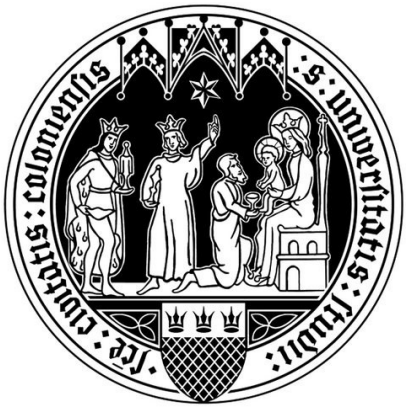
Emotional Cue Effects on Choice Impulsivity



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To Levi

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General Introduction

Every day, we are facing decisions - big and small. The first one might arise as early as we wake up in the morning. Should I hit the snooze button and get ten extra minutes of sleep or should I get up on time to set out for a productive day at work? Later on, I might deliberate on spending my money on the not necessarily needed MacBook and a balanced bank account and in the evening, I may have to consider, whether small immediate pleasures like smoking or feasting outweigh the larger future reward of a good health. Such decisions are intertemporal ones. They require a trade-off between costs and benefits that occur at different points in time (Kreidel et al., 2021).

When given a choice, humans and many animals tend to prefer smaller but sooner (SS) over larger but later (LL) rewards. This common tendency is referred to as *delay* or *temporal discounting* (TD), and implies the devaluation of delayed rewards as a function of time (Ainslie, 1975; Frederick et al., 2002; Mazur & Coe, 1987). It becomes obvious, that future-reward devaluation has far-reaching consequences for wealth, health and contentment of the individual but also affects society as a whole (Frederick et al., 2001; Golsteyn et al., 2014; Kreidel et al., 2021). The question of how much to invest for the future is central to a multitude of policy matters, spanning education, healthcare, retirement planning, energy and the environment (Ericson & Laibson, 2018). Due to the significance and ubiquity of intertemporal decisions it is hardly surprising, that they have been subject of extensive research across multiple academic disciplines, such as psychology, cognitive neuroscience, behavioral economics and public policy (Frederick et al., 2002; Urminsky & Zauberman, 2014).

In experimental settings, intertemporal choice can be assessed via pen-and-paper questionnaires (Kirby & Marakovic, 1996) or computerized tasks (e.g., Peters & Büchel, 2009). In both cases, participants are usually provided with a series of choices between a smaller amount of a reward (e.g., money or food), which can be received immediately and a larger amount of the given reward, obtainable after a certain delay (e.g., "Would you prefer 20 € today or 34 € in 40 days?"; Myerson & Green, 1995; Weinztok et al., 2021). By manipulating temporal delays and reward amounts of the available options across choices, researchers can assess the degree to which an individual devaluates or discounts rewards over time. A quantification of this behavioral tendency is provided by an individual's *discount rate* (Peters & Büchel, 2011; Scholten et al., 2019).

On the intraindividual level, intertemporal choice behavior is considered to be fairly stable (Bruder et al., 2021; Kirby, 2009; Odum, 2011) and evidence suggests that a genetic component may play a role in shaping these reward preferences (Anokhin et al., 2015; Mackillop, 2013). Although TD is a common and widespread phenomenon in humans (and many other animals), an exaggerated preference for smaller but sooner and especially immediate rewards is considered an indicator of choice impulsivity and decreased self-control (Frederick et al., 2002). Consequently, increased TD is associated with numerous health-related actions or lack thereof, such as a reduced probability of monitoring blood

pressure and cholesterol, going to dental checkups, working out, receiving vaccinations and adhering to medical treatment (Bickel, 2015).

Moreover, a growing body of research has underlined the relevance of TD in the context of multiple clinical conditions and psychiatric disorders (Bickel, 2015), thus rendering excessive future-reward devaluation a transdiagnostic process (Bickel et al., 2019). Due to its role in various disorders, a shared behavioral pattern may provide novel perspectives on their common underlying features (Amlung et al., 2019).

In this respect, examination of TD may be promising as it could help to inform transdiagnostic treatments by identifying target behavioral processes and by providing indicators of treatment response (Levin et al., 2018). Recent meta-analyses and narrative reviews have reported *increased* TD in several clinical populations typically associated with impulsive behavior (Bulley & Schacter, 2020), including substance abuse, attention-deficit/hyperactivity disorder, schizophrenia, problem gambling and obesity (Amlung et al., 2019). Simultaneously, *decreased* discounting has been found in subpopulations suffering from anorexia nervosa or obsessive–compulsive personality disorder (OCD; Amlung et al., 2019; Lempert et al., 2019). These findings suggest TD to be conceptualized as a continuum, with extreme values on either side to be associated with mental ill health. Differences with regard to their location and relative distance on this dimension cannot only inform our understanding of (classically/categorically defined) mental disorders but may also shed light on the feasibility of TD as treatment target in the attempt of improving transdiagnostic symptoms (Amlung et al., 2019). These considerations nicely resonate with the objectives of the US National Institute of Mental Health (NIMH) and the proposed Research Domain Criteria (RDoC) framework (Cuthbert & Insel, 2013; Insel et al., 2010), which aims to define the core aspects of cognitive, perceptual and social processing, with the goal of discovering new targets for treating mental health disorders (Amlung et al., 2019).

Interestingly, despite its high intraindividual trait-like stability, TD is susceptive to within-subject change (Lempert et al., 2019). Multiple studies revealed that short-term state manipulations via various kinds of pharmacological agents, environmental stimuli or external emotional cues can affect TD in both healthy and clinical subgroups (Dixon et al., 2006; Foerde et al., 2016; Lempert & Phelps, 2016; MacKillop et al., 2011; Mathar et al., 2022a; Mathar et al., 2022b; Miedl et al., 2014; Wagner et al., 2020; Wagner et al., 2022). Elucidating mechanisms contributing to such state manipulations can foster identification of risky situational conditions potentially triggering impulsive/short-sighted real-world behaviors. Simultaneously, knowledge about modes of action can promote development of above-mentioned interventions.

The current dissertation project specifically focusses on emotional visual cues, proved capable to affect both cognitive processes and intertemporal choice behavior on a broad front (e.g., Dolan, 2002; Herman et al., 2018; Kim & Zauberman, 2013; Shang et al., 2020; Sheldon et al., 2020; Wilson & Daly, 2004; Zadra & Clore, 2011).

Studies investigating emotional cue effects on TD can be classified along multiple dimensions. Cue exposure might be implemented via cues of positive and/or negative valence (Cai et al., 2019; Guan et al., 2015), which can be presented in auditory (Daniel et al., 2015) or visual domains (Simmank et al., 2015), using block-wise (e.g., Otterbing & Sela, 2020) or trial-wise (Luo et al., 2014) experimental designs.

When findings from emotional cue exposure studies on TD are reviewed, they appear highly heterogenous. While various studies reported increased TD in response to *negative* or aversive cue exposure (e.g., Guan et al., 2015; Sohn et al., 2015), others failed to find such effects (e.g., Luo et al., 2014). In contrast, presenting *positive* words, videos or images (e.g., babies, puppies or happy older couples) alongside intertemporal choice options was found to foster patient decisions in some experiments (Ifcher & Zarghamee, 2011; Pyone & Isen, 2011), but many others yielded null results (Augustine & Larsen, 2011; Hirsh et al., 2010; Simmank et al., 2015). Among literature exploring emotional cue effects on TD, highly appetitive erotic cues take a special role. Block-wise exposure to appetitive and especially erotic visual cues prior to TD tasks has been found to reliably elevate devaluation of future rewards (Cheng & Chiou, 2018; Chiou et al., 2015; Gracia & Huertas-Garcia, 2016; Kim & Zauberman, 2013; Otterbing & Sela, 2020; van den Bergh et al., 2008; Wilson & Daly, 2004), a finding that seems to be most pronounced in male participants (Cheng & Chiou, 2018; Kim & Zauberman, 2013; Wilson & Daly, 2004). However, studies applying a trial-wise cue presentation in conjunction with available choice options yielded mixed results (Guan et al., 2015; Luo et al., 2014; Simmank et al., 2015).

Looking at these inconsistent findings is somewhat unsatisfactory and the questions arise – why do emotional cue effects appear so heterogeneous, and which underlying mechanisms may explain these seemingly contradictory findings? With regard to the somewhat more consistent finding of elevated TD following negative and block-wise erotic cue exposure, it might be speculated that a minimum of two complementary processes likely play a role in shaping cue-evoked alterations of reward preference.

The first one is *physiological arousal*. Physiological arousal is known to be related to risky decision-making (Galentino et al., 2017; Loewenstein et al., 2001; Phelps et al., 2014) and recent studies indicated that trial-wise arousal changes, assessed through pupil dilation, are choice-predictive during TD (e.g., Lempert et al., 2016). However, the degree to which rather complex emotional cue effects on TD can be traced back to phasic variations in short-term arousal has not been tested before and remains unclear. In case of highly arousing erotic stimuli, some authors have argued that erotic cue exposure might alter subjective time perception in a way that future durations are perceived as longer (Kim & Zauberman, 2013; Laube & van den Bos, 2020). However, others reasoned that a tonic upregulation of the reward circuitry by highly appetitive erotic stimuli may be the underlying critical feature, facilitating reward approach behavior in other domains (e.g., approach behavior towards food or monetary rewards; van den Bergh et al., 2008).

In line with these ideas, both erotic and aversive cues have been found to elevate sympathetic arousal signals (Bradley et al., 2008; Finke et al., 2017; Kinner et al., 2017). Simultaneously, block-wise erotic cue exposure can indeed increase activity in (dopaminergic) brain areas involved in reward processing, including ventral striatum (VS), orbitofrontal cortex (OFC) and ventral tegmental area (VTA; Gola et al., 2016; Markert et al., 2021; Stark et al., 2019; Wehrum-Osinsky et al., 2014).

However, whether these physiological and/or neuronal mechanisms contribute to aforementioned cue effects on TD still has to be tested. Further, assessing behavioral adaptations in response to appetitive erotic cues in healthy participants may be of particular importance to improve our understanding of maladaptive behaviors in clinical groups, especially in addiction. A transfer of knowledge from healthy to (sub-) clinical samples appears both promising and plausible, especially when mental health and associated behavioral characteristics (e.g., cue-evoked impulsivity) are considered from a dimensional perspective.

Appetitive cues refer to all environmental or external stimuli signaling potential availability of reward or other beneficial (i.e., appetitive) outcomes. Such outcomes might comprise primary (e.g., food, water or sex) or secondary reinforcers (e.g., money). Primary reinforcers are stimuli that serve to satisfy universal basic needs and drives, and have innate and unlearned value to the organism (O'Doherty, 2009). Secondary reinforcers only become effective through individual learning processes (Kelleher & Gollub, 1962). They acquire value via pairing with primary reinforcers (O'Doherty, 2009) or other sources of pleasure. Following this reasoning, drugs might be considered secondary reinforcers as their (reinforcing) properties are learned through repeated association with pleasure and the brain's reward circuit activation. Meta-analyses show that processing of primary and secondary reinforcers mostly occurs in overlapping brain regions (e.g., Sescousse et al., 2013). Moreover, both of them share at least three defining features: they are pleasant and physiologically arousing, they can foster spontaneous approach behavior and they may satisfy (physiological) needs (Li, 2008). By means of operant or classical conditioning processes, these features might be transferred to signaling cues, which can thereby acquire motivational and/or rewarding properties themselves (Berridge, 2007). In light of these findings, understanding how primary reward-signaling erotic cues affect myopic choice behavior in controls might inform us about the maladaptive attraction-mechanisms of addiction-related cues, whose presence can trigger subjective and physiological craving responses as well as drug consumption and relapse even after years of abstinence (Robinson & Berridge, 1993; Vafaie & Kober, 2022).

To sum up, ample evidence suggests that future-reward devaluation can be regarded as a common and trait-like characteristic, suitable as an indicator for choice impulsivity. Excessive discounting is apparent in a multitude of psychiatric disorders, rendering it a transdiagnostic marker and possible intervention target (Amlung et al., 2019; Levitt et al., 2023). Exposure to emotional cues has been found to affect TD. However, precise contributing mechanisms lie largely in the dark. Especially in trial-wise experimental designs, short-term fluctuations of physiological arousal, which is inextricably linked to emotional stimulus processing, appears as a possible candidate that may partly dissolve

previous contradictory cue effects on TD. Block-wise cue exposure to appetitive (erotic) stimuli might exert their effect on TD via upregulation of the dopaminergic reward circuitry, possibly fostering approach behavior towards immediately available rewards. Exploring such mechanisms in healthy participants might inform our understanding and conceptualization of dysregulated behaviors and decision-making processes in various psychopathologies (e.g., addiction).

This dissertation project had multiple aims. In study 1, we assessed whether increased TD can be evoked following *trial-wise* exposure to visual erotic and equally arousing aversive cues – enabling us to disentangle valence- and arousal-related effects. Further, we aimed to test whether trial-wise indices of autonomous nervous system (ANS) activity can account for significant and unique variance over and above behavioral cue effects. ANS proxies comprised pupil size, heart rate and electrodermal activity, which allowed us to investigate trial-by-trial fluctuations of arousal with high temporal resolution. In study 2, we used functional magnetic resonance imaging (fMRI) to directly measure the effects of *block-wise* erotic cue exposure on both, neuronal reward circuit activity and subsequent TD. Moreover, we assessed hypothesized associations between (dopaminergic) reward-system reactivity and behavioral cue-reactivity as measured by alterations in TD.

In the upcoming sections, I will first elaborate on the theoretical background and methodology used in this dissertation project. Next, I will present the two studies we conducted to elucidate mechanisms involved in emotional cue effects on TD. In the end, main study results will be summarized and put into context before I will give a short outlook for upcoming research.

Theoretical Background

This thesis aims to contribute to a better understanding of physiological and neuronal mechanisms involved in emotional cue effects on temporal discounting (TD) – a measure of choice impulsivity. To do so, a few basic concepts must be introduced. First, I will briefly delineate the various facets of (choice-) impulsivity. Impulsivity is a multidimensional concept, where components might be independent of one another and reflect distinct aspects of behavior (Herman et al., 2018). Next, I will outline the origins of the concept of intertemporal choice and TD, respectively (note that in the following, these terms are used interchangeably). TD was early identified as a promising way to approximate impulsive tendencies, but viewpoints and modeling of such behavior strongly evolved over time. Thereafter, I will condense empirical findings on emotional cue effects on TD and present theoretical frameworks that may be able to integrate them. Lastly, I will address the physiological and neuronal (reward-) systems that are assumed to be involved in emotional cue effects on TD.

So, what does impulsivity mean? According to the Diagnostic and Statistical Manual of Mental Disorders (DSM-V) "*Impulsivity refers to hasty actions that occur in the moment without forethought, which may have potential for harm to the individual (e.g., darting into the street without looking)*" (APA, 2013). Similarly, Moeller et al. (2001) describe impulsivity as a predisposition for rapid, unplanned actions in response to external and internal stimuli without considering potential negative consequences of these actions. Several aspects might be inferred from these definitions.

First, impulsivity is regarded a maladaptive feature. It is commonly accepted that impulsivity is foremost a "normal" aspect of human behavior, and every individual exhibits a characteristic level of impulsive tendency (Evenden, 1999; Herman et al., 2019). It was also argued that, especially in everyday situations, fast, impulsive or spontaneous actions can be beneficial, as they enable to seize opportunities, gain new experiences and might constitute a reasonable strategy when facing limited time and resources (Dickman, 1990; Gigerenzer et al., 1999). However, as every "normal" characteristic, it can manifest in a pathological manner when extremely pronounced, forming a core feature of a number of psychiatric disorders and clinical conditions (Amlung et al., 2019; Lempert et al., 2019).

Second, definitions emphasize that impulsivity might be seen as a trait-like predisposition and/or behavioral feature susceptible to external and environmental conditions, which gives rise to a differentiation between trait and state impulsivity (Antons & Brand, 2018; Halvorson et al., 2021; Hamilton et al., 2015). Trait impulsivity is regarded a stable personality characteristic, predisposing individuals to engage in impulsive behaviors across a variety of situations and contexts over time (McKillop et al., 2016). It is often assessed using global self-report questionnaires like the Barratt-Impulsiveness-Scale (BIS; Barratt, 1959; Patton et al., 1995), where individuals are asked to indicate to what degree statements like: "I am restless at theaters or lectures", "I often have extraneous thoughts when thinking" or "I buy things on impulse" are true, thereby yielding three different (sub-) types or factors of impulsivity (motor, cognitive and non-planning). Self-report measures are fast and easy to acquire from large numbers of individuals and appear generally reliable (King et al., 2014). Further, they have been found to possess predictive and discriminant validity for risky behaviors and mental health (Berg et al., 2015; Halvorson et al., 2021). However, they do have a few important limitations. Self-reports heavily rely on introspection, as individuals are required to recall past prototypical behaviors across a wide range of time and situations – resulting in a reconstructive process that may be biased (Santana et al., 2022). Recall accuracy is influenced by various factors, including memory encoding, recollection and/or emotional significance of memories (Halvorson et al., 2021; Hunt et al., 2003; Robinson & Clore, 2002).

Standardized computerized tasks may enable a reduction of such biases, and a more objective measurement of different (behavioral) facets of impulsivity under different internal and external states. Broadly, these tasks can be classified into two major categories: those measuring impulsive action (or motor impulsivity) and those assessing impulsive choice (Herman et al., 2019; King et al., 2014).

Impulsive action refers to the inability to inhibit a prepotent behavioral response, resulting in fast and often inaccurate actions (Brunner & Hen, 1997). These may be further divided into impulsive actions relating to refraining from initiating an action (action restraint) versus stopping an action that has been initiated (action cancelation; Eagle et al., 2008; Schachar et al., 2007). Widely applied tasks are the Stop Signal Task (SST; Logan, 1994), the Go/No Go task (GNG; Hogg & Evans, 1975) or the 5-Choice Serial Reaction Time Task (5-CSRTT; Carli et al., 1983).Whereas the SST and the GNG both require subjects to respond to go-signals and to inhibit their responses to stop-signals, in the 5-CSRTT, subjects must react to a stimulus, which can occur in one of five locations. Premature responses, which occur before the stimulus appears, are indicative of impulsive (motoric) behavior or action (Herman et al., 2018).

In the context of impulsive choice, risk/uncertainty-based (e.g., Iowa gambling task in human subjects (IGT; Bechara et al., 1994) or the rat gambling task in animal studies (rGT; de Visser et al., 2011; Zeeb et al., 2009)) and delay-based (intertemporal choice task) paradigms can be differentiated. Whereas the former implies decision-making between small-but-certain and larger-but-uncertain rewards, participants solving intertemporal choice tasks must indicate their preference for SS or LL rewards (Ainslie, 1975; Mazur & Coe, 1987).

In humans, principal component analysis (PCA) also confirmed the above-mentioned trisection: (1) self-reported impulsivity, (2) impulsive action and (3) impulsive choice (Broos et al., 2012). This independence is also emphasized by study results reporting, if anything, small associations between the three measures of impulsivity (Broos et al., 2012; McCarthy et al., 2018).

In light of the multi-dimensional nature of the impulsivity construct, it should be noted, that the current dissertation exclusively focuses on intertemporal choice as a measure for (choice-) impulsivity. The following section will give a short overview over early considerations of this concept, covering theoretical perspectives from different disciplines as well as modeling of behavior.

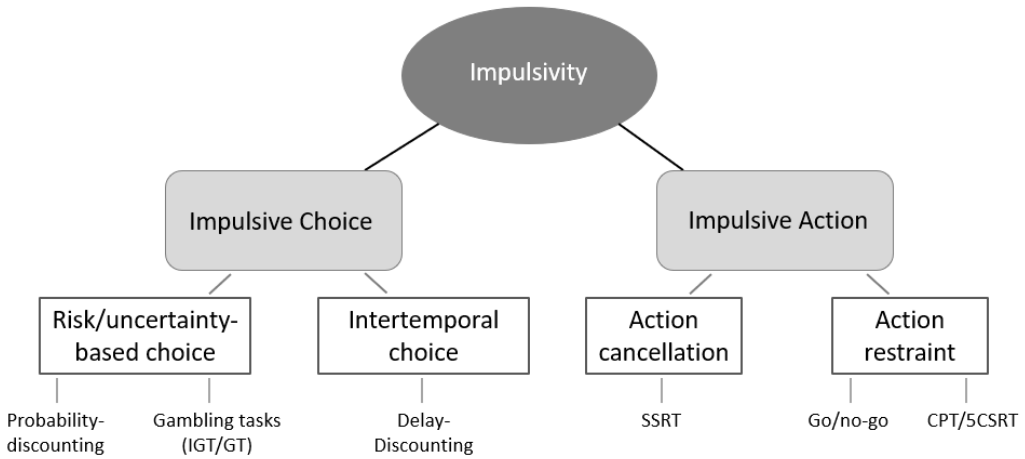

Figure 1. Different facets of impulsivity and associated tasks. IGT: Iowa gambling task; GT: gambling task; SSRT: stop-signal reaction time task; CPT: continuous performance test; 5CSRT: five-choice serial reaction time task. Figure adapted and modified from Winstanley and colleagues (2010)

The Concept of Intertemporal Choice

Reflections on intertemporal choice and related concepts occurred surprisingly early. During the 5th century BC, Plato already reasoned that outcomes that are distant in *time* are diminished in perception just as are objects farther away in *space*. Crucially, he considered this a bias, arguing that the appropriate way to make a choice between options was to disregard the delay of the outcome and concentrate on its magnitude, similar to how we neglect distance when determining the height of distant objects (Read et al., 2018). In modern times, the topic of intertemporal choice has been deliberated for more than two hundred years and until recently has been narrowed to the field of economics. Initially taking a broad economic perspective, Adam Smith (1776) already elaborated on the importance of intertemporal choice for the prosperity of nations. He was concerned about why wealth differed among nations and emphasized that national wealth would benefit from a higher amount of labor allocated to the production or accumulation of future capital and lower amounts of present consumption than would spontaneously occur in a market economy (Garrison, 1998). Later on, John Rae (1834) was the first who reasoned about the sociological and psychological factors influencing such allocation tendencies. According to Rae "the effective desire of accumulation" could be viewed as a societal or psychological characteristic that varies between countries and influences a society's savings and investments (Frederick et al., 2002). He reasoned such a trait (in fact mirroring societal intertemporal choice behavior) to be the product of various promoting and/or limiting factors. Whereas the tendency to demonstrate self-restraint ("the extent of the intellectual powers, and the consequent prevalence of habits of reflection, and prudence, in the minds of the members of society") would promote far-sighted behavior (capital accumulation), uncertainty of human living conditions as well as the excitement resulting from the prospect of immediate consumption would foster myopic societal tendencies (Frederick et al., 2002).

Shifting perspectives, Eugen von Böhm-Bawerk (1889) and Irving Fisher (1930) later reasoned about which characteristics affected the *individual* preference for immediate over delayed utility (Frederick et al., 2002). Whereas Böhm-Bawerk argued that increased present-focused decision-making in humans might generally result from of a systematic underestimation of distant future wants, Fisher first proposed that every individual is characterized by its own *individual rate of impatience*. He assumed this rate to be strongly related to objective (size and risk of future income) but also subjective factors (foresight, strength of will, habit, uncertainty, selfishness, influence of fashion). Thus, during the nineteenth and early twentieth century, subjective utility (de-) valuation across time points was already seen as a complex combination of different intertemporal motives.

However, in 1937 Paul Samuelson proposed his new seminal model of *Discounted Utility* (DU-model), which amalgamated and reduced these psychological and sociological motives into a single mathematical parameter, the discount rate, which allowed to describe intertemporal preference across time points (Sellitto et al., 2011). In short, the DU-model assumes a fixed decrement in the subjective utility of delayed outcomes over time, described by an exponential function (Eq. 1):

$$DU(x,t) = U(x) * e^{(-kt)} \quad \text{Eq.1}$$

$DU(x,t)$ represents the utility of receiving outcome x at time t, while $U(x)$ denotes the utility of receiving the same outcome immediately. The k parameter depicts the individual discount rate, where higher values imply more pronounced discounting. Due to the exponential term, the DU-model treats each time period equivalently, suggesting human choice to be consistent over time, no matter how far it is projected into the future. Thus, a waiting period of e.g., ten days from today should be treated the same way as a waiting period of ten days in a year from now (Peters & Büchel, 2011), a property referred to as *dynamic consistency* (Berns et al., 2007). After its introduction, the exponential DU-model gained popularity especially among economists as a tool for evaluating intertemporal choices. Its simplicity and similarity to present financial value and actuarial models made it the main normative model in this field.

However, starting from the 1980s, critiques of the DU-model began to surface, as human behavior was found to be largely inconsistent with exponential discounting in various empirical studies (Frederick et al., 2002; Green & Myerson, 2004; Loewenstein, 1988; Soman et al., 2005). These *anomalies* or deviations from the DU-model rose concerns and questions about its validity.

From Anomalies to New Models

The probably most common result from intertemporal choice studies is that small reward magnitudes are discounted more than large ones (for a given delay). This finding has been replicated across numerous studies involving both real and hypothetical monetary rewards (e.g., Ainslie & Haendel, 1983; Andersen et al., 2013; Ballard et al., 2017; Green et al., 1997; Smith & Peters, 2022; Thaler, 1981; Wagner et al., 2020). For instance, Thaler (1981) discovered that delaying amounts of $4.000, $350 and $60 by a year resulted in a discount of 29%, 34% and 139%, respectively. This calculation was based on the immediate amounts that would make the individual indifferent between the two options (indifferent here means that both options are equal in subjective value (SV)). Within the same study (Thaler, 1981), it was also observed that discount rates are lower when choosing among delayed losses than delayed gains - a phenomenon called *sign-effect* or *gain-loss asymmetry* (Benzion et al., 1989; Frederick et al., 2002). In experimental settings such effect might become apparent in participants becoming indifferent between receiving e.g., $10 now and $21 in one year (discount rate: 110%) and indifferent between losing $10 now and losing $15 twelve months later (discount rate: 50%; Loewenstein & Prelec, 1992). Additional intertemporal choice "anomalies" include the *date-delay-effect,* which implies that expressing time as a duration (e.g., six months) results in higher discount rates for future outcomes compared to expressing it as a specific date (e.g., September 21), or the *delay-speedup-asymmetry,* which describes the observation that discount rates are greater when people are confronted with decisions that involve delaying anticipated rewards than for decisions that involve expediting rewards (Read & Loewenstein, 2000).

However, the empirical finding that was most difficult to reconcile with the normative DU-model is that discount rates are, in fact, not stable but actually decrease over time. This is because the SV of a LL reward diminishes more slowly, as it becomes more delayed, than the SV of a SS reward (Green & Myerson, 2004; Kirby, 1997; Lempert & Phelps, 2016). For instance, when participants were asked to state the amount of money they would need in one month, one year or ten years to become indifferent to receiving $15 immediately, responses indicated an average annual discount rate of 19% over ten years, 120% over one year and 345% over one month (Thaler, 1981; van den Bos & McClure, 2013). Such choice pattern can be better approximated via hyperbolic discounting models (see Figure 2), which were introduced by Chung and Herrnstein (1961), strongly advocated by Ainslie (1975) and further elaborated by Mazur and Coe (1987). One-parameter hyperbolic discounting models assume that utility of delayed rewards or punishments at a given point in time (DU) is discounted as follows:

$$DU(x,t) = U(x)/(1 + k * t) \qquad \text{Eq.2}$$

U(x) again denotes the utility of receiving an outcome x immediately. The k parameter depicts the individual discount rate, and t is the time or delay until the outcome is received.

There is ample evidence that hyperbolic models fit temporal discounting data better than exponential models (e.g., Frederick et al., 2002; Green & Meyerson, 2004, McKerchar et al., 2009). Moreover, unlike exponential models they can account for so-called preference reversals. This refers to our somewhat irrational human tendency to make future-oriented plans (e.g., stop smoking to live healthy) when outcomes are distant, but reverse our choices in favor of short-term rewards when the actual future is reached (Kalenscher & Pennartz, 2008; Story et al., 2014). In experimental settings this might be indicated by individuals who choose (A) €20 in one year over (B) €10 in six months, but choose (B') €10 today over (A') €20 in six months (Seinstra et al., 2018).

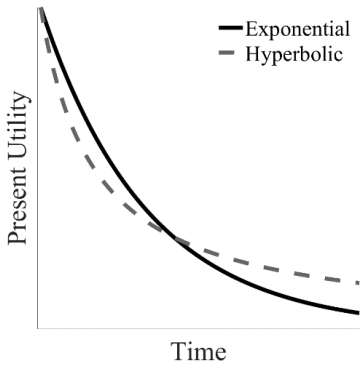

Figure 2. Exponential vs. hyperbolic discounting. In exponential models each time step is treated equally, represented by stable utility devaluation over time. Contrarily, in hyperbolic models, devaluation speed decreases over time.

It should be noted that multiple (two-parameter) extensions have been proposed to both the exponential and hyperbolic models (Ebert & Prelec, 2007; Mazur, 1987; Myerson & Green, 1995; Rachlin, 2006), trying to account for the observation that discounted values at shorter delays are typically over-estimated and discounted values at longer delays are often under-estimated (McKerchar et al., 2009). However, due to its simplicity and parsimony, one-parameter hyperbolic models have widely spread in temporal discounting research (Peters et al., 2012).

To sum up, the previous chapters illustrate that people often tend to deviate from previously conceptualized rational and steady reward devaluation over time. These deviations became apparent in various so-called *anomalies*, emphasizing that otherwise highly constant discount rates appear susceptible to both the context or framing of the given choice options as well as to external and internal influencing variables (see Lempert & Phelps (2016) for a review). This dissertation project focusses on incidental emotions as one such (powerful) influencing variable.

Malleable Intertemporal Choice – Emotional Cue Effects

From a classical point of view, the entire mental process of decision-making ought to be completely rational – a structured procedure centered on maximizing utility (Olson, 1965; Verweij et al., 2015). From this perspective, the domain of rational thinking and decision-making aimed to neglect/avoid emotions, which were often regarded as confounds, capable to bias reasoning (Barnes & Thagard, 1966; Livet, 2010).

From a theoretical perspective, two types of emotional influences on choice are distinguished. Integral emotions are directly related to the decision at hand and arise from the options being considered and the outcomes associated with them, e.g., the fear of losing money when choosing between investments (Lerner et al., 2015). Incidental emotions are not directly related to the current decision. They may be triggered by something unrelated to the decision, but can still influence the decision-making process – often without awareness (Engelmann & Hare, 2018). Visual emotional cues without any information value fall into this category.

Current models emphasize dimensionality of emotions, which means they are evaluated on continuous scales instead of being classified as separate and distinct categories (Cacioppo et al., 2000; Pfister & Böhm, 2008; Russell, 1980). The *circumplex model of affect* has been among the most prevalent representations of affect (Remington et al., 2000), and postulates that each emotional state can be expressed as a linear combination of two dimensions: valence and arousal (Posner et al., 2008). While both of them are thought to originate from distinct but related neurophysiological systems, the specific emotions experienced are determined by the relative activation of each dimension (Colibazzi et al., 2010; Gerber et al., 2008; Posner et al., 2005, 2009; Russel, 1980). This internal model structure largely mirrors self-reports on subjective emotional experiences and has also been validated via factor analysis

and scaling procedures applied to emotional terms and facial expressions (Feldman-Barrett & Russell, 1998; Kring et al., 2003; Russell, 1980; Watson & Tellegen, 1985).

As assumed, emotions can indeed bias or affect various cognitive processes, including attention (Garcia-Garcia et al., 2010), perception (Vuilleumier, 2015), memory encoding (i.e., the encoding, storage and retrieval of information; Tyng et al., 2017) and associative learning (Ono et al., 1995). Critically, multiple lines of research indicate that incidental emotions have far-reaching influence on decision-making in general and on (value-based) intertemporal choice in particular (Lempert & Phelps, 2016). The next section will give a brief overview over key empirical findings.

Empirical Findings

Studies exploring emotion effects on intertemporal choice differ in the way they evoke incidental emotions. While some assess the influence of longer lasting mood inductions (Lerner et al., 2013) or acute stress (Haushofer et al., 2021) on subsequent reward devaluation, others examine choice adaptations following or during exposure to (mostly visual) external emotional cues (e.g., Kim & Zauberman, 2013; Simmank et al., 2015). As both experiments of this dissertation project focused on the latter, the upcoming section mainly reviews results from similar approaches. To improve internal structuring, I will first successively review findings from studies utilizing negatively and positively valanced cues in general before I will turn to the specific class of erotic stimulus material.

Several studies indicate that negative or aversive cues can affect TD. A majority of them reported increased discount rates following cue exposure. For example, Guan and colleagues (2015) observed significantly more myopic SS choices when participants were primed with negative compared to neutral or positive images. Sohn and colleagues (2015) investigated emotional arousal effects on TD using positive, negative and neutral cues. On every trial, two pictures of the same (emotional) category were presented, followed by the SS and LL reward options. Results showed increased TD following negative cue-exposure. Similar results have been observed following presentation of negative words (Augstine & Larsen, 2001) or negative connoted video material (Lerner et al., 2013), in both healthy and (sub-) clinical populations (e.g., Cai et al., 2019). Some authors argued that the above-mentioned findings might reflect an increased tendency to seek immediate gratification or short-term pleasures in order to compensate negative emotions (Tice et al., 2001). However, contrasting findings of negative cue effects on TD raise doubt about this interpretation. In a study from Luo and colleagues (2014) individuals were instructed to keep a happy, fearful or neutral facial expression in mind while performing a TD task. They observed an increase in *patient* choice patterns (increased LL preference) when fearful compared to happy facial expressions were maintained. The authors argued for a so-called *inhibition-spillover-effect*, which might cause a suppression of reward-seeking behavior following fear induction. However, it should be noted that this methodological approach is not completely comparable to classical cue exposure designs, using external stimulus presentation.

Findings from studies using positive (non-erotic) affective stimuli appear even more mixed. Above-mentioned studies from Guan et al. (2015), Cai et al. (2019) and Luo et al. (2014) also included happy stimuli in their cue-set or asked participants to keep happy expressions in mind. While results from Guan and colleagues (2015) indicated increased patience following "happy primes", reward preference did not differ between positive and neutral conditions in studies from Cai et al. (2019) and Luo et al. (2014). Similarly, unaltered discounting following positive but non-erotic stimulus material was reported by Simmank et al. (2015). In 2011, Ifcher and Zarghamee (2011) employed short movie clips while Pyone and Isen (2011) used words to elicit positive or neutral emotions, and both studies demonstrated that positive affect decreased TD. Conversely, Augustine and Larsen (2011) as well as Hirsh and colleagues (2010) did not observe a decrease in TD rates, even though they used the same type of affect induction.

Instead of using visual imagery of happy stimuli (e.g., faces, older couples, pets), Li (2008), relied on cues of primary rewards (i.e., food). In their study, participants viewed and evaluated multiple images of appealing desserts (vs. non-appetitive nature photographs) prior to completion of a TD questionnaire. Interestingly, such cue exposure led to significantly more monetary SS vs. LL choices indicating increased out-of-domain choice impulsivity. Individuals exposed to appetitive food stimuli also reported a higher probability of making unplanned purchase decisions (Li, 2008).

In a similar vein, multiple studies indicated that increased sexual arousal can crucially affect impulsive decision-making. For instance, Ariely & Loewenstein (2006) showed that increased sexual arousal heightened the readiness for impulsive decisions and reduced self-control in a sexual context: sexually aroused participants were more willing to engage in sexual risk-taking behavior compared to individuals in a control group. Moreover, a growing body of research reported that preceding or concurrent processing of visual erotic cues can affect intertemporal choice (Cheng & Chiou, 2017; Chiou et al., 2015; Gracia & Huerta-Garcia, 2016; Kim & Zauberman, 2013; Otterbing & Sela, 2020; van den Bergh et al., 2008; Wilson & Daly, 2004).

In a study from Wilson & Daly (2004), male and female participants were first required to rate photos showing attractive and unattractive individuals of opposite sex. Subsequently, they completed a TD task. Men who had first rated photos of attractive women exhibited a significantly higher discount rate than men who rated photos of unattractive women. The same effect could not be identified for female participants. These asymmetric findings nicely resemble previous evidence, showing that visual sexual cues seem to have a stronger appetitive effect on men than on women (Hamann et al., 2004; Rupp & Wallen, 2008). Van den Bergh and colleagues (2008) conducted several studies that also support the influence of erotic cues on TD. Among men who rated erotic photos of women, a stronger discount rate was observed in a TD task compared to men who rated landscape photos. This effect was also evident when men were asked to examine and rate (female) underwear on various criteria compared to men who rated outerwear. However, while more recent studies applying block-wise designs confirmed these

findings (e.g., Kim & Zauberman, 2013), trial-wise approaches yielded mixed results (Simmank et al., 2015; Sohn et al., 2015).

Theoretical Considerations

Several theoretical accounts have been proposed, aiming to contribute to a better understanding of the role of emotions and emotional cue effects in decision-making processes. Classical but still popular dual-system models assume that behavior results from an interplay of two (opposing) mental processes (Cohen, 2017; Heatherton & Wagner, 2011; Hofmann et al., 2009; Kahneman 2011; Metcalfe & Mischel, 1999; Thaler & Shefrin, 1981). While these models come in various flavors, they all agree on the idea that behavior is governed by two distinct systems - commonly referred to as System I and System II (Inzlicht et al., 2021).

System I, which is also termed the “impulsive”, “automatic”, “hot”, “reflexive” system or simply “the doer”, is associated with emotions and reacts quickly and reflexively to the motivational-affective value of unconditioned and conditioned stimuli (Inzlicht et al., 2021). Specifically, "hot" processes are especially driven by the visceral and motivational appeal of *immediately* available stimuli in close temporal and spatial proximity (Hirsh et al., 2010; Loewenstein, 1996; Metcalf & Mischel, 1999). The impulsive system is assumed to focus on short-term gratification, exhibiting an urge to approach and promoting inflexible and automatic behaviors (Hofmann et al. 2009). In contrast, it places only little value on distant or effort-based stimuli (Ainslie, 1974; Apps et al., 2015; Mischel et al., 1972; Westbrook et al., 2013). Neuronally, it is often linked to upregulated subcortical brain activity in key areas of both reward and emotion processing (e.g., VS, nucleus accumbens (NAc), amygdala, insula; Lopez et al., 2014).

The “cool” or controlled System II acts slower, more reflectively and is able to exert cognitive-control necessary to prioritize long-term goals. Further, it allows for flexible responses to the environment by overriding impulsive tendencies and has been associated with increased lateral prefrontal cortex activity during choice (Berkman et al., 2011; Heatherton & Wagner, 2011). With regard to intertemporal decision-making, the System I/System II framework might suggest, that participants choose impulsively (SS choice) or show more self-control (LL choice) depending on which of the two systems currently dominates or shows increased activation, respectively. Cue-evoked emotional arousal should put much more weight on the “hot” system, resulting in increased short-sighted behavior (Li, 2008; Luo et al., 2014; Metcalfe & Mischel, 1999). However, the model does neither predict whether arousal of either valence (negative and or/positive) is sufficient to induce such systematic imbalance nor does it discuss which underlying mechanisms might play a role.

Hypothesized Physiological Mechanisms

Taking a neuro-physiological perspective, the question arises which mechanisms may be involved in the above-mentioned emotional cue effects on TD? As already outlined, it appears plausible that two core processes or systems could play a role in shaping alterations of reward preference. First, variation of dopaminergic neurotransmission might contribute to variations in approach behavior towards immediate rewards, especially following erotic cue exposure (van den Bergh et al., 2008). Second, physiological arousal systems might play a role, which could also explain changes in TD in response to negative/aversive cues (Lempert & Phelps, 2016). In the upcoming sections, I will briefly introduce both systems and discuss their roles in shaping intertemporal choice and choice impulsivity, respectively.

The Dopaminergic System

Dopamine (3,4-dihydroxyphenethylamine; DA) is a chemical compound and neuromodulatory molecule. It primarily acts as a neurotransmitter in the central nervous system (CNS) and is strongly implicated in a wide range of behavioral and cognitive functions, including movement (Alm, 2021; Joshua et al., 2009), memory (Clos et al., 2019), motivation (Bromberg-Martin et al., 2010; Grogan et al., 2020) and reward processing (Berridge & Kringelbach, 2008; Schultz, 1998). Together with norepinephrine (NE) and epinephrine it belongs to the class of catecholamines (Carlsson, 1959).

DA is the simplest molecule in its class, comprising a benzene ring with two hydroxyl side groups and an amine group attached via an ethyl chain (Vallone et al., 2000). Biosynthesis of DA involves a series of enzymatic reactions, starting from the non-essential amino acid tyrosine (Musaccio, 2013), which is obtained through dietary sources or synthesized within the body from phenylalanine (Fernstrom & Fernstrom, 2007). Tyrosine is transported into dopaminergic neurons and converted into L-DOPA by the enzymes tyrosine-hydroxylase (TH) or tyrosinase. Within cytoplasm, L-DOPA is then metabolized to DA by aromatic L-amino acid decarboxylase (AADC; Meiser et al., 2013). As dopamine is incapable of passing the blood-brain barrier (Obray et al., 2022), it must be synthesized within neurons to carry out its CNS functions. Once DA is synthesized, it can be stored in synaptic vesicles and released into the synaptic cleft in response to incoming presynaptic action potentials (Beaulieu & Gainetdinov, 2011). DA itself represents an intermediary product in the synthesis of NE and epinephrine (Meiser et al., 2013).

Physiological effects of DA release are mediated by dopaminergic receptors, which are widely expressed across the brain (Rangel-Barajas et al., 2015) and all act as metabotropic receptors (De Felice, 2017). Unlike ionotropic receptors, which are directly coupled to ion channels and mediate fast synaptic transmission, metabotropic receptors are indirectly linked to intracellular signaling pathways through heterotrimeric G-proteins, that can activate or inhibit downstream effectors (Offermanns, 2021). In humans (and all other mammals) there are five DA receptor subtypes that fall into two categories (D1-like, D2-like), depending on their structural and pharmacological properties (Martel & McArthur, 2020).

D1-like receptors, including D1- and D5-receptors, are coupled to G_s-proteins and stimulate the production of cyclic adenosine monophosphate (cAMP), a second messenger that can activate protein kinase A (PKA) and related agents. These agents can foster short-term postsynaptic depolarization processes and excitability by phosphorylation and activation of ion channels, permeable for positively charged molecules (e.g., calcium or glutamate; Greengard et al., 1999). Further, PKA-mediated phosphorylation of CREB (cAMP response element-binding protein) can activate gene expression and lead to changes in synaptic plasticity and long-term potentiation (LTP) implicated in learning and memory (Huganir & Nicoll, 2013). In contrast, D2-like receptors, which include the D2, D3, and D4 subtypes, are coupled to $G_{i/o}$ proteins which inhibit both, the production of cAMP and subsequent activation of PKA, thereby fostering postsynaptic hyperpolarization and neuronal inhibition (Neve et al., 2004).

While D1-like receptors are primarily found post-synaptically, showing highest concentrations in the striatum, NAc, olfactory tubercle, and prefrontal cortex (PFC), D2-like receptors can be found both pre- and post-synaptically, with greatest abundance in the striatum (Cortes et al., 1989; Jaber et al., 1996; Missale et al., 1998). D2-like receptors have a 10 up to 100 times greater affinity for DA and thus, can be activated even in a low-DA state, while D1 receptors require higher DA-concentrations (Martel & McArthur, 2020).

DA signaling operates on two timescales: via rapid-acting (phasic) signals and via slow-acting (tonic) signals (Floresco et al., 2003; Grace, 1991). Phasic signals (bursts) refer to the release of large amounts of DA into the synaptic cleft due to action potential discharge in the dopaminergic neuron. This leads to high intrasynaptic DA concentrations, capable of stimulating postsynaptic receptors. Following exocytosis and receptor binding, DA is removed from the synaptic cleft by the dopamine transporter (DAT) in a milliseconds range (Klein et al., 2019) to prevent it from escaping into the extrasynaptic space. In contrast, tonic DA (varying along timescales of seconds to minutes) represents low concentrated DA molecules apparent in the extrasynaptic space. This may result from either sustained activity in DA terminals causing overflow from the synaptic clefts or from presynaptic glutamate receptors being stimulated by freely diffusing glutamate neurotransmitters, causing DA release from the presynapse (Grace, 2000).

Although there is only a small number of dopaminergic neurons in the human brain (approximately 400.000; Schultz, 2007), whose cell bodies are located in few small areas, their axons are widespread, exhibiting significant impact on (sub-) cortical targets (Björklund & Dunnet, 2007). Dopaminergic neurons constitute a diverse set of cells, primarily found in the mesencephalon and diencephalon, with a smaller population present in the olfactory bulb. Within the mesencephalon, these cells are clustered in the substantia nigra pars compacta (SN), the ventral tegmental area (VTA), and the retrorubral field (RRF; Hosp et al., 2011; Menegas et al., 2015). The axons of these neurons constitute the three main dopaminergic pathways in the brain, including the nigrostriatal, mesocortical and mesolimbic pathways (Arisa-Carrión et al., 2010).

Nigrostriatal projections originate from the SN and extend their efferent fibers to caudate-putamen nucleus in the striatum. This pathway appears strongly implicated in the control of motor function and learning capabilities (Bourdy et al., 2014; Matsumoto et al., 1999). In particular, this pathway regulates the procedural aspects of movements and motivated behaviors by projecting to the more dorsal basal ganglia areas where both behavioral and cognitive habits are learned and stored (Amaya & Smith, 2018; Malvaez & Wassum, 2018). Mesolimbic and mesocortical pathways traverse more medially and arise from DA neurons located in the VTA (Arrias-Carrión & Pöppel, 2007). Whereas mesolimbic DA neurons mainly project to the NAc and the olfactory tubercle but also innervate the septum, amygdala and the hippocampus, the mesocortical DA efferents target prefrontal, cingulate and perirhinal cortices (Arrias-Carrión et al., 2010).

Mesocortical and mesolimbic (DA) projection areas are often summarized as the *mesocorticolimbic system*, which contributes to executive functions, including working memory, cognitive control and flexibility as well as attention (Cools, 2008; Hirano, 2021), but especially appears heavily involved in motivation, reward learning and reward processing (Kelley & Berridge, 2002).

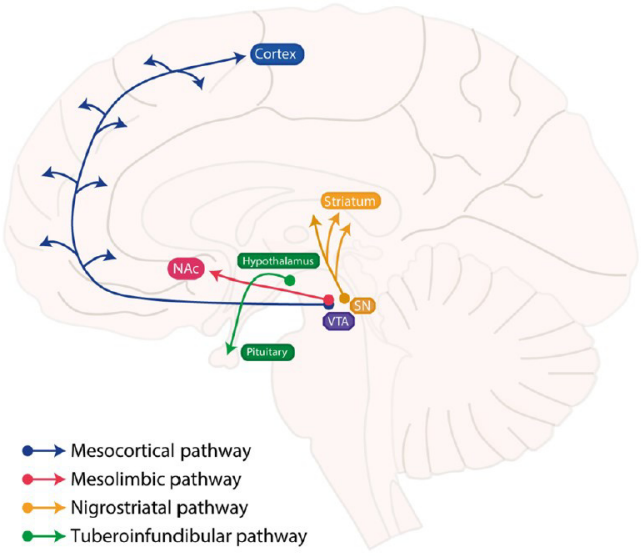

Figure 3. Dopaminergic pathways in the brain: The mesocortical pathway (blue), the mesolimbic pathway (red), the nigrostriatal pathway (yellow) and the tuberoinfundibular pathway (green, not of special interest here); Figure adapted from Xu & Yang (2022), but also see Klein et al., (2019).

Dopaminergic Reward Processing

Research on reward processing in the brain was initiated by Olds and Milner (1954). Their experiments involved implanting electrodes into different brain regions of rats and providing them with a lever to press. Lever presses could induce small electric currents with high precision – as they evoked action potentials in a few thousand neurons within a millimeter sphere around the electrode. Interestingly, the

authors observed that rats strongly increased lever presses to receive more electric shocks to their brains (up to 2000 presses per hour), when electrodes where located in specific regions (including NAc and septum; Olds, 1956). In these cases, rats tended to repeat lever pressing until exhaustion, even ignoring food, water or potential mating partners (Olds & Milner, 1954; Olds, 1956). Such findings seemed to suggest that Olds and Milner discovered a physical correlate for reward in the brain (Schultz, 2016). Subsequent studies indicated that catecholamines played a crucial role in these effects (Wise, 1978) and that DA, rather than NE, was the primary transmitter involved in the brains' reward circuitry (Mason, 1984).

For many years, DA was therefore referred to as the "pleasure chemical" (Kringelbach & Berridge, 2010), related to the prediction and anticipation of rewards as well as associated approach behavior (Arias-Carrión & Pöppel, 2007). More recent compelling evidence from electrophysiological studies suggests that DA activity may also play a role in learning about reward outcomes, by detecting violations in our expectations, called prediction errors (PEs) (Diederen & Fletcher, 2021; Schultz et al., 1997; Schultz, 2016). Such Reward PEs (RPEs) indicate whether received outcomes are better or worse than expected, yielding positively and negatively signed RPEs, respectively (Den Ouden et al., 2012; Gunasekera et al., 2022). These RPEs seem to be coded via increased or decreased spiking frequency of DA neurons (Valdés-Baizaba et al., 2020). However, the sign (positive/negative) and size of RPEs can only be computed, when the brain "knows" how much an individual currently values specific outcomes (Levy & Glimcher, 2012). Put differently, the brain must store an expected value, to which the actual outcome can be compared. The assignment of a subjective value (SV) to an objective outcome is complex as multiple kinds of information or reward attributes must be integrated. These for example might comprise type, magnitude, probability or timing of the outcome (Lak et al., 2014; Padoa-Schioppa, 2011). In intertemporal choice tasks, attribute integration is crucial, as reward magnitude should increase and the delay until receipt should decrease SV. Evidence suggests that such integration might be implemented by a so-called *valuation system* comprising ventromedial prefrontal cortex (vmPFC; including the OFC), VS and posterior cingulate cortex (PCC; see e.g., Kable & Glimcher, 2007). These regions largely resemble core hubs of the mesocorticolimbic system mentioned above and play a key role in the representation of incentive values for primary (e.g., sweet juice), secondary (e.g., money), immediate or delayed rewards (Chib et al., 2009; Kable & Glimcher, 2007; Kable & Glimcher, 2010; Knutson & Ballard, 2009; Lempert et al., 2017; Peters & Büchel, 2010). Moreover, it has been shown, that discounted SV (incorporating delay and reward information), modeled by a hyperbolic function indeed correlates with blood oxygen level dependent (BOLD)-signals in the OFC and the VS (Peters & Büchel, 2009).

Crucially, processing of various primary rewards, including food or erotic visual stimuli are likewise associated with upregulated activity in dopaminergic reward or valuation circuitry (e.g., Gola et al., 2017; Oren et al., 2022; Stark et al., 2019). Specifically, Sescousse and colleagues (2013) conducted a large-scale meta-analysis, showing that the processing of primary and secondary reinforcers

(food-related, erotic and monetary rewards) largely takes place in overlapping brain regions including the VS, anterior insula, thalamus, amygdala and vmPFC.

Moreover, fMRI analyses revealed increased BOLD responses in the VS to conditioned *cues* that reliably preceded primary rewards (Wang et al., 2016), like pleasant liquids (O'Doherty et al., 2002) and odors (Gottfried et al., 2002), or secondary rewards including money (Knutson et al., 2001) – findings suggesting that triggered mesolimbic activation might in fact mirror motivational aspects of reward-directed (approach) behavior (Volkow et al., 2017).

These findings on *cue-evoked* (dopaminergic) reward system upregulation appear promising, as they may also inform certain cue-reactivity phenomena in addiction. During the emergence of an addiction, there is a rising number of stimuli that become experientially linked (conditioned) to the drug, thereby increasing the likelihood of being exposed to drug-predictive cues (Volkow et al., 2019). Evidence suggests a hypodopaminergic state in the VS at baseline (Samaha et al., 2021, Trifilieff & Martinez, 2013) and decreased activation of brain reward regions in response to receipt of non-drug rewards, such as food, sexual stimuli or money, in individuals addicted to drugs compared with controls (Alonso-Alonso et al., 2015; Blum et al., 2012; Carelli & West, 2014; Enzi et al., 2015; Parvaz et al., 2012). Simultaneously, and seemingly in contrast to this, they exhibit exaggerated phasic DA bursts in response to drug-predicting cues, implying hypersensitization. Such drug-cue exposure has been shown to elicit a strong subjective urge for drug consumption (craving; Volkow et al., 2019) and drug-seeking behavior (Perry et al., 2014). Craving responses are strongly linked to VS BOLD signaling (Breiter et al., 1997) and accompanying (striatal) DA release (Volkow et al., 2011; Wong et al., 2006). Studies in animal models show that conditioned cues evoke tendencies of approach behavior, which can be eliminated via striatal lesioning or by DA depletion (Nicola et al., 2005; Parkinson et al., 2002). These results align well with the *incentive sensitization theory*, which postulates that compulsive reward or drug seeking stems from an excessive attribution of incentive salience (or *wanting*) to reward predicting cues, brought on by progressive neuroadaptations in DA projections within mesocorticolimbic circuitry (Berridge et al., 2009).

The spatial overlap during processing of primary and secondary rewards and associated cues, as well as the involvement of DA in modulating subsequent behaviors may indicate that the impact, especially of erotic cues on TD examined in the current project, likely is accompanied by variations in dopaminergic neurotransmission. The next paragraph briefly summarizes key findings of DA effects on TD.

Dopaminergic Involvement in Intertemporal Choice

Evidence on dopaminergic involvement in intertemporal choice stems from multiple sources. As already mentioned, various psychiatric disorders that are presumably linked to a dopaminergic imbalance have

been associated with both, steeper (ADHD, schizophrenia, addiction) as well as shallower (anorexia nervosa, OCD) TD (Amlung et al., 2019; Lempert et al., 2019).

Further, contextual manipulations assumed to interact with DA neurotransmission have also been proven to affect TD. Replicating previous findings (Dixon et al., 2006), Wagner and colleagues (2022) showed that exposure to real-life gambling venues can increase TD in problematic gamblers compared to controls. The authors interpreted their effects in light of incentive sensitization theory (Berridge, 2016; Robinson & Berridge, 2001), proposing that addiction-related environments might have fostered DA release - thereby increasing preference for immediate rewards.

More direct pharmacological approaches including animal or human participants likewise indicate that dopaminergic tone can modulate TD. Specifically, in most animal studies, the ability to delay gratification was impaired by decreased DA transmission (Cardinal et al., 2000; Denk et al., 2005; Floresco et al., 2008; Koffarnus et al., 2011; van Gaalen et al., 2006; Wade et al., 2000) but improved by medium-sized increases (D'Amour-Horvat et al., 2021). However, administration of higher doses of DA-releasing drugs like amphetamine pointed to dose-dependent effects, with small increases in DA improving performance on TD tasks and larger doses leading to impairments (D'Armour-Horvath & Leyton, 2014). It must be noted, that the interpretation of pharmacological DA effect is often hampered by the use of different pharmacological agents, which differentially act on striatal (e.g., haloperidol; Sebel et al., 2017) and/or more frontal (e.g., tolcapone; Magalona et al., 2013) DA levels.

Studies including human participants report even more ambiguous results (Arrondo et al., 2015; Cools, 2008; de Wit, 2002; Hamidovic et al., 2008; Kayser et al., 2012; Petzold et al., 2019; Pine et al., 2010; Wagner et al., 2020; Weber et al., 2016). For example, de Wit and colleagues (2002) reported that elevation of dopaminergic neurotransmission via acute d-amphetamine administration led to a decrease in impulsive decision-making on three different tasks, including two assessing behavioral inhibition and one assessing the relative value of immediate vs. delayed rewards. However, this effect was not replicated (Acheson & de Wit, 2008). Likewise, administration of the D2/D3-receptor agonist pramipexole had no significant effect on measures of impulsivity in another study (Hamidovic et al., 2008). Conversely, Pine and colleagues (2010) reported evidence for steeper TD under a high DA state, induced via L-DOPA (vs. placebo) administration in healthy participants. Simultaneously, D2-receptor antagonist haloperidol did not affect TD. Three other studies reported decreased TD in response to D2/D3-receptor antagonists (Arrondo et al. 2015; Wagner et al., 2020; Weber et al., 2016), which likely reduced DA levels, although opposite interpretations have also been formulated (Wagner et al., 2020).

In summary, these findings seem rather puzzling, as administration of both, DA-increasing and DA-decreasing drugs have been found to elevate and diminish impulsive choice. To reconcile these findings Petzold and colleagues (2019a) proposed an inverted-u-model of DA effects (Cools et al., 2008) on value-based decision-making. In their study, administration of 150 mg L-DOPA had no main effect on impulsive choice. Instead, they found that after L-DOPA intake, more-impulsive individuals became less impulsive but low-impulsive individuals made more impulsive choices on a TD task. The authors

reasoned that low-impulsive individuals (presumed optimal DA signaling) might have been "overdosed" with L-DOPA, therefore demonstrating increased TD, whereas the opposite was observed in more-impulsive individuals (presumed suboptimal baseline dopaminergic signaling) – an interpretation that was later supported by findings from Positron-Emission-Tomography (PET; Petzold et al., 2019b). Resembling such an inverted-u-effect, Kayser and colleagues (2012) observed that subjects with greater baseline impulsivity scores assessed via Barratt-Impulsiveness-Scale (BIS; Barratt, 1959) demonstrated larger declines in TD following tolcapone administration, while subjects with lower baseline impulsivity scores demonstrated smaller declines or even increases in TD.

Underlying reasons for such an inverted-u-shape are manifold. As outlined above, DA is strongly implicated in SV-coding, a crucial process for both intertemporal choice and reward learning (Peters & Büchel, 2010; Schultz, 2016a). Specifically, value-related BOLD fluctuations have been detected in the PCC but especially in vmPFC and the VS (e.g., Kable & Glimcher, 2007). It might be speculated, that blunted (striatal) neurotransmission could therefore impair representation of option values. Simultaneously, strong elevations of DA could promote ceiling effects, which likewise would prevent differentiation e.g., between SS and LL option values. Such effects might especially foster impulsive choice, as higher utility of LL options is not represented accordingly. Early findings already confirmed that a heightened dopaminergic tone can reduce phasic DA signaling (Grace, 1995; Grace, 2000).

This might also explain why individuals suffering from addiction (presumed low DA baseline levels), who generally exhibit increased choice impulsivity, can be triggered by phasic DA-eliciting drug-cues to show even stronger myopic behavior. Miedl and colleagues (2014) showed that neural representation of reward value during TD in gamblers was strongly affected by the degree of craving evoked by arousing gambling-related cues. The authors reported that a positive correlation with model-based SV in midbrain and striatal structures was evident in low-craving trials, but was reversed in high-craving trials. Further, TD was steeper during presentation of high versus low craving stimuli. These findings suggest that highly arousing cues may affect TD via a disruption of SV coding, thereby diminishing perceived differences between LL and SS rewards.

Regarding highly appetitive (erotic) cue effects assessed in the current project (study 2), these findings might suggest that healthy controls (optimal baseline DA signaling) might be pushed to the right side of the inverted-u-function when exposed e.g., to a block-wise series of DA prompting erotic stimuli prior to a TD task. However, such interpretation remains speculative.

Autonomic Arousal Systems

Processing of emotional stimulus material might not only interact with dopaminergic neurotransmission but will most likely also induce short-term fluctuations in physiological arousal. These fluctuations should be evident following both highly appetitive (e.g., erotic) and aversive (e.g., humiliation) stimuli.

Such a general effect, largely independent of the valence and specific content of the cue-material, might be able to shed light on the aforementioned ambiguous findings on cue-evoked changes in TD – especially for those, stemming from trial-wise designs. This was explicitly tested in study 1 of the current dissertation project. The upcoming chapters will therefore shortly introduce the main constituents, contributing to the human physiological/autonomous arousal state. Further, they will briefly summarize theoretical accounts and empirical findings on how arousal (induced by external cues and/or pharmacological agents) might interact with decision-making processes and measures of choice impulsivity in particular.

Physiological Sub-divisions & Signaling

Definitions of arousal vary and often include autonomic, behavioral or cognitive dimensions (Lendner et al., 2020). Autonomic or physiological arousal refers to "*aspects of arousal shown by physiological responses, such as increases in blood pressure and rate of respiration and decreased activity of the gastrointestinal system. Such primary arousal responses are largely governed by the sympathetic nervous system (SNS), but responses of the parasympathetic nervous system (PNS) may compensate or even overcompensate for the sympathetic activity*" (American Psychological Association dictionary, 2023).

The SNS and PNS together represent the two main divisions of the vegetative or autonomic nervous system (ANS), a complex and involuntarily acting network, that supplies internal organs, smooth muscles and secretory glands in order to preserve internal physiologic homeostasis (Karemaker, 2017; Patel, 2015). Although the enteric nervous system (ENS) is sometimes referred to as a third, partly independent sub-division (Gibbons, 2019), it is not of central importance here.

The SNS is governed by upper motor neurons (i.e., neurons superior to the spinal cord) that originate from the hypothalamus (Patel, 2015). Efferents travel down the hypothalamospinal tract, passing the brain stem until they reach preganglionic cells, located in the intermediolateral (IML) cell column of the thoracolumbar division of the spinal cord (Portillo et al., 1996). From there, their short, myelinated and cholinergic fibers project to the para- and prevertebral ganglia, where they synapse with postganglionic neurons (Karemaker, 2017). Postganglionic fibers then extend throughout the organ systems of the body, where they mostly release norepinephrine (NE), capable to bind to adrenergic receptors located on target effectors (Drake et al., 2005; Gibbons, 2019). The extensive ramification of postganglionic efferents in the periphery also explains the diverse and simultaneous bodily reactions that follow upon SNS activation. The associated reactions are often subsumed under the term "fight-or-flight response", which prepares the organism for stress, heightened demands or danger (Zagila & Mongillo, 2017). These include heart rate accelerations, increases in blood pressure, respiration and blood flow to the muscles (Cannon, 1967). Moreover, bronchioles, pupils and blood vessels to the heart dilate, catecholamines (including adrenaline) are emitted from the adrenal medulla, stored glycogen is

released to provide energy and sweating increases (Patel, 2015). The sympathetic nervous systems' actions are coordinated with other neural or hormonal stress responses, such as elevations in corticotropin and cortisol secretion (Chaves et al., 2021).

Whereas the SNS is strongly implicated in "fight-or-flight", the PNS is often considered as its antagonist or counterpart representing a "rest-and-digest" or "feed-and-breed" system (Waxenbaum et al., 2023). Preganglionic neurons of the PNS originate from several brainstem and spinal cord nuclei and exit the central nervous system (CNS) through the 3rd, 7th, 9th, and 10th cranial nerves and four different sacral nerves (Janig & Habler, 2000; Shields, 1993). While most cranial nerves predominantly supply motor and sensory functions to focal structures located in the head and neck region (e.g., the eyes (3rd cranial nerve), the face (7th cranial nerve) or throat (9th cranial nerve)), the 10th nerve (vagus nerve) innervates the viscera of the thorax and the abdomen, including the heart, lungs, stomach, pancreas, small intestine, upper half of the large intestine and the liver (Satsangi & Brugnoli, 2018). In fact, 75% of all parasympathetic fibers are part of the vagus nerve (McCorry, 2007).

Contrasting the SNS, the peripheral PNS lacks a continuous string of ganglia along the vertebral column. Instead, their parasympathetic preganglionic nerves directly travel to the target organ being innervated where they synapse with specific terminal postganglionic neurons. As a result, the parasympathetic system typically produces more localized and discrete effects, stimulating only specific tissues at any given time, whereas the SNS often produces more diffuse discharges upon activation (McCorry, 2007). The central neurotransmitter in the PNS is acetylcholine – for both preganglionic and postganglionic neurons. Whereas the preganglionic receptors are nicotinic, postganglionic receptors are muscarinic in type (Lindh & Hokfelt, 1990). Increased PNS activation typically results in constriction of pupils and bronchial muscles, decreased heart rate and blood pressure and increased production of saliva and mucus as well as urine secretion (Gibbons 2019).

Although SNS and PNS are often described as independent subsystems it is important to note that almost all target areas of the body are innervated by both of them (Waxenbaum et al., 2019). Therefore, the net internal autonomic arousal state might always be understood as weighted sum from both ANS inputs.

In experimental contexts, multiple studies revealed that ANS activity can be successfully altered via various kinds of pharmacological agents (Becker et al., 2012) or external stimuli presented across all sensory modalities (Bari et al., 2018; Horio et al., 2000; Laohakangvalvit et al., 2023; Munoz et al., 2022; Triscoli et al., 2017). In particular, visual emotional stimuli and salient cues of either valence have been observed to induce changes of the internal arousal state, approximated via pupillometric and electrodermal measures, electrocardiography, electromyography or respiratory indices (Bradley et al., 2008; Finke et al., 2017; Kinner et al., 2017; Sato et al., 2021; Wilhelm et al., 2017).

Moreover, affective stimulus processing might not only trigger downstream activity changes in peripheral targets and effector organs, but is also strongly associated with heightened neurotransmission in several brainstem nuclei, that have been characterized as key origins of monoaminergic ascending

fibers (Levinson et al., 2023). Besides serotonergic dorsal raphe nucleus (Luo et al., 2015), noradrenergic locus coeruleus (LC) is of special importance here. The LC is the primary noradrenergic brainstem nucleus in the brain (Bouret & Richmond, 2015; Mather et al., 2016), and is coactivated in parallel to sympathetic systems to rapidly adapt and respond to urgent and salient stimuli (Aston-Jones et al., 1991). This close functional relationship is facilitated by close interconnections with paraventricular nucleus (PVN) of the hypothalamus, one of the key sources of sympathetic signaling. Specifically, release of corticotropin releasing factor (CRF) from PVN during stress responding is associated with increased LC neuronal firing rate and heightened brainstem NE release (Curtis et al., 2012; Lavicky & Dunn, 2010; Page & Abercrombie, 2015). Although depicting one of the smallest, the LC is the most extensively projecting nucleus in brain (Aston-Jones & Waterhouse, 2016). Its efferents reach all of the other neuromodulatory nuclei (e.g., dorsal raphe nucleus) and project to thalamic nuclei, septum, hippocampus, basal lateral amygdala and almost all cortical regions (Loughlin et al., 1986). In fact, LC afferents, targeting α_1-, α_2-, and β-receptor subtypes are the only source of NE innervation to these structures (Samuels & Szabadi, 2008; Sara & Bouret, 2012). Regarding these diverse ascending projections associated with cue-evoked autonomic/sympathetic processing and related brainstem signaling, it appears plausible to suggest, that arousal might affect stimulus processing and behavior on a broader front.

Theoretical Perspectives – Arousal & Behavior

From a theoretical point of view, relative SNS and ANS activity serves two functions. As alterations of the physiological arousal state seem to evolve somewhat automatically, it first has informative value for the individual, acting as a "saliency detector" for the environment, indicating what degree of activation is currently needed. Simultaneously, physiological arousal generally enables the organism to adequately react to the changing conditions of its surrounding. In view of these considerations, it is not surprising, that multiple accounts already proposed how physiological arousal and related bodily states might interact with behavior and decision-making in particular.

For example, Loewenstein (1996) coined the term "visceral factors" to explain how arousal, related to various internal states, including hunger, sexual desire, mood and emotions or physical pain, can affect relative desirability of goods and actions. He stated, that visceral factors are especially triggered by spatial or temporal proximity and availability of a desired object, which in turn might foster a feeling of being "out of control" and a behavioral tendency to respond impulsively. Loewenstein reasoned, that an improved understanding of the underlying mechanisms might help to explain the often-observed discrepancy between behavior and self-interest.

Other influential theories, including the somatic markers hypothesis (SMH), emphasized that autonomic bodily signals such as arousal responses are crucial for decision-making (Bechara, 2004; Bechara & Damasio, 2005; Bechara et al., 1997), as they may entail and transfer information value

regarding available response options or the anticipated outcome of a decision – even without conscious awareness (Bechara et al., 1994, 1997; Wagar & Dixon, 2006). Specifically, Bechara and Damasio (2004) noted that healthy participants engaged in a card-based gambling task (GT; Bechara et al., 2000b) generated increased anticipatory skin conductance responses (SCRs), when they pulled a card from a disadvantageous risky deck, even before picking up the card. Simultaneously, anticipatory SCRs were absent in a vmPFC lesion group, predicting impaired task performance (Dunn et al., 2006).

More cognitive/perceptual accounts also highlight the possibility, that arousal elicited via various sources can sometimes enhance or impair perception and memory, depending on the current situational context. Specifically, it was proposed that a heightened arousal state would additionally boost the processing of already salient stimuli while processing of relatively less salient stimuli would be impaired (*Arousal-biased Competition Theory* (ABC theory); Lee et al., 2014; Mather & Sutherland, 2011).

Empirical evidence – Arousal, Stimulus Processing & Behavior

Empirical evidence suggests that fluctuations of autonomic arousal (state) are indeed strongly associated with alterations in stimulus processing and cognition, as well as (value-based) decision-making.

It is well established, that autonomic arousal and accompanying NE release significantly influence the processing of external stimuli. Specifically, early studies in monkey auditory cortex (Foote et al., 1975), hippocampus (Segal & Bloom, 1976) and cerebellum (Freedman et al., 1977) suggested, that NE upregulation reduces spontaneous cell firing to a greater extent than stimulus-evoked discharge, thus yielding a net increase in *signal-to-noise ratio* (Aston-Jones & Waterhouse, 2016). These findings nicely resonate with recent human and animal studies indicating that short-term arousal signals might contribute to minimizing the impact of prior expectations and biases on evidence accumulation and decision formation within perceptual tasks (de Gee et al., 2014, 2017; de Gee, 2020; Krishnamurthy et al., 2017; Nassar et al., 2012; Urai et al., 2017). Moreover, these effects might be subsumed under the proposed general cognitive function of (prefrontal) NE, which is assumed to facilitate sensory processing but may also enhance cognitive flexibility and executive function, attention and offline memory consolidation (Berridge & Spencer, 2016; Roosendaal & Herman, 2017; Sara & Bouret, 2012). Whereas NE neurotransmission is rather advantageous, if not necessary for regular PFC functioning, especially during demanding executive control tasks, NA effects on PFC functions appear dose dependent, following an inverted-u-function (Sara & Bouret, 2012). When a critical threshold is exceeded, NE levels might impair PFC-dependent executive functions (Arnsten, 2009).

When it comes to (value-based) decision-making, evidence suggests a potential role of physiological arousal in shaping choice behavior. For example, Wemm & Wulfert (2017) showed that in male participants, elevated heart rate (HR), associated with heightened SNS signaling was linearly related to riskier choices on the Iowa Gambling Task (IGT). Similarly, Persson and colleagues (2018)

observed that higher levels of measured electrodermal activity (EDA; i.e., skin conductance) accompanied increased risk-taking behavior, but only when decisions were made under limited temporal resources. Studer & Clark (2011) used a roulette betting task to assess psychophysiological signals (EDA, HR), while participants were engaged in risky decision-making. In 50% of the trials, participants could actively select the size of the bet (active-choice trials). In the other half of the trials, the bet size was fixed (no-choice trials). The authors observed that EDA during active selection of a risky option, increased with the bet size, a finding that replicated in a more recent study (Studer et al., 2016). These findings appear in accordance with predictions derived from somatic marker hypothesis (SMH; Bechara & Damasio, 2005), stating that psychophysiological arousal might be used as an indicator variable for the degree of uncertainty or risk of available choice options. Relatedly, various studies found that e.g., pupil size, a sensitive marker of physiological arousal is affected by uncertainty across learning (Muller et al., 2019) and in perceptual decision tasks (Lempert et al., 2015). However, above-mentioned findings do not clarify whether physiological arousal itself has an independent/specific effect on actual choice behavior or whether it depicts a correlate of the implied and perceived risk. Addressing this issue, more recent studies, capable to quantify physiological arousal during the processing of risky choice options *prior* to the decision, found that enhanced physiological arousal adaptively decreases risk-taking, especially when participants are engaged in highly risky lottery tasks (FeldmannHall et al., 2016).

In sum, these findings might indeed emphasize an informative value of physiological arousal for the individual, which scales with the extent of riskiness/uncertainty during a choice that is currently carried out. Simultaneously, when perceived before an actual decision is made, these arousal signals can be used, fostering preferences of certain options. However, it should also be noted that such interpretation is challenged by recent findings showing that arousal-related pupil dilation following highly salient auditory sounds could not successfully predict trial-level RTs or risk taking (Sullivan et al., 2021).

In the context of intertemporal choice, evidence on the role of physiological arousal is still scarce, especially regarding short-term, phasic arousal. For example, Lempert and colleagues (2016) used pupillometry to assess participants' trial-wise arousal state during a TD task. Interestingly, they found that greater pupil dilation during processing of delayed choice options was associated with an increased likelihood of choosing the LL reward. However, their experimental design could not rule out that these effects where at least partly driven by higher subjective value (SV) of the presented delayed vs. immediate rewards. Other studies explored the association between spontaneously occurring (e.g., Fung et al., 2017), or pharmacologically altered (e.g., Lempert et al., 2017) tonic arousal levels and TD. Fung and colleagues (2017) were the first who showed that cardiac signals were independently associated with TD. Specifically, they found that over the entire experimental interval, individuals with higher heart rates had a tendency towards lower discount rates. These findings complement or support claims from several personality theories, stating that impulsivity might be associated with baseline hypo-arousal (Zuckerman, 1969). Pharmacological approaches entailing administration of NE altering

medication yielded mixed findings, reporting reduced TD following NE upregulation in rats (Bizot et al., 2011; Schippers et al., 2016) while comparable results are largely absent in humans (Herman et al., 2019; Lempert et al., 2017).

Summary

What we know so far is, that temporal discounting (TD) depicts a promising tool to assess choice impulsivity. Research has shown that humans but also animals engaged in TD tasks often deviate from previously conceptualized stable and uniform utility devaluation, especially when exposed to emotional stimuli. What we do not know is, which mechanisms are driving these effects. Tonic variations in dopaminergic neurotransmission as well as short-term-physiological arousal depict two important candidates, as they both have been observed to interact with decision-making on a larger scale. The use of different and complementary experimental designs (block-wise vs. trial-wise), methodologies (fMRI vs. psychophysiology) as well as arousing stimuli of opposing valence (positive vs. negative), might enable us to successfully track down contributions of both systems to alterations in TD. Moreover, improving our knowledge about the underlying features implicated in stimulus-evoked (increased) choice impulsivity might also foster a better understanding of maladaptive cue-reactivity responses in mental ill health, especially in addiction. These constitute the major aims of this dissertation project.

Methods

The upcoming chapter is structured as follows: First, I will introduce key psychophysiological (pupil size, electrodermal activity, heart rate; study 1) and neuroscientific (fMRI; study 2) indices and methods used in the current project to quantify cue-evoked variation of the internal arousal state and reward-system (re-) activity. Second, I will summarize analytical approaches to approximate the degree of TD following emotional cue exposure and illustrate how arousal and reward-system fluctuations can be directly related to choice behavior.

Autonomic Arousal Measures

Pupil Size

Any visual perception starts with light entering the eye through the pupil. The pupil itself is a transparent spherically shaped aperture in the center of the eye (Beatty & Lucero-Wagoner, 2000). The diameter of the human pupil varies roughly between 2 and 10 mm (Mathot, 2018), with an average size of approximately 3 mm under normal lighting conditions (Loewenfeld & Lowenstein, 1999; Sirois &

Brisson, 2014). Pupil size is determined by the activity of two autonomically innervated smooth iris muscles, working antagonistically to control the amount of light falling through the pupil onto the retina. First, the sphincter pupillae, which encircles the pupil like a cord and actively decreases pupil size when it contracts (Mathot, 2018). The sphincter muscle is innervated by the parasympathetic branch of the autonomic nervous system (ANS), which provides homeostatic balance (i.e., keeping the body in stable condition) and regulates rest and digest functions (Mathot, 2018; McCorry, 2007). This resonates with the finding, that pupils are relatively small when we are relaxed. The main waypoints across the parasympathetic constriction pathway are the following: Incoming light is processed by retinal photoreceptors converging on downstream bipolar and subsequent ganglion cells. Visual information further travels along the optic nerve (axons of ganglion cells), passing the optic chiasma and the pretectal olivary nuclei (PN) until the Edinger-Westphal nucleus (EWN) in the midbrain is reached. From here, efferents project via the oculomotor nerve (III) to the ciliary ganglion (CG). Postganglionic fibers, then reach the iris sphincter muscle via short fibers of the ciliary nerve, which evoke pupillary constriction by acetylcholine release at the neuromuscular junction (Hall & Chilcott, 2018).

The counterpart of the sphincter is the dilator muscle. It actively increases pupil size by contracting radially oriented muscle fibers, which pull the interior of the iris outward (Steinhauer et al., 2022). This muscle is innervated by the sympathetic nervous system (SNS), the ANS-subsystem, which is critically involved in arousal and alertness responses and prepares the body for physical action (McCorry, 2007). The association between pupil dilation and the SNS explains why pupils are enlarged when we are aroused. The sympathetic dilation pathway is a subcortical pathway, originating from the hypothalamus and the locus coeruleus (LC), that targets the iris dilator muscle (Mathot, 2018). More specifically, the interconnected LC and hypothalamus likewise project to the intermedio-lateral column (IML) of the spinal cord. Efferents from the IML project to the superior cervical ganglion (SCG), which in turn innervates the iris dilator muscle via the alpha-adrenergic receptors, which causes the pupil to dilate (McKoy et al., 2022). Apart from this main dilatory pathway, the LC can also directly inhibit the EWN, which means LC activity causes pupil dilation not only by actively enhancing noradrenergic dilation processes, but also by inhibiting the parasympathetic constriction pathway at the level of the EWN (Steinhauer et al., 2004).

Multiple studies indicated that dilatory pupil responses can be used as a reliable and accessible measure of NE levels (Aston-Jones & Cohen, 2005; Koss, 1986) and LC activity, respectively (Joshi, 2020). Global arousal levels captured via electroencephalography (EEG) and pharmacological agents interacting with the LC-NE system both affect pupil size and LC activity (Chu & Bloom, 1973; Hong et al., 2014; Koss, 1986; Phillips et al., 2000). Further, LC neural firing patterns are closely related to pupil size in rodents and monkeys (Joshi et al., 2016; Varrazani et al., 2015). Human research confirmed covariation of pupil size and BOLD activity in the LC (Murphy et al., 2014), but also found this relationship to be modulated by brain states (Megemont et al., 2022). Although dilatory responses are

also partly influenced by other neurotransmitters like serotonin, these effects are known to be mediated via variations of the LC-NE system (Yu et al., 2004).

LC neurons adopt two modes of action, a tonic and a phasic mode (Aston-Jones & Cohen, 2005; van den Broeke et al., 2019). While tonic activity refers to a baseline level of neuronal discharge (1-6 Hz), phasic activity, which is characterized by short-term bursts of higher frequency firing (10–15 Hz), can be superimposed (Aston-Jones et al., 1999; Kane et al., 2017; Poe et al., 2020). Tonic LC activity is closely related to the sleep-waking cycle (Hayat et al., 2020). It is lowest or even absent in states of drowsiness or slow wave sleep, and is heightened during active waking (Takahashi et al., 2010), increased attention (Sara, 2009) and arousal (Carter et al., 2010). Phasic LC activity on the other hand, is closely related to the processing of salient sensory information or to novel or behaviorally-relevant stimuli (Cole et al., 2022; Vazey et al., 2018; Zhao et al., 2019).

Similar to LC activity and resembling their close relationship, pupil size is also based on two analogous components: a baseline component, comprising slow changes in pupil size for sustained periods of time, and a phasic response, characterized by an event-related transient change (Beatty, 1982). Especially phasic dilatory responses are well documented following internal events like imagination (Laeng & Sulutvedt, 2014; Sulutvedt et al., 2018) or mental effort (Kahneman & Beatty, 1966) and external events like sudden sounds (Zekfeld et al., 2018) or trial-wise processing of arousing visual stimuli of positive (e.g., erotic; Finke et al., 2017; Rieger et al., 2012) and negative valence (Bradley et al., 2008; Kinner et al., 2017). The pupil's role as indicator of emotional arousal is further supported by its close relationship to other established measures of ANS activity like heart rate (HR) or skin conductance responses (SCR; Bradley et al., 2008; Kinner et al., 2017; Wang et al., 2018).

In the first study of this dissertation project, we were particularly interested in the impact of cue-related short-term arousal fluctuations on intertemporal choices. Therefore, we applied a trial-wise design, aiming to capture phasic pupil (dilatory) responses associated with the processing of highly affective stimuli (represented by erotic, aversive vs. neutral images).

Pupillometry data were acquired by a RED500 remote eye-tracking device, which uses infrared illumination of the retina (Sensomotoric Instruments (SMI)). The system enables contact-free measurement of eye-movements and pupil size, while head movements are compensated by tracking the corneal reflex. However, to ensure optimal data quality, participants were also instructed to place their heads on a chin rest at a distance of 60 cm from both, eye-tracking device and the monitor. Raw pupil data were sampled in millimeter units, with a frequency of 500 Hz, and without using online filters. Critical time stamps within the experiment (e.g., image onsets) were marked by trigger events, which were sent to an acquisition laptop via ethernet connection. Trigger events were then used to divide continuous pupil data stream into task-relevant segments. Segmented pupil data was averaged and divided by median pupil size from the preceding inter-trial interval to receive a cue-evoked phasic pupillary response relative to the tonic baseline signal for each trial. Precise details on pupil data analysis can be found in the methods section of study 1.

Electrodermal Activity

Electrodermal activity (EDA) is a direct measure of the current conductive properties of the skin, which are typically under control of eccrine sweat gland activity (Cacioppo et al., 2007; Martin & Venables, 1980; Posada-Quintero & Chon, 2020). Thermoregulation is the primary function of most of the more than three million sweat glands (Greco et al., 2016), although those located on the plantar and palmar sides of the hand are also known to contribute to grasping ability and mechanical friction, rather than temperature control (Critchley, 2002; Posada-Quintero & Chon, 2020). Contrasting with pupil size, sweat gland activity is solely innervated by the SNS, mainly by the sudomotor nerves (Braithwaite et al., 2015). Such exclusiveness is supported by studies, which simultaneously recorded sympathetic action potentials in peripheral nerves and EDA. A high correlation between bursts of sympathetic nerve activity and phasic changes in EDA was reported (Bouscein, 2013; Wallin, 1981). As mentioned above, SNS upregulation increases the autonomic arousal state and prepares the organism for actions, necessary for fight-or-flight (Critchley, 2002; McCorry, 2007). The exclusive innervation by sympathetic branches of the ANS without any "contamination" by parasympathetic activity explains why the EDA is probably the most widely used index of changes in sympathetic arousal (Braithwaite, 2015).

Efferents controlling sudomotor and sweat gland activity, originate in the posterior hypothalamus. Fiber strands travel ipsilaterally along the pontine tegmentum and medullary (reticular) nuclei before synapsing in the sympathetic ganglia. In response to stimulation, postganglionic sympathetic nerves release acetylcholine (Ach), which triggers sweat secretion from eccrine glands (Hu et al., 2017).

Both, sympathetic and electrodermal activity are closely linked to emotional processing and arousal (Critchley et al., 2002; Horvers et al., 2021; Rahma et al., 2022). This coupling is mirrored by a multitude of studies reporting increased EDA in response to visual (Bradley et al., 2008; D'Hondt et al., 2010; Ventura-Bort et al., 2022) or auditory (Brouwer et al., 2013) arousing cues and during socially stressful (e.g., TSST; Greco et al., 2023; Liu & Zhang, 2020) or cognitively demanding tasks (e.g., mental arithmetic; see Kim et al., 2019). Further, fMRI studies enabled a characterization of how CNS activity covaries with changes in EDA (Gertler et al., 2020). Brain regions found to be engaged during affective, somatosensory-motor and cognitive stimulus-evoked EDA included posterior and mid-cingulate, left amygdala, right anterior insula and left posterior insula. These associations were found irrespective of the task characteristics and demands at hand (Beissner et al., 2013).

Akin to pupil size, there are two main components that constitute the compound EDA or skin conductance (SC) signal (see Figure 4). Tonic phenomena include slow shifts of the baseline skin conductance level (SCL) and background characteristics of the signal, which create a moving baseline per individual (Braithwaite, 2015), relatively stable in a second's range (Bouscein, 2012). Variations in the SCL are thought to reflect slow changes in the ANS dynamics and autonomic arousal (Braithwaite et al., 2015; Greco et al., 2016). Phasic activity or skin conductance responses (SCRs) comprise faster reacting elements of the EDA signal (Greco et al, 2016; Horvers et al., 2021). SCRs might occur

spontaneously or in response to external stimuli. While spontaneous or *unspecific* SCRs occur with no identifiable stimulus that elicits the response, SCRs are usually defined as *event-related* if its peak exceeds a specific a-priori defined threshold and occurs in close temporal proximity to stimulus onset (Dawson et al., 2000).

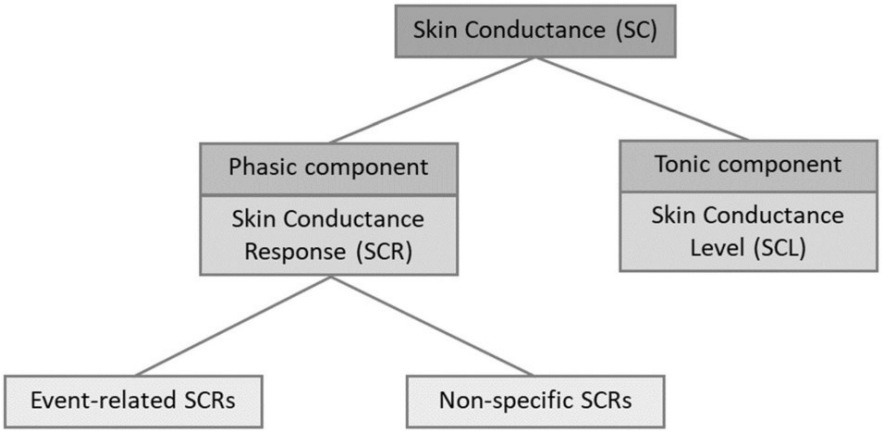

Figure 4. Main components of skin conductance/electrodermal activity (adapted from Horvath et al., 2021)

Event-related SCRs are typically triggered 1-5 s post stimulus presentation (Dawson et al., 2000) and are best captured by a monophasic right-skewed distribution, characterized by a steep increase of skin conductance (SC), with a slow recovery (Boucsein, 1992). The duration of the recovery phase strongly depends on the SCR amplitude but can take up to approximately twenty seconds (Kelsey et al., 2018). The minimum amplitude threshold, a phasic response has to reach to be classified as SCR, typically ranges between 0.01 and 0.05 microsiemens (μS; Braithwaite, 2015).

Measures to quantify phasic SCRs include the amplitude (maximum deflection in predefined interval), rise time (time taken from SCR onset to reach peak amplitude), onset latency (time until pre-set SCR threshold is reached) or half recovery time (time from SCR peak to 50% recovery of SCR amplitude) (Benedek & Kaernbach, 2010; Braithwaite et al., 2015).

In study 1 of the project, we were primarily interested in short term arousal fluctuations, which we aimed to capture via trial-wise calculated phasic EDA responses following exposure to highly arousing images. To extract phasic signal proportions from the tonic baseline level we used so-called *continuous decomposition analysis* (CDA; Benedek & Kaernbach, 2010).

As mentioned before, sudomotor nerve activity causes sweat secretion from eccrine glands, which in turn evokes changes in SC (Benedek & Kaernbach, 2010). From a theoretical perspective, CDA assumes that sudomotor nerve activity can be quantified as a total driver signal, which is convolved with an impulse response function (IRF) to produce the raw EDA. Tonic and phasic fractions contribute to the total driver signal (see Eq. 3).

$$EDA = (Driver_{Tonic} + Driver_{Phasic}) * IRF \quad \text{Eq.3}$$

Following this idea, CDA first uses deconvolution (which reverses the process of convolution and simply implies the division of the raw EDA by the IRF), to derive a total driver signal, comprised from tonic and phasic fractions (Eq. 4).

$$\frac{EDA}{IRF} = Driver_{total} = (Driver_{tonic} + Driver_{Phasic}) \quad \text{Eq.4}$$

Next, transient impulse sections (phasic) and inter-impulse intervals (tonic) are detected in the total driver signal by finding zeros in its first time-derivative. Interpolated inter-impulse intervals are then considered as tonic driver fraction. In the end, the tonic SC activity is recovered by convolution of the tonic driver with the IRF. Phasic driver fraction can be calculated by simply subtracting the tonic driver from the total driver signal (Benedek & Kaernbach, 2010).

Automatic continuous decomposition analysis routines (including tonic and phasic driver extraction) were performed using the *Ledalab* toolbox (Benedek & Kaernbach, 2010) implemented in Matlab (Mathworks). We focused on the phasic driver fraction for all subsequent statistical analyses. Details on all computed single trial measures can be found in the study 1 protocol.

Raw EDA data were acquired via a Biopac MP160 data acquisition system (Biopac Systems, Inc), using a sampling frequency of 2000 Hz. Further, we connected an EDA100c amplifier module with a gain of 5 µS/V, 10 Hz low pass filter and DC high pass filter settings. Disposable Ag/AgCl electrodes were attached to the index- and middle finger of the non-dominant hand, pre-gelled with isotonic gel (Biopac Gel 101) to ensure optimal signal transmission. Raw data were recorded in microsiemens (µS). Before each measurement, we validated the functionality and response of the EDA device. To this end, we performed two simple dynamical tests and simultaneously checked signal characteristics after electrodes were attached to the subject. Specifically, we used startle stimuli, namely, deep breaths and a sudden external loud sound, which should evoke an increase in SCL about 1-5 s thereafter. These tests were implemented to detect so-called “non-responders”, which show almost no EDA response despite subjective arousal (Figner & Murphy, 2011). However, all subjects participating in study 1 showed adequate responsivity.

Heart Rate

Complementing pupil dilation and EDA, we assessed cue-evoked changes of the heart rate (HR) to characterize short-term fluctuations of emotional arousal.

The heart is the key element of our cardiovascular system. It acts as a pump, moving blood through various kinds of vessels (i.e., arteries, capillaries, veins) thereby providing necessary oxygen and nutrients to the body (Gordon et al., 2015). The heart is composed of four morphologically and

functionally distinct chambers, including the right atrium, right ventricle, left atrium and left ventricle (Litviňuková et al., 2020). Deoxygenated blood from the right ventricle is pumped through pulmonary arteries to the lungs. Here, wastes are removed, the blood becomes oxygenated and re-enters the left atrium via the pulmonary veins. Oxygenated blood next moves across the mitral valve to the left ventricle. When the left ventricle contracts, blood is moved through the aorta and is propelled out across the body (Marieb & Hoehn, 2013; Tortora & Derrickson, 2017).

To act as a pump, our cardiac system (heart) needs electrical input. The input or electrical innervation stems from autorhythmic cells located at the sinoatrial node (SA), spontaneously generating pacemaker potentials, which initiate each cardiac contraction (Coote & Cauhan, 2016). Specifically, spontaneous depolarization of the SAs autorhythmic fibers creates an electrical signal that projects through the atria to the atrioventricular node (AV). From the AV the electrical impulse is passed on via the "Bundle of His", right and left bundle branches, and Purkinje fibers to the ventricular muscle, evoking ventricular contraction (systole; Biopac Systems).

Whereas the *P-wave* of a recorded electrocardiogram (ECG) represents depolarization and contraction of muscle cells in the atria, the characteristic *QRS-complex* is evoked by depolarization of the right and left ventricles. Ventricular contraction (ventricular systole) and associated ejection of oxygenated blood to the body occurs after the onset of the QRS-complex and extends into the S-T segment. The *T-wave* represents repolarization of bilateral ventricles (see Figure 5.; Shaffer et al., 2014).

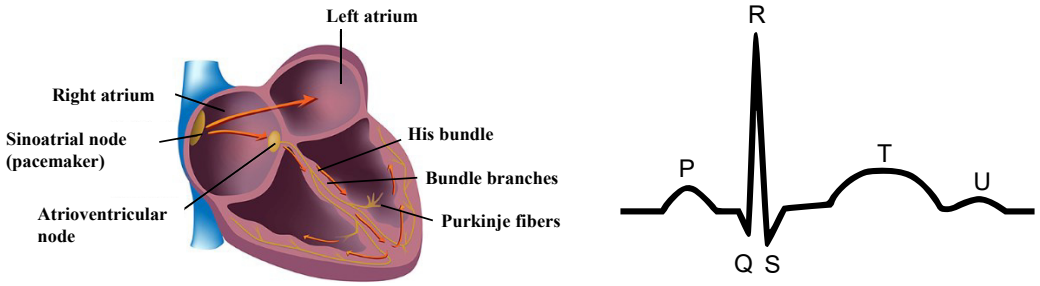

Figure 5. Left: Schematic illustration of heart chambers and associated innervation (Figure adapted and modified from Alila Medical Media/Shutterstock.com); Right: Key components of the cardiac cycle

Although the heart appears like a closed loop system, which in general produces its own beat, contraction strength and especially the heart rate (beats per minute (bpm)) are strongly affected by sympathetic and parasympathetic subdivisions of the ANS (Campos et al., 2018).

At rest, the PNS influence on the heart predominates (Shaffer et al., 2014). It decreases automaticity and excitability of the SA node, thereby decreasing average heart rate to around 75 bpm. SA node's intrinsic firing rate (without any modulation), decreases with age from an average 107 bpm at 20 years to 90 bpm at 50 years (Opthof, 2000). Parasympathetic preganglionic neurons (P1N) originate from the medulla oblongata (especially from the nucleus ambiguous) and the dorsal motor nucleus of the vagus nerve (Hopkins et al., 1996). Neuronal projections travel through bilateral vagus

nerves to the atrial and ventricular myocardium (i.e., heart muscle; Campos et al., 2018). Here acetylcholine and vasoactive intestinal peptides are released (Silvani et al., 2016; Spyer, 2011), binding to muscarinic (mainly M2) receptors. As a result, specific potassium channels open, promoting a hyperpolarized state following enhanced PNS activity (Silvani et al., 2016). HR decreases almost linearly with the parasympathetic preganglionic discharge rate (Berntson et al., 1995).

In contrast, sympathetic postganglionic neurons innervate the SA and AV node via the intrinsic cardiac nervous system and the myocardium (Biopac Systems). Increased activity in these afferents is followed by norepinephrine (NE) and epinephrine release and binding to beta-adrenergic (β1) receptors located on cardiac muscle fibers (Shaffer et al., 2014). This facilitates spontaneous depolarization in the SA and AV nodes, which in turn increases HR and strengthens the contractility of the atria and ventricles (Shaffer et al., 2014). HR increases almost linearly with the frequency of sympathetic postganglionic discharge (Berntson et al., 1995).

In sum, sympathetic and parasympathetic cardiac controls work in antagonistic ways and exert opposing regulatory effects on myocardial activity. Measured HR represents the net effect of the neural output of the parasympathetic (vagus) nerves, which slow HR, and the sympathetic nerves, which accelerate it (Shaffer et al., 2014). However, SNS and PNS affect the HR at different time frames (Silvani et al., 2016). Whereas parasympathetic nerves exert their effects more rapidly (<1 s), changes in sympathetic activity take effect from approximately 5 s post stimulus onset (Nunan et al., 2010).

To capture short-term autonomic changes associated with emotional image processing, we focused on phasic changes in HR immediately (0-5 s) post stimulus onset. We calculated the instantaneous HR per minute by dividing 60 by the current R-wave-to-R-wave (RR) interval, measured in seconds, which denotes the time between consecutive R-waves at the center of the QRS-complexes. This first interval following a stimulus encounter is typically marked by a vagally (i.e., parasympathetically) mediated HR suppression or deceleration, denoted as *orienting response* (OR; Hare, 1972). We captured the OR using a weighted average approach (Graham, 1978; Velden & Wölk, 1987), yielding mean HR changes in 0.5 s bins relative to a 2 s baseline prior to image onset. The OR represents an automatic allocation of cognitive or attentional resources promoting increased sensory receptivity and deepened encoding of information from the environment (Graham, 2021). There is strong evidence that this type of stimulus reaction is increased following both, pleasant and unpleasant stimuli (Abercrombie et al., 2008; Bradley et al., 2001; Jönsson & Hansson-Sandsten, 2008).

Similar to EDA, we measured cardiovascular activity using Biopac systems' hard- and software (MP 160; Biopac Systems), including an ECG100C amplifier module with a gain of 2000 normal mode, 35 Hz low pass notch filter and 0.5 Hz/1.0 Hz high pass filter. Disposable circular contact electrodes were filled with isotonic paste and attached according to the lead-II configuration. Details on all computed single trial measures, can be found in study 1 protocol.

Summary of Psychophysiological Indices

In Study 1 of the current dissertation project, we used three different measures to quantify short-term fluctuations of physiological arousal, evoked by visual affective stimuli (images). Those are pupil size, electrodermal activity and heart rate. These three measures are partially complementary, as they rely on sympathetic and parasympathetic inputs to different extents. Pupil size is under control of SNS and PNS afferents, but especially dilatory pathways are tightly linked to SNS activity. Heart rate is likewise modulated by both branches of the ANS, but especially short-term orienting responses in a range of seconds post stimulus onset, mainly resembling PNS input. Lastly, EDA is solely under sympathetic control. Simultaneously using all three methods enabled us to comprehensively monitor and extract single-trial cue-responses with good temporal resolution, which we later used in computational models to investigate arousal effects on TD (study 1; see section "Analysis of Intertemporal Choice").

Functional Magnetic Resonance Imaging

Functional Magnetic Resonance Imaging (fMRI) was introduced in the early nineties of the last century (Bandettini et al., 1992; Bandettini, 2012; Kwong et al., 1992, 2012; Ogawa et al., 1992). As a variant of classical or conventional Magnetic Resonance Imaging (MRI), it is intended to depict dynamic patterns in brain activation, caused by local changes in neural metabolism (Chen & Glover, 2015; Soares et al., 2016). FMRI is non-invasive and has unparalleled spatial specificity, characteristics that contributed to its widespread use across neuroscientific, psychological or medical professions.

Mapping of functional brain activity relies on a phenomenon called the *blood oxygenation level dependent* (BOLD) contrast, first demonstrated in rats (Ogawa & Lee, 1990) and later in humans (Bandettini et al., 1992). The BOLD contrast depends on two distinct phenomena. First, the working brain requires a continuous supply of glucose and oxygen (O_2). As the brain has no storage of O_2, there must be continuous delivery by cerebral blood flow (CBF; Buxton, 2009). Local increases in neural (and glial) discharge and associated increases in aerobic and anaerobic O_2 consumption trigger the delivery of oxygenated hemoglobin through vasodilation (Chen & Glover, 2015; Malonek & Grinvald, 1996; Raichle et al., 1976). This increases CBF to the region. Moreover, the local oxygen demands are transiently overcompensated, which results in a net increase in local oxygenation for several seconds (Chen & Glover, 2015). The amplification of the oxy-/deoxy-hemoglobin ratio directly affects the magnetic characteristics of the local tissue, resulting in an elevated MRI signal relative to the surrounding area (Soares et al., 2016). In particular, whereas deoxygenated hemoglobin is paramagnetic, which induces local magnetic field distortions, oxygenated hemoglobin has diamagnetic properties, and does not strongly interfere with the magnetic field (Schandry, 2011).

The physical foundation of MRI is nuclear magnetic resonance (NMR) and was first described by Felix Bloch and Edward Purcell in 1946, for which they were both awarded the nobel prize for

physics in 1952 (Grover et al., 2015). In fact, MRI is used to detect hydrogen (H^+) nuclei in water molecules that are present throughout the entire body and brain (water molecules comprise more than 75% of brain tissue by weight; Blinkov & Glezer, 1968; Deoni, 2010). Positively charged protons within hydrogen nuclei are constantly rotating along their axis, a quantum-mechanic atomic property denoted as *spin* (Deoni, 2010). As a spinning motion of an electrically charged object generates a magnetic field, each hydrogen proton can be conceived as a tiny bar magnet exhibiting a non-zero vectoral force, called *magnetic moment*, with random orientation in three-dimensional space (Mastrogiacomo et al., 2019). When a strong external magnetic field B_0 is applied, spinning protons align either in parallel with (low-energy state) or anti-parallel (high-energy state) to the external field. Further, the protons have an angular momentum due to its rotation, so they will *precess* around the B_0 axis, reminding of the wobbling motion of a gyroscope (Grover et al., 2015). Although most of these magnetic moments cancel each other out, there is a small excess of spinning protons oriented parallel with B_0, which provide the net magnetization vector M_0 in the longitudinal direction (longitudinal magnetization; Grover et al., 2015; Loued-Khenissi et al., 2018). The precession speed of the protons is described by the Larmor-equation and is directly proportional to the applied external field strength (Buxton, 2010).

It is this precessing motion, that causes the protons' sensitivity and receptivity to incoming radiofrequency energy (RF; Sprawls, 2000). When matching the protons precession rate (the resonant frequency of NMR), short RF impulses (separated from each other by a *repetition time*) delivered to the tissue will tip precessing protons away from the B_0 axis and cause them to synchronize, which in turn creates a transverse magnetization relative to B_0. Such pulses are usually described by the *flip angle* they evoke (e.g., a 90° pulse or a 60° pulse; Buxton, 2010; Sprawls, 2000). Simultaneously, a sub-portion of protons undergoes a transition from the parallel to the anti-parallel state, leading to a decrease in overall longitudinal magnetization (M_0; Brown et al., 2007).

This newly created transverse magnetization precesses around B_0, and creates a detectable signal in the radiofrequency coil of the MR scanner (Buxton, 2010). The position of the spins in three-dimensional space can be determined by means of magnetic field gradients, which slightly alter the protons' precession speed in single layers of brain tissue. As RF energy is only transferred when pulse frequency matches precession speed, changes in magnetization and relaxation can be precisely located (Sprawls, 2000).

As soon as the RF impulse is turned off, magnetization recovers back to equilibrium via two processes. First, individual protons return to their original parallel or anti-parallel orientation (relative to B_0), restoring longitudinal magnetization and releasing adsorbed energy back to the surrounding tissue (spin-lattice-interaction). This process is called T_1-relaxation (Deoni, 2010; Mastrogiacomo et al., 2019). Second, individual precessing protons start to de-synchronize, and adsorbed energy is released by spins following mutual interference (spin-spin interaction), which in turn reduces transverse magnetization. This process is called T_2-relaxation (Deoni, 2010; Mastrogiacomo et al., 2019). As a convention, the T_1 relaxation time (constant) is specified in terms of the time required for the longitudinal magnetization

to reach 63% of its initial maximum. Contrary, the T_2-constant is the time required until only 37% of the initial transverse magnetization is still present (Sprawls, 2000). However, it must be noted that pure T_2-decay only occurs in completely homogeneous magnetic fields (B_0). As mentioned above, paramagnetic deoxygenated hemoglobin located within blood vessels can induce local field inhomogeneities, speeding up the desynchronization of the spinning protons and the loss of transverse magnetization (Sprawls, 2000). This fastened decay of transversal magnetization is described as T_2*-relaxation.

As T_1-, T_2- and T_2*-relaxation times directly depend on spin-lattice-interaction and spin-spin interactions, it is not surprising that these time constants are affected by local biophysical and biochemical environments and differ for tissues with different composition (Sprawls, 2000). Relaxation properties of the tissues can then be used to generate contrast images based on the differences in T_1 (i.e., T_1-weighted image) and in T_2 /T_2* (i.e., T_2-weighted image) relaxation times (Mastrogiacomo et al., 2019). Likewise, BOLD activity changes can be depicted via T_2*-weighted images, in which active and oxygenated (diamagnetic) brain areas exhibit stronger magnetization (i.e., signal emitted to the RF coil) resulting in a brighter appearance in the image (Volkow, 1997).

T_2*-relaxation and thus BOLD signal change is optimally depicted using fast MR sequences like *gradient-echo planar imaging* (EPI). Such sequences can be further accelerated by using so-called *multiband imaging*, which allows for the simultaneous acquisition of multiple brain slices at a time (Feinberg & Setsompop, 2013).

As acquired raw fMRI data are typically mixed with non-neural sources of variability, several preprocessing steps must be taken to identify nuisance sources and artifacts (noise) and reduce their effect on the data (Esteban et al., 2019). These typically entail motion and distortion correction, co-registration of T_1-images to functional images, normalization and spatial smoothing (Soares et al., 2016; but see methods section of study 2 for details of the applied preprocessing pipeline).

Next, preprocessed fMRI data are analyzed using classical statistical methods. The most common approach to analyze fMRI images from each participant is to use general linear models (GLM). Using GLMs, we can define one or multiple regressors, or independent (predictor) variables, to fit a model to a specific outcome measure or dependent variable, respectively. The dependent variable in our case is the BOLD time series measured at each voxel *Y* (i.e., volume element as analogy to pixel) (Arco et al., 2018; Friston et al., 1994). The GLM (Eq. 5) is used to model the voxel signal (*Y*) at each timepoint as a weighted sum of multiple predictor variables (X_1-X_n), which are multiplied by a corresponding regression coefficient (β_1-β_n). Moreover, the GLM also includes an intercept (β_0; i.e., representing the expected value of the response variable when all predictor variables (covariates) are set to zero) and an error term (ε; Pernet, 2014).

$$Y = ß_0 + ß_1 * X_1 + ß_2 * X_2 + \cdots + ß_n * X_n + \varepsilon \quad \text{Eq.5}$$

Predictor variables or regressors usually represent specific experimental events of interest (e.g., stimulus presentation onsets), parametric modulators of such events (e.g., stimulus magnitudes) and other covariates possibly affecting BOLD signal variation (e.g., age or sex). Further, irrelevant nuisance regressors might be incorporated to account for variance unrelated to experimental events (e.g., motion or drifts). Regressors that are included in the model are additionally convolved with a hemodynamic response function (HRF). The HRF characterizes the theoretical course of the BOLD signal that emerges after exposure to a short, isolated stimulus (Poldrack et al., 2011).

Commonly used fMRI analysis software (e.g., Statistical Parametric Mapping (SPM); Friston, 2011) typically models the HRF with a set of gamma functions, that gradually rise 1-2 s post stimulus, peak after ~5-6 s, and then return to baseline about 12 s after the stimulus occurred. Typically, a small undershoot appears, before it stabilizes after ~25-30 s (Buxton et al., 2004; Handwerker et al., 2012; Miezin et al., 2000; Soares et al., 2016).

In the end, this GLM approach aims to create an ideal fitted time-series for the BOLD response within each voxel, so that we can use the estimated beta-weights (regression coefficients) for each regressor for the upcoming statistical analyses.

During first-level analysis, we assess task-related effects for every individual. Specifically, we can examine, whether beta-weights from different regressors differ significantly (using t- or f-tests) from an implicit baseline or between different experimental conditions. In the second-level-analyses, data from all individuals are pooled together and analyzed to examine experimental effects across the group (Poldrack et al., 2011). Here, random effects models can be employed to consider variability present both within individual subjects and across different subjects in the dataset (Chen et al., 2013; Friston et al., 2005). Results from the statistical analysis can be visualized in statistical parametric maps, depicting the respective test statistic for each voxel in the brain (e.g., *t-maps*). Such t-maps, resembling task-related changes in BOLD activity can be color-coded and superimposed onto a structural (T_1) brain image.

As the same GLM and statistical test is applied to up to hundreds of thousands of voxels (and their time courses), significant results will arise by pure chance (Type I errors). This is known as the *multiple comparison problem* in fMRI (Loued-Khenissi et al., 2018). There are several methods to control such elevated error rates. These for example include Bonferroni Correction or *familywise error rate* (FWER). Bonferroni Correction would rescale the single-voxel threshold to "maintain" an error probability of 5% at the global level. This is accomplished by testing each individual hypothesis at a significance level of α/N, where N denotes the number of tests or voxels, respectively. However, this approach is too conservative for fMRI data, because the time courses at each voxel are in fact not independent (Loued-Khenissi et al., 2018). In contrast, familywise error (FWE) correction, accounts for the spatial (auto-) correlation of voxel activity according to *Random Field Theory* (RFT), thereby essentially reducing the number of tests performed. The degree of roughness (the inverse of smoothness) of the whole-brain voxel activity map can thus be used to identify the appropriate threshold

corresponding to a desired FWER (Logan & Rowe, 2004; Loued-Khenissi et al., 2018; Nichols & Hayasaka, 2003). However, it is often the case, that task-related differences in BOLD activity are assumed to particularly occur in specific a-priori defined brain regions (regions of interest, ROIs). Therefore, FWE correction approaches can be restricted to voxels within these areas, which essentially reduces the number of statistical tests. This approach is known as small volume correction FWE (Poldrack et al., 2011). For a detailed introduction to (functional) magnetic resonance imaging and corresponding analyses the reader is referred to the textbooks of Poldrack et al. (2011) or Sprawls (2000).

In study 2 of the current project we were particularly interested in BOLD activity changes associated with the processing of highly erotic (vs. neutral) visual stimuli to quantify the degree of erotic cue-reactivity (or erotic arousal, respectively). Such changes, we reasoned, could have contributed to previously reported findings on increased choice impulsivity following appetitive cue exposure. We specifically focused on a set of ROIs, associated with attention and reward processing, that showed high differential responsivity to erotic image content in previous studies (Gola et al., 2016; Markert et al., 2021; Stark et al., 2019; Wehrum-Osinsky et al., 2014). These areas comprised the VS, dorsal and ventral anterior cingulate cortex (dAcc/vAcc), OFC, amygdala, thalamus, hypothalamus, insula, VTA and lateral occipital cortices (lOcc). To quantify the effect of erotic cue-reactivity on TD more directly, we also extracted beta-weights for the contrast erotic>neutral from reward-related subcortical (VS, VTA) and prefrontal (dlPFC) areas, and assessed whether erotic cue-reactivity predicted changes in a subsequent TD task on the subject level. In addition, we used model-based fMRI to assess more subtle cue effects on TD. In model-based fMRI, we can examine the functional correlates of latent cognitive processes that may underlie observed behavior. Specifically, parameter estimates derived from computational models (e.g., a choice of a specific option or an options' subjective value (SV)) can be used as parametric regressors or predictor variables in the GLM to determine brain regions showing a response profile consistent with that model (Gläscher & O'Doherty, 2010; O'Doherty et al., 2007). We first assessed core neural effects underlying TD, that is SV-related BOLD fluctuation in vmPFC, striatum and posterior cingulate and LL-choice-related activity in dlPFC (Bartra et al., 2013; Clithero & Rangel, 2014; Kable & Glimcher, 2007; Peters & Büchel, 2009; Smith et al., 2018). We also assessed whether lateral PFC (lPFC) activity in response to LL reward presentation differed following erotic vs. neutral cues. For details on the fMRI data acquisition, the implemented preprocessing pipeline, as well as first- and second-level modeling of the cue exposure phases and the TD task, the reader is referred to the methods section of study 2.

Analysis of Intertemporal Choice

Both studies of the current project used classical TD tasks to approximate the degree of choice impulsivity. As already mentioned, TD refers to the tendency to discount the value of delayed options

as a function of time (Green et al., 1997), which might lead people to prefer SS over LL rewards. Multiple ways have been proposed, how behavior in TD tasks can be adequately quantified. Broadly speaking, those can be classified into model-based and model-free approaches.

The perhaps most simple and reasonable model-free measure of TD is the relative fraction of SS choices compared to all valid choices made (Eq. 6).

$$TD_{model-free} = \frac{Choices_{SS}}{(Choices_{SS} + Choices_{LL})} \quad \text{Eq.6}$$

Moreover, devaluation of LL rewards can also be quantified via computation of the area under the empirical discounting curve (AUC; Myerson et al., 2001). The AUC corresponds to the area under the connected data points that describe the decrease of the SV (y-axis) of the LL over time (x-axis). These connected data- or so-called *indifference points* can be identified using a three-step procedure. First, a logistic function is fitted to the choices made for each delay, which approximates the probability to choose the LL- vs. the SS-option. Second, the LL amount is identified, at which the logistic function takes a value of 0.5 (the functions' inflection point), denoting the point at which both reward types are valued equally by the respective participant (i.e., the participant is "indifferent"). Each delay can then be expressed as a proportion of the maximum delay and plotted against the normalized subjective (discounted) value as a fraction of the objective monetary amount (Yoon et al., 2017). Lastly, the area under the curve can be estimated by dividing the total area into trapezoids (trapezoidal rule) that are summed up (Bourget & Delouis, 1993). The borders of each of the trapezoids are represented by two consecutive delays (x_1, x_2) depicted on the x-axis and the corresponding SVs (y_1, y_2) on the y-axis. Specifically, the area of each of the trapezoids was computed as follows (Myerson et al., 2001; Eq. 7):

$$A = \frac{x_2 - x_1}{\left(\frac{(y_1 + y_2)}{2}\right)} \quad \text{Eq.7}$$

The sum across trapezoids then corresponds to the individual AUC, and smaller AUC-values indicate steeper discounting (Basile & Toplak, 2015).

Such model-free or model-agnostic measures of TD have several advantages. They can be easily derived and depict a straightforward measure of behavioral preference. In addition, they avoid potential issues with parameter estimation or the commitment to a specific mathematical framework (e.g., hyperbolic vs. exponential discounting).

However, more effortful cognitive modeling of TD behavior appears even more promising. In general, cognitive models use mathematical formalizations that help to deepen our understanding of human behavior and ideally give insights into underlying mental processes that may drive it (Farrell & Lewandowsky, 2018; Yarkoni & Westfall, 2017). Derived model parameters may be linked to partly unique cognitive sub-processes, so variation in parameter estimates may inform us about *which* aspects

within decision-making processes are affected by experimental manipulation. Although numerous models have been proposed to describe the devaluation process of future rewards as a function of time (Bleichrodt et al., 2009; Ebert & Prelec, 2007; Killeen, 2009; Loewenstein & Prelec, 1992; Mazur, 1987; McKerchar et al., 2009; Rachlin, 2006; Samuelson, 1937; Yi et al., 2009), exponential and especially hyperbolic models are the most frequently used (Molloy et al., 2020; Peters et al., 2012). In these two model specifications, the decrease in SV of a delayed reward (*A*) over time (*D*) is described using an exponential (Samuelson, 1937; Eq. 8) or hyperbolic (Mazur, 1987; Eq. 9) function:

$$SV = A * \exp(-kD) \quad \text{Eq.8}$$

$$SV = A/(1 + kD) \quad \text{Eq.9}$$

Whereas exponential models formalize a constant rate of reward devaluation, irrespective of the delay to reward receipt, hyperbolic models assume a decreasing devaluation rate as the delay to receiving the reward increases, meaning that the SV of the reward decreases more rapidly for shorter delays and more slowly for longer delays (Chapman & Elstein, 1995). As this pattern is often observed, especially in human participants, hyperbolic models show superior fit to most data sets (McKerchar et al., 2009).

Based on those findings, both studies of the current project assumed hyperbolic discounting of future rewards, which was slightly adapted to the applied experimental design (trial-wise vs. block-wise, see below). Study 1 had two objectives. First, we aimed to explore trial-wise effects of erotic, aversive and neutral visual cue exposure on TD. Second, we assessed whether single-trial physiological arousal measures could partly predict behavioral variation in discounting. We first modeled TD of delayed rewards in the neutral condition using the above mentioned classical hyperbolic formula (Mazur & Coe 1987; Green & Myerson 2004; Peters & Büchel, 2011):

$$SV_{(LL_t)} = \frac{A_t}{(1 + exp(k) * D_t)} \quad \text{Eq.10}$$

A_t denotes the objective amount of the LL option and D_t the associated delay in trial *t*. The parameter *k* describes the participant-specific discount rate, which determines speed of reward devaluation over time. Note that *k* was modeled in log-space to increase numerical stability of the model. We used a standard softmax action-selection choice rule (see Eq. 11), often used in the context of reinforcement-learning and decision-making to model the probability of choosing the LL option in a given trial *t* (Sutton & Barto, 2018). The softmax models the (LL-) choice probability as a sigmoid function of SS- and LL-subjective value differences. It further allows to model choice stochasticity, using a *ß*-parameter, which accounts for the fact that choice is not entirely driven by the value of the encountered options. A *ß*-value

of zero reflects random choice behavior with equal choice probabilities for all options. Higher *ß*-values indicate a higher reliance on option values.

$$P_{(LL)} = \frac{exp(SV_{LL} * ß)}{exp(SV_{SS} * ß) + exp(SV_{LL} * ß)} \quad \text{Eq.11}$$

In order to assess condition-related differences in reward devaluation (*k*) and choice stochasticity (*ß*) we slightly extended the above-mentioned formulas by adding so-called shift parameters ($S_{Ero_{k/ß}}, S_{Avr_{k/ß}}$), which allowed for trial-wise *variation* of both parameters depending on the current condition (erotic or aversive; see Eq. 12, Eq. 13).

$$k_{(t)} = k_{neut} + I_{Ero(t)} * S_{Ero_k} + I_{Avr(t)} * S_{Avr_k} \quad \text{Eq.12}$$

$$ß_{(t)} = ß_{neut} + I_{Ero(t)} * S_{Ero_ß} + I_{Avr(t)} * S_{Avr_ß} \quad \text{Eq.13}$$

I_{Ero} and I_{Avr} are dummy variables identifying the respective experimental conditions (erotic vs. aversive). Trial-wise estimates for *k* and *ß* can then be used to calculate the SV of the LL reward as well as the probability to choose the respective option (see Eqs. 10 & 11 above).

In order to assess whether single-trial physiological arousal measures could partly predict behavioral variation in TD over and above condition effects, we set up two additional models. The first model included two additional terms ($EroPupil_{k/ß}$ and $AvrPupil_{k/ß}$) in the trial-wise estimation of $k_{(t)}$ and $ß_{(t)}$. These terms allowed us to model variations in *k*- and *ß* due to the current arousal state, which was not explained by experimental condition alone. In this first model (Eqs. 14 & 15), the arousal state was approximated via single-trial pupil size, which appeared to be the most sensitive arousal proxy (see chapter "Pupil Size" in the methods section above for details on the calculation of trial-wise pupil estimates).

$$k_{(t)} = exp(k_{neut} + (I_{Ero(t)} * S_{Ero_k}) + (I_{Ero(t)} * Pupil_{(t)} * EroPupil_k) + (I_{Avr(t)} * S_{Avr_k}) + (I_{Avr(t)} * Pupil_{(t)} * AvrPupil_k)) \quad \text{Eq.14}$$

$$ß_{(t)} = ß_{neut} + (I_{Ero(t)} * S_{Ero_ß}) + (I_{Ero(t)} * Pupil_{(t)} * EroPupil_ß) + (I_{Avr(t)} * S_{Avr_ß}) + (I_{Avr(t)} * Pupil_{(t)} * AvrPupil_ß) \quad \text{Eq.15}$$

I_{Ero} and I_{Avr} again depict dummy variables coding the experimental condition and S_{Ero} and S_{Avr} denote subject-specific parameters modeling changes in log(*k*) and *ß* depending on the condition in the current trial *t*. $EroPupil$ and $AvrPupil$ capture additional condition-specific variation in the model parameters (log(*k*), *ß*) due to trial-wise pupil-linked arousal. These modulated *k*- and *ß*-parameters can then be used to calculate the *SV* of the LL option and the respective choice probabilities.

Although pupil size appeared to be the most sensitive arousal proxy, we set up a second model to examine a pure arousal effect on TD irrespective of experimental conditions. As mentioned earlier, pupil size, EDA and ECG measures can be regarded complementary, as they capture sympathetic and parasympathetic fractions of autonomic activation to a different extent. We therefore first removed dummy variables and condition-specific shift parameters from the model. Next, we included single-trial estimates of all three physiological arousal measures and assessed their effect on the trial-wise estimates of *k*- and *ß*-parameters (see Eqs. 16 & 17).

$$k_{(t)} = exp\left(k_{base} + \left(Pupil_{(t)} * PupilReg_k\right) + \left(ECG_{(t)} * EcgReg_k\right) + \left(EDA_{(t)} * EdaReg_k\right)\right) \quad \text{Eq.16}$$

$$ß_{(t)} = ß_{base} + \left(Pupil_{(t)} * PupilReg_ß\right) + \left(ECG_{(t)} * EcgReg_ß\right) + \left(EDA_{(t)} * EdaReg_ß\right) \quad \text{Eq.17}$$

Here, *PupilReg*, *EcgReg*, *EdaReg* represent the three arousal regressors modelling changes in log(*k*) and *ß* as a function of trial-wise mean estimates in pupil size, heart rate or skin conductance.

Modeling of TD in study 2 of the current project was highly similar. In this study we assessed block-wise appetitive (erotic) vs. neutral cue exposure effects on subsequent TD while participants underwent fMRI. We again modeled TD in the neutral condition using the above mentioned classic standard hyperbolic formula (see Eq. 10) and captured condition-specific variations in *k* and *ß* (i.e., due to erotic cue exposure) by respective shift-parameters ($S_{Ero_{k/ß}}$; see Eqs. 12 & 13).

However, this time, we reasoned that cue exposure might affect TD beyond a modulation of log(*k*) (which captures steepness of the discounting function), e.g., by inducing an overall offset in the discounting function. This approach increases model flexibility, which also addresses a common problem of classical one-parameter hyperbolic and the exponential discounting models, which often over-estimate discounted values at shorter delays and under-estimate discounted values at longer delays (McKerchar et al., 2009). To capture such effects, we set up another model that allowed for an offset of the discounting function as a whole in the neutral condition (modelled by the parameter $\omega_{Neut_{SV}}$), which might be differentially affected by erotic cue exposure (S_{Ero_ω}, Eq. 18).

$$SV_{(LL)} = SV_{(LL)} * (\omega_{neut} + I_{Ero(t)} * S_{Ero_\omega}) \quad \text{Eq.18}$$

Here $SV_{(LL)}$ denotes the discounted SV of the LL reward. ω_{neut} is the offset parameter in the neutral condition, which additionally can be shifted in the erotic condition (S_{Ero_ω}).

Hierarchical Bayesian Modeling

In the upcoming section I will give a short introduction to the principles of Hierarchical Bayesian Modeling and associated parameter estimation techniques we applied to find the best fitting parameters of the cognitive models described above. For a detailed overview of the described concepts, the reader is referred to Kruschke (2015) as well as Farrell and Lewandowsky (2018).

So, what is Bayesian modeling? Bayesian modeling describes a statistical approach that is based on the Bayes' theorem of conditional probabilities, a mathematical formulization that allows us to update our beliefs or probabilities of an event occurring, in light of new information (i.e., new data; van de Schoot et al., 2014). Specifically, the theorem postulates that for any two events A and B, the probability of A, given B has already occurred (denoted as P(A|B)), is given by:

$$P(A|B) = \frac{P(B|A)*P(A)}{P(B)} \quad \text{Eq.19}$$

Here P(A|B) is the conditional probability of A given B, P(B|A) is the conditional probability of B given A and P(A) and P(B) describe the unconditional probabilities of the events A and B.

As an everyday example, consider a person going to a psychotherapist showing symptoms of a specific clinical disorder. The therapist already has a suspicion, which has to be validated using a diagnostic test. The probability of having the disorder (event A), given the test is positive (event B), can be expressed as P(disorder|positive test). To calculate this probability, the therapist can use Bayes' theorem to update the prior probability of the disorder (P(disorder)) based on the test results. The therapist would need to know the sensitivity and specificity of the test, which are the probabilities of a true positive and true negative test result, respectively. Let us assume the test has a sensitivity of 0.8 (80%) and a specificity of 0.9 (90%) and the prior probability of the disorder (i.e., population prevalence) to be 0.1 (10%). The probability of having the disorder, given a positive test, can then be calculated using the following equation: P(disorder|positive test) = P(positive test|disorder) * P(disorder) / P(positive test) = 0.8 * 0.1 / (0.8 * 0.1 + 0.1 * 0.9) = 0.47. So, even in case of a positive test, the probability of having the disorder is 47%, pointing to the need of multiple tests and additional information to finally confirm a clinical diagnosis (Although the fact that the patient consults the therapist on its own accord would already represent relevant prior information, this is neglected in the above performed calculations). This example illustrates how Bayes' theorem can be used to incorporate new information (test results) into our understanding of the probability of an event (the presence of a disorder) and update prior beliefs or probabilities.

In the context of Bayesian cognitive modeling we now aim to estimate the parameter values of our chosen model for each of our participants, given their (mostly behavioral) data to update our prior beliefs. For this purpose, we adapt the formula of conditional probability (Eq. 19) as follows:

$$P(\theta|D) = \frac{P(D|\theta)*P(\theta)}{P(D)}$$ Eq.20

Here, P(θ|D) denotes the posterior distribution, which approximates the probability distribution over the parameter values, given the data. The posterior distribution density is maximal for the most likely parameter value. P(θ) is the prior distribution. The prior distribution describes initial beliefs or assumptions we have about participants' parameter values before new data is incorporated (Wilde & Li, 2019). Prior distributions can take multiple forms, used to express the a-priori degree of uncertainty about the expected parameter values and are roughly classified as informative or non-informative (Lemoine, 2019). Uniform priors are rather non-informative as they assign equal probabilities to all values within a certain (plausible) range. In contrast, e.g., Gaussian prior distributions can be regarded informative. Their mean represents the assumed most likely value of the parameter, while the standard deviation represents the degree of uncertainty around the mean (van de Schoot et al., 2014). The choice of a prior distribution appears crucial, as it can have a non-neglectable impact on the results of the analysis. Especially, the choice of informative priors (e.g., Gaussian priors) should be made with care, and it is important to have a good estimate of its mean and standard deviation, to avoid introducing (non-justified) biases into the analysis (Depaoli et al., 2020). Informative priors can for example be based on the posterior distribution of a given parameter from previous studies. The likelihood, $P(D|\theta)$, represents the probability of having obtained the data D, given our prior values of the parameters. $P(D)$, sometimes termed marginal likelihood or evidence, describes the overall probability of the data, regardless of any specific parameter values. It serves as a normalization factor, scaling the obtained posterior to the range of probabilities (0-1) leaving relative posterior probabilities of parameter values unaffected (Farrell & Lewandowsky, 2018). Therefore, the above-mentioned formula can be simplified to:

$$P(\theta|D) \propto P(D|\theta) * P(\theta)$$ Eq.21

which states, that an unknown posterior distribution is proportional to the likelihood times the prior. This is important as the posterior distribution cannot be derived analytically. However, if we can compute the terms on the right-hand side of the equation, we can draw samples from the posterior distribution (Farrell & Lewandowsky, 2018).

Markov Chain Monte Carlo (MCMC) sampling (Robert & Casella, 2010) describes a strong class of computational algorithms used to approximate complex probability distributions in Bayesian statistics. It allows for the generation of samples from a posterior distribution, even when the distribution is intractable or difficult to compute analytically (van Ravenzwaaij et al., 2020). Further, it can handle high-dimensional parameter spaces. The basic idea behind MCMC sampling involves creating a Markov Chain, a random process starting at an initial value, which can be provided or randomly chosen. From this starting point, the process navigates through the parameter space of the model, sampling parameter values with higher posterior probability more frequently. Due to this probability-dependent sampling,

the MCMC sampler creates a representative sample from the target- or posterior distribution (Smith, 2007).

There are several popular MCMC algorithms, including Metropolis-Hastings (Metropolis & Hastings, 1953), Gibbs sampling (Geman & Geman, 1984), or the Hamiltonian Monte Carlo (HMC; Duane et al., 1987), which all enable an approximation of the target distribution, given a large number of samples, but differ in how new samples are generated from this distribution during each iteration. In Metropolis-Hastings, new samples are created by proposing a candidate sample from a proposal distribution, and then accepting or rejecting it based on the acceptance probability, which is calculated using the ratio of the height of the posterior at the proposal to the height at the current sample (Farrell & Lewandowsky, 2018). In Gibbs sampling, a new sample is generated by sampling from the conditional distribution of each variable, given the current values of the other variables in the model. This is done for each variable in the multivariate distribution (Casella & George, 1992). Hamiltonian Monte Carlo (HMC) is a variation of the Metropolis-Hastings algorithm that allows for more efficient exploration of the parameter space by considering the underlying geometry (gradient) of the target distribution, to guide the proposal of new states (Kruschke, 2015).

How can we ensure that the above-mentioned sampling processes yield valid approximations of the posterior distribution? There are multiple pitfalls in MCMC sampling that have to be addressed. First, samples drawn using step-by-step MCMC algorithms are not completely independent but will show some degree of autocorrelation. To tackle this issue, as a convention only every i-th sample of the Markov Chain can be kept, a procedure termed thinning (South et al., 2022). Another problem is multimodality, which points to the fact that the posterior distribution may have multiple modes, and the MCMC sampler may get stuck in one mode, failing to explore other regions of the distribution and finding the true parameter values (Larjo & Lähdesmäki, 2015). To address multimodality, one can run multiple chains starting from different initial values to more effectively explore the state space (Yao et al., 2020). If there is a truly best fitting parameter, all chains equally should roughly converge on this value. One way to assess this chain convergence is to examine the convergence diagnostic, $\hat{R}$ (Gelman & Rubin, 1992), which indicates the ratio of the between-chain variance to the within-chain variance. A ratio close to 1 suggests that chains mixed or converged adequately. Another problem concerns heightened sensitivity to initial conditions or starting values, which should be addressed by techniques such as specifying a burn-in (period), where the initial samples are discarded to foster the probability that the Markov Chains can converge to the true underlying distribution (South et al., 2022). Lastly, a more general and coarse approach to evaluate the validity of the drawn samples is to compare key indices of the posterior (e.g., mean or median) to model-free indices of behavior. For instance, in the context of TD, one could assess whether the estimated discounting parameter log(k) is closely associated to the fraction of SS choices or the AUC.

What makes above-mentioned Bayesian modeling hierarchical? The term “hierarchical” points to the underlying structure of the model we set up to depict complex relationships or dependencies in

the data. A core feature of hierarchical models is that they acknowledge the presence of individual variation of e.g., behavior, but simultaneously posit there is a systematic pattern governing this variation (Lewandowsky & Farrell, 2018). Such governance within hierarchical or multi-level models can be depicted by higher-/group- level variables (or "parent" variables) that influence the probability distributions of the variables at the lower levels (or "child" variables; Gopal et al., 2012). Hierarchical models are most suitable, when we attempt to model data that have a nested or grouped structure, which is often apparent in data collected from multiple individuals belonging to a certain group or data collected in different experimental conditions (Mertens et al., 2017). In the context of computational modeling, individual data are captured via so-called subject-level parameters ("child" variable), which can be drawn from hyper- or group-level parameters (parent variable). Hyperparameters and subject-level parameters form a joint parameter space and can be fitted simultaneously (Rouder & Lu, 2005). This joint fitting in hierarchical modeling appears promising, as it enables sharing of information between the multiple levels of the model that can improve the estimation of model parameters, which simultaneously appear to be more robust to outliers and data noise (Kruschke, 2015; Wang & Blei, 2018). This increased robustness is partly due to a process called *shrinkage*, which refers to the fact, that single-subject parameter values are shrunk (pulled closer) towards the estimates of the hyperparameter (Gelman & Pardoe, 2012; Katahira, 2016).

Examination of the resulting hyperparameter (posterior-) distributions, representing different experimental conditions or participant subgroups, allows us to infer several kinds of information. For example, we can assess key indices like their means or medians, or calculate a difference distribution and assess its deviation from zero. To evaluate whether such deviation is substantial or "meaningful", we can examine highest density intervals (HDIs), a summary measure for probability distributions, which denotes a value-range containing a specified proportion of the probability mass (e.g., 95% or 99%; Joshi et al., 2023). If specified HDIs show no overlap with zero, this can be interpreted as first evidence that parameters differ meaningfully. Further we can calculate so-called *directional* (dBFs) or *undirected* (BF01) *Bayes Factors*. DBFs (corresponding to the ratio of the posterior mass of difference- or shift-parameter distribution below zero to the mass above zero) can be computed to test the degree of evidence for increases vs. decreases of parameter values (Dienes, 2014). BF01 are based on the Savage-Dickey Ratio (SDR) and quantify the degree of evidence for a null model that would restrict a parameter of interest at a given value (e.g., $S_{Ero} = 0$) against an alternative model, where the parameter can vary freely. SDR can be calculated by dividing the height of the prior distribution at a given value by the height of the posterior at the same value (Dickey & Lientz, 1970; Marsman & Wagenmakers, 2017). While a positive dBF of e.g., 5, would suggest that an increase of parameter value is five times more likely than a decrease, the reverse is true for negative values. Simultaneously, a BF01 of 5 would imply that the null model is five times more likely than the alternative full model and a BF01 of 1/5 = .2 would suggest the opposite. In general, Bayes Factors between 1 and 3 can be considered as anecdotal evidence, Bayes Factors above 3 as moderate evidence and Bayes Factors above 10 as strong evidence for a

parameter increase or the null model. Likewise, the inverse of these values reflect evidence in favor of the opposite hypothesis (Beard et al., 2016).

To sum up, above-mentioned characteristics of hierarchical Bayesian models and inference derived from parameter posterior distributions illustrate key advantages compared to classical frequentist statistical approaches. Bayesian modeling enables the incorporation of prior information we have about the range and/or distribution of model parameters or measurements. Such prior information or belief can be directly fed into a-priori multi-level model specifications to consider dependencies in the data. Further, it allows sequential accumulation of knowledge as we can use evidence derived from previous model fits for upcoming prior definitions. By using posterior distributions, Bayesian models also provide a natural framework for quantifying uncertainty in parameter estimates, which is not, or only to limited extent, possible in frequentists approaches that often deliver point estimates (Gelman, et al., 2013). Lastly, results from Bayesian models, such as Bayes Factors have a clear and intuitive interpretation, which appears especially useful when we aim to assess evidence for (or direction of) an effect following experimental manipulation (Gelman & Hill, 2006).

In study 1, parameter posterior distributions were estimated via Markov Chain Monte Carlo Gibbs sampling as implemented in JAGS (Version 4.2) using R (Version 3.5.1; R Development Team, 2018) and the r2jags package (Plummer, 2003). In study 2, parameter estimation was implemented via MCMC no-U-turn (Hamiltonian Monte Carlo) sampling (NUTS; Hoffmann & Gelman, 2014) implemented in STAN (Carpenter et al., 2017) using R (Version 3.5.1; R Development Team, 2018) and the rstan Package (Stan Development Team and others, 2018). Relative model fit was assessed via the *loo* package in R using the Widely-Applicable Information Criterion (WAIC), a method for estimating pointwise out-of-sample prediction accuracy from a fitted Bayesian model using the log-likelihood evaluated at the posterior simulations of the parameter values (Vehtari et al., 2017). Put differently, WAIC depicts a measure that helps us to assess the relative performance of different Bayesian models in explaining or fitting our observed data, while penalizing for model complexity. Lower values of WAIC indicate better out-of-sample prediction performance.

Publications

Summaries

This dissertation project and the two conducted studies presented below aim to contribute to a better understanding of emotional cue effects on choice impulsivity as measured by temporal discounting (TD) behavior. While there is a broad consensus on the fact that various contextual factors and external (emotional) cues can affect otherwise highly stable TD, findings to date still appear mixed and involved mechanisms remain elusive. Investigating such mechanisms might be promising for multiple reasons:

First, TD appears altered in a range of psychiatric disorders and clinical conditions. While some disorders have been characterized by increased TD (e.g., addiction) others show the opposite (e.g., anorexia nervosa; Amlung et al., 2019; Lempert et al., 2019). These findings have rendered TD (approximating choice impulsivity) a promising transdiagnostic process (Bickel et al., 2019), i.e., a process or behavior exhibited across disorders whose examination may provide novel insights into common underlying features of the different psychopathologies as well as factors contributing to their development, maintenance or exacerbation (Amlung et al., 2019). Moreover, when TD is considered a relevant (latent) factor of multiple rather different disorders, knowledge about mechanisms that *change* that latent factor appears of high theoretical but also practical relevance as it may inform potential interventions.

TD entails at least two subprocesses. These are *valuation* of the immediate and delayed choice options (rewards) and *cognitive control* (Peters & Büchel, 2011). When emotional (e.g., erotic) cues are capable to affect TD (as previously observed), it appears plausible that they potentially act via a disruption of one of these two subprocesses (or both). Similar results have been observed in individuals suffering from gambling disorder (Miedl et al., 2014). Here, highly arousing gambling cues interfered with neuronal valuation signatures, which may have prevented a representation of objective value differences, thereby fostering immediate reward preference. However, whether such interference "requires" addiction-related stimuli or whether it can also be triggered via highly appetitive erotic cues in healthy individuals remains unclear. Alternatively, especially highly appetitive cues like erotic images could act via a more general upregulation of activity in (dopaminergic/mesolimbic) reward areas, fostering approach behavior towards immediate rewards. Moreover, processing of highly emotional cues (of either valence) will always be inextricably linked to elevated short-term ANS responses in the individual. However, whether such arousal signals also contribute to cue-evoked alterations in TD likewise remains an open question.

Answers to the question of how emotional cues influence impulsive choice in healthy controls might also notably inform our understanding of real-world *cue-reactivity* responses in (subclinical) addiction, where a heightened responsivity to addiction-related cues, evident on subjective (craving),

physiological and neuronal levels, can favor impulsive and often maladaptive decision-making or even relapse in abstinent individuals.

In the following, I will briefly summarize the main procedures and results from the two studies. Afterwards the published versions of both papers will be presented.

Summary study 1. Trial-wise exposure to visual emotional cues increases physiological arousal but not temporal discounting (published in "Psychophysiology" in 2022)

In study 1 we addressed previous contradictory findings on trial-wise emotional cue effects on TD. Both, highly appetitive and aversive visual stimuli presented during choice have been found to elevate TD, but other studies also reported reductions in TD or null effects. We reasoned, this discrepancy might be attributed to cue-evoked arousal fluctuations. Moreover, previous study designs were often unable to adequately disentangle valence and arousal related effects. In study 1 we therefore used highly appetitive (erotic), equally arousing aversive and neutral visual cues that were separately presented during temporal discounting trials. Complementary psychophysiological measures (pupil size, heart rate, electrodermal activity) were recorded to approximate autonomous nervous system (ANS) activity. Trial-wise arousal estimates were calculated and fed into computational models to assess short-term cue-evoked ANS effects on TD. Despite robust ANS responding following erotic and aversive stimuli indicated by pupil dilations and phasic heart rate responses, we detected no condition effects on TD nor did we find evidence for substantial variations in TD due to the momentary physiological arousal state. These results speak against a general physiological arousal effect of visual emotional stimuli on choice impulsivity.

One might argue, that although TD is not reliably affected by short-term cue exposure and related arousal fluctuations, more slower tonic elevations of neuronal reward circuit activity following block-wise cue presentation might change intertemporal choice. Moreover, such a design might more closely reflect real-world situations in which for example formerly addicted individuals are exposed to drug cues or come across public places associated with past drug consumption. Previous studies on block-wise appetitive cue effects (compared to trial-wise designs) yielded more consistent results, often reporting increased TD. However, these studies did not assess whether neuronal signaling in key (dopaminergic) brain areas might bear information that could explain upregulated impulsive choice on a broader scale.

Summary study 2. Erotic cue exposure increases neural reward responses without modulating temporal discounting (Published in "Imaging Neuroscience" in 2023)

In study 2, we used fMRI to assess the effects of *block-wise* erotic vs. neutral cue exposure on both, neuronal reward circuit activity and subsequent TD. Moreover, we investigated potential associations between reward-system-reactivity in key dopaminergic brain areas and changes in TD. Although it appears highly plausible, that such modes of action might likewise contribute to previously reported

appetitive cue effects in healthy individuals as well as drug cue effects in addicted subgroups, this was not tested before. In a within-subjects study, participants were first exposed to a 15-minute cue exposure phase, including a presentation of highly appetitive, pre-rated erotic or neutral visual stimuli (depending on the condition of the current testing day). Immediately after, subjects performed a classical TD task. Both experimental phases were performed during fMRI assessment.

As hypothesized, erotic compared to neutral stimuli strongly increased neuronal activity in attention and reward circuitries. Replicating previous findings, subjective value-coding was evident in vmPFC, VS, and cingulate cortex and increased dlPFC activity was associated with more future-oriented LL choices. However, TD was not substantially affected by erotic vs. neutral cue exposure and upregulated activity in key dopaminergic areas was not sufficient to explain myopic approach behavior towards immediate rewards.

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ORIGINAL ARTICLE

Trial-wise exposure to visual emotional cues increases physiological arousal but not temporal discounting

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Abstract

Humans and many animals devalue future rewards as a function of time (temporal discounting). Increased discounting has been linked to various psychiatric conditions, including substance-use-disorders, behavioral addictions, and obesity. Despite its high intra-individual stability, temporal discounting is partly under contextual control. One prominent manipulation that has been linked to increases in discounting is the exposure to highly arousing appetitive cues. However, results from trial-wise cue exposure studies appear highly mixed, and changes in physiological arousal were not adequately controlled. Here we tested the effects of appetitive (erotic), aversive, and neutral visual cues on temporal discounting in 35 healthy male participants. The contribution of single-trial physiological arousal was assessed using comprehensive monitoring of autonomic activity (pupil size, heart rate, electrodermal activity). Physiological arousal was elevated following aversive and in particular erotic cues. In contrast to our preregistered hypothesis, steepness of temporal discounting was not significantly affected by emotional cues of either valence. Aversive cues tended to increase decision noise. Computational modeling revealed that trial-wise arousal only accounted for minor variance over and above aversive and erotic condition effects, arguing against a general effect of physiological arousal on temporal discounting.

KEYWORDS

arousal, decision-making, heart rate, pupillometry, skin conductance, temporal discounting

1 | INTRODUCTION

Many decisions are associated with consequences that differ in temporal proximity and reward magnitude. Temporal discounting (TD), the tendency to favor smaller-but-sooner over larger-but-later rewards, is common in humans (Peters & Büchel, 2011) and many animals (Kalenscher & Pennartz, 2008). Alterations in TD are associated with a range of psychiatric conditions and problematic behaviors, including addiction, substance abuse and attention-deficit hyperactivity disorder (Amlung et al., 2019; Bickel et al., 2019; Jackson & MacKillop, 2016; Wiehler & Peters, 2015). TD exhibits stability over weeks ($r = .91$; Simpson & Vuchinich, 2000), months ($r = .77$–$.80$; Arfer & Luhmann, 2017), and even 1 year ($r = .71$; Kirby, 2009), and across different testing environments (Bruder et al., 2021; Odum, 2011). TD is therefore regarded as a trait-like characteristic (Smith & Hantula, 2008).

However, despite its trait-like stability, TD can be modulated by contextual factors (Lempert et al., 2016; Peters & Büchel, 2011). The format of time and reward information

directly influences choice behavior (Lempert et al., 2016). TD is attenuated when delays are expressed in terms of the date of reward delivery (Read et al., 2005), when future rewards are paired with participant-specific episodic cues (Bromberg et al., 2017; Peters & Büchel, 2010; Rösch et al., 2021) or when reward amounts are increased (Green et al., 1997).

In the context of TD, modulatory effects of appetitive cues have also long been discussed. For example, men might discount rewards more steeply following exposure to arousing pictures of opposite-sex faces or erotica (Kim & Zauberman, 2013; Van den Bergh et al., 2008; Wilson & Daly, 2004). Such effects are often interpreted as reflecting the activation of a motivation/reward system by highly rewarding erotic stimuli, which in turn could facilitate reward approach behavior in other domains (Van den Bergh et al., 2008). This resonates with the observation that erotic cues robustly activate reward-related brain circuits including ventral striatum and orbitofrontal cortex (Gola et al., 2016; Stark et al., 2005; Wehrum-Osinsky et al., 2014). Furthermore, primary reinforcers such as appetitive (erotic) or food cues might promote out-of-domain immediate (monetary-) reward preferences (Li, 2008; Yeomans & Brace, 2015). Participants exhibiting steeper discounting showed increased responses to positive reward feedback in ventral striatum (Hariri et al., 2006). Effects of appetitive cues in healthy participants might also share conceptual similarities with so-called *cue-reactivity* responses in addiction, reflecting increased subjective, physiological, and neural responses to addiction-related cues in substance-use-disorders and behavioral addictions (Courtney et al., 2015; Starcke et al., 2018; Volkow et al., 2010).

However, there is some heterogeneity with respect to modulations of TD via affective cues. Luo et al. (2014) primed participants with fearful and happy faces in a trial-wise design. Fearful faces were associated with a *reduction* in TD. In contrast, Guan et al. (2015) showed that trial-wise presentation of aversive cues *increased* discounting, whereas Simmank et al. (2015) observed no effects of erotic cue exposure across lean and obese participants.

In sum, the effects of affective cues on TD are mixed. Many studies use a blocked presentation of a series of appetitive (erotic) *and/or* aversive stimuli to examine effects on TD (Cai et al., 2019; Kim & Zauberman, 2013). Although such designs are suitable to robustly detect cue effects on decision-making if they exist, they are ill-suited to reveal short-term behavioral or psycho-physiological changes that accompany individual decisions.

Such cue effects might in part be driven by activation of ascending catecholaminergic brainstem arousal systems, as salient stimuli, irrespective of their valence, are associated with phasic discharges of neurons in the locus coeruleus (LC), the primary noradrenergic brainstem nucleus (Bouret & Richmond, 2015; Chen & Sara, 2007; Mather et al., 2016). Phasic LC activity increases noradrenaline release across cortex, facilitating sensory stimulus processing (Howells et al., 2012; Mather et al., 2016; Moxon et al., 2007). In line with these findings, cortical responses to non-salient stimuli can be elevated when time-locked with phasic LC photoactivation (Vazey et al., 2018).

LC activity is tightly linked to pupil dilation (Aston-Jones & Cohen, 2005; Joshi et al., 2016) in humans (Murphy et al., 2014) as well as in primates (Varazzani et al., 2015). Due to the association between phasic LC activity and cortical noradrenaline release, pupil dilation is often used in conjunction with other measures such as cardiovascular (ECG) and electrodermal activity (EDA) to examine short-term changes in arousal levels (Bradley et al., 2008). Pupil responses are increased following both aversive (Kinner et al., 2017) and erotic stimuli (Finke et al., 2017) and might track ongoing task demands and choice processes (Alnæs et al., 2014; van der Wel & van Steenbergen, 2018). Finally, trial-wise arousal changes are choice-predictive during TD (Lempert et al., 2016). In sum, appetitive cues might modulate TD under some conditions (Guan et al., 2015; Luo et al., 2014) but whether such effects can be traced back to variations in short-term physiological arousal remains unclear.

Here we address this issue, expanding upon previous work in three ways. First, we applied a trial-wise design that allowed us to disentangle arousal- and valence-related effects. Second, we comprehensively monitored psycho-physiological arousal (pupil size, cardiovascular activity, electrodermal activity). Finally, we quantified arousal-related effects on individual decisions using a hierarchical Bayesian computational modeling scheme. Based on the literature (see above), we pre-registered the following hypotheses (https://osf.io/swp4m/): On the behavioral level, we predicted increased TD following both erotic and aversive cues. Further, we hypothesized that arousing stimuli (irrespective of valence) would lead to increased physiological arousal (pupil dilation, skin conductance response amplitudes, heart rate deceleration). We also hypothesized that difficult trials (high decision conflict) would result in a more pronounced pupil dilation indicating high cognitive effort. Finally, we predicted that higher baseline working memory would be negatively associated with steepness of discounting behavior (Shamosh et al., 2008).

2 | METHOD

2.1 | Participants

Thirty-five heterosexual male participants took part in the study (mean ± *SD* (age) = 24.3 ± 5.1; range 18–38 years). All subjects were non-smokers, fluent German speakers,

reported normal or corrected-to-normal vision and had no history of neurological or psychiatric disorders. All experimental procedures were approved by the ethics committee of the German Psychological Society (DGPs), and participants provided informed written consent prior to participation in the study. Participants were recruited online and included mainly university students. A preregistered sample size of $n = 29$ was determined a priori via a power analysis using G*Power (Faul et al., 2007). This effect size estimate was based on previous studies investigating cue effects on TD (average effect size across three studies: Cohen's $d = 0.49$; alpha error prob. = 0.05; power = 0.80; Kim & Zauberman, 2013; Sohn et al., 2015; Wilson & Daly, 2004).

2.2 | Experimental set-up

Participants were seated in a shielded, dimly lit room 60 cm from a 24-inch LED screen (resolution: 1366 × 768; refresh rate: 60 Hz). The subjects placed their chin and forehead in a height-adjustable chinrest. They were instructed to minimize blinks and to focus on the screen center throughout the experiment. Stimuli were presented centrally at 600 × 600 pixels superimposed on a gray background. Stimulus presentation was implemented using Psychophysics toolbox (Version 3.0.14) for MATLAB (R2017a; MathWorks, Natick, MA).

2.3 | Affective cues

We screened several image databases for stimulus selection, including the International Affective Picture system (IAPS), the Nencki Affective Picture System (NAPS) as well as EmoPics (Lang et al., 2008; Marchewka et al., 2014; Wessa et al., 2010). In addition, we performed a google search. We created a preliminary stimulus set consisting of 376 erotic, aversive, and neutral images which were roughly matched for image content and complexity. As all pictures displayed humans stimuli can be considered as social cues. In a preceding pilot study, the preliminary set was rated concerning valence and arousal levels by an independent sample ($n = 10$). Based on those ratings, we selected 288 images (96 erotic/aversive/neutral). Erotic and aversive images were comparable in their arousal levels (mean ± *SD* arousal = erotic: 6.98 ± 0.52; aversive: 7.04 ± 0.82, $p = .115$), but differed in terms of their valence (mean ± *SD* valence = erotic: 7.57 ± 0.49; aversive: 2.50 ± 0.69, $p < .001$). Neutral images differed in both dimensions (arousal: 1.59 ± 0.25; valence: 5.63 ± 0.49). Further details on the pilot study image ratings and statistics are provided in the supplement (see Figure S1). Using MATLAB's SHINE toolbox, images were converted to grayscale and matched according to mean intensity (mean ± *SD* = erotic: 0.42 ± 0.0009; neutral: 0.42 ± 0.001; aversive: 0.42 ± 0.001; $p = .133$) and contrast (mean ± *SD* contrast = erotic: 0.19 ± 0.01; neutral: 0.19 ± 0.001; aversive: 0.19 ± 0.01; $p = .347$). Details of physical image properties and associated analyses are depicted in the supplement (see Figure S2).

2.4 | Data acquisition

For quantification of cue-evoked physiological responses throughout the experiment, we assessed three different measures of autonomic nervous system activity, pupil size, heart rate, and skin conductance. Pupillometry data were collected using a RED-500 remote eye-tracking system (sampling frequency [SR]: 500 Hz; Sensomotoric Instruments) which uses invisible infrared illumination of the retina. Heart rate and skin conductance data were acquired by Biopac systems hard- and software (SR: 2000 Hz; MP 160; Biopac systems, Inc). For cardiovascular recordings, an ECG100C amplifier module with a gain of 2000 normal mode, 35 Hz low pass notch filter, and 0.5 Hz/1.0 Hz high pass filter was included in the recording system. Disposable circular contact electrodes were attached according to the lead-II configuration. Isotonic paste (Biopac Gel 100) was used to ensure optimal signal transmission. For electrodermal recordings, we used an EDA100c amplifier module with a gain of 5 μS/V, 10 Hz low pass filter, and DC high pass filter settings. Activity was derived from the index- and middle finger of the non-dominant hand using disposable Ag/AgCl electrodes, pregelled with isotonic gel. Participants responses from the behavioral tasks were recorded via keyboard and mouse.

2.5 | General procedure

Data collection was carried out on two separate testing days with an interval of 3–7 days. On day one, participants were informed about the experimental procedure and provided informed consent. They then completed a behavioral pretest, a series of questionnaires, and a number of working memory tasks. On day two, participants completed the TD task with trial-wise affective picture presentation and physiological recordings.

2.5.1 | Behavioral pretest and subject-specific trial generation

Participants performed a short behavioral pretest (96 trials) of a TD task. On each trial, participants chose between a fixed immediate reward of 20€ (smaller-sooner,

SS) and a variable delayed amount (larger-later, LL). LL reward amounts were calculated by multiplying the SS amount with 16 factors (1.05, 1.055, 1.15, 1.25, 1.35, 1.45, 1.55, 1.65, 1.85, 2.05, 2.25, 2.55, 2.85, 3.05, 3.45, and 3.85), and combined with a set of six delays (2, 6, 15, 29, 62, or 118 days), yielding a total of 16 * 6 = 96 trials. Participants were instructed explicitly about the task structure and performed 12 practice trials. We then used the pretest choice data to estimate an a-priori discount-rate via Maximum-Likelihood estimation assuming a hyperbolic model (Equation 1) and a Softmax choice rule (Equation 2) (Green & Myerson, 2004).

$$SV_{(\mathrm{LL})} = \frac{A}{(1 + \exp(k) * D)}, \quad (1)$$

$$P_{(\mathrm{chosen})} = \frac{\exp(SV_{\mathrm{chosen}} * ß)}{\exp(SV_{\mathrm{other}} * ß) + \exp(SV_{\mathrm{chosen}} * ß)}. \quad (2)$$

The hyperbolic model describes the decrease in the subjective value of a delayed option (LL) over time. The amount of the larger but later reward (A) which is delivered after a specific delay (D in days) is devalued by the subject's specific discount-rate (k, here modeled in log-space) that weights the influence of time on the subjective value (SV). Higher k-parameter reflects an increased devaluation of the LL over time or more impulsive choice preferences. As choice preferences are affected by subject-specific noise, we used a sigmoid (softmax) function (Equation 2) to estimate choice probabilities (Sutton & Barto, 1998). Here, $ß$ scales the influence of value differences on choice probabilities. Lower values of $ß$ indicate a high choice stochasticity whereas higher values indicate that choices depend more on value differences.

We then used this pretest-based discount rate to calculate indifference points (ID-points) for each participant for three different delay vectors ([1, 7, 14, 28, 65, 90]; [1, 7, 14, 30, 55, 100]; [1, 7, 14, 32, 60, 80]). ID-points reflect the LL-amount at which a participant is expected to be indifferent between the SS and LL options. For every participant, the three delay-vectors were randomly assigned to the experimental conditions (erotic, aversive, neutral). The indifference amounts per delay were then used to compute participant-specific choice options. To this end, for each delay in each condition, we drew 10 random samples from normal distributions centered at the respective ID-points, with standard deviation of 4, and six additional samples linearly spanning the interval between 20 and a subject-specific maximum yielding 96 subject-specific trials per condition.

After completion of the behavioral pretest, participants underwent a short working memory test battery, including digit- (forward & backward), operation-, and listening span tasks (Redick et al., 2012; van den Noort et al., 2008; Wechsler, 2008). Finally, participants completed several questionnaires on demographic, health, and personality data that will be reported elsewhere.

2.5.2 | TD task with affective pictures

On day 2, participants performed the experimental version of the TD task including the erotic, aversive, and neutral cues derived from the pilot study. Subjects were seated in a dimly lit, electrically and acoustically shielded test room with their head placed on the chinrest. After the ECG- and EDA, electrodes were attached and the eye-tracker was calibrated (9-point calibration), the discounting task was started.

Here, participants performed 288 choices between a smaller sooner reward of 20€ immediately available and one of the subject-specific delay/LL-reward pairs generated from the pretest. The overall trial structure is outlined in Figure 1. Every trial started with the presentation of one of the 96 neutral, aversive or erotic images which were presented in the screen center for 2000 ms. Then the LL-reward and the associated delay were superimposed on the image (e.g. 38€, 14 days). After 3000 ms the image and the LL-reward disappeared and the decision screen was presented. Here, participants chose between one of two symbols which corresponded to the available options (SS: circle; LL: square). The chosen option was then highlighted for another 1000 ms. The intertrial-interval (ITI) was marked by a white fixation cross superimposed on a grayscale scrambled image with a randomized presentation time between 5500 and 6000 ms sampled from a uniform distribution. The scrambled image was exactly matched to the affective picture set in terms of mean pixel intensity and contrast. Experiment administration and behavioral recording were controlled by MATLAB (MATLAB 2017a; The MathWorks, Inc., Natick, Massachusetts) on an IBM compatible PC running on Windows 10. After completion of the discounting task, participants were thanked and fully debriefed.

2.6 | Data analysis

Data analysis was conducted using MATLAB and R. For frequentist statistical approaches including within-subjects repeated-measures variables (e.g. rmANOVA) we report Greenhouse-Geisser-corrected p-values, degrees of freedom, and epsilon values if the assumption of sphericity was violated. Effect sizes of significant results ($p < .05$) are reported as proportion of explained variance (partial

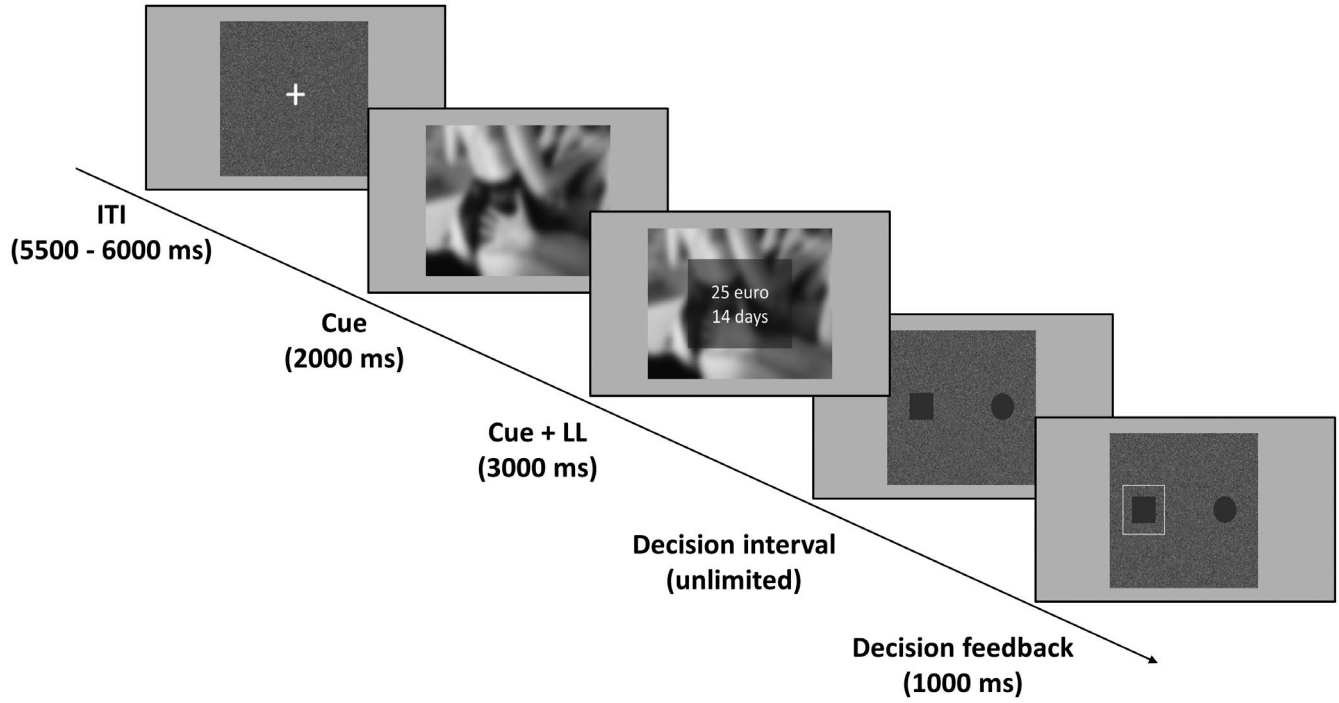

FIGURE 1 Example trial from the experimental temporal discounting task. ITI, intertrial-interval (onset to onset); LL, larger-later reward

eta squared). For follow-up tests, Bonferroni correction for multiple comparisons was applied.

2.6.1 | Analysis of choice data

To quantify TD, we used two complementary approaches. As a model-free approach, we computed the area under the empirical discounting curve AUC (Myerson et al., 2001). Our model-based approach then utilized adapted versions of the hyperbolic model (Mazur, 1987) and the softmax choice rule (Equations 1 and 2, see above).

Model-free approach

Model-free approaches avoid potential issues with parameter estimation or the commitment to a specific mathematical framework (e.g. hyperbolic vs. exponential discounting). We computed the area under the empirical discounting curve (AUC) as a model-free measure of discounting (Myerson et al., 2001), corresponding to the area under the connected data points that describe the decrease of the subjective value (*y*-axis) over time (*x*-axis). Each delay is expressed as a proportion of the maximum delay and plotted against normalized subjective (discounted) value as a fraction of objective value. The area of the resulting trapezoids was computed as follows (Myerson et al., 2001):

$$A = \frac{x_2 - x_1}{\left(\frac{(y_1 + y_2)}{2}\right)}. \quad (3)$$

The sum across trapezoids then corresponds to the individual AUC. AUC values were compared between neutral, aversive, and erotic cue conditions using repeated measurement ANOVA. Here, smaller *AUC*-values indicate steeper discounting.

Computational modeling

We used hierarchical Bayesian modeling to fit adapted versions of the hyperbolic model with softmax action selection. For each parameter (log(k) & softmax $ß$), we fit group-level distributions for the neutral condition from which individual subject parameters were drawn. To model (cue-) condition effects, we fit two separate group-level distributions modeling deviations from the neutral condition for aversive and erotic cues, respectively ("shift"-parameters, Equations 4 and 5) (Pedersen et al., 2017).

$$k_{(t)} = \exp\left(k_{\text{neut}} + I_{\text{Ero}\,(t)} * S_{\text{Ero}_k} + I_{\text{Avr}\,(t)} * S_{\text{Avr}_k}\right), \quad (4)$$

$$ß_{(t)} = ß_{\text{neut}} + I_{\text{Ero}\,(t)} * S_{\text{Ero}_ß} + I_{\text{Avr}\,(t)} * S_{\text{Avr}_ß}, \quad (5)$$

Here, I_{Ero} and I_{Avr} are dummy-coded indicator variables coding the respective experimental conditions (erotic vs. aversive) and S_{Ero} and S_{Avr} are the subject-specific parameters modeling changes in log(k) and $ß$ depending on the condition on trial t. These trial-wise estimates for k and $ß$ were then used to calculate the subjective value (*SV*) of

the larger later reward (LL) as well as the probability to choose the respective option (see Equations 1 and 2, see above). Parameter posterior distributions were estimated via Markov chain Monte Carlo (MCMC) as implemented in JAGS (Version 4.2) using R (Version 3.5.1) and the r2jags Package (Plummer, 2003). The prior distributions for the group-level parameters of the hierarchical model are listed in Table 1. JAGS model code is publicly available at OSF (https://osf.io/bk64d/). Model convergence was assessed via the Gelman-Rubinstein convergence diagnostic $\hat{R}$ and values of $1 \leq \hat{R} < 1.03$ were considered acceptable. We ran 2 chains with a burn-in period of 1.280 k samples and a thinning factor of 2. About 20 k samples were then retained for further analysis. For details on MCMC convergence, see Gelman and Rubin (1992).

We evaluated cue effects on parameter estimates using Bayesian statistics (see Kruschke, 2010). Specifically, we analyzed the posterior distributions of parameters modeling group mean condition effects (as reflected in the S_{Ero} and S_{Avr} parameters, see Equations 4 and 5 above) by computing their highest density intervals (HDI) and assessed their overlap with zero. Furthermore, we calculated *undirected* Bayes factors based on the Savage-Dickey method to quantify relative evidence for a null model that would restrict a parameter of interest at a given value (e.g. *SEro/SAvr* = 0) against an alternative model where the parameter is free to vary. The undirected Bayes factor in favor of the null model (BF_{01}) equals the ratio of the posterior ordinate to the prior ordinate at a given point of interest (see Marsman & Wagenmakers, 2017 for details). To directly test the degree of evidence for directional effects, we also computed so-called *directional* Bayes factors (dBFs) for erotic (S_{Ero}) and aversive (S_{Avr}) shift parameters for log(k) and β. A dBF corresponds to the ratio of the posterior mass of the shift-parameter distribution below zero to the posterior mass above zero (Marsman & Wagenmakers, 2017). Bayes factors (BF_{01}/dBFs) above 3 can be interpreted as moderate evidence in favor of the null model (BF_{01}) or a decreasing effect (dBF) on the parameter, while Bayes factors above 12 are interpreted as strong evidence (Beard et al., 2016). Bayes factors below 0.33 are likewise interpreted as moderate evidence in favor of the alternative model or an increasing effect on the respective parameter.

As individual subject parameters were drawn from group-level distributions, and parameter estimates cannot be considered independent we did not include a classical frequentist statistics approach (as preregistered) to assess differential cue effects on choice.

TABLE 1 Priors of group-level parameter means

Parameter	Group mean prior
$\text{Log}(k_{\text{neut}})$	Uniform (−15, 3)
β_{neut}	Uniform (0, 5)
$SEro_k$	Normal (0, 1)
$SAvr_k$	Normal (0, 1)
$SEro_\beta$	Normal (0, 0.2)
$SAvr_\beta$	Normal (0, 0.2)

Note: Ranges (uniform distribution), means and variances (normal distributions) were chosen to cover numerically plausible values.

2.6.2 | Analysis of physiological data

Pupil data

Pupil data were first divided into segments ranging from 1000 ms before, until 5000 ms after image onset. Next, segments were screened for outliers and implausible values. Here, we slightly adjusted our preregistered pre-processing protocol to better control for putative artifacts. We defined outliers as values which exceed the respective trial mean by more than two standard deviations (Finke et al., 2017). Such outliers (2.9% of all data within relevant epochs) and missing data points due to blinks or other artefacts (4.2% of all data within relevant epochs) within the trial were linearly interpolated. Trials including more than 12% missing datapoints or outliers were excluded from further analyses (8.2% of trials on average). Subjects exhibiting more than 90% invalid trials were completely discarded from further analyses ($n = 2$). Next, pupil data were down-sampled to 20 Hz by means of a moving average filter and median baseline-corrected. As the appearance of the choice options starting at 5 s post image onset might induce changes in luminance and additional pupil responses, we calculated the mean pupil diameter for the whole image presentation interval (0–5 s) excluding dilation data from the decision period (see Preregistration). Further, mean pupil size was calculated in ten bins of 0.5 s following image onset. Pupil size measures were compared between cue conditions using repeated measurements analysis of variance (ANOVA).

Heart rate data

Heart rate data were visually screened and manually corrected for major artifacts. We linearly interpolated these intervals via Biopacs built-in connect-endpoints-algorithm. We used custom MATLAB routines to detect QRS-complexes within ECG-data because Biopacs's peak detection algorithm (preregistered) missed complexes in multiple subjects resulting in a strong underestimation of heart rates. Nonetheless, one subject had to be discarded due to poor data quality which resulted in an unreliable R-wave detection. To investigate phasic heart rate changes in response to erotic, aversive, and neutral

cues in real-time, we adopted a weighted average approach (Graham, 1978; Velden & Wölk, 1987). We used the interbeat-interval length to calculate the mean heart rate change in 0.5 s bins relative to an 2 s baseline prior to image onset. Trials containing implausibly low (HR < 30) or high (HR > 180) heart rate frequencies were completely discarded. Interbeat-intervals and the corresponding heart rate were weighted by their respective real time fraction in the bin. The resulting weighted means across the whole image presentation interval (0–5 s) as well as within the respective time bins for all three conditions were compared using repeated measurements ANOVA.

Skin conductance data

We manually screened electrodermal activity data and corrected for major artifacts and signal losses. These intervals were again linearly interpolated via Biopacs built-in connect-endpoints-algorithm. To achieve an improved detection and exclusion of rapid transients, drifts and other more subtle artifacts we extended and adapted our preregistered preprocessing steps in the following way: Raw data were first low-pass filtered (1 Hz) and smoothed by a moving average filter (63 samples). Next, data were down-sampled to 62.5 Hz to reduce computational load. Instead of using Biopacs built-in analysis routine to derive phasic activity from the raw signal (preregistered), we used Ledalab's automated continuous decomposition analysis routines to decompose skin conductance (SC) data into its tonic and phasic components which in turn reflect underlying sudomotor nerve activity (Benedek & Kaernbach, 2010a, 2010b). As sweat gland activity typically lags behind sympathetic nervous system changes, we calculated the maximum value of phasic activity and the response latency of the first significant SCR within a time window of 1–6 s post image onset (significant SCR amplitude threshold of 0.03 μS). In an exploratory approach we further assessed the total number of evoked SCR's, the sum of amplitudes of all significant SCR's as well as the mean phasic activity within the respective time window. The different outcome measures were compared between cue-conditions using repeated measurements ANOVA.

Further evaluation of physiological cue responses

After evaluation of cue effects on autonomic nervous system activity (pupil dilation, heart rate, EDA) we next explored associations amongst physiological measures on the single-subject level. For this purpose, we used the single-trial mean changes in pupil diameter, heart rate, and phasic electrodermal activity to compute Pearson's correlation coefficients. Single-trial data were standardized within subject. Using one-sample *t*-tests, we determined whether the mean of the Fisher *z*-transformed correlation coefficients differed from zero. Furthermore, we calculated cue-reactivity indices for each measure by computing difference scores between the mean response to erotic versus neutral images and aversive versus neutral images, respectively. To explore potential associations between the different physiological cue-reactivity effects, these difference scores were correlated across participants via Pearson's correlations.

2.6.3 | Analysis of arousal effects on TD

Correlation analysis

We next explored the association between the estimated erotic and aversive shift-parameters from the hierarchical model (Equations 4 and 5) and physiological cue-reactivity indices (see above). That is, we correlated within-subject physiological difference scores (physiological responses following erotic vs. neutral trials [erotic cue-reactivity], aversive vs. neutral trials [aversive cue-reactivity]) with model-based measures of behavioral effects ($S_{\mathrm{Ero}(k,ß)}$, $S_{\mathrm{Avr}(k,ß)}$).

Computational modeling

In the next step, we investigated physiological arousal effects on choice behavior on the single-trial level. As cue-reactivity was most robustly associated with changes in pupil diameter (see Figure 2), we initially used within-subject standardized pupil size as a proxy for the single-trial arousal level. To quantify effects of arousal on choice behavior, we included additional parameters (*EroPupil*(k,$ß$), *AvrPupil*(k,$ß$)) modeling changes k- and $ß$ due to the current arousal state, over and above effects of the experimental condition, as follows (see Equations 6 and 7):

$$k_{(t)} = \exp\left(k_{\mathrm{neut}} + \left(I_{\mathrm{Ero}\,(t)} * S_{\mathrm{Ero}_k}\right) + \left(I_{\mathrm{Ero}\,(t)} * \mathrm{Pupil}_{(t)} * \mathrm{EroPupil}_k\right) + \left(I_{\mathrm{Avr}\,(t)} * S_{\mathrm{Avr}_k}\right) + \left(I_{\mathrm{Avr}\,(t)} * \mathrm{Pupil}_{(t)} * \mathrm{AvrPupil}_k\right)\right), \quad (6)$$

$$ß_{(t)} = ß_{\mathrm{neut}} + \left(I_{\mathrm{Ero}\,(t)} * S_{\mathrm{Ero}_ß}\right) + \left(I_{\mathrm{Ero}\,(t)} * \mathrm{Pupil}_{(t)} * \mathrm{EroPupil}_ß\right) + \left(I_{\mathrm{Avr}\,(t)} * S_{\mathrm{Avr}_ß}\right) + \left(I_{\mathrm{Avr}\,(t)} * \mathrm{Pupil}_{(t)} * \mathrm{AvrPupil}_ß\right), \quad (7)$$

Here I_{Ero} and I_{Avr} again denote dummy-coded indicator variables coding the experimental condition and S_{Ero} and S_{Avr} are the subject-specific parameters modeling changes in log(k) and $ß$ depending on the condition in the current trial t. *EroPupil* and *AvrPupil* capture additional condition-specific variation in the model parameters (log(k), $ß$) due to trial-wise pupil dilation. These modulated k- and $ß$-parameters were then used to calculate the subjective value (*SV*) of the delayed option and the respective choice probabilities. The single-subject parameters *EroPupil* and *AvrPupil* were again drawn from group-level normal distributions, with mean and variance hyper-parameters that were themselves estimated

from the data. The prior distributions for the group-level parameters of the hierarchical model, the individual-level parameters as well as all relevant model equations are publicly available at OSF (https://osf.io/bdwfa/).

In a final model, we examined trial-wise arousal effects irrespective of the experimental condition, and jointly for all three physiological measures (pupil size, heart rate, EDA). Instead of fitting choice data with a logistic model on the single-subject level, using standardized mean pupil-size, heart rate, and phasic electrodermal activity as regressors (as preregistered), we adapted the above-mentioned hierarchical model as follows: Erotic and aversive shift-parameters which captured condition-dependent changes in log(k)- and β were removed from the model. Instead, we now included three arousal regressors (*PupilReg*, *EcgReg*, *EdaReg*) modeling changes in log(k) and β as a function of trial-wise mean changes in pupil size, heart rate, or skin conductance (Equations 8 and 9):

$$k_{(t)} = \exp\left(k_{\text{base}} + \left(\text{Pupil}_{(t)} * \text{PupilReg}_k\right) + \left(\text{ECG}_{(t)} * \text{EcgReg}_k\right) + \left(\text{EDA}_{(t)} * \text{EdaReg}_k\right)\right), \quad (8)$$

$$\beta_{(t)} = \beta_{\text{base}} + \left(\text{Pupil}_{(t)} * \text{PupilReg}_\beta\right) + \left(\text{ECG}_{(t)} * \text{EcgReg}_\beta\right) + \left(\text{EDA}_{(t)} * \text{EdaReg}_\beta\right). \quad (9)$$

Again, priors and model code are publicly available at OSF (https://osf.io/ajxkd/). As a complementary analysis, we also tested whether trial-wise measures of pupil size, heart rate, and phasic electrodermal activity directly influenced the probability of making smaller-sooner versus larger-later choices (0 = SS choice vs. 1 = LL-choice; preregistered analysis). Therefore, we performed a linear mixed model analysis (glmer package in R) to investigate single-trial arousal effects on choice, with "subject" as random effect. All three arousal regressors (Pupil, ECG, EDA) were z-standardized within-subject.

2.6.4 | Data and code availability

Behavioral and physiological data as well as JAGS model code is available on the Open Science Framework (https://osf.io/dtwg3/files).

3 | RESULTS

3.1 | Physiological cue responses

Analysis of the physiological data proceeded in the following steps. First, we examined cue-evoked changes in autonomic nervous system activity. We did this separately for each physiological measure (pupil size, heart rate, electrodermal activity [EDA]). Next, we used Pearson's correlations to assess the associations between evoked physiological responses following image onset on the single-trial level as well as the concordance between differential responses to erotic and aversive image content (difference scores, see above). Unless otherwise stated, all analyses were conducted as preregistered (https://osf.io/swp4m/).

3.1.1 | Pupil diameter change

Evoked changes in pupil size following affective image presentation are depicted in Figure 2. After an initial dip reflecting a small initial light reflex (Beatty & Lucero-Wagoner, 2000) at around 0.5 s post image onset, we observed a substantial pupil dilation response, differently pronounced for erotic, aversive, and neutral pictures (Figure 2a–c). A two-factor repeated measures ANOVA (within factors: image condition, time bin [0.5 s/bin]) showed a significant main effect for image condition ($F[2,64] = 91.17$, $p < .001$, $\eta_p^2 = 0.74$, $\varepsilon = 0.08$). Post-hoc t-

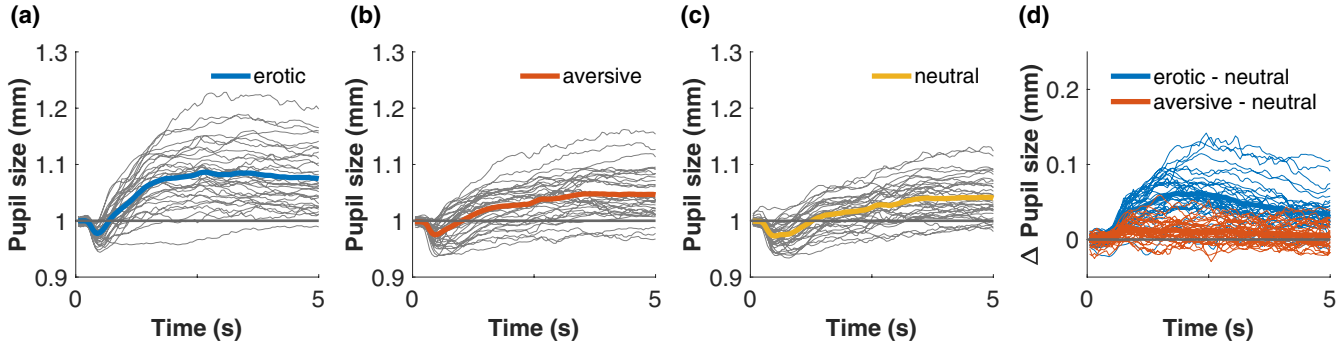

FIGURE 2 Baseline-corrected grand average pupil responses (in mm) following erotic (a), aversive (b) and neutral (c) image onset; Thin gray lines depict mean single-subject pupil trajectories. Intra-individual contrasts in pupil size following image presentation are depicted in (d); blue lines: erotic—neutral; red lines: aversive—neutral

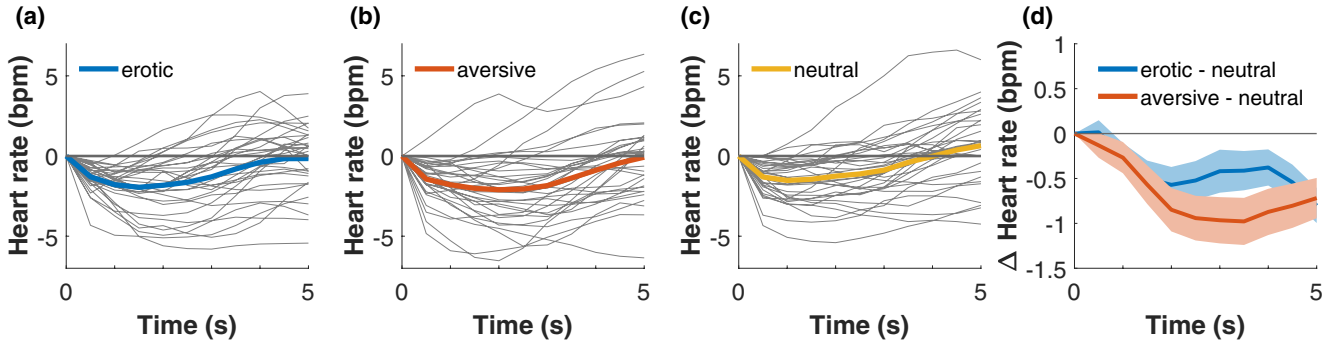

FIGURE 3 Baseline-corrected grand average heart rate changes (in bpm) following erotic (a), aversive (b) and neutral (c) image onset; Thin gray lines depict single-subject heart rate trajectories; Grand average contrasts of average heart rate change are shown in (d); blue line: erotic—neutral; red line: aversive—neutral. Shaded areas depict standard errors (SE)

tests indicated increased pupil dilation responses following aversive compared with neutral stimuli, ($t_{(\text{aversive, neutral})} = 4.49$, $p < .001$, $\text{CI}_{\text{Diff}(95\%)} = [0.005;0.01]$), a pattern which was even more pronounced for erotic stimuli ($t_{(\text{erotic, neutral})} = 10.47$, $p < .001$, $\text{CI}_{\text{Diff}(95\%)} = [0.03;0.05]$; $t_{(\text{erotic, aversive})} = 9.36$, $p < .001$, $\text{CI}_{\text{Diff}(95\%)} = [0.03;0.04]$).

Furthermore, we observed a significant interaction effect of the factors image condition and time bin ($F[18,576] = 43.30$, $p < .001$, $\eta_p^2 = 0.58$, $\varepsilon = 0.08$). As illustrated in Figure 2d, condition-dependent differences in pupil size emerged between the first and second bins, increased until the 5th bin and then slightly decreased over time. All pairwise comparisons are depicted in Table S1 (supplementary materials). Intraindividual contrasts indicated that in particular the increased pupil responses to erotic stimuli were highly consistent between subjects (Figure 2d).

3.1.2 | Heart rate change

Heart rate decelerated in response to image onset irrespective of image condition, likely reflecting an initial orienting response (Hare, 1972). In accordance with previous studies, the deceleration pattern was numerically most prominent for erotic and aversive image conditions (Figure 3a,b,d; Abercrombie et al., 2008). However, a repeated measurements ANOVA (within factors: image condition, time bin [0.5 s/bin]) did not reveal a significant main effect for image condition ($F[2,66] = 1.74$, $p = .196$, $\varepsilon = 0.11$). The interaction of the factors image condition and time bin indicated differences in heart rate deceleration at trend level across timepoints ($F[18, 594] = 3.00$, $p = .052$, $\varepsilon = 0.11$), which were most pronounced 3–3.5 s post image onset.

3.1.3 | Electrodermal activity change

To evaluate possible cue effects on alterations in electrodermal activity, we assessed the latency of the first-evoked skin conductance response (SCR) as well as the maximum phasic peak following image presentation (Figure 4a,b). Contrary to our expectations, we did not find differential effects of image condition on those measures (Latency (SCR): $F[2,68] = 0.13$, $p = .876$; Phasic activity: $F[2,68] = 1.41$, $p = .252$).

In an additional exploratory analysis (not preregistered), we extracted three additional measures to quantify cue-evoked electrodermal responses and compared them between image conditions: the sum of SCR amplitudes, the number of SCR's, as well as mean phasic activity within the interval 1–6 s post image onset. Sum of SCR amplitudes and mean phasic activity did not differ between conditions, whereas repeated measures ANOVA indicated significant differences in the number of SCR's between conditions ($F[2,68] = 4.17$, $p = .020$, $\eta_p^2 = 0.11$). There was a greater mean number of SCR's following erotic images (mean ± Std = 83.31 ± 33.13) compared with aversive (mean ± Std = 77.83 ± 28.96) and neutral (mean ± Std = 78.06 ± 31.10). However, none of the pairwise comparisons survived Bonferroni correction. Cue effects on all three exploratory measures are shown in Figure S3 (supplementary materials).

3.1.4 | Associations amongst physiological measures

We next conducted an exploratory analysis to examine associations amongst the three physiological measures using two complementary approaches. First, we used the

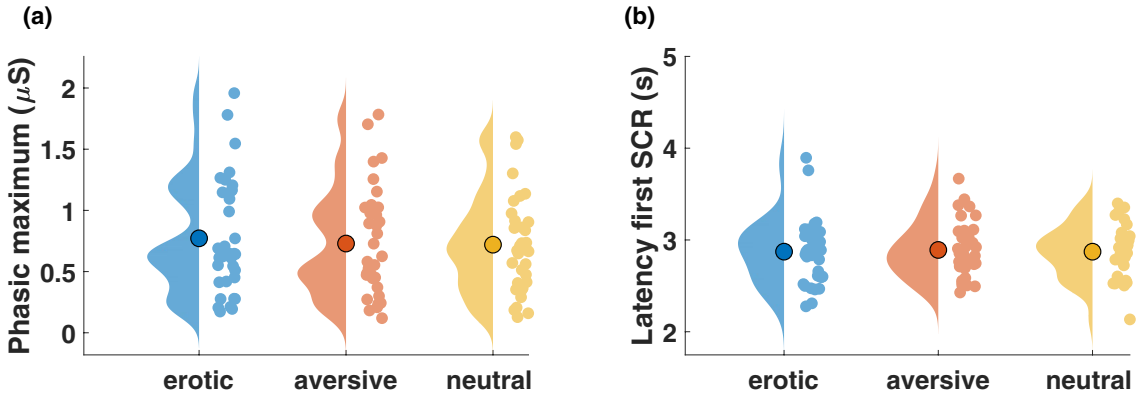

FIGURE 4 Maximum value of phasic activity (a) and latency of first skin conductance response (SCR) (b) in the interval 1–6 s post image onset. Colored dots depict single-subject means. μS = microsiemens

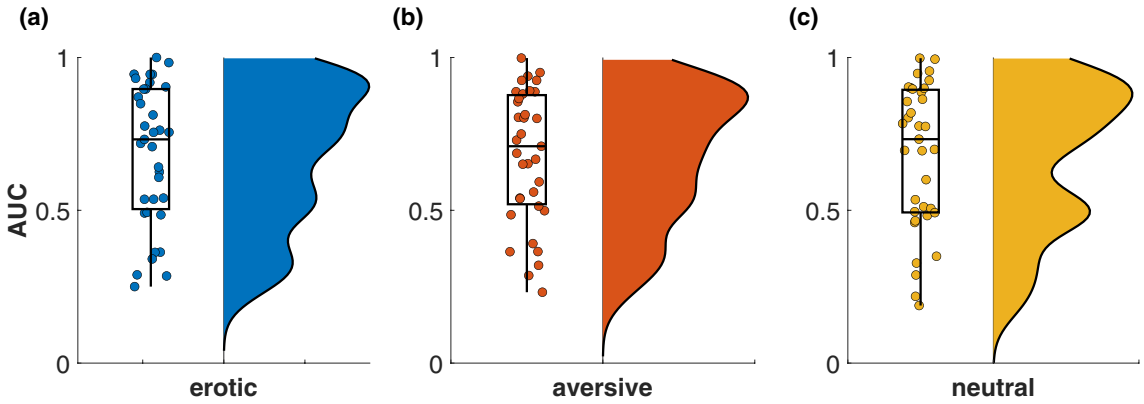

FIGURE 5 Area under the empirical discounting curve (AUC) for erotic (a), aversive (b) and neutral (c) cue conditions. Dots depict single-subject AUCs (means)

single-trial mean changes in pupil diameter, heart rate, and phasic electrodermal activity to compute Pearson's correlation coefficients. Then, concordance between differential responses to erotic and aversive image content was assessed between all three physiological measures. These analyses revealed if anything small associations (range (r): −.03 to .26). A detailed description of all conducted correlational analyses and respective results are depicted in Figures S4 and S5 (supplementary materials).

3.2 | Cue effects on TD

Having thus confirmed trial-wise changes in physiological arousal, we next quantified condition-specific changes in TD. We used model-free and computational modeling approaches, as preregistered (https://osf.io/swp4m/).

3.2.1 | Model-free approach

Applying repeated measures ANOVA on the area under the empirical discounting curve (AUC) revealed no significant differences between erotic (mean (AUC) = 0.69), aversive (mean (AUC) = 0.68), and neutral (mean (AUC) = 0.68) conditions (F[2,68] = 0.29, p = .753; Figure 5).

3.2.2 | Computational modeling

Using hierarchical Bayesian modeling, we fit adapted versions of the hyperbolic model with softmax action selection to the choice data. To estimate changes in discounting behavior due to erotic or aversive cue exposure, we fit group-level distributions for the neutral condition from which individual subject parameters were drawn. Subject-specific S_{Ero} and S_{Avr} parameters (Equations 4 and 5) then modeled trial-wise condition-specific changes in log(k) and β.

Examination of the posterior distributions of $S_{\text{Ero}(k)}$ and $S_{\text{Avr}(k)}$ from the computational model suggested a small decrease in discounting following erotic stimuli (95.01% of posterior distribution of $S_{\text{Ero}(k)}$ fell below zero). Bayes factor analysis revealed that this reduction following erotic cues was more likely than an increase, given the data (dBF = 19.78), but still highly compatible with a null

model (BF_{01} = 7.48). This suggests that these data are 7.48 times more likely to be observed under a null hypothesis assuming $S_{Ero(k)}$ to be equal to zero. Similarly, posterior distribution of $S_{Avr(k)}$ showed a substantial overlap with zero (dBF = 0.27), indicating that steepness of discounting likewise did not change in response to aversive cues (BF_{01} = 10.62; Figure 6a,b, Table 2).

Further, β-parameters slightly decreased following aversive cue exposure, pointing toward an increase in decision noise. Inspection of the posterior distribution showed that 97.16% of $S_{Avr(\beta)}$ fell below zero and directional Bayes factor (dBF = 40.37) indicated that an increase in decision noise following aversive stimuli was 40.37 times more likely than a decrease, given the data. However, undirected Bayes factor (BF_{01} = 1.134) yielded comparable evidence for the null and alternative model. We found no modulation of decision noise following erotic cues (dBF = 0.71; BF_{01} = 6.12) (Figure 6d,e; Table 2).

To validate the approach, we also fitted a non-hierarchical version of our model to the choice data and directly tested whether shift-parameters on log(k) and softmax(β) significantly differed from zero. This analysis revealed that, although variance in the posterior distributions from these individual-subject models was substantially greater (as expected due to the shrinkage imposed by the hierarchical model), both approaches converged to very similar group-level effects (see Table S4 and Table 2). Partly confirming results from the hierarchical model, t-tests indicated a significant decrease in β-parameter following aversive cues ($t(34) = -2.36$, $p = .024$, Cohen's $d = -0.398$). However, this effect did not survive Bonferroni correction, and the analysis was not preregistered. No other parameters significantly differed from zero. As effect size estimates may be biased by the shrinkage of variance imposed by the hierarchical structure, we also report summary statistics and classical effect sizes (Cohen's d) based on non-hierarchical model in the supplement (see Table S4).

We also explored associations between $S_{Ero(k)}$ and $S_{Avr(k)}$ and model-free measures (AUC values (3.2.1), larger-later choice proportions). Correlations between model parameters and model-free measures were consistently in the expected direction (see Figure S7, supplementary materials).

TABLE 2 Summary statistics of the posterior distributions of computational shift-parameters (Main model)

Parameter	Mean	*SD*	dBF	BF_{01}
SEro(k)	−0.055	0.061	19.780	7.480
SAvr(k)	0.050	0.313	0.270	10.619
SEro(β)	0.010	0.078	0.710	6.116
SAvr(β)	−0.062	0.081	40.370	1.134

Abbreviations: BF_{01}, undirected Bayes factor in favor of null model; dBF, directional Bayes factor; *SD*, standard deviation.

3.3 | Arousal effects on TD

Although indices of TD were only little affected by experimental cue conditions we next explored whether behavioral shift-effects (S_{Ero}, S_{Avr}) were related to changes in physiological arousal (indexed via pupil responses) on

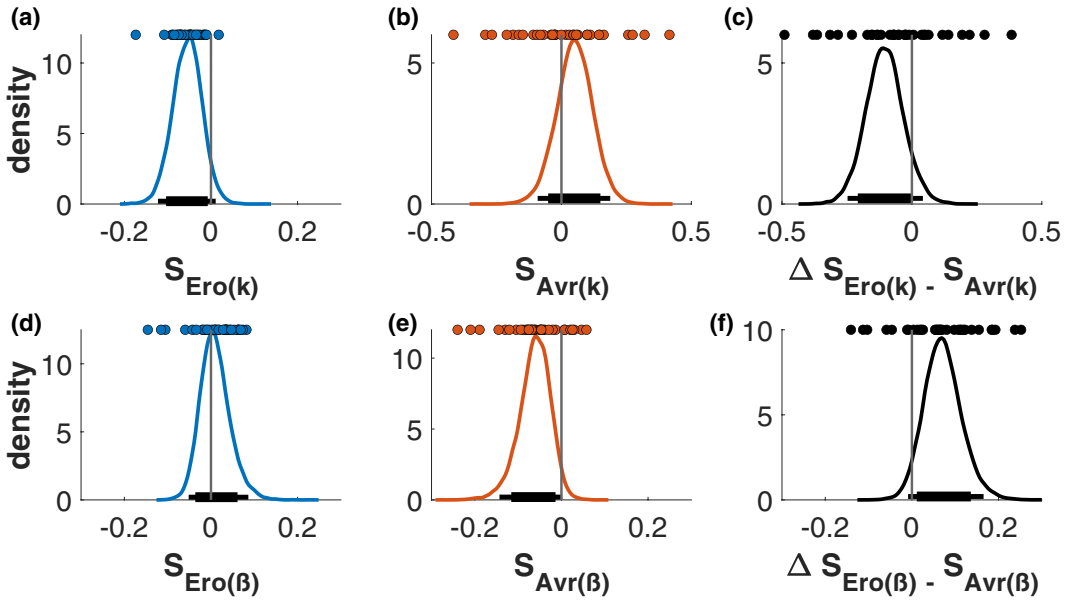

FIGURE 6 Posterior distributions for erotic (S_{Ero}; blue) and aversive (S_{Avr}; red) shift-parameters as well as their differences (black); (a–c) Log(k); (d–f) Softmax (β); Colored dots depict single-subject means. Thick and thin horizontal lines indicate 85% and 95% highest density intervals

the subject level. We extracted the means of the posterior distributions of S_{Ero}-, and S_{Avr}-parameters per participant and computed Pearson's correlations between those means and the difference scores between the average pupil response to affective (erotic & aversive) and neutral stimulus material (exploratory analysis). These analyses revealed overall small and non-significant associations (Figure S8, supplementary materials).

We next examined whether the single-trial arousal predicted trial-wise changes in TD (exploratory analysis). As in particular pupil responses reliably differentiated between cue conditions (see Figure 2), we initially focused on this measure. Arousal level was quantified via mean single-trial pupil dilation and evaluated in terms of its modulating effect on discounting behavior. Specifically, we set up an additional hierarchical Bayesian model in which trial-wise parameters ($\log(k)$ and β) were allowed to vary both according to the cue condition ($S_{Ero(k,\beta)}$, $S_{Avr(k,\beta)}$) and according to the trial-wise arousal level as reflected in pupil dilation responses ($EroPupil_{(k,\beta)}$, $AvrPupil_{(k,\beta)}$; see Equations 6 and 7; exploratory analysis).

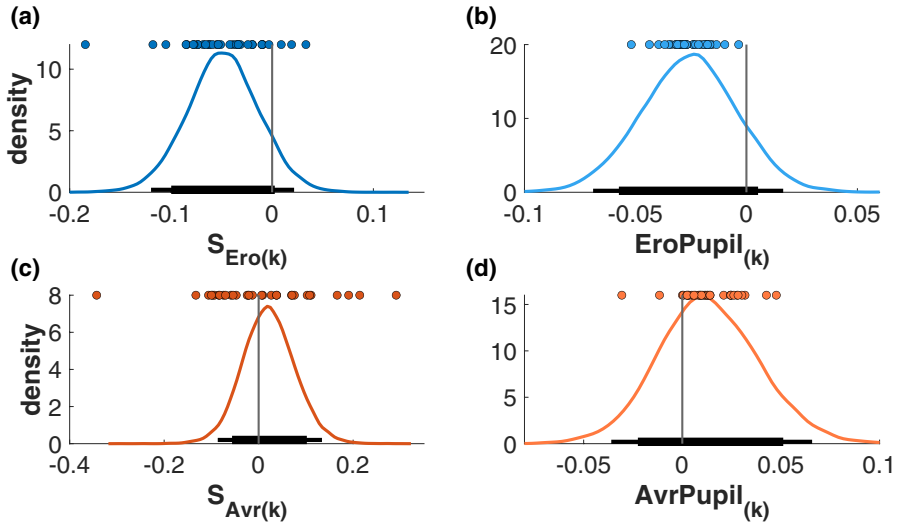

FIGURE 7 Posterior distributions for erotic ($S_{Ero(k)}$) and aversive ($S_{Avr(k)}$) shift parameters on $\log(k)$ (a, c) and shift parameters due to single trial arousal state following erotic ($EroPupil_{(k)}$) and aversive ($AvrPupil_{(k)}$) stimuli (b, d). Colored dots depict single subject means. Thick and thin horizontal lines indicate 85% and 95% highest density intervals

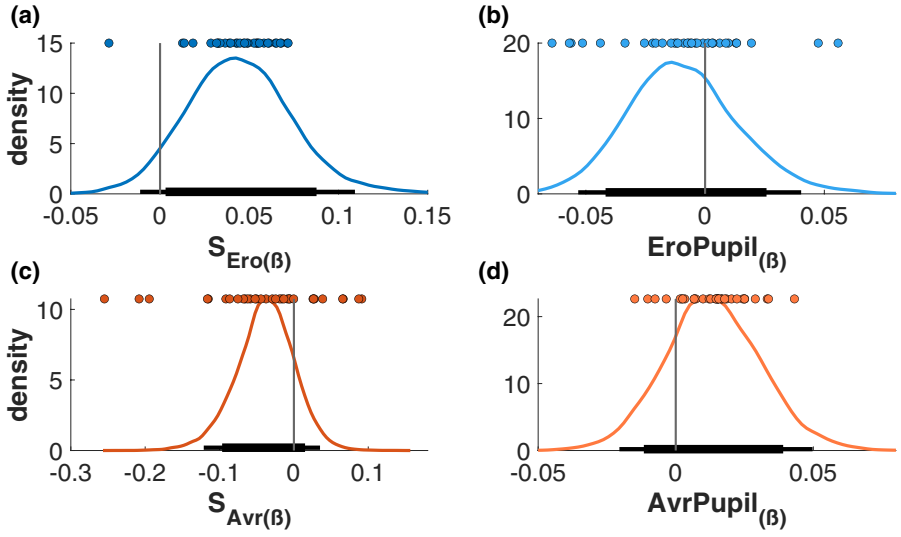

FIGURE 8 Posterior distributions for erotic ($S_{Ero(\beta)}$) and aversive ($S_{Avr(\beta)}$) shift parameters on β (a, c) and shift parameters due to single trial arousal state following erotic ($EroPupil_{(\beta)}$) and aversive ($AvrPupil_{(\beta)}$) stimuli (b, d). Colored dots depict single subject means; Thick and thin horizontal lines indicate 85% and 95% highest density intervals

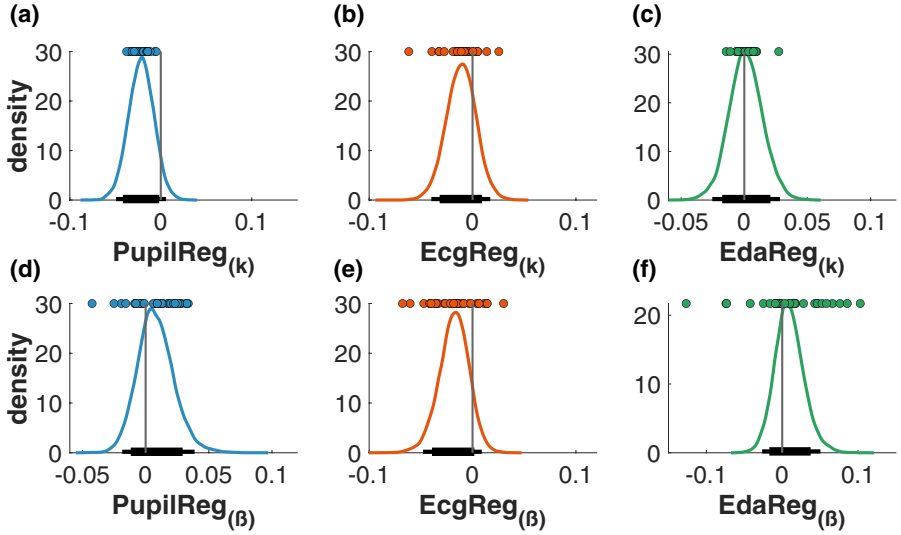

FIGURE 9 Posterior distributions depicting single trial pupil (a & d) heart rate (b & e) and skin conductance (c & f) effects on choice. Colored dots depict single subject means. Thick and thin horizontal lines indicate 85% and 95% highest density intervals

We reproduced the small attenuation of log(k) in the erotic condition (see Figure 6a) also in this model. As can be seen from Figure 7a, 91.34% of the posterior distribution for $S_{\mathrm{Ero}(k)}$ fell below zero. Again, the associated directional Bayes factor (dBF = 11.62) indicated that a decrease in log(k) following erotic cue exposure was more likely than an increase. This effect was independent of the trial-wise arousal level but somewhat less pronounced than in the model without a pupil predictor (Figure 6). This was due to the fact that trial-wise pupil dilation ($EroPupil_{(k)}$) also exhibited a small negative effect on log(k) (Figure 7b, dBF = 8.70, 88.29% of the posterior distribution fell below zero). However, inspection of undirected Bayes factors based on Savage-Dickey density ratios (BF_{01}) indicated that all shift-effects on log(k) in this model were highly compatible with a null hypothesis assuming $S_{\mathrm{Ero}(k)}$ and $S_{\mathrm{Avr}(k)} = 0$. See Table S7 for details on all undirected and directed Bayes factors. Similarly, posterior distributions for $S_{\mathrm{Avr}(k)}$ and $AvrPupil_{(k)}$ both showed a substantial overlap with zero (Figure 7c,d, $\mathrm{dBF}_{\mathrm{SAvr}(k)} = 0.57$, $\mathrm{dBF}_{\mathrm{AvrPupil}(k)} = 0.43$).

Posterior distributions of the $S_{\mathrm{Ero}(ß)}$-parameter (Figure 8a) indicated that decision noise slightly decreased (softmax ($ß$) increased) in response to erotic stimuli while it increased in response to aversive image content ($S_{\mathrm{Avr}(ß)}$) (Figure 8c, $\mathrm{dBF}_{(SEro(ß))} = 0.05$; $\mathrm{dBF}_{(SAvr(ß))} = 5.88$). The effect of single-trial arousal state on decision noise in the erotic condition ($EroPupil_{(ß)}$) was of inconclusive directionality (Figure 8b, dBF = 2.09), whereas, if anything, this association was positive for aversive cues ($AvrPupil_{(ß)}$; Figure 8d, dBF = 0.28). However, inspection of undirected Bayes factors yielded $\mathrm{BF}_{01} > 1$ for all parameters, indicating that all cue-induced variation in decision noise (softmax ($ß$)) in this model was compatible with a null model (Table S7).

We next assessed arousal effects on TD irrespective of overall condition effects. Single-trial mean pupil diameter, heart rate, and phasic electrodermal activity were included in the trial-wise computation of log(k)- and $ß$ (see Equations 8 and 9), yielding separate estimates of the effects of each physiological measure on log(k) and $ß$. Posterior distributions for all three effects are depicted in Figure 9. Whereas trial-wise pupil response and heart rate change were both, if anything, associated with decreases in discounting ($\mathrm{dBF}_{PupilReg(k)} = 17.98$, $\mathrm{dBF}_{EcgReg(k)} = 3.41$), phasic electrodermal activity showed no systematic association with log(k) ($\mathrm{dBF}_{EdaReg(k)} = 0.92$; see Figure 9a–c). In contrast, whereas single-trial heart rate change was negatively associated with softmax($ß$) ($\mathrm{dBF}_{EcgReg(ß)} = 9.27$), pupil diameter and phasic electrodermal activity were not systematically associated with decision noise (Figure 9d–f; $\mathrm{dBF}_{PupilReg(ß)} = 0.37$; $\mathrm{dBF}_{EdaReg(ß)} = 0.46$). As expected, undirected Bayes factors yielded $\mathrm{BF}_{01} > 1$ for all included arousal-regressors (see Table S8).

Although steepness of the TD curve (log(k)) and decision noise (softmax $ß$) showed no substantial variation due to trial-wise arousal we tested whether measures of pupil size, heart rate, and phasic electrodermal activity *directly* influenced the probability of making smaller-sooner versus larger-later choices in each trial (0 = SS choice vs. 1 = LL choice; preregistered analysis). Interestingly, this revealed a significant negative effect of electrodermal activity (EDA) on choice ($ß = -0.058$; $z = -2.446$; $p = .014$), such that increased trial-wise skin conductance levels increased the likelihood of SS choices. We found no other significant main or interaction effects (See Table S9, supplementary materials).

As effects of physiological measures on log(k) and $ß$ might be affected by habituation, we investigated cue-evoked physiological responses over the course of the experiment. To this end, trials of pupil diameter, heart rate, and phasic electrodermal activity data, were binned into three time-bins separately for neutral, erotic, and aversive cue conditions. There was overall limited evidence for habituation across measures (Figure S9, supplementary materials). For example, cue-evoked pupil dilation significantly decreased over time, but this effect was numerically small, and pupil dilation still differentiated reliably between cue conditions across all phases of the experiment. Heart rate and electrodermal activity data also showed small but non-significant reductions in evoked responses.

4 | DISCUSSION

Here we investigated the effects of erotic, aversive, and neutral visual cues on TD in a trial-wise design. We used comprehensive monitoring of autonomic nervous system (ANS)-activity in response to cue presentation to assess contributions of trial-wise physiological arousal to TD modulations. Physiological arousal was robustly elevated following aversive and in particular erotic cue exposure. Contrary to our predictions, steepness of TD was not reliably affected following erotic or aversive cues. Decision noise tended to increase (rather than decrease) in response to aversive stimuli, but an overall null effect could not be ruled out. Trial-wise arousal only accounted for minor variance over and above aversive and erotic condition effects.

4.1 | Cue effects on autonomic activity

Autonomic activity was assessed using three complementary measures (pupil size, heart rate, electrodermal activity), which are differentially affected by sympathetic and parasympathetic branches of the nervous system (Bradley et al., 2008). Whereas changes in skin conductance responses are mainly driven by sympathetic activity (Dawson et al., 2007; Posada-Quintero et al., 2016; Venables & Christie, 1980), modulations of heart rate (Berntson et al., 1997) as well as pupil size (Fotiou et al., 2000; Loewenfeld, 1999; Steinhauer et al., 2004) result from an interplay of parasympathetic and sympathetic afferents.

Cue-evoked arousal modulations were successfully captured by pupil dilation. A small onset-related pupil constriction was followed by a long-lasting dilation response which was substantially increased for both erotic and aversive cues, confirming previous findings of appetitive (Finke et al., 2017) and aversive stimulus processing (Kinner et al., 2017). A direct comparison confirmed previous findings of increased responses to erotica (Bradley & Lang, 2015; Bradley et al., 2008; Henderson et al., 2014). Such dilatory pupil responses have been observed following various cues with high motivational and behavioral relevance, including engaging sounds (Partala et al., 2000), task-relevant stimuli (Kahneman & Beatty, 1966), and surprising events (Preuschoff, 2011), which have been closely linked to phasic activations of locus coeruleus (LC) neurons (Aston-Jones & Bloom, 1981, but see Aston-Jones & Cohen, 2005) and concomitant norepinephrine (NE) release (Abercrombie et al., 1988). Increased pupil dilation following both appetitive and aversive cues in our study might therefore reflect phasic modulations of the LC-NE-system.

Pupil dilation can be traced back to sympathetic and parasympathetic inputs (Schumann et al., 2020). Whereas pupil constriction is controlled via parasympathetic innervation of the pupillae sphincter, pupil dilation is controlled by sympathetic afferents to the dilator pupillae muscle of the iris (Andreassi, 2000; Loewenfeld, 1999). In our data, we observed no substantial cue-effects on the initial pupil constriction. However, late dilatory responses clearly discriminated between conditions, suggesting that this effect might be mediated by sympathetic involvement.

Heart rate (HR) was also modulated by cue type. A short-latency heart rate deceleration was most pronounced for aversive and erotic cues. Such vagally mediated HR suppression is assumed to reflect an initial orienting response (OR; Hare, 1972), denoting an epoch of increased sensory receptivity and deepened encoding during pleasant and unpleasant stimulus perception (Abercrombie et al., 2008). In line with previous literature (Bradley et al., 2001; Jönsson & Hansson-Sandsten, 2008), our data indicate that such deceleration patterns appeared to be more stable following aversive stimuli. However, although the observed heart rate responses might reflect modulations of parasympathetic nervous system activity by erotic and aversive cues, moderately high single-subject variance prevented significant condition differences.

Contrary to our pre-registered hypotheses, participants exhibited no overall increase in skin conductance response (SCR) amplitudes following erotic or aversive images compared with neutral. Exploratory analyses revealed largest SCR-amplitudes following erotica in the first third of the experiment, an effect that substantially habituated over time, thereby reducing overall condition differences (see Supplemental Materials). SCR's are known to be sensitive to habituation (Steiner & Barry, 2014). In addition to SCR-amplitudes, the number of evoked SCR's following erotic images was numerically (but not significantly)

increased compared with aversive and neutral conditions. However, contrasting with prior studies (Kinner et al., 2017; Vujovic et al., 2014), participants showed no increased electrodermal responsiveness to aversive image content. The reasons for this could be manifold. Although SCR's are a well-established measure of ANS-activity in response to pleasant and aversive stimuli (Bernat et al., 2006; Christopoulos et al., 2019), sex differences in affective picture processing have been observed (Bradley et al., 2001). Women exhibit greater physiological reactivity to aversive material compared with men (Chentsova-Dutton & Tsai, 2007; Lithari et al., 2010). In contrast, SCR's in men are largest in response to erotic cues (Bradley et al., 2001). The fact that we only recruited male participants might have, at least partly, contributed to the lack of SCR modulation by aversive stimuli. We also used relatively short inter-trial intervals (ITIs; 5.5–6 s). As skin conductance responses can be considered a slowly reacting measure of emotional arousal, evolving SCRs were possibly affected by the recovery slope of preceding one (Benedek & Kaernbach, 2010a). Although we applied a nonnegative deconvolution approach that partly compensates for such effects, and is suitable to also estimate phasic skin conductance responses in fast succession, we cannot rule out that longer ITIs would have resulted in stronger differential SCR effects (Benedek & Kaernbach, 2010a).

In sum, we found considerable evidence that arousal (pupil size, heart rate) was successfully modulated by our experimental conditions.

4.2 | Cue effects on TD

Although exposure to erotic and aversive stimuli induced substantial changes of physiological arousal (pupil size, heart rate), steepness of TD was not significantly affected by emotional cues. This was reflected in both, model-free (AUC; Myerson et al., 2001) and model-based (hyperbolic discounting model; Mazur, 1987) measures of choice impulsivity. Results from the computational model indicated that a decrease in discounting following erotica was more likely than an increase (dBF = 19.78). However, this effect was also more compatible with a null model than with the alternative model including condition effects.

Earlier studies found that exogeneous cues might modulate TD (Herman et al., 2018). More specifically, blockwise presentation of appetitive (Li, 2008) and especially erotic cues (Kim & Zauberman, 2013; Van den Bergh et al., 2008; Wilson & Daly, 2004) prior to TD tasks increased discounting. This has been attributed to an out-of-domain wanting for immediate pleasure (present orientation) in response to primary reinforces like erotic picture stimuli (Van den Bergh et al., 2008). Such effects might be mediated by an elevated dopaminergic tone in reward-related brain areas following sustained presentation of highly appetitive rewards like erotic stimuli (O'Sullivan et al., 2011; Redouté et al., 2000). This matches previous evidence showing that pharmacological manipulation of dopaminergic neurotransmission can directly influence discounting behavior (Petzold et al., 2019; Pine et al., 2010; Wagner et al., 2020) though overall, the corresponding human literature is small and heterogeneous (D'Amour-Horvat & Leyton, 2014). In stark contrast, studies investigating trial-wise cue effects on TD report highly mixed results. Studies observed increased (Guan et al., 2015; Sohn et al., 2015), or decreased (Luo et al., 2014) discounting following negative primes, and increased (Sohn et al., 2015) or unaltered (Simmank et al., 2015) discounting in response to erotic cues.

Reasons for this high variability could be manifold. Multiple mechanisms might contribute to trial-wise cue effects, potentially with opposite directionality. Animal studies suggest that both highly arousing appetitive and aversive stimuli induce a graded release of noradrenaline in cortex (NE; Ventura et al., 2008). In humans, highly arousing cues of either valence increase pupil dilation (Finke et al., 2017; Kinner et al., 2017), a measure associated with locus coeruleus (LC) activity (Aston-Jones & Cohen, 2005). NE agonists might reduce several forms of impulsivity (Robinson et al., 2008) and directly increase the preference for larger later rewards (Bizot et al., 2011). Further, Yohimbine, an α_2-adrenergic receptor antagonist that increases NE release reduced discounting in humans (Herman et al., 2019; Schippers et al., 2016). Short-term increases in NE release via erotic or aversive stimuli might therefore foster more patient choice patterns.

At the same time, stimulus-evoked physiological arousal is inextricably linked to emotional processing (Herman et al., 2018). Various studies observed increased TD following negative emotional priming (Guan et al., 2015; Lerner et al., 2013; Moore et al., 1976)—findings that correspond to the idea that experiencing emotional distress might foster desire for immediate pleasure and reward (Tice et al., 2001). Other studies report that positive stimuli, imagining positive future events or a positive mood state, can reduce discounting (Guan et al., 2015; Liu et al., 2013; Rösch et al., 2021; Weafer et al., 2013). Although these findings do not remain unchallenged (Luo et al., 2014; Simmank et al., 2015), they might support the notion of opposing valence-driven cue effects on TD. Such processes might also have contributed to the observations of the present study, which suggested little to no modulatory effect of erotic and aversive cues on decision-making. More complex interaction effects remain possible, such that e.g. single-trial changes in noradrenergic activity might have reduced the preference for immediate

reward following both erotic and aversive cues, whereas emotional processing in response to aversive image onset might have selectively increased wanting of immediately available rewards.

Further, when comparing results across trial-wise cue-exposure studies, it is crucial to consider event sequences within single trials, which might affect value integration and choice preferences. Sohn et al. (2015) investigated emotional arousal effects on TD using positive, negative, and neutral cues. On every trial, two pictures of the same category were presented, followed by the presentation of the smaller sooner (SS) and larger later (LL) rewards. Similarly, Guan et al. (2015) first displayed negative (arousing), neutral, or happy primes. The SS and LL options appeared both shortly after. In contrast, in the present study, cues were presented alone for 2 s, and subsequently the LL option was superimposed. The immediately available SS option (20€) was never shown throughout the experiment (Kable & Glimcher, 2007; Miedl et al., 2014; Peters & Büchel, 2009). Therefore, neural coding of the LL-reward (Miedl et al., 2014; Strait et al., 2015) may have been selectively increased by preceding erotic cues, and decreased by aversive cues. However, whether the small and non-significant bias toward less impulsive choice in the erotic condition is a consequence of such coding remains speculative. Further, if this is true, superimposing varying smaller but sooner rewards (SS) onto emotional image cues might reverse the effects observed here. Further work is required to examine the impact of such experimental design choices on cue-exposure effects.

We observed robust cue-evoked changes in arousal, in particular for pupil dilation (see above). However, modeling revealed that trial-wise arousal had little to no effects on $\log(k)$ and β. Small attenuating effects of erotic cues on $\log(k)$ persisted, even when trial-wise pupil dilation was included in the model. Although the erotic effect was further attenuated, this was not the case for the aversive cue effects, arguing against a general valence-independent effect of physiological arousal on discounting.

In a final control model, we tested whether single-trial physiological measures affected $\log(k)$, irrespective of overall condition effects. Confirming previous results, posterior distributions indicated if anything small (decreasing) and non-significant effects of pupil and heart rate regressors on the discount rate which were both highly compatible with a null model. Complementing this approach, we also tested whether trial-wise arousal indices directly influenced the probability of making smaller-sooner versus larger-later choices (0 = SS choice vs. 1 = LL-choice) using a linear-mixed model analysis. Interestingly, this yielded a significant negative effect of electrodermal activity (EDA) on choice, indicating that increased trial-wise skin conductance levels were associated with an increased likelihood of SS choices. As trial-wise arousal (comprising EDA) did not modulate the steepness of TD (quantified via $\log(k)$-parameter), the observed increased preference for the immediate choice options here might be explained by an offset of the TD curve as a whole, under heightened electrodermal activity. However, as electrodermal responses did not reliably differentiate between cue conditions this finding should be interpreted with care.

Posterior distributions from the hierarchical model indicated that an increase in decision noise following aversive cues (decreased β) was far more likely than a decrease, given the data. This effect was also reproduced in the non-hierarchical modeling scheme (see Supplement), but did not survive correction for multiple comparisons. Although this effect was also compatible with a null model, it might reflect a reduced impact of value differences on choices. This could be attributable to distraction (Dolcos & McCarthy, 2006; Stout et al., 2020) and/or increased demands for emotion regulation (Dolcos & McCarthy, 2006; Ochsner et al., 2004), impeding successful value integration. However, unaltered decision noise following highly arousing erotic stimuli again argues against an underlying arousal-driven effect.

Previous research indicated that pupil size tracks task demand cognitive load, as well as memory and decision processes (Kahneman & Beatty, 1966; van der Wel & van Steenbergen, 2018). In the context of TD, relative value equivalence (RVE), a proxy for choice difficulty, scales with pupil dilation (Lempert et al., 2016). Therefore, we predicted pupil size to be differentially increased in response to high decision conflict (i.e. small trial-wise subjective value differences of SS and LL rewards). However, this was not the case (see Supplemental Materials). In contrast to previous approaches, in the current study participants performed a behavioral pretest prior to the actual experiment to estimate individual a-priori discount rates, which were then used to create individually tailored choice options. Therefore, choice sets contained a disproportional high number of difficult high-conflict trials. Although this procedure can improve parameter estimation, it likely decreased variance in choice difficulty which in turn might have impeded the detection of corresponding associations with pupil dilation.

The present study has several limitations that need to be acknowledged. First, although our data indicate alterations of ANS-activity following erotic and aversive cues (Wang et al., 2018), we did not directly assess subjective arousal. However, psychophysiological ANS-measures and subjective measures tend to co-vary (Aguado et al., 2018; Lang et al., 1990). Moreover, pupil dilation during mental imagery covaries with subjective arousal (Henderson et al., 2018). We also conducted a pilot study where image characteristics of the stimulus set were

pre-rated by an independent sample. The obtained ratings suggest that erotic and aversive stimuli modulated subjective arousal. However, future studies might complement physiological recordings in response to affective cue presentation by self-reported arousal. Second, we focused on male participants because erotic cue effects on TD have been primarily examined in male subjects (Kim & Zauberman, 2013; Van den Bergh et al., 2008; Wilson & Daly, 2004). Men and women might differ in their neurophysiological reactivity to affective stimulus material and emotional processing (Bradley et al., 2001; Lithari et al., 2010; Wrase et al., 2003), and future studies should extend the present approach and include participants from both sexes. Further, our pre-registered power analysis suffers from two shortcomings. First, we erroneously included both between- and within-subject studies for effect size estimation. Second, we did not take the within-subject correlation of TD adequately into account. However, even when focusing on effect size estimates derived from the two most comparable studies (Guan et al., 2015; Sohn et al., 2015), we had adequate power to detect behavioral (main) effects of the reported size (power > 0.99). However, effect size estimates from only few studies using different approximations of TD might be biased. Future studies might aim for a bigger sample size to (a) confirm the present main effects of cue condition on TD and (b) assess further modulatory influence of physiological arousal on choice.

Taken together, while appetitive and aversive cues caused a substantial modulation of the physiological arousal state, behavioral effects on TD were at most small. Whereas steepness of TD was not affected by emotional cues of either valence, aversive cues tended to increase decision noise. Previous trial-wise cue-exposure effects on discounting were mixed, but physiological arousal was not explicitly controlled. Using extensive computational modeling and physiological monitoring, we found no strong evidence for a major influence of trial-wise physiological arousal levels on TD.

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CONFLICT OF INTEREST

There are no conflicts of interest.

AUTHOR CONTRIBUTIONS

Kilian Knauth: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Software; Validation; Visualization; Writing – original draft; Writing – review & editing. **Jan Peters:** Conceptualization; Funding acquisition; Methodology; Resources; Software; Supervision; Validation; Writing – review & editing.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

FIGURE S1. Pilot study image ratings ($n = 10$) of erotic, aversive and neutral cues (A: Arousal; B: Valence); Small colored dots depict single-subject means

FIGURE S2. Physical properties of erotic, aversive and neutral cues (A: Mean pixel intensity; B: Standard deviation of pixel intensities (contrast))

FIGURE S3. Sum of SCR amplitudes (A), number of significant SCR's (B) and mean phasic activity (C) in the interval 1–6 s post image onset; Small colored dots depict single-subject means; μs = microsiemens

FIGURE S4. Mean within-subject associations (r) between physiological measures (pupil, heart rate [HR], electrodermal activity [EDA]) in response to cue presentation; Small gray dots depict single-subject coefficients

FIGURE S5. Associations amongst physiological cue-reactivity indices (difference scores; pupil, heart rate [HR], electrodermal activity [EDA])

FIGURE S6. Single-subject posterior distributions for erotic (S_{Ero}; blue) and aversive (S_{Avr}; red) shift-parameters as well as their differences (black); A–C: Log(k); D–F: Softmax (β); Colored dots depict single-subject means. Dotted lines indicate grand average across all subjects

FIGURE S7. Associations between model-free (AUC, LL-choice proportions) and model-based measures ($S_{Ero(k)}$, $S_{Avr(k)}$) of discounting behavior. r = Pearson's correlation coefficient

FIGURE S8. Association between pupillary cue-reactivity indices (difference scores) and erotic- (A, B) and aversive (C, D) shift-parameters ($S_{Ero(k,\beta)}$, $S_{Avr(k,\beta)}$)

FIGURE S9. Cue-evoked physiological responses over the course of the experiment; Valid trials of pupil size (A), heart rate (HR; B) and phasic electrodermal activity data (EDA; C), were binned into three bins separately for neutral, erotic and aversive cue conditions; Shaded areas depict standard errors (SE)

FIGURE S10. (A) Grand average pupil trajectories as a function of trial difficulty following larger later (LL) reward onset; dotted lines depict standard errors (SE's) (B) Mean single-subject pupil responses for the interval (LL-onset until decision screen onset)

FIGURE S11. (A) Grand average pupil trajectories as a function of trial difficulty following image onset; solid/dotted lines = real/modeled data (GLM); (B) Unstandardized regression weights of LL-reward presentation on pupil size split by trial difficulty level

FIGURE S12. Reaction time (RT) differences as a function of trial difficulty (easy, medium, hard). Dotted lines depict grand mean across all participants ± standard errors (SE's)

FIGURE S13. Physiological (pupil size) and behavioral (RT) indices of cognitive effort and their association. Dots depict single subject beta coefficients from the mixed models: (1) RT ~ difficulty + condition + difficulty * condition + (1|Subject); (2) Pupil Size ~ difficulty + condition + difficulty * condition + (1|Subject)

FIGURE S14. Association between mean standardized working memory score (WMC) and neutral log (k)-parameter from the computational shift-model

TABLE S1. Pairwise comparisons of cue-evoked mean pupil dilation (Interaction effect: time bin (0.5 s/bin) × condition)

TABLE S2. Correlation statistics (r_{means}) quantifying single-trial concordance between physiological measures (pupil, heart rate [HR], electrodermal activity [EDA])

TABLE S3. Correlation statistics quantifying concordance between physiological cue-reactivity indices (difference scores; pupil, heart rate [HR] & electrodermal activity [EDA])

TABLE S4. Summary statistics for the main model (non-hierarchical version)

TABLE S5. Correlation statistics quantifying associations between model-free (AUC, LL-choice proportions) and model-based measures ($S_{Ero(k)}$, $S_{Avr(k)}$) of discounting behavior

TABLE S6. Correlation statistics quantifying the association between behavioral (shift-parameters; ($S_{Ero(k,\beta)}$, $S_{Avr(k,\beta)}$)) and pupillary cue-reactivity indices (difference scores)

TABLE S7. Summary statistics of the posterior distributions of computational shift-parameters (Pupil model)

TABLE S8. Summary statistics of the posterior distributions of computational shift-parameters (Arousal model)

TABLE S9. Results from linear mixed model assessing trialwise arousal effects on choice (0 = SS choice vs. 1 = LL-choice)

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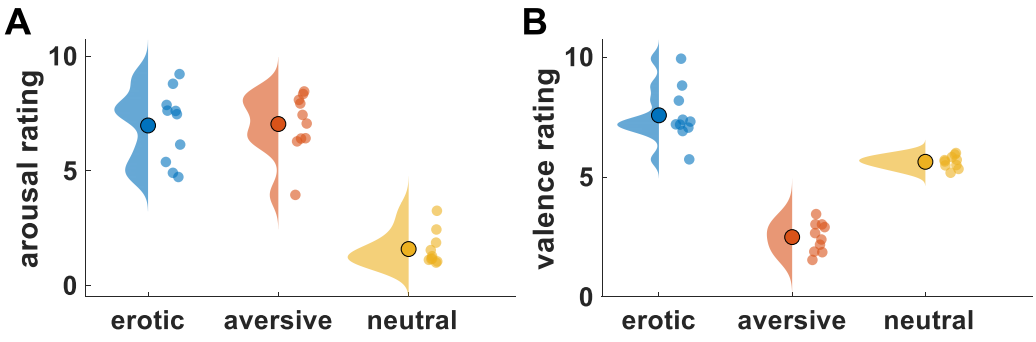
Supplementary Materials

(*Study 1: Trial-wise exposure to visual emotional cues increases physiological arousal but not temporal discounting*)

Pilot study ratings of stimulus material used in the study

We used repeated measures analysis of variance (rmANOVA) to compare image ratings (arousal, valence) between conditions. Results showed that arousal ratings clearly differed between conditions (F[2,190] = 9961.70; p < .001; η_p^2 = 0.99; ε = 0.61; Figure S1). Post-hoc ttests revealed, that arousal levels were comparable for erotic and aversive cues ($t_{(\text{erotic, aversive})}$ = -1.59; p = .346; $CI_{Diff(95\%)}$ = [-0.14;0.02]) but differed for neutral image condition ($t_{(\text{erotic, neutral})}$ = 188.04; p < .001; $CI_{Diff(95\%)}$ = [5.33;5.45]); $t_{(\text{neutral, aversive})}$ = -92.49; p < .001; $CI_{Diff(95\%)}$ = [-5.57;-5.34]).

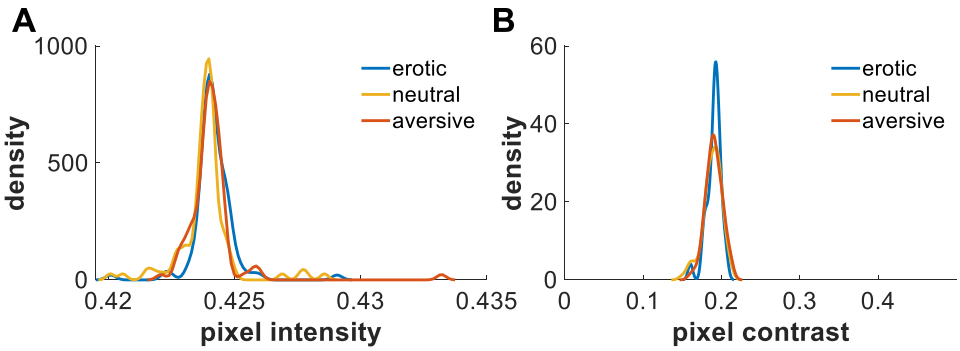
Valence ratings also differed between cue conditions (F[2,190] = 1720.40; p < .001; η_p^2 = 0.95; ε = 0.87; Figure S1). Post-hoc ttests showed, that erotic and aversive images differed in their rated valence ($t_{(\text{erotic, aversive})}$ = 51.13; p < .001; $CI_{Diff(95\%)}$ = [4.88;5.27]). Neutral images differed from both erotic and aversive image conditions ($t_{(\text{erotic, neutral})}$ = 27.76; p < .001; $CI_{Diff(95\%)}$ [1.80;2.08]; $t_{(\text{neutral, aversive})}$ = 34.76; p < .001; $CI_{Diff(95\%)}$ = [2.96;3.32]).



Supplementary Figure S1. Pilot study image ratings (n = 10) of erotic, aversive and neutral cues (**A:** Arousal; **B:** Valence); Small colored dots depict single-subject means.

Physical properties of stimulus material used in the study

Using MATLABS SHINE toolbox, images of all three experimental conditions were matched with respect to mean pixel intensity (F[2, 285] = 2.03, p = .133; mean ± SD = erotic: 0.42 ± 0.001; neutral: 0.42 ± 0.001; aversive: 0.42 ± 0.001) and pixel contrast (F[2,285] = 1.06, p = .347; mean ± SD = erotic: 0.19 ± 0.012; neutral: 0.19 ± 0.001; aversive: 0.19 ± 0.01) (Figure S2).



Supplementary Figure S2. Physical properties of erotic, aversive and neutral cues (**A**: Mean pixel intensity; **B**: Standard deviation of pixel intensities (contrast)).

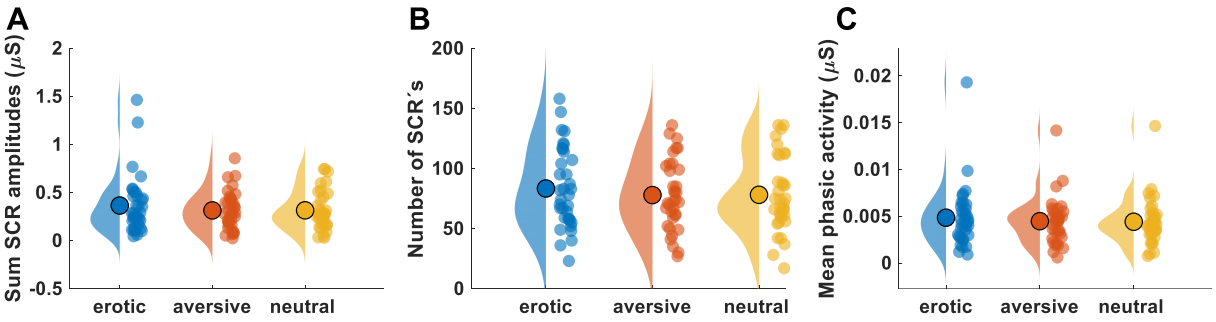
Supplementary Table S1. Pairwise comparisons of cue-evoked mean pupil dilation (Interaction effect: time bin (0.5s/bin) x condition).

Time Bin	Condition (1)	Condition (2)	Difference	StdErr	*p-value*	Lower bound	Upper bound
1	erotic	aversive	0.002	0.0001	.287	0.001	0.004
1	erotic	neutral	0.002	0.001	.298	0.001	0.004
1	aversive	neutral	0.0002	0.001	1.000	-0.003	0.003
2	erotic	aversive	0.02	0.002	< .001*	0.013	0.024
2	erotic	neutral	0.03	0.002	< .001*	0.023	0.035
2	aversive	neutral	0.01	0.002	< .001*	0.007	0.015
3	erotic	aversive	0.04	0.004	< .001*	0.027	0.045
3	erotic	neutral	0.05	0.004	< .001*	0.037	0.058
3	aversive	neutral	0.01	0.003	< .001*	0.005	0.018
4	erotic	aversive	0.05	0.005	< .001*	0.036	0.059
4	erotic	neutral	0.06	0.005	< .001*	0.047	0.072
4	aversive	neutral	0.01	0.002	< .001*	0.006	0.018
5	erotic	aversive	0.05	0.005	< .001*	0.038	0.062
5	erotic	neutral	0.06	0.006	< .001*	0.046	0.074
5	aversive	neutral	0.01	0.002	< .001*	0.005	0.016
6	erotic	aversive	0.05	0.005	< .001*	0.033	0.059
6	erotic	neutral	0.06	0.006	< .001*	0.042	0.070
6	aversive	neutral	0.01	0.002	< .001*	0.004	0.017
7	erotic	aversive	0.04	0.005	< .001*	0.027	0.052
7	erotic	neutral	0.05	0.006	< .001*	0.034	0.062
7	aversive	neutral	0.01	0.002	.002*	0.003	0.014
8	erotic	aversive	0.04	0.005	< .001*	0.023	0.047
8	erotic	neutral	0.04	0.005	< .001*	0.030	0.056
8	aversive	neutral	0.01	0.002	.005*	0.002	0.014
9	erotic	aversive	0.03	0.004	< .001*	0.020	0.042
9	erotic	neutral	0.04	0.005	< .001*	0.025	0.050
9	aversive	neutral	0.01	0.003	.054	0.000	0.013
10	erotic	aversive	0.03	0.004	< .001*	0.019	0.040
10	erotic	neutral	0.04	0.004	< .001*	0.024	0.046
10	aversive	neutral	0.01	0.003	.115	0.000	0.012

Note. Asterisks indicate significant correlations on the $p < .05$ level (Bonferroni corrected). StdErr = standard error; Lower and upper bounds describe the 95% confidence interval.

Exploratory analysis on skin conductance responses following image presentation

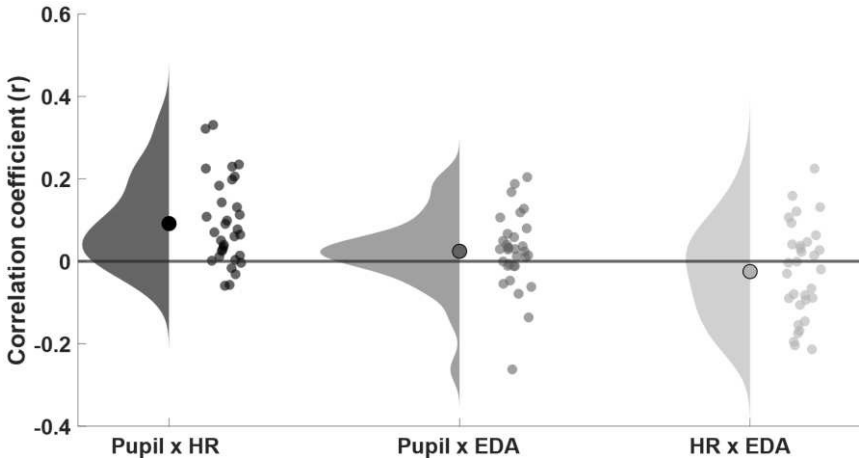
A repeated measures ANOVA indicated that while the sum of SCR amplitudes and mean phasic activity did not differ between experimental conditions (erotic, aversive, neutral), there was a higher mean number of evoked SCR´s following erotic images (mean ± Std = 83.31 ± 33.13) compared to aversive (mean ± Std = 77.83 ± 28.96) and neutral ones (mean ± Std = 78.06 ± 31.10) (Figure S3). However, none of the pairwise comparisons survived Bonferroni correction.



Supplementary Figure S3. Sum of SCR amplitudes **(A)**, number of significant SCR´s **(B)** and mean phasic activity **(C)** in the interval 1-6 seconds post image onset; Small colored dots depict single-subject means; *μs* = microsiemens.

Within-subject correlation of physiological measures in response to cue presentation

Within-subject cue-evoked changes in all three physiological measures (pupil size, heart rate, EDA) were at most weakly correlated (Figure S4, Table S2). Pupil size showed a small but significant mean correlation with heart rate change in response to image presentation (r_{mean} = .09, p < .001). Single-subject data indicated that while some subjects showed substantial associations, correlations were around zero in other participants. In contrast, pupil- and heart rate change both showed no associations with phasic electrodermal activity following image onset (Pupil / EDA: r_{mean} = .02, p = .142; HR / EDA: r_{mean} = -.03, p = .227).



Supplementary Figure S4. Mean within-subject associations (*r*) between physiological measures (pupil, heart rate (HR), electrodermal activity (EDA)) in response to cue presentation; Small gray dots depict single-subject coefficients.

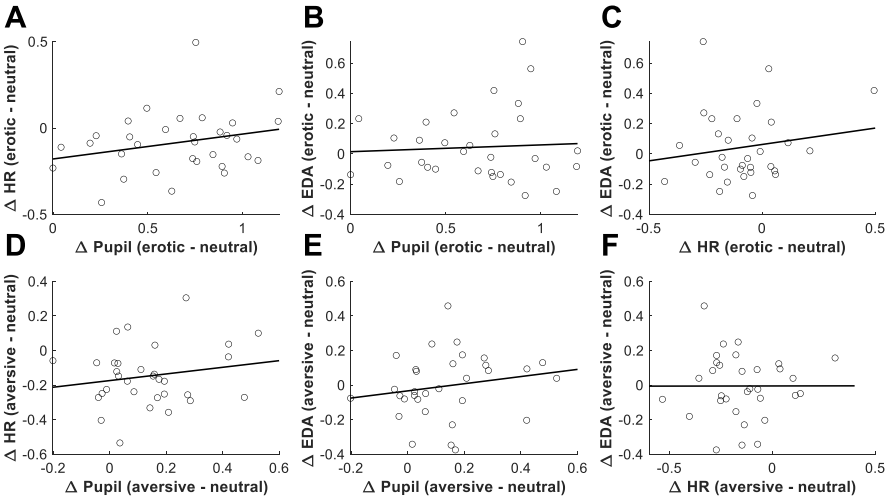
Supplementary Table S2. Correlation statistics (r_{means}) quantifying single-trial concordance between physiological measures (pupil, heart rate (HR), electrodermal activity (EDA)).

Measures	r_{mean}	**CI**	***p*-value**
Pupil x HR	.09	[0.05; 0.13]	< .001*
Pupil x EDA	.02	[-0.01; 0.06]	.142
HR x EDA	-.03	[-0.07; 0.02]	.227

Note. Asterisks indicate significant correlations on the $p < .05$ level; *r* = Pearson's correlation coefficient; CI = 95% confidence interval.

Associations amongst physiological cue-reactivity indices

After we examined the trialwise associations between physiological measures in general, we assessed subjects´ cue-reactivity response in every physiological measure as well as their concordance. To this end, we calculated difference scores between the mean response to erotic and neutral and between aversive and neutral content respectively. Next, we used Pearson's correlations to quantify the association between those difference scores. As evident from Figure S5 (**A & D**), the above-mentioned selective increase in pupil diameter following erotic and aversive image content compared to neutral showed only small and non-significant associations to cardiovascular cue-reactivity. Subjects showing most pronounced differences in heart rate change between conditions exhibited only small cue-reactivity effects in pupil diameter ($r = .26$, $p = .148$). In addition, heightened cue-related pupil responses to aversive images were slightly and non-significantly associated with increased phasic electrodermal activity (Figure S5 (**E**); $r = .19$, $p = .310$). Detailed correlation statistics between physiological cue-response measures are depicted in Table S3.



Supplementary Figure S5. Associations amongst physiological cue-reactivity indices (difference scores; Pupil, Heart Rate (HR), Electrodermal Activity (EDA)).

Supplementary Table S3. Correlation statistics quantifying concordance between physiological cue-reactivity indices (difference scores; Pupil, Heart Rate (HR) & Electrodermal Activity (EDA)).

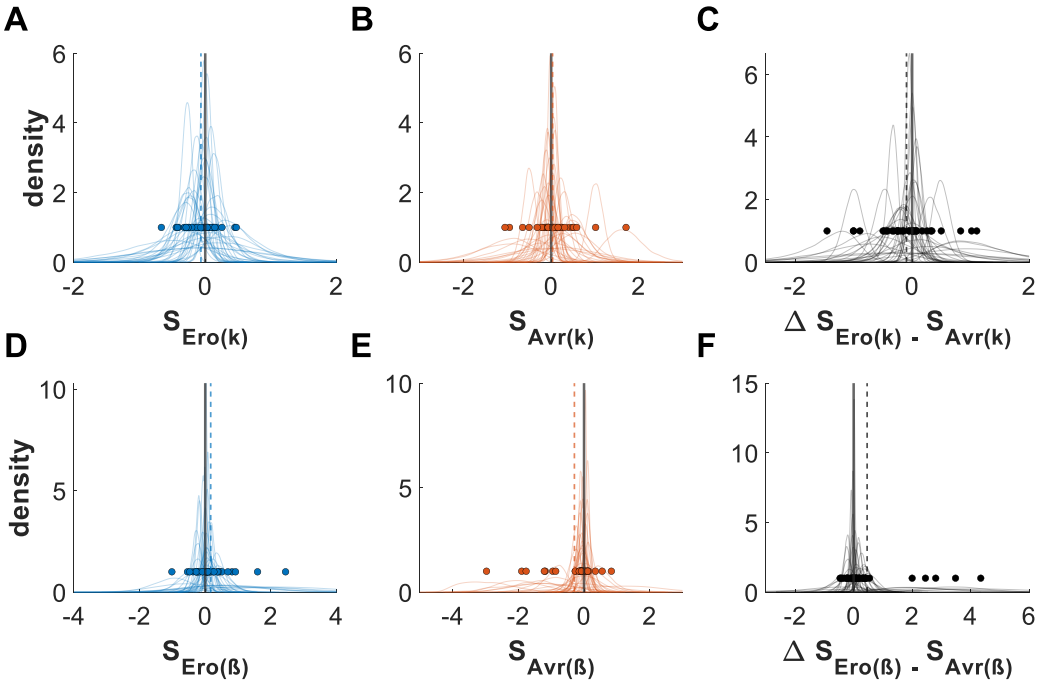
Physiological measures	**Δ Contrast**	**Correlation coefficient (*r*)**	**CI**	***p-value***
Pupil x HR	Erotic - neutral	.26	[-0.10; 0.56]	*.148*
	Aversive - neutral	.18	[-0.18; 0.50]	*.315*
Pupil x EDA	Erotic - neutral	.06	[-0.29; 0.40]	*.740*
	Aversive - neutral	.19	[-0.17; 0.50]	*.310*
HR x EDA	Erotic - neutral	.16	[-0.20; 0.48]	*.375*
	Aversive - neutral	.002	[-0.35; 0.35]	*.993*

Note. *r* = Pearson's correlation coefficient; CI = 95% confidence interval.

Assessment of erotic and aversive shift-effects on the single-subject-level

To validate parameters from the hierarchical modeling approach, we fitted a non-hierarchical version of the same hyperbolic model with softmax action selection to the choice data (see 2.6.2). We also examined whether estimates for erotic and aversive shift parameters significantly differed from zero via ttests (see Table S4). This analysis revealed that mean shift-parameters from the single subject model went into the same direction as group parameters from the hierarchical counterpart. However, variance in the posterior distributions from these individual-subject models was of course substantially greater than the estimates from the hierarchical model, due to parameter shrinkage. Ttest results indicated a significant decrease in β-parameter following aversive cues ($t(34) = -2.36$, $p = 0.024$, Cohen's $d = -0.398$), confirming an increase in decision noise. However, this effect did not survive Bonferroni

correction. No other parameters significantly differed from zero. Those results thus closely resemble results from the hierarchical model.



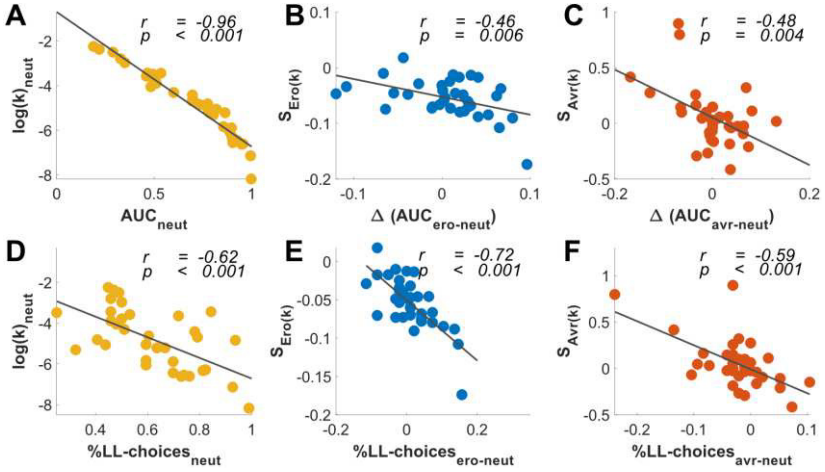
Supplementary Figure S6. Single-subject posterior distributions for erotic (S_{Ero}; blue) and aversive (S_{Avr}; red) shift-parameters as well as their differences (black); **A-C**: Log(k); **D-F**: Softmax (β); Colored dots depict single-subject means. Dotted lines indicate grand average across all subjects.

Supplementary Table S4. Summary statistics for the main model (non-hierarchical version)

Parameter	Median	Range (min, max)	Cohen's d	t-statistic	*p-value*
SEro(k)	-0.041	[-0.668, 0.473]	-0.271	-1.606	0.118
SAvr(k)	-0.044	[-1.057, 1.710]	0.064	0.378	0.708
SEro(ß)	0.059	[-1.017, 2.448]	0.275	1.627	0.113
SAvr(ß)	-0.072	[-2.972, 0.833]	-0.398	-2.355	**0.024***

Note. SD = standard deviation.

Associations between model-free and model-based measures of temporal discounting



Supplementary Figure S7. Associations between model-free (AUC, LL-choice proportions) and model-based measures ($S_{Ero(k)}$, $S_{Avr(k)}$) of discounting behavior. *r* = Pearson's correlation coefficient.

Supplementary Table S5. Correlation statistics quantifying associations between model-free (AUC, LL-choice proportions) and model-based measures ($S_{Ero(k)}$, $S_{Avr(k)}$) of discounting behavior.

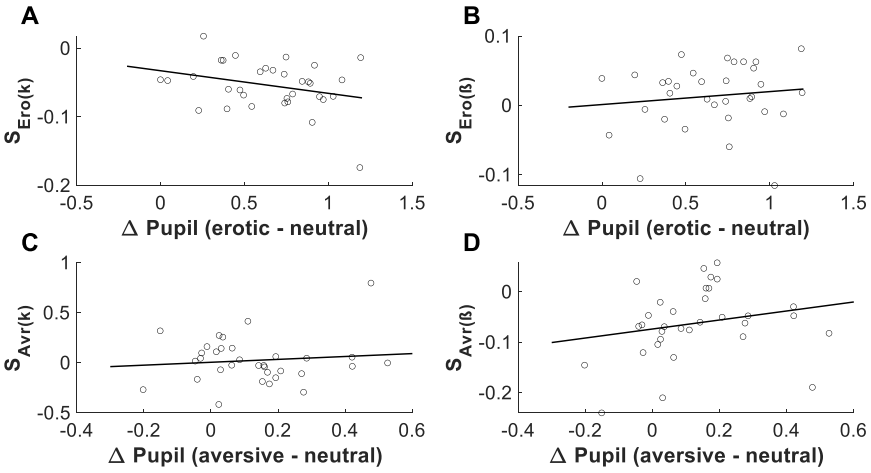
Measure (1)	Measure (2)	Correlation coefficient (*r*)	CI	*p-value*
$Log(k)_{neut}$	AUC_{neut}	-.96	[-.98; -.93]	< .001*
	% $LL\text{-}choices_{neut}$	-.62	[-.79; -.36]	< .001*
$S_{Ero(k)}$	Δ ($AUC_{ero\text{-}neut}$)	-.46	[-.69; -.15]	.006
	% $LL\text{-}choices_{ero\text{-}neut}$	-.72	[-.85; -.51]	< .001*
$S_{Avr(k)}$	Δ ($AUC_{avr\text{-}neut}$)	-.48	[-.70; .17]	.004
	% $LL\text{-}choices_{avr\text{-}neut}$	-.59	[-.77; -.32]	< .001*

Note. Asterisks indicate significant correlations on the $p < .05$ level; *r* = Pearson's correlation coefficient; CI = 95% confidence interval.

Association of behavioral (shift-parameters) and pupillary cue-reactivity indices (difference scores)

The magnitude of erotic shift-parameter on log(*k*) ($S_{Ero(k)}$) showed a slightly non-significant negative association with differential pupil responses to erotic stimuli, indicating that subjects exhibiting increased responses to erotic images also showed a more pronounced decrease in their discounting behavior in the erotic condition ($r = -.29$, $p = .096$; Figure S8, **A**). There was no comparable association for the aversive condition ($r = .11$, $p = .546$). In addition, elevated pupil responses to affective stimulus material (erotic & aversive) were positively associated with respective *ß*-shift parameters ($S_{Ero(ß)}$, $S_{Avr(ß)}$; Figure S8, **B** & **D**) assuming that an increased physiological cue-response was associated with less decision noise. Despite non-significant, this effect was more pronounced for aversive image condition

(Aversive: r = .22, p = .220; Erotic: r = .13, p = .487). Detailed correlation statistics are depicted in Table S6.



Supplementary Figure S8. Association between pupillary cue-reactivity indices (difference scores) and erotic- (**A, B**) and aversive (**C, D**) shift-parameters ($S_{Ero(k,\beta)}$, $S_{Avr(k,\beta)}$).

Supplementary Table S6. Correlation statistics quantifying the association between behavioral (shift-parameters; ($S_{Ero(k,\beta)}$, $S_{Avr(k,\beta)}$)) and pupillary cue-reactivity indices (difference scores).

Measures	Correlation coefficient (*r*)	CI	*p-value*
Δ Pupil$_{(ero\text{-}neut)}$ x S$_{Ero(k)}$	-.29	[-0.58; 0.05]	*.096*
Δ Pupil$_{(avr\text{-}neut)}$ x S$_{Avr(k)}$	.11	[-0.24; 0.44]	*.546*
Δ Pupil$_{(ero\text{-}neut)}$ x S$_{Ero(ß)}$	.13	[-0.23; 0.45]	*.487*
Δ Pupil$_{(avr\text{-}neut)}$ x S$_{Avr(ß)}$	.22	[-0.13; 0.52]	*.220*

Note. r = Pearson's correlation coefficient; CI = 95% confidence interval.

Supplementary Table S7. Summary statistics of the posterior distributions of computational shift-parameters (Pupil model).

Parameter	dBF	BF_{01}
SEro(k)	11.62	11.475
SAvr(k)	0.570	17.120
EroPupil(k)	8.700	22.465
AvrPupil(k)	0.430	35.616
SEro(ß)	0.050	2.267
SAvr(ß)	5.880	3.290
EroPupil(ß)	2.090	7.716
AvrPupil(ß)	0.280	8.542

Note. dBF = directional Bayes Factor; BF_{01} = undirected Bayes Factor in favor of null model.

Supplementary Table S8. Summary statistics of the posterior distributions of computational shift-parameters (Arousal model).

Parameter	dBF	BF_{01}
PupilReg(k)	17.980	22.034
EcgReg(k)	3.410	53.577
EdaReg(k)	0.920	76.523
PupilReg(ß)	0.370	13.267
EcgReg(ß)	9.270	6.653
EdaReg(ß)	0.460	10.178

Note. dBF = directional Bayes Factor; BF_{01} = undirected Bayes Factor in favor of null model.

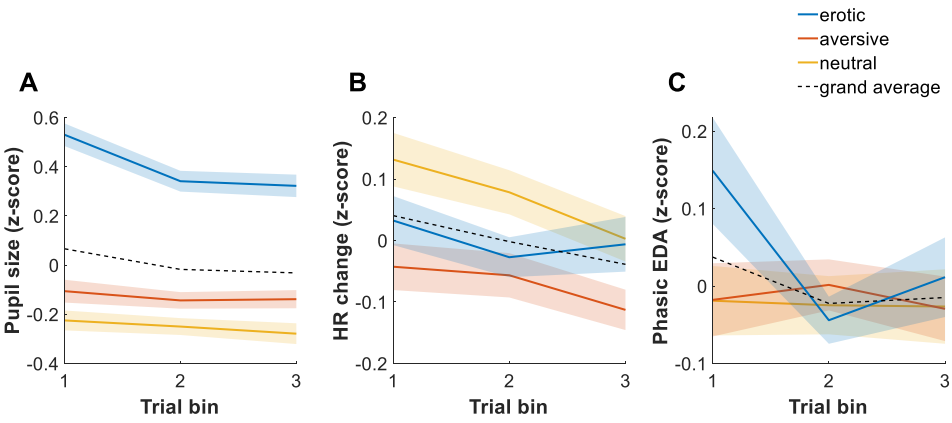
Supplementary Table S9. Results from linear mixed model assessing trialwise arousal effects on choice (0 = SS choice vs. 1 = LL-choice).

Fixed Effects	Estimate	Std.	z-	*p*-
(Intercept)	0.448	0.151		**0.003***
Pupil	0.030	0.024		0.206
ECG	0.031	0.024		0.196
EDA	-0.058	0.024	-	**0.014***
Pupil*ECG	0.008	0.025		0.738
Pupil*EDA	0.005	0.023		0.816
ECG*EDA	-0.007	0.018	-	0.719
Pupil*ECG*EDA	-0.018	0.015	-	0.244

Note. Std. Error = standard error;

Habituation of physiological cue response

We assessed habituation processes of evoked physiological responses to image presentation over the course of the experiment. To this end, we separately z-scored and binned pupil, heart rate and electrodermal activity data (trial means) into three trial bins. Using separate repeated measures ANOVA, we compared evoked physiological responses over the course of the experiment (within factor: time bin). As shown in Figure S9 (**A**), evoked pupil responses slightly decreased over trial bins (F[1, 32] = 4.18, p = .028, η_p^2= 0.12, ε = 0.82). Similar patterns were numerically apparent for evoked heart rate responses and phasic electrodermal activity data (EDA) but both did not reach significance (Heart Rate: F[1, 33] = 1.46, p = .240; **B;** EDA**:** F[1, 34] = 0.58, p = .498, ε = 0.66 ; **C**).



Supplementary Figure S9. Cue-evoked physiological responses over the course of the experiment; Valid trials of pupil size (**A**), heart rate (HR; **B**) and phasic electrodermal activity data (EDA; **C**), were binned into three bins separately for neutral, erotic and aversive cue conditions; Shaded areas depict standard errors (SE).

Evaluation of physiological and behavioral indices of cognitive effort

Analysis

As pupil dilation appears sensitive to various internal states or cognitive manipulations, including mental arithmetic, memory processes and decision formation (van der Wel & van Steenbergen, 2018), we hypothesized, that high decision conflict during temporal discounting would likewise result in an elevated pupil dilation indicating high cognitive effort irrespective of cue condition. This effect should be most pronounced following LL-onset and might last until a decision is made. Here, we slightly deviated from our preregistered analysis plan (analysis of trial difficulty- and cue-condition effects on pupil dilation in two separate general linear models (GLMs; https://osf.io/swp4m/)). Instead, we used three complementary approaches. First, mean pupil size starting at larger later reward (LL) onset until decision screen onset was compared between easy, medium and hard trials using repeated measures ANOVA. For every subject we determined trial difficulty by classifying all trials into three terciles depending on the numeric subjective value (SV) difference between smaller sooner and the larger later options. Second, as cognitive conflict might cumulate and reach its peak immediately before a decision between SS and LL-options is made, we used a linear mixed model to analyze whether median pupil size in the interval 1 second prior to decision (button press) differed between trial difficulty levels (easy, medium, hard). We added cue condition (erotic, aversive, neutral) as well as the interaction of cue condition and trial difficulty as fixed effects while fitting a random effect for subject. Third, using a

Pupil Response Estimation Toolbox (PRET) we constructed a general linear model (GLM) to examine trial difficulty- and cue-effects on pupil dilation (Denison et al., 2020). We defined two sustained boxcar regressors, spanning the periods of image- and LL-reward presentation. Both regressors were convolved with a pupil response function (PRF) of the form:

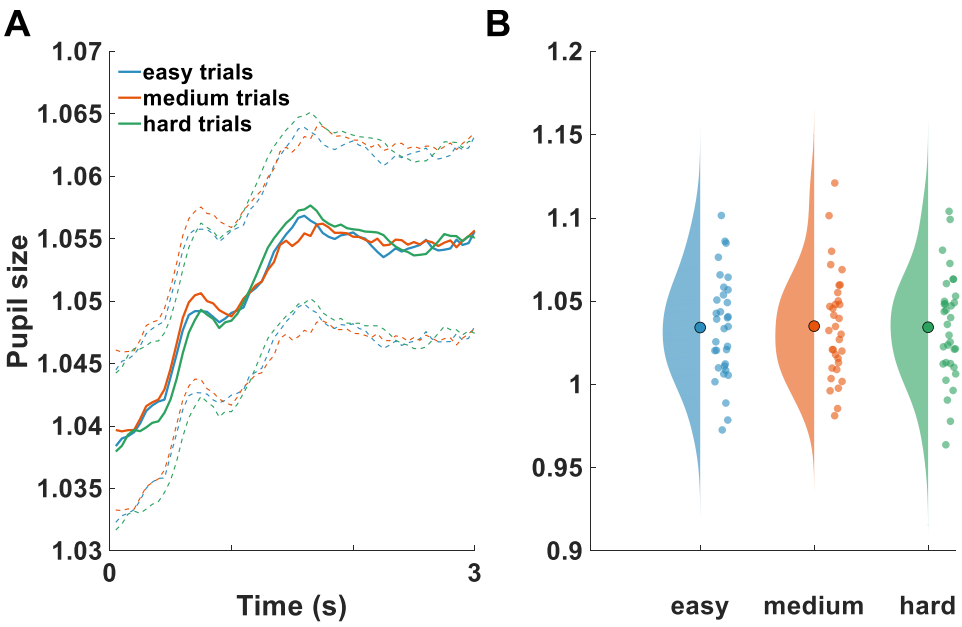
(1) $h(t) = t^n * e^{-nt/tmax}$

Here, *h* is the predicted pupil size, *t* is the time in ms, *n* controls the shape of the function, and *tmax* controls its temporal scale as it is the time of the maximum (Hoeks & Levelt, 1993). To examine interaction effects, single trial data were fitted separately for all cue conditions and trial difficulty levels. Fitted boxcar amplitudes for LL-reward presentation were compared using rmANOVA (within factors: cue condition, trial difficulty).

As trial difficulty might also affect behavioral markers sensitive to cognitive effort, like reaction times (RT), we again used the above mentioned linear mixed model to assess effects of trial difficulty, experimental condition and their interaction (fixed effects) on reaction times, fitting a random effect for every subject. To investigate whether trial difficulty effects on behavioral and physiological indices are associated on the subject level, we extracted single-subject fixed effect estimates from the above mentioned linear mixed models on pupil and reaction times and implemented a Pearson's correlation analysis.

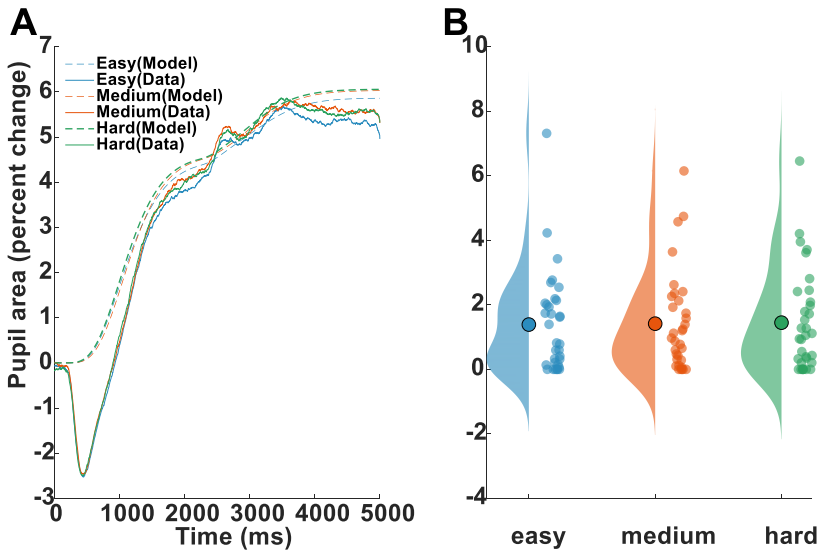
Results

Pupil trajectories in response to easy, medium and hard trials are depicted in Figure S10 (**A**). There was a substantial pupil dilation in response to larger later reward onset which reached a plateau approximately 1.5 seconds post LL presentation. Repeated measures ANOVA revealed that trial difficulty did not further change mean evoked pupil response ($F[2,64] = 0.12$, $p = .830$, $\varepsilon = 0.76$).



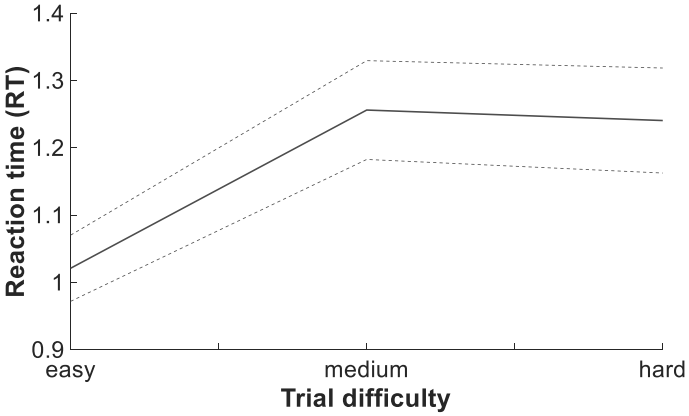
Supplementary Figure S10. **(A)** Grand average pupil trajectories as a function of trial difficulty following larger later (LL) reward onset; dotted lines depict standard errors (SE´s) **(B)** Mean single-subject pupil responses for the interval (LL-onset until decision screen onset).

To assess mental effort effects on pupil dilation in more detail, we used a linear mixed model to quantify trial difficulty and condition effects on median pupil size within the last second interval prior to decision. Complementing previous results, we identified a significant main effect for experimental condition F[1,261], $p < .001$, replicating enhanced pupil responses following erotic and aversive images compared to neutral. There was no further significant main effect for trial difficulty (F[1,261], $p = .375$) or interaction effect between trial difficulty and condition (F[1,261], $p = .451$) in that specific trial period. Two sustained boxcar regressors spanning the intervals of image- and LL-reward presentation, each convolved with a pupil response function, were used to model trialwise pupil trajectories. As trial difficulty effects should first emerge following LL-presentation, we compared boxcar amplitudes for this second regressor using repeated measures ANOVA (within factors: Cue condition, Trial difficulty). While results from the general linear model (GLM) confirmed the missing trial difficulty effect on pupil size (F[2,64] = 0.09, $p = .922$) we found a significant main effect of cue condition indicating that this second dilatory process was most pronounced for neutral image condition, followed by aversive and erotic, possibly indicating a ceiling effect (F[2,64] = 21.63, $p < .001$; mean ± SD: neutral = 2.05 ± 2.01, aversive = 1.67 ± 1.94, erotic = 0.53 ± 0.78). Raw and modeled pupil trajectories as well as boxcar amplitudes split by difficulty levels are depicted in Figure S11.



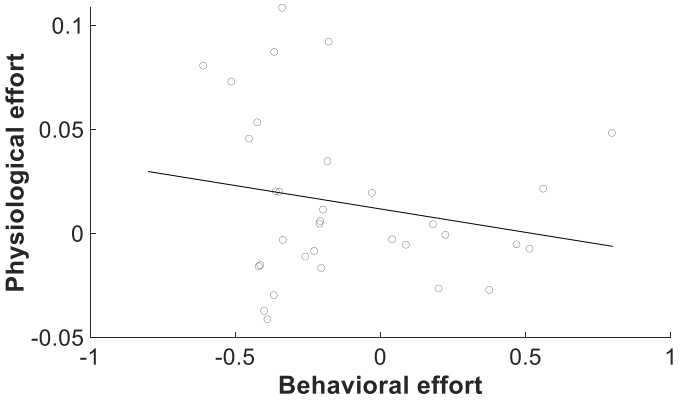
Supplementary Figure S11. **(A)** Grand average pupil trajectories as a function of trial difficulty following image onset; solid/dotted lines = real/modeled data (GLM); **(B)** Unstandardized regression weights of LL-reward presentation on pupil size split by trial difficulty level.

As cognitive effort was not visible in differential physiological responses (pupil dilation) we explored whether trial difficulty was captured by behavioral markers of cognitive effort. To this end, we again used a linear mixed model to assess effects of trial difficulty and experimental condition (fixed effects) on reaction times (RT). Results showed a significant main effect of trial difficulty level on reaction times ($F[1,277]$, $p = .029$), indicating slower RT´s for medium and hard trials compared to neutral (medium vs easy: $t(6.514)$, $p < .001$); hard vs easy: $t(6.08)$, $p < .001$, see Figure S12). RT´s for hard and medium trials did not differ significantly ($t(-0.43)$, $p = .902$). There were no further significant main or interaction effects.



Supplementary Figure S12. Reaction time (RT) differences as a function of trial difficulty (easy, medium, hard). Dotted lines depict grand mean across all participants ± standard errors (SE's).

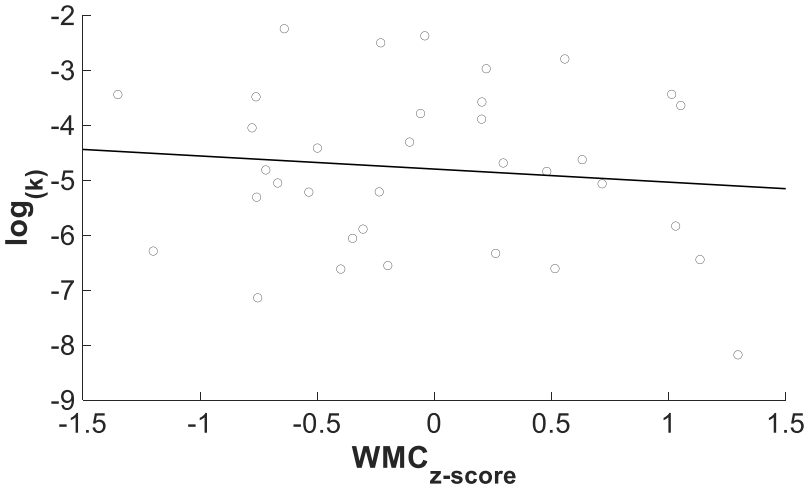
We also tested whether behavioral (RTs) and physiological (pupil dilation) indices of cognitive effort showed associations on the subject level. By this means, we extracted single-subject fixed effect estimates from the above mentioned linear mixed models on pupil and reaction times and implemented a Pearson's correlation analysis. As shown in Figure S13, there seemed to be no strong interdependency between both measures (r = -.20, p = .260, $CI_{(95\%)}$ = [-.51; .15]).



Supplementary Figure S13. Physiological (pupil size) and behavioral (RT) indices of cognitive effort and their association. Dots depict single subject beta coefficients from the mixed models: **(1)** RT ~ difficulty + condition + difficulty*condition + (1|Subject); **(2)** Pupil Size ~ difficulty + condition + difficulty*condition + (1|Subject).

Association of working memory capacity (WMC) and temporal discounting

As working memory capacity (WMC) is often negatively associated with measures of choice impulsivity like temporal discounting we tested whether this is the case in our data. We calculated a working memory compound score for every participant, that is the mean z-score from four different working memory tasks (forward/backward digit span, operation/listening span; Redick et al., 2012; van den Noort et al., 2008; Wechsler, 2008). Next, we implemented Pearson's correlation between working memory scores and estimated neutral log(k)-parameters from the computational shift model (see Eqs. 4 & 5). Results showed no substantial association between WMC and estimated neutral log(k)-parameters (r = -.11, p = .526, $CI_{(95\%)}$ = [-.43; .23]; Figure S14).



Supplementary Figure S14. Association between mean standardized working memory score (WMC) and neutral log (*k*)-parameter from the computational shift-model.

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Research Article

Erotic cue exposure increases neural reward responses without modulating temporal discounting

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ABSTRACT

Humans prefer smaller sooner over larger later rewards, a tendency denoted as temporal discounting. Discounting of future rewards is increased in multiple maladaptive behaviors and clinical conditions. Although temporal discounting is stable over time, it is partly under contextual control. Appetitive (erotic) cues might increase preferences for immediate rewards, although evidence to date remains mixed. Reward circuit activity was hypothesized to drive increases in temporal discounting following cue exposure, yet this was never tested directly. We examined erotic vs. neutral cue exposure effects on subsequent temporal discounting in a preregistered within-subjects study in healthy male participants (n = 38). Functional magnetic resonance imaging assessed neural cue-reactivity, value-computations, and choice-related effects. We replicated previous findings of value-coding in ventromedial prefrontal cortices, striatum, and cingulate cortex. Likewise, as hypothesized, lateral prefrontal cortex activity increased during delayed reward choices, potentially reflecting cognitive control. Erotic cue exposure was associated with increased activity in attention and reward circuits. Contrary to preregistered hypotheses, temporal discounting was unaffected by cue exposure, and cue responses in reward circuits did not reliably predict changes in behavior. Our results raise doubts on the hypothesis that upregulation of (dopaminergic) reward systems following erotic cue exposure is sufficient to drive myopic approach behavior towards immediate rewards.

Keywords: appetitive cue effects, temporal discounting, choice impulsivity, model-based fMRI

1. INTRODUCTION

People and many animals devalue future rewards as a function of time, resulting in an increased preference for immediate rewards (temporal discounting (TD); Kalenscher & Pennertz, 2008; Peters & Büchel, 2011). Despite high intra-individual stability (Bruder et al., 2021; Enkavi et al., 2019; Kirby, 2009), TD varies substantially across individuals (Peters & Büchel, 2011; Soman et al., 2005). High discount rates are observed in clinical groups exhibiting impulsive and/or short-sighted behavior (Bulley & Schacter, 2020), including gambling disorder, substance abuse, impulse control disorders, or lesions to the prefrontal cortices (Amlung et al., 2019; Garofalo et al., 2022; Lempert et al., 2019; Peters & D'Esposito, 2016; Weinsztok et al., 2021).

TD can be affected by environmental factors and cues (Lempert & Phelps, 2016; Peters & Büchel, 2011). In men, TD increases following block-wise presentation of arousing images of opposite-sex faces or erotica (Kim & Zauberman, 2013; Van den Bergh et al., 2007; Wilson & Daly, 2004), stimuli which possess inherently rewarding or appetitive qualities and elicit basic emotional responses (Klucken et al., 2013). More recent results support a more fine-graded association between visual appetitive

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stimulus processing and impulsivity, possibly moderated by internal motivational (e.g., mating mindset; see Chiou et al., 2015) or metabolic (e.g., hunger; see Otterbring & Sela, 2020) conditions (Chiou et al., 2015; Otterbring & Sela, 2020). Such internal states might foster active approach behavior towards immediate rewards.

Previous studies hypothesized that an upregulation of reward circuitry following appetitive cue exposure might drive this effect (Van den Bergh et al., 2007). Indeed, exposure to primary reinforcers including appetitive (erotic) cues increases activity in reward circuits, including ventral striatum (VS), orbitofrontal cortex (OFC), and ventral tegmental area (VTA; Brand, Snagowski, et al., 2016; Gola & Draps, 2018; Gola et al., 2016, 2017; Golec et al., 2021; Klein et al., 2020; Markert et al., 2021; Stark et al., 2019, 2022; Voon et al., 2014; Wehrum-Osinsky et al., 2014). Such exposure might also lead to a bias towards short-term rewards (Li, 2008; Mathar et al., 2022; Yeomans & Brace, 2015) possibly driven by increased dopamine (DA) release. Cortical and striatal dopamine tone have been shown to modulate TD (Arrondo et al., 2015; Cools, 2008; de Wit, 2002; Hamidovic et al., 2008; Kayser et al., 2012; Petzold et al., 2019; Pine et al., 2010; Wagner et al., 2020; Weber et al., 2016), although overall directionality of DA effects appears still mixed (D'Armour-Horvat & Leyton, 2014).

Erotic cue processing and a resulting present orientation in healthy participants might share conceptual similarities with cue-reactivity in addiction, referring to increased subjective, physiological, and neural responses to addiction-related cues (Courtney et al., 2015; Starcke et al., 2018; Volkow et al., 2010; Zhou et al., 2019). Exposure to gambling-related cues can drive increases in TD in gambling disorder (Dixon et al., 2006; Miedl et al., 2014; Wagner et al., 2022). Moreover, increased ventral striatal reactivity to erotic visual stimuli has been associated with the self-reported symptoms of Internet pornography addiction (Brand, Snagowski, et al., 2016), pornography use (Gola et al., 2017), and compulsive sexual behaviors (CSB; Gola & Draps, 2018; Voon et al., 2014).

The study of appetitive cue effects on TD in healthy participants might thus inform our understanding of maladaptive behaviors in clinical groups and potential interventions.

To sum up, there is considerable evidence that exposure to highly appetitive (erotic) cues can increase TD (Kim & Zauberman, 2013; Otterbring & Sela, 2020; Wilson & Daly, 2004) and that erotic cues upregulate activity in reward-related (dopaminergic) regions (Gola et al., 2016; Stark et al., 2005, 2019; Wehrum-Osinsky et al., 2014). However, the degree to which neuronal (erotic) cue-reactivity in these areas directly contributes to changes in TD remains unclear.

The current study addressed these issues in the following ways. First, extending previous work, we used fMRI to directly measure the effects of erotic cue exposure on reward circuit activity and subsequent temporal discounting. Second, we linked reward-system-reactivity to TD. Based on the previous literature, we preregistered the following hypotheses (https://osf.io/w5puk/):

- *Behavioral hypotheses*
  - H1: Temporal discounting will be selectively increased following erotic cue exposure. This effect will be driven by an enhanced bias towards smaller but sooner options
- *Neuronal hypotheses—replication of previous study findings*
  - H2: The subjective value (SV) of the delayed rewards (LL) will be coded in striatal and ventromedial prefrontal areas (vmPFC; see Peters & Büchel, 2009)
  - H3: Lateral prefrontal cortex activity (LPFC) will be increased during choices of LL vs. SS rewards (see Hare et al., 2014; Smith et al., 2018)
  - H4: Erotic vs. neutral cues will upregulate activity in a set of a priori-defined regions related to the processing of visual erotic stimuli (see Stark et al., 2019; a detailed procedure on ROI definition is outlined in the methods section)
- *Neuronal hypotheses—novel insights (linking neuronal cue effects to temporal discounting)*
  - H5: Lateral prefrontal cortex (lPFC) activity at onset of LL-option onset will be reduced following erotic vs. neutral cues
  - H6: Increased reward-system-reactivity (erotic> neutral) within key dopaminergic regions (Nacc, VTA) and reduced LPFC activity in response to erotic cues will both be positively associated with cue-induced increases in TD

2. MATERIALS AND METHODS

2.1. Participants

Based on mean effect size estimates from two previous studies on erotic cue exposure effects on TD (Kim & Zauberman, 2013; Wilson & Daly, 2004), a power analysis (G*Power; Faul et al., 2007) yielded a preregistered sample size of N = 31 when taking a test-retest reliability estimate of TD into account (Enkavi et al., 2019) (effect size Cohen's

f = 0.22, error probability α = .05, power = .80; F-tests, number of groups: 1; number of measurements: 2; correlation between repeated measures: 0.65). To account for potential drop out and data loss, we tested a total sample of 38 participants. Two participants dropped out after the first testing session. fMRI data from one additional participant was lost due to technical error at the MRI environment, while behavioral data was preserved. The final sample therefore consisted of N = 36 male participants (mean age ± SD (range) = 31.2 ± 7.5 (20-50)). Participants were recruited via advertisements on Internet bulletin boards, mailing lists, and local notices. Main inclusion criteria included male gender, right-handedness, heterosexuality, normal or corrected-to-normal vision, no alcohol or drug abuse, no psychiatric, neurological, or cardiovascular disease (past or current), and no pacemakers or other ferromagnetic materials on the body. All experimental procedures were approved by the institutional ethics committee of the University of Cologne Medical Center (application number: 17-045), and participants provided informed written consent prior to participation in the study.

2.2. Appetitive cues

During each of the fMRI sessions, participants underwent two analogous cue exposure phases and performed two different decision-making tasks (see Tasks & Procedure section 2.3). Depending on the experimental condition of the day, participants were exposed to either erotic or neutral visual stimuli. Experimental images were partly derived from IAPS database, Nencki Affective Picture System (NAPS), EmoPics (Lang et al., 2008; Marchewka et al., 2014; Wessa et al., 2010) and from a google search. Our preliminary stimulus set consisted of 220 erotic and neutral images which were roughly matched for image content and complexity. In a preceding pilot study, the preliminary set was rated concerning valence and arousal levels by an independent sample. The most arousing erotic (N = 90) and the least arousing neutral images (N = 90) were included into our experimental image pool. Consequently, erotic and neutral cues differed in arousal (erotic: 65.07 ± 3.51, neutral: 4.89 ± 3.39; $t_{(178)}$ = 140.67, p < 0.001) and valence (erotic: 64.92 ± 3.39, neutral: 48.90 ± 9.84; $t_{(178)}$ = 14.59, p < 0.001). We ensured that images were matched on intensity (erotic: 0.46 ± 0.09, neutral: 0.45 ± 0.14; $t_{(178)}$ = 0.26, p = 0.79) and contrast (erotic: 0.19 ± 0.04, neutral: 0.19 ± 0.03; $t_{(178)}$ = -0.47, p = 0.64). Control scrambled images were created by randomly shuffling pixel locations, thereby preserving intensity and contrast. Unique image sets were created for each participant and for each cue phase by randomly drawing 40 intact and 20 scrambled control images without replacement from their respective image pools (N = 90).

2.3. Tasks & procedure

The current study was conducted as one group within-subject design, including two experimental conditions (erotic vs. neutral). Data collection took place on two testing days with an approximate interval of 11 days (mean ± SD (range) = 11.31 ± 12.62 (1-70)). Each day, participants performed two decision-making tasks and two cue-exposure phases during fMRI. After introduction to the experimental set-up and scanning-preparation, participants completed the first cue-exposure phase. The cue phase consisted of 40 neutral or appetitive (erotic) images (depending on the condition on that day) and 20 scrambled control images which should be passively viewed. Each image was shown on the screen for a fixed duration of 6 s. To maintain participants' attention, 10 trials were randomly chosen, in which participants had to indicate (via keypress) whether the last presented image depicted a person or not. We included an intertrial-interval (ITI) between consecutive image presentations, which was marked by a white fixation cross. The duration of the ITI was sampled from a poisson distribution (M = 2 s; range: 1-9 s). The total duration of the cue phase was 10 min. Following the first cue phase, participants completed 128 trials of a classical delay-discounting task (Peters & Büchel, 2009). On each trial, participants chose between a fixed immediate reward of 20€ (SS) and a variable delayed amount (LL). Every trial started with the presentation of the available LL-reward and the associated delay (e.g., 38€, 14 days). The LL-reward was depicted centrally on the screen for a fixed duration of 2 s. LL-presentation was followed by a short jitter interval which was marked by a white fixation cross. The jitter interval was included to better differentiate phases of valuation (LL-presentation phase) and choice for conducted fMRI analyses (see below). The duration of the jitter interval was sampled from a poisson distribution (M = 2 s; range: 1-9 s) and was followed by the decision screen. Here, participants chose between one of two symbols corresponding to the two options (SS: circle; LL: square). The response window was 4 s. The chosen option was highlighted for 1 s. The ITI was again marked by a white fixation cross with a presentation duration sampled from a poisson distribution (M = 2 s; range: 1-9 s). An example trial is depicted in Figure 1.

The LL-rewards were calculated beforehand by multiplying the SS-amount with two different sets of multipliers,

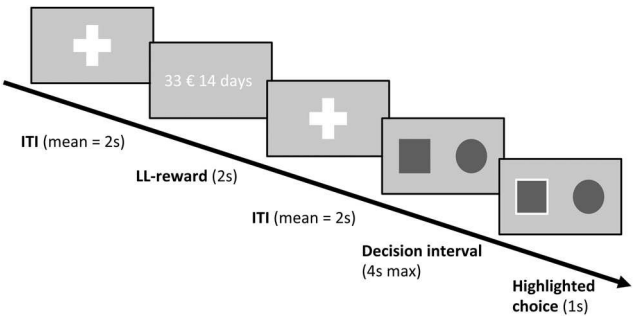

Fig. 1. Example trial from the delay discounting task. Larger later reward (LL) presentation was preceded and followed by short jitter intervals (ITI), marked by white fixation crosses; Durations for the jitter intervals were sampled from a poisson distribution (M = 2 s; range: 1-9 s); Thereafter, the decision screen was presented. The fixed smaller sooner reward (SS; 20€) was never shown throughout the experiment.

differing slightly across days (Set 1: [1.01 1.02 1.05 1.10 1.15 1.25 1.35 1.45 1.65 1.85 2.05 2.25 2.65 3.05 3.45 3.85]; Set 2: [1.01 1.03 1.08 1.12 1.20 1.30 1.40 1.50 1.60 1.80 2.00 2.20 2.60 3.00 3.40 3.80]). We likewise used two sets of delays (Set 1: [1 3 5 8 14 30 60 122 days]; Set 2: [2 4 6 9 15 32 58 119 days]). Multiplier and delay combinations were randomly assigned to testing days per participant. Participants were instructed explicitly about the task structure and performed 10 test trials during a practice run within the scanner. In accordance with previous studies (Green et al., 1997; Mathar et al., 2022; Wagner et al., 2020), we used hypothetical choice options. However, note that discount rates for real and hypothetical rewards are highly correlated and similarly processed on the neuronal level (Bickel et al., 2009; Johnson & Bickel, 2002).

Following the TD task, participants underwent a second analogous cue phase, which was then followed by a reinforcement learning task (Two-Step task). This task is preregistered separately and will be reported elsewhere.

The second day followed exactly the same structure, with the exception of the cue phases. Depending on the condition on the first day, participants were presented with images from the other condition (neutral or erotic). The sequence was counterbalanced between participants (50% of the participants started with the erotic cue condition, and the other 50% were first presented with neutral cues). After completing the scanning session on the second day, participants performed three short working memory tasks (operation span (Foster et al., 2015), listening span (van den Noort et al., 2008), and digit span (Wechsler, 2008)) on a laptop and filled out a computerized questionnaire battery as well as a demographic survey. However, note that data from demographic, health, and personality questionnaires will be reported elsewhere.

2.4. Data analysis

2.4.1. Behavioral data analysis of intertemporal choice

We used two different approaches to quantify impulsivity as measured by the TD task. Our model-based approach assumed hyperbolic devaluation of delayed rewards (Green & Myerson, 2004; Mazur, 1987) and a softmax choice rule for modeling subjects' intertemporal decisions. For model-free analysis, we directly focused on actual choice preferences of SS- and LL-options.

Model-agnostic approach. A model-free analysis can avoid problems associated with the choice for a particular theoretical framework (e.g., hyperbolic discounting) or extreme parameter estimates that result in skewed distributions. The latter might yield problems for statistical approaches that require normally distributed variables. We therefore simply computed the relative proportion of SS-choices for every participant and condition (neutral vs. erotic) to obtain a model-agnostic measure of TD (Eq. 1).

$$TD_{model-agnostic} = \frac{Choices_{SS}}{(Choices_{SS} + Choices_{LL})} \quad (1)$$

Computational modeling. We used hierarchical Bayesian modeling to fit a hyperbolic discounting model with softmax action selection to the choice data. This approach enables to separately assess cue condition effects on both steepness of temporal discounting and decision noise which cannot be disentangled via model-free approaches.

For each parameter (discount rate k, modeled in log-space, and inverse temperature $ß$), we fit separate group-level Gaussian distributions for the neutral condition from which individual subject parameters were drawn. To model condition effects on each parameter, we fit separate group-level distributions modeling deviations from the neutral condition for erotic cues, respectively ("shift"-parameter; Eqs. 2-3). Whereas higher k-parameters reflect an increased devaluation of the LL over time or more impulsive choice preferences, $ß$ scales the influence of value differences on choice probabilities. Lower values of $ß$ indicate a high choice stochasticity, whereas higher values indicate that choices depend more on value differences.

$$k_{(t)} = exp(k_{neut} + I_{Ero(t)} * S_{Ero_k}) \quad (2)$$

$$ß_{(t)} = ß_{neut} + I_{Ero(t)} * S_{Ero_ß} \quad (3)$$

Here, I_{Ero} is a dummy-coded indicator variable coding the experimental condition (1 = erotic, 0 = neutral) and S_{Ero} are subject-specific parameters modeling changes in log(k) and $ß$ depending on the condition in trial t. Computation of the discounted subjective value (SV) of the larger later option (LL) for a given delay D and amount A in a given trial then uses the standard hyperbolic model (Eq. 4):

$$SV_{(LL)} = \frac{\mathrm{LL}}{\left(1+(k_{(t)} * D)\right)} \quad (4)$$

However, cue exposure might also affect TD beyond a modulation of log(k), for example, by inducing an overall offset in the discounting function. To account for such effects, we examined another model that allowed for an offset in the discounting function in the neutral condition (modeled by the parameter $\omega_{Neut_{SV}}$), which might then again be differentially affected by erotic cues (S_{Ero_ω}, Eq. 5).

$$SV_{(LL)} = SV_{(LL)} * (\omega_{neut} + I_{Ero(t)} * S_{Ero_\omega}) \quad (5)$$

Because a positive $\omega_{Neut_{SV}}$ would indicate a subjective value of the LL that exceeds the objective amount (at delay = 0), the range of the offset-parameter was restricted between 0 and 1. Finally, subjective values of SS- and LL-options as well as modulated inverse temperature parameter $ß$ (Eq. 3) were then used to calculate trial-wise choice probabilities according to a softmax choice rule:

$$P_{(chosen)} = \frac{exp(SV_{chosen} * ß_{(t)})}{exp(SV_{other} * ß_{(t)}) + exp(SV_{chosen} * ß_{(t)})} \quad (6)$$

In summary, we compared two models: Model 1 (*Base-model*) only included $S_{Ero_ß}$ and S_{Ero_k} to assess cue exposure effects on ß and log(k). Model 2 (*Offset-model*) additionally included a potential change in the offset, S_{Ero_ω}.

Parameter estimation. Posterior parameter distributions were estimated via no-U-turn sampling (NUTS; Hoffmann & Gelman, 2014) implemented in STAN (Carpenter et al., 2017) using R (R Core Team, 2022) and the RStan Package (Stan Development Team, 2018). Prior distributions for the group-level parameters are listed in Table 1. Group mean priors were derived from posterior means and standard deviations from a recent study from our group, based on the Base-model (Mathar et al., 2022). STAN model code for all models is publicly available at OSF (Base-Model: osf.io/6uz8g; Offset-Model: osf.io/mgjx5). Model convergence was assessed via the Gelman-Rubinstein convergence diagnostic $\hat{R}$, and values of $1 \leq \hat{R} < 1.05$ were considered acceptable. We ran 4 chains with a burn-in period of 1500 samples and no thinning. 4000 samples were then retained for further analysis. For details on MCMC convergence, see Gelman & Rubin (1992). We used Bayesian statistics (see Kruschke, 2010) to evaluate cue effects on model parameters of the best fitting model. Relative model fit was assessed via the loo-package in R using the Widely-Applicable Information Criterion (WAIC), where lower values reflect a superior fit of the model while considering its complexity (Vehtari et al., 2017; Watanabe, 2010).

Table 1. Priors of group-level parameter means

Base-model	Parameter	Group mean prior
	k	Normal (-4.2, 2.01)
	S_{Ero_k}	Normal (.15, .64)
	$ß$	Normal (.51, .3)
	$S_{Ero_ß}$	Normal (.02, .11)
Offset-model	Parameter	Group mean prior
	k	Normal (-4.2, 2.01)
	S_{Ero_k}	Normal (.15, .64)
	$ß$	Normal (.51, .3)
	$S_{Ero_ß}$	Normal (.02, .11)
	ω	Uniform (0, 1)
	S_{Ero_ω}	Normal (0, .4)

We analyzed posterior distributions of group mean condition effects (as reflected in the S_{Ero} parameters, see Eqs. 2, 3, and 5 above) by computing their highest density intervals (HDI) and assessed their overlap with zero. We further report *undirected* Bayes factors (BF01) based on the Savage-Dickey-Density Ratio, which quantify the degree of evidence for a null model that would restrict a parameter of interest at a given value (e.g., S_{Ero} = 0) against an alternative model where the parameter can vary freely (see Marsman & Wagenmakers, 2017 for details). To test the degree of evidence for increases vs. decreases in parameter values, we computed *directional* Bayes factors (dBFs) for condition effects. A dBF corresponds to the ratio of the posterior mass of the shift-parameter distribution below zero to the posterior mass above zero (Marsman & Wagenmakers, 2017). We considered Bayes Factors between 1 and 3 as anecdotal evidence, Bayes Factors above 3 as moderate evidence, and Bayes Factors above 10 as strong evidence. Likewise, the inverse of these values reflects evidence in favor of the opposite hypothesis (Beard et al., 2016).

Posterior predictive checks. We used posterior predictive checks to assess the degree to which the included models (Base-model, Offset-model) reproduced key

patterns in the data, in particular the change in LL choice proportions across delays. For this purpose, we simulated 4000 datasets from each model's posterior distribution and plotted the mean observed proportion of LL choices and the simulated LL choice proportions across delay. This was done separately for both conditions (neutral, erotic).

2.4.2. fMRI data acquisition

MRI images were acquired on a 3 Tesla Magnetom Prisma Fit system (Siemens, Erlangen, Germany) equipped with a 64-channel head coil. Task stimuli were presented on an MR compatible screen and a rearview mirror system. Participants responded with their index and middle fingers on a two-button box, held in their right hand. Psychophysics Toolbox Version 3.52 implemented within MATLAB R2019b software (The Mathworks Inc., MA, USA) was used for stimulus presentation and behavioral data collection. Functional images were acquired in 5 separate runs (Cue phase1, TD, Cue phase 2, Two-step (first half), Two-step (second half)) by utilizing a multiband gradient echo-planar imaging (mb-EPI) sequence with repetition time (TR) = 0.7 s, echo time (TE) = 37 ms, flip angle = 52°, field of view (FOV) = 208 mm, voxel size = 2 mm^3 isotropic (slice thickness = 2 mm, no gap), and multiband acceleration factor of 8. Each volume consisted of 72 transverse slices acquired in alternating order from the anterior-posterior commissure plane. The 5 runs contained ~7700 volumes for each participant and ~90 min of total scan time per day.

2.4.3. fMRI data analysis

Preprocessing and analyses of fMRI data was performed using SPM12 (v7771; Wellcome Trust Centre for Neuroimaging) implemented in MATLAB R2019b (The MathWorks), and the FMRIB Software Library (FSL; Version 6.0.4; Jenkinson et al., 2012). Prior to statistical analysis, the first five functional volumes were discarded to allow for magnetic saturation. Functional images were corrected for motion and distortion artifacts using the FSL tools MCFLIRT and topup (Andersson et al., 2003; Smith et al., 2004). Next, anatomical T1-images were co-registered to functional images and normalized to the Montreal Neurological Institute (MNI) reference space using the unified segmentation approach in SPM12 (voxel size after normalization: [2,2,2] mm). Finally, we normalized functional images using the ensuing deformation parameters, and smoothed using a 6 mm full-width-half-maximum Gaussian kernel.

Cue phase

1^{st}/2^{nd} level modeling. Both testing days entailed two separate cue exposure phases (session 1 & 2). Note that to examine cue effects on TD, we only focused on the first cue exposure session directly preceding the TD task. In each cue phase, participants viewed 40 intact and 20 scrambled images. Depending on the condition of the day, intact images depicted either everyday scenes and portraits of people (neutral condition) or nude women (erotic condition).

Using SPM12, functional images from each day were analyzed using a general linear model (GLM). Each GLM examined the sustained activity during the presentation of intact and scrambled image types using boxcar regressors (duration = 6 s) which were convolved with the canonical hemodynamic response function (HRF). To account for residual variance caused by subject movement, we included the following nuisance regressors: 24 motion parameters (6 motion parameters relating to the current and the preceding volume, respectively, plus each of these matrices squared, see Friston et al., 1996), mean signal extracted from the ventricular cerebrospinal fluid (CSF), and a matrix containing motion-outlier volumes (identified by assessing global intensity differences between subsequent volumes; threshold: >75th percentile + 2.5 * interquartile range of the global signal).

Contrast images for intact and scrambled image presentation from the cue exposure phases ($Cuephase1_{Erotic}$; $Cuephase1_{Neutral}$) were then entered into a second-level random effects model (flexible factorial design; factors: subjects, visibility (intact, scrambled), condition (erotic, neutral)) to evaluate BOLD-activity changes attributable to erotic image content. Variances for all factors were set to: *equal.* We included a main effect for "subject" and an interaction term for the factors "visibility" and "condition."

We ran two analyses to evaluate neural effects of neutral vs. erotic cues. First, to replicate erotic cue effects (vs. intact neutral cues), we examined a priori-defined regions-of-interest (ROIs) related to the processing of visual erotic stimuli (see H4; Stark et al., 2019). The ROI mask was created using the group-level results (t-map) for the contrast erotic>neutral from Stark et al. (2019). For this purpose, we first used custom MATLAB code to filter out all voxels whose t-values fell below a cut-off of 6. Thereby we only kept the "most significant" voxels, showing increased responsiveness to erotic stimulus content. We then used small volume family wise error (FWE) correction ($p < 0.05$) across the entire mask to control for multiple comparisons. Further whole-brain effects

of visual cue exposure are reported at an FWE-corrected threshold ($p < 0.05$; peak-level).

Second, we tested for associations between reward-system activity (erotic>neutral) within key dopaminergic (Nacc, VTA) and prefrontal (DLPFC) regions and behavioral cue effects on TD following erotic vs. neutral cue exposure (see H6). In more detail, we assessed associations between neuronal cue-reactivity-responses within the first cue phase ($Erotic_{session1}$>$Neutral_{session1}$) and subject-specific shift-parameters ($S_{Ero(k)}$, $S_{Ero(\omega)}$), capturing condition-specific changes in TD. Associations were quantified via Bayesian correlations (using JASP (JASP Team, 2022; Version 0.14.3)) separately for predefined subcortical (Nacc, VTA) and cortical (DLPFC) ROIs.

To extract VTA activity, we first constructed an anatomical mask based on Stark and colleagues (2019; see above). Specifically, we used reported peak coordinates from the group contrast erotic>neutral (VTA: -6, -8, -10 and the mirrored location) as centers of two 10 mm spherical ROIs, which we then combined into a bilateral mask. For Nacc, we focused on the striatal cluster within the "reward" mask based on two meta-analyses, provided by the Rangel Neuroeconomics lab (http://www.rnl.caltech.edu/resources/index.html). This mask combines bilateral striatum, vmPFC, posterior cingulate cortex (PCC), and anterior cingulate cortex (ACC). Lastly for DLPFC, we built a custom mask based on previous studies reporting increased DLPFC-activity during LL vs. SS choices (Smith et al., 2018; see below). To calculate brain-behavior correlations, we first identified peak voxels from our group-level contrast erotic(intact)>neutral(intact) within the mentioned VTA, striatum, and DLPFC masks and extracted parameter estimates from these voxels for each participant.

Delay-discounting-task

1st/2nd level modeling. On both testing days, the first cue exposure phase was followed by a classical delay discounting task (see methods section 2.3). Functional images from both days (i.e., conditions) were analyzed separately using general linear models (GLM) implemented in SPM12. Each GLM included the following regressors: (1) the presentation of the larger later option (LL) as event regressor (duration = 2 s), standardized discounted subjective value (SV) as parametric modulator (computed based on the best-fitting model), (3) the onset of the decision period as stick regressor (duration = 0 s), and (4) the choice (LL vs. SS) as parametric modulator. Invalid trials on which the participant failed to respond within the response window (limit: 4 s) were modeled separately. All regressors were convolved with the canonical hemodynamic response function as provided by SPM12. Residual movement artifacts were corrected by using the same nuisance regressors as for the cue phase (see above).

We hypothesized subjective value (SV) of delayed rewards to be encoded in ventral striatal (VS) and ventromedial prefrontal areas (vmPFC) and that lateral prefrontal cortex activity (DLPFC) would be increased during choices of LL rewards (see H2 & H3). Further, we predicted that DLPFC activity during delayed reward presentation would be reduced following erotic cue exposure (see H5). To test H2 and H3, we entered the respective contrast images of parametric effects of subjective value (SV) and the chosen option (LL vs. SS) into separate second-level random effects models. We focused on predefined ROIs implicated in TD SV-computations (H2; Bartra et al., 2013; Clitero & Rangel, 2014) and choice behavior (H3; Smith et al., 2018). Specifically, H2 was tested using again the combined "reward" mask, which was provided by the Rangel Neuroeconomics lab (http://www.rnl.caltech.edu/resources/index.html), and combines bilateral striatum, vmPFC, PCC, and ACC. To test H3, we again used the above-mentioned DLPFC-mask created on findings on LL vs. SS choices (Smith et al., 2018). To control for multiple comparisons, we applied small volume correction (SVC; $p < 0.05$, peak-level) across the reward mask (H2) or the DLPFC mask (H3).

Finally, we tested for condition-related (erotic vs. neutral) differences in prefrontal activation related to the onset of the LL-rewards (H5). For this purpose, LL-onset regressors were directly compared between neutral and erotic image conditions on the group level. Here, we again used the above-mentioned preregistered DLPFC-ROI (Smith et al., 2018) for SVC ($p < 0.05$, peak-level).

2.4.4. Deviations from preregistered analyses

This study was preregistered (https://osf.io/w5puk). We deviated from the preregistered analyses in the following ways: First, based on mean effect size estimates from two previous studies on erotic cue exposure effects on TD, we preregistered a minimum sample size of n = 31 to reach a power of .80 (effect size Cohen's f = 0.22, error probability α = .05). To account for potential dropout, we aimed for a final sample size of n = 40. Due to technical issues of the MRI scanning environment, the final sample consisted of 38 subjects which was further reduced to 36, as two participants voluntarily dropped out of the experiment. Nevertheless, this still exceeds the minimum

sample size by 5, indicating that we had enough power to detect potential erotic cue effects on TD.

Second, we slightly deviated from our planned computational modeling approach to quantify erotic cue effects on TD. We initially preregistered three models which all used hierarchical Bayesian modeling to fit variants of the hyperbolic model with softmax action selection to the choice data. However, two of the preregistered models suffered from two shortcomings (Model 2 & 3 in the preregistration). First, they both assumed cue-induced SV-offsets *only in the erotic condition*, thereby selectively increasing flexibility and predictive power in one condition. To correct this asymmetry, we now allowed for an offset of the discounting function in the neutral condition, which again could be differentially modulated by erotic cues (see Model 2, section 2.4.1). Second, the preregistered offset-parameter was initially defined as additive. However, validation analyses revealed that this formulation yielded implausible SVs (e.g., $SV_{LL} < 0$) in a few individuals who exhibited extremely unbalanced choice behavior (e.g., only very few SS or LL choices). Therefore, we changed the model formulation to a multiplicative offset (see Eq. 5).

3. RESULTS

The results section is structured as follows. In accordance with our preregistered analysis plan, we first report the results of the replication analyses for the fMRI data for subjective value coding (H2), intertemporal choice (H3), and erotic cue processing (H4). Next, we report behavioral and modeling results regarding effects of cue exposure on TD (H1). Finally, to link neuronal cue-reactivity to TD, we report findings from two separate analyses. First, we assessed cue exposure effects on DLPFC activity at the during LL-reward presentation (H5). Second, we examined between-subjects associations between erotic reward-system-responsivity within key dopaminergic (Nacc, VTA) and prefrontal (DLPFC) areas, and alterations in TD (H6).

3.1. Neuronal correlates of subjective discounted value

We hypothesized subjective value (SV) coding of delayed rewards in striatal (VS) and ventromedial prefrontal areas (vmPFC; see Peters & Büchel, 2009; see H2). Our GLM incorporated the onset of the LL-option as event regressor (duration = 2 s) and the standardized discounted subjective value (SV) of the LL option as parametric modulator. SVs were based on the best-fitting *Offset-model* (methods section 2.4.2, lowest WAIC, see below). We used a combined "reward" ROI mask provided by the Rangel Neuroeconomics lab (http://www.rnl.caltech.edu/resources/index.html). This mask combines bilateral striatum, vmPFC, PCC, and ACC and was used for small-volume correction.

Figure 2A shows brain activation that covaried with subjective discounted value of larger later rewards across experimental conditions (main effect across *erotic* and *neutral*). ROI analysis replicated previous findings on subjective value coding in a large cluster within medial prefrontal cortex (peak coordinates x, y, z (in mm): 2, 54, -10; z-value = 5.83, $p_{SVC} < 0.001$), posterior cingulate cortex (PCC; -10, -34, 38; z-value = 4.38, $p_{SVC} = 0.005$), and right ventral striatum/caudate (VS; 4, 10, 2; z-value = 4.22, $p_{SVC} = 0.010$)—confirming hypothesis H2. Parameter estimates extracted from vmPFC, PCC, and VS peak voxels illustrate that this effect was evident in the vast majority of individual participants (see Fig. 2B). Value-related activity in predefined ROIs did not differ between experimental conditions (no suprathreshold clusters for the contrasts: erotic>neutral or neutral>erotic). When running separate analyses for each condition, significant SV coding was confirmed in mPFC, PCC, and VS in the erotic condition ($p_{SVC} < 0.05$). In the neutral condition, this was true for the mPFC, VS reached trend level (see Supplementary Table S1). T-maps from the respective group-level contrasts are publicly available at OSF (https://osf.io/9uzm8/).

3.2. Neuronal correlates of intertemporal choice

We predicted increased dorsolateral prefrontal cortex activity (DLPFC) during choices of LL vs. SS rewards (Smith et al., 2018; see H3). Our GLM included the onset of the decision period as event regressor (duration = 0 s) and the selected option (LL vs. SS) as parametric modulator. We built (and preregistered) a custom (left) DLPFC-mask based using a 12 mm sphere centered at the group peak coordinates for the contrast "LL- vs. SS-choice" reported by Smith and colleagues (2018) (peak coordinates (x = -38, y = 38, z = 6)).

This ROI analysis replicated increased activity in left DLPFC associated with LL vs. SS choices across conditions (main effect across *erotic* and *neutral*; peak coordinates: -40, 48, 4; z-value = 4.26, $p_{SVC} = 0.003$; see Fig. 3), confirming hypothesis H3. We found no suprathreshold clusters for the contrasts: erotic>neutral or neutral>erotic. This effect was also confirmed in our preregistered ROI when each condition was analyzed separately (Supplementary Table S2). T-maps from the

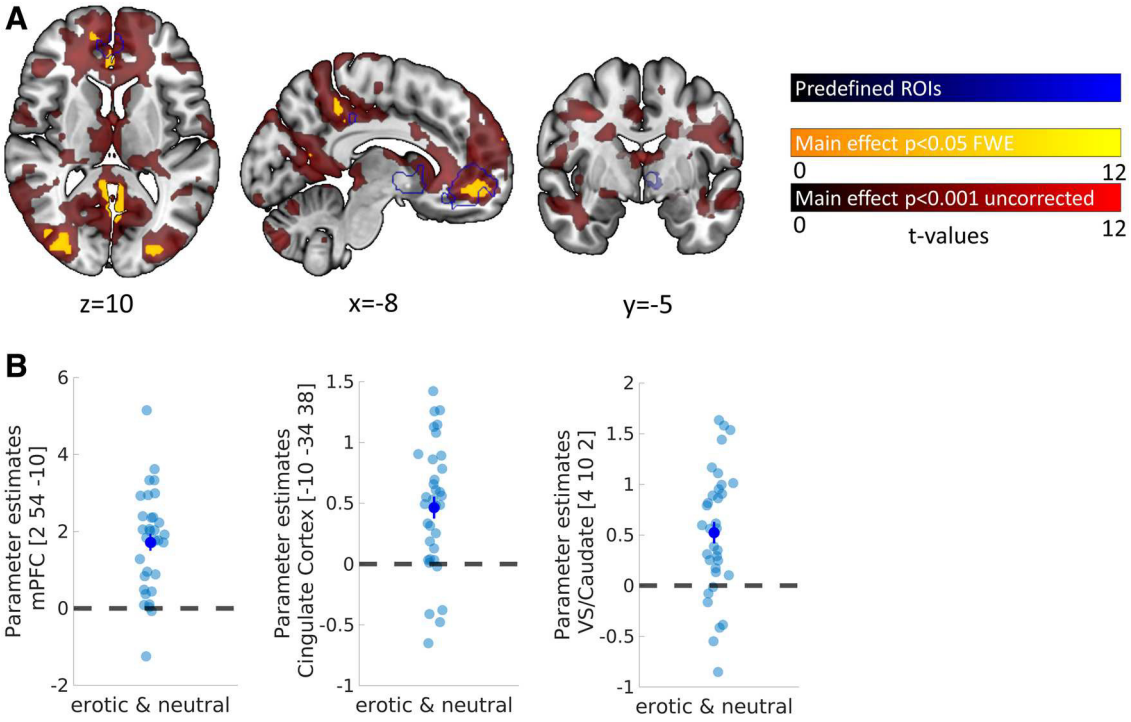

Fig. 2. Neuronal correlates of subjective value (SV). (A) Display of the parametric SV-regressor (main effect across conditions); red, $p < 0.001$ (uncorrected); yellow, whole-brain FWE-corrected $p < 0.05$; blue, preregistered regions of interest from reward mask (see above); (B) Extracted *ß*-estimates of each participant extracted from medial prefrontal cortex (mPFC), posterior cingulate cortex (PCC), and ventral striatum/caudate (VS) peak coordinates of the parametric SV-regressor; error bars denote SEM.

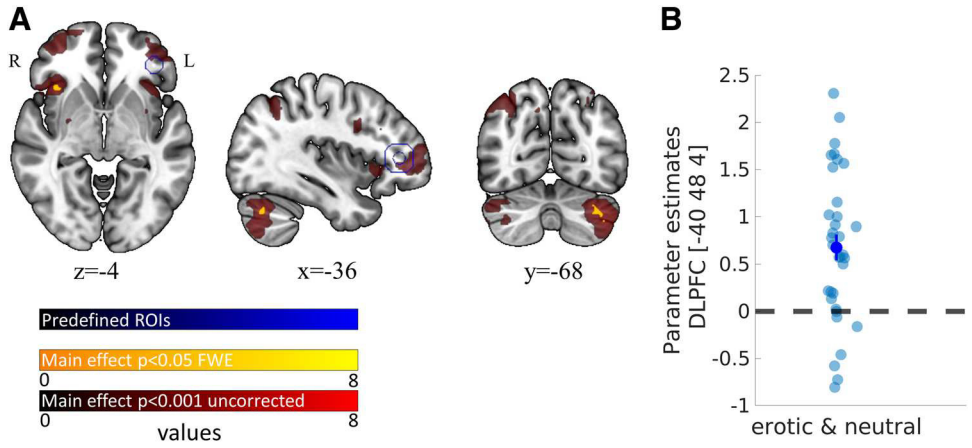

Fig. 3. Neuronal correlates of larger-later (LL) vs. smaller-sooner (SS) choices. (A) LL>SS contrast (main effect across conditions); red, $p < 0.001$ (uncorrected); yellow, whole-brain FWE-corrected $p < 0.05$; blue, predefined regions of interest from custom DLPFC mask (see above); (B) *ß*-estimates of each participant extracted from left DLPFC peak coordinates; error bars denote SEM.

respective group-level contrasts are publicly available at OSF (https://osf.io/9uzm8/).

Subsequent whole-brain (FWE-corrected) analysis revealed two additional clusters coding for LL vs. SS choices across conditions (main effect across *erotic* and *neutral*), located in the right insular cortex (36, 20, -4; z-value = 5.38, $p_{FWE} = 0.007$) and the cerebellum (-34, 66, -34, z-value = 5.28, $p_{FWE} = 0.012$). We found no suprathreshold clusters for either condition contrast (erotic>neutral; neutral>erotic) using whole-brain FWE correction ($p < 0.05$).

In an exploratory whole-brain approach, we also checked for brain activity associated with choices of the immediately available option, that is the smaller but sooner option/reward (SS). Here, we found that brain activity within a multitude of cortical (cerebellum, mid-cingulate, bilateral insula, mid-frontal cortex) but especially subcortical regions (bilateral caudate, right putamen, thalamus, hippocampus) positively correlated with SS-choices across both experimental conditions (see Supplementary Fig. S1). For the condition contrasts, erotic>neutral and neutral>erotic however, no voxels survived whole-brain FWE correction ($p < 0.05$).

3.3. Appetitive cue effects on neuronal reward circuitry

We predicted (erotic-) cue effects on TD to be at least partly moderated by activations in neuronal reward circuits (Li, 2008; Stark et al., 2019; Yeomans & Brace, 2015). During the cue exposure phase, participants were exposed to 40 intact (erotic or neutral) and 20 scrambled control images. Analyses only focused on the first cue exposure session directly preceding the TD task. We ran a flexible factorial random-effects model (factors: visibility (intact/scrambled), condition (erotic/neutral)) and preregistered ROIs based on a previous study (Stark et al., 2019; see methods section for details). ROI analyses applied small-volume FWE correction ($p < 0.05$) across the entire mask.

A sanity check confirmed widespread functional responses across occipital and ventral temporal cortices for the intact vs. scrambled contrast (see Supplementary Fig. S2).

As depicted in Figure 4, (intact) erotic, compared to (intact) neutral cue exposure was associated with increased activity in widespread cortical and subcortical

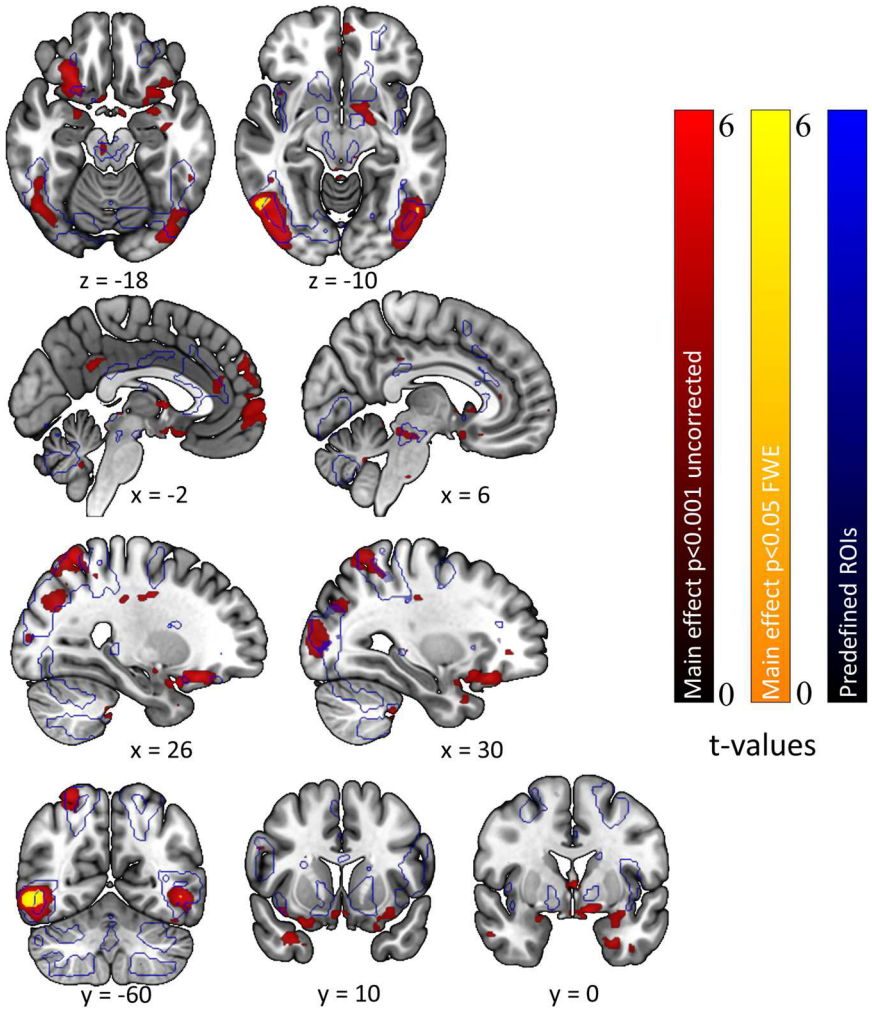

Fig. 4. Neuronal correlates of (intact) experimental image processing (erotic>neutral). Red, $p < 0.001$ (uncorrected); yellow, whole-brain FWE-corrected $p < 0.05$; blue, predefined regions of interest from ROI mask (see above).

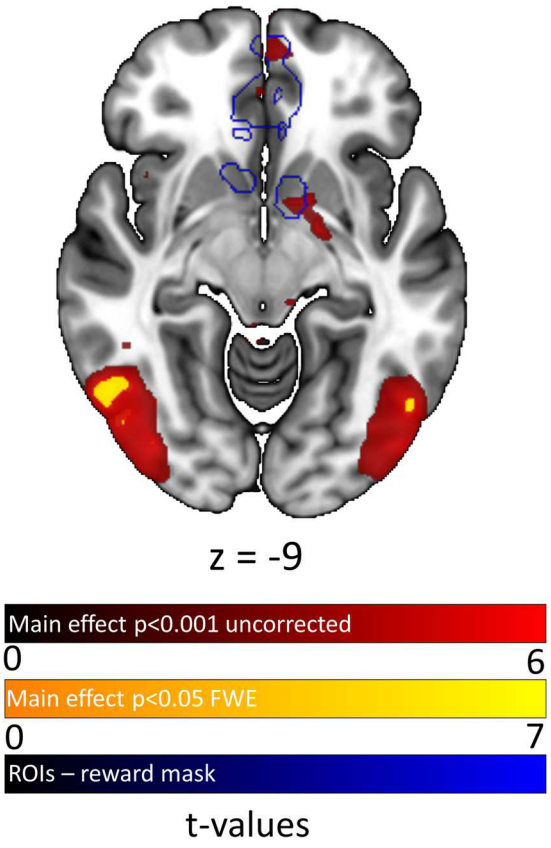

Fig. 5. Neuronal correlates of (intact) experimental image processing (erotic>neutral). Red, $p < 0.001$ (uncorrected); yellow, whole-brain FWE-corrected $p < 0.05$; blue, regions of interest from reward mask (not preregistered, see above).

regions. Our preregistered ROI analysis revealed increased activity in four large posterior (cortical) clusters for erotic vs. neutral cues, including right inferior temporal cortex (52, -60, -4; z-value = 6.25, $p_{SVC} < 0.001$), left inferior occipital cortex (-48, -68, -6; z-value = 5.42, $p_{SVC} = 0.001$), right superior parietal cortex (26, -60, 62, z-value = 4.76, $p_{SVC} = 0.013$), and right middle occipital cortex (28, -72, 30; z-value = 4.51, $p_{SVC} = 0.036$).

We had predicted subcortical activations in reward-related brain regions (e.g., VS, vmPFC) to be linked to erotic cue exposure (H4), but many subcortical effects fell just beyond the preregistered ROI-mask based on Stark et al. (2019). We therefore followed up with a second (not preregistered) ROI analysis using the above-mentioned "reward" mask, based on two meta-analyses, provided by the Rangel Neuroeconomics Lab (http://www.rnl.caltech.edu/resources/index.html). Small-volume correction was again applied across the entire mask. As expected, this confirmed highly robust bilateral effects in the VS/caudate (left: -10, 2, -10; z-value = 4.59; $p_{SVC} = 0.002$; right: 4, 6, 2;

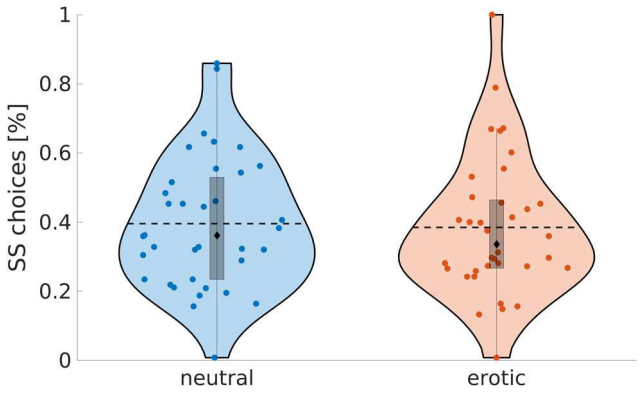

Fig. 6. Percentage of smaller-sooner choices split by experimental condition (neutral vs. erotic). Colored dots = single subjects; Dashed lines = condition means; Black diamonds = condition medians; The edges of the boxes depict the 25th and 75th percentiles, and the whiskers extend to the most extreme datapoints the algorithm considers to be not outliers.

z-value = 3.70; $p_{SVC} = 0.047$) and the vmPFC (-6, 58, -2; z-value = 4.54; $p_{SVC} = 0.002$; see Figure 5).

A t-map depicting all activations associated with erotic>neutral image processing is publicly available at OSF (https://osf.io/9uzm8/). We also checked for increased brain activity following neutral compared to erotic image presentation. However, here we identified no suprathreshold clusters.

3.4. Appetitive cue effects on intertemporal choice

Having thus replicated previous findings on subjective value coding (H2), intertemporal choice (H3), and erotic stimulus processing (H4) (Peters & Büchel, 2009; Smith et al., 2018; Stark et al., 2019), we next assessed condition-related changes in TD behavior.

3.4.1. Model-agnostic approach

Contrary to our hypothesis (H1), TD was not differentially affected by appetitive cue exposure (see Fig. 6). In the neutral condition, the SS-option was chosen in 39.6% of trials whereas in the erotic condition the SS-option was chosen in 38.5% of trials ($t_{(35)} = 0.714$, $p = 0.480$).

3.4.2. Computational modeling

Model comparison revealed that choice data were best captured by a hyperbolic model with an additional SV-offset-parameter ω, in addition to parameters accounting for choice consistency (β) and steepness of TD (log(k);

Table 2. Summary of the WAICs of all included hyperbolic models in all sessions

	Neutral condition		Erotic condition		Combined	
Model	WAIC	Rank	WAIC	Rank	WAIC	Rank
Base-model	2654.537	2	2699.152	2	5365.867	2
Offset-model	2292.945	1	2453.293	1	4771.835	1

Note. Ranks are based on the lowest WAIC.
WAIC, Widely applicable information criterion.

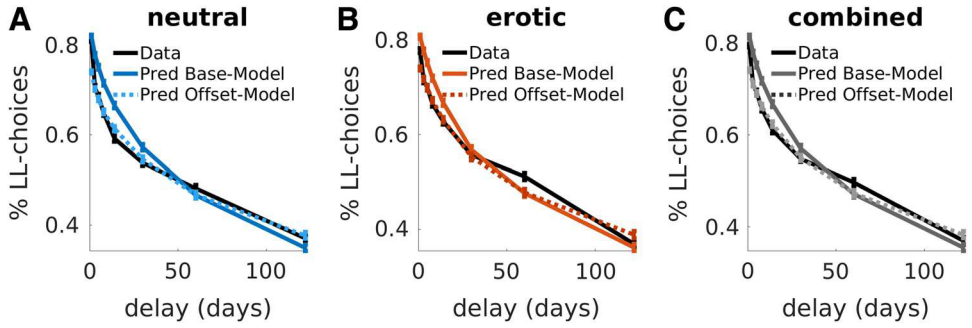

Fig. 7. Group-level posterior predictive checks for the included temporal discounting models (Base-model, Offset-model). Here, we plotted the mean observed proportion of LL-choices and the simulated LL-choices from both models for each delay. Specifically, we created 4k simulated data sets from each model's posterior distribution. For each simulated participant, we calculated the fraction of LL-choices across eight delay bins. Next, we calculated group average proportion of LL-choices for each delay and associated standard errors (vertical bars). Simulated data were then overlaid over the observed choice data. We did this separately for the neutral (A) and erotic (B) conditions as well as for the combined datasets (C).

Offset-model). This model comparison replicated across conditions (neutral, erotic), and was confirmed in the combined model including parameters modeling condition effects (see Table 2). The superior fit of the offset-model was also reflected in choice predictions. The Offset-model accounted for around 82.2% (Base-model: 79.6%) of all decisions (Supplementary Table S3, Supplementary Fig. S3). Finally, posterior predictive checks confirmed that LL-choice proportions across delays were much better accounted for by the Offset-model (Fig. 7). All further analyses therefore focused on the Offset-model. However, note that due to an extreme behavioral choice pattern (only one single SS-choice in both conditions), data from one participant could not be explained by our winning model and was excluded from all further analyses.

Examination of the posterior distributions of the best-fitting model then confirmed the model-agnostic results. TD (log(k); Fig. 8A) was not substantially affected by erotic cue exposure ($SERO_{(k)}$; Fig. 8B), such that the highest density intervals for $SERO_{(k)}$ substantially overlapped with zero. These data were more likely to be observed under a null hypothesis assuming $SERO_{(k)}$ to be equal to zero (BF01 = 4.11). Interestingly, SV-offset parameters $\omega_{neutral}$ clearly differed from one in all participants, emphasizing the general utility of this additional parameter to account for a choice bias irrespective of delay. However, the observed data were much more compatible with the null model where the condition effect in the offset was equal to zero (BF01 = 43.18; Fig. 8C, D), strongly suggesting the offset was not modulated by erotic cue exposure. Likewise, data for the $SERO_{(\beta)}$ parameter were much more compatible with the null model, indicating that the change in stochasticity following erotic cue exposure was equal to zero (BF01 = 18.473, see Fig. 9A, B). See Table 3 for summary statistics and Bayes factors of the posterior distributions of all relevant parameters. For completeness, posterior distributions and Bayes factors from the inferior Base-model are reported in the supplement (Supplementary Fig. S4, Supplementary Table S4).

To confirm the validity of our modeling approach, we also examined associations between $SEro_{(k)}$ and model-free measures of TD (SS-option choice proportions). Correlations between model parameters and model-free measures were consistently in the expected direction (see Supplementary Fig. S5, Supplementary materials).

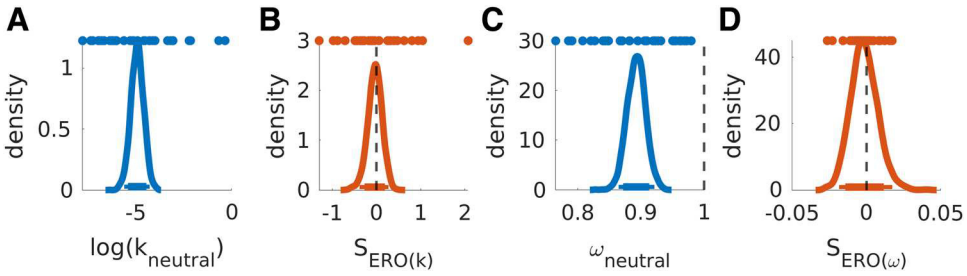

Fig. 8. Posterior distributions for $\log(k_{neutral})$ and $\omega_{neutral}$ (A, C) as well as associated erotic shift parameters ($SERO_{(k, \omega)}$, B, D). Colored dots depict single-subject posterior means. Thick and thin horizontal lines indicate 85% and 95% highest density intervals.

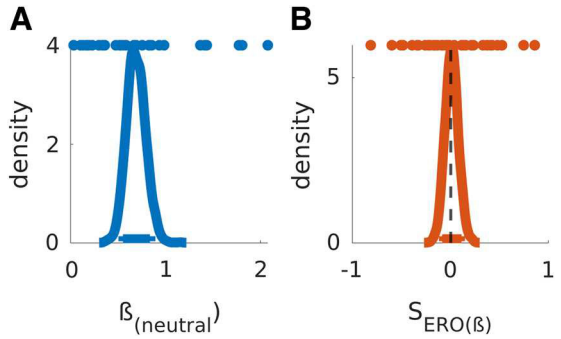

Fig. 9. Posterior distributions for $ß_{neutral}$ (A) and $SERO_{ß}$ (B). Colored dots depict single-subject means. Thick and thin horizontal lines indicate 85% and 95% highest density intervals.

Table 3. Summary statistics of the posterior distributions of computational shift-parameters (offset-model)

Parameter	Mean	SD	dBF	BF_{01}
$SERO_{(k)}$	-0.050	0.634	1.450	4.113
$SERO_{(\omega)}$	-0.001	0.009	0.800	43.184
$SERO_{(ß)}$	0.008	0.377	1.380	18.473

Note. BF_{01}, undirected Bayes factor in favor of null model; dBF, directional Bayes factor; SD, standard deviation.

3.5. Appetitive cue effects on neuronal and behavioral indices of temporal discounting

Despite increased (sub-) cortical processing of erotic compared to neutral cues, TD did not differ between experimental conditions. We next assessed the preregistered links between neuronal cue-reactivity and TD. We first report cue exposure effects on DLPFC activity during LL-reward presentation (H5), possibly indicating changes in (prefrontal) cognitive control. We next show between-subjects associations between erotic reward-system-responsivity within key dopaminergic (Nacc, VTA) and prefrontal (DLPFC) areas, and changes in TD (H6).

Recall that we reasoned (and preregistered) that cue effects on TD reported in previous studies (Kim & Zauberman, 2013; Van den Bergh et al., 2007; Wilson & Daly, 2004) might be due to cue-induced changes in prefrontal control regions and subcortical reward circuits. We tested the first prediction by comparing (left) DLPFC activity during LL-reward presentation (duration = 2 s) between experimental conditions (H5) using the preregistered DLPFC mask and small volume correction (12 mm sphere, peak coordinates (x = -38, y = 38, z = 6); Smith et al., 2018). Contrary to our hypothesis, we found no differences in DLPFC activity for the contrasts erotic> neutral or neutral>erotic. Likewise, on the whole-brain level no voxels survived FWE ($p < 0.05$) correction. A t-map depicting all activations associated with erotic> neutral LL-reward processing is publicly available at OSF (https://osf.io/9uzm8/).

Next, we tested associations between neuronal cue-reactivity-responses within key dopaminergic (Nacc, VTA) and prefrontal (DLPFC) areas and subject-specific condition effects on behavior ($SERO_{(k)}$, $SERO_{(\omega)}$, H6), capturing individual differences of cue effects. Associations were quantified via Bayesian correlations (using JASP) separately for peak voxels from preregistered subcortical (Nacc, VTA) and cortical (DLPFC) ROIs (see methods section for details). We found no evidence for a significant correlation between functional cue-reactivity towards erotic cues and change in discounting behavior ($SERO_{(k)}$, $SERO_{(\omega)}$). Contrarily, associations between cue-evoked changes in log(k) ($SERO_{(k)}$) and subcortical ROI activity (Nacc, VTA) yielded highest BF01 (Nacc: 4.226; VTA: 4.663), indicating moderate evidence for a model assuming no association between dopaminergic brain activity and changes in *steepness* of TD. This model was approximately 4 to 4.5 times more likely than an alternative model given the data (see Table 4, upper panel; Supplementary Fig. S6, Supplementary materials).

Table 4. Correlation statistics quantifying associations between brain activity in key dopaminergic (VS/Nacc, VTA) and prefrontal (DLPFC) areas and subject-specific shift-parameters (SERO(k), SERO (ω)) at the subject level

(A) Peak-voxel approach				
ROI peak voxel [x,y,z]	Model parameter	Correlation coefficient (r)	CI	BF01
DLPFC [-30, 36, 4]	$SERO_{(k)}$	-0.259	[-0.531, 0.085]	1.638
	$SERO_{(\omega)}$	-0.239	[-0.516, 0.105]	1.932
VS/Nacc [-10, 2, -10]	$SERO_{(k)}$	0.083	[-0.252, 0.393]	4.226
	$SERO_{(\omega)}$	-0.242	[-0.518, 0.102]	1.881
VTA [-10, 0, -12]	$SERO_{(k)}$	-0.018	[-0.340, 0.309]	4.663
	$SERO_{(\omega)}$	-0.240	[-0.517, 0.104]	1.911
(B) Mean cluster activity approach				
ROI	Model parameter	Correlation coefficient (r)	CI	BF01
DLPFC	$SERO_{(k)}$	-0.146	[-0.445, 0.194]	3.378
	$SERO_{(\omega)}$	-0.403	[-0.635, -0.068]	0.332
VS/Nacc	$SERO_{(k)}$	0.061	[-0.272, 0.376]	4.432
	$SERO_{(\omega)}$	-0.416	[-0.644, -0.083]	0.264
VTA	$SERO_{(k)}$	-0.117	[-0.422, 0.221]	3.801
	$SERO_{(\omega)}$	-0.218	[-0.501, 0.125]	2.237

Notes. ROI: Region of interest; CI: 95%-confidence interval; BF_{01}, undirected Bayes factor in favor of null model; (A) Peak-Voxel approach: Beta-values were extracted from single peak-voxels within each ROI/sub-cluster; (B) Mean cluster activity approach: Average beta-values extracted from respective ROI/sub-cluster.

However, we reasoned that characterizing cue-reactivity responses solely based on one peak-voxel could be problematic—potentially yielding biased estimates. Using mean voxel activity across the whole region of interest or respective sub-clusters might increase robustness (of approximations). In an exploratory approach, we therefore extracted average beta-values for the contrast erotic>neutral from above-mentioned VTA and DLPFC masks and the striatal cluster included in the reward mask. This analysis confirmed the non-significant association between $SERO_{(k)}$ and brain activity across all three ROIs. Simultaneously, previous numerically negative correlation between $SERO_{(\omega)}$ and cue-reactivity within DLPFC and the ventral striatum (VS) was now even more pronounced, indicating that higher erotic cue-reactivity within these regions now appeared (significantly) associated with an increased preference for immediate (SS-) reward (see Table 4, lower panel; Supplementary Fig. S7, Supplementary materials). Although Bayes Factors (BF01) indicated at least moderate evidence for this association (DLPFC = 0.332: VS = 0.264), findings from this exploratory analysis should be interpreted with caution.

4. DISCUSSION

Here, we followed up on the literature on erotic cue exposure effects on TD (Kim & Zauberman, 2013; Mathar et al., 2022; Van den Bergh et al., 2007; Wilson & Daly, 2004). We expanded previous work by leveraging a pre-registered fMRI approach to assess cue exposure-related activity changes in prefrontal and subcortical reward-related brain areas, and by linking these effects to TD. We first replicated a range of effects from the imaging literature on TD, including subjective value coding in vmPFC, striatum, and cingulate cortex (Peters & Büchel, 2009), and increased left DLPFC activity for LL vs. SS choices (Smith et al., 2018). We also replicated the finding of increased visual and subcortical reward-related responses for erotic vs. neutral cues (Gola et al., 2016; Markert et al., 2021; Stark et al., 2019; Wehrum-Osinsky et al., 2014). However, these effects did not lead to increased TD, neither overall, nor in preregistered between-subject correlations focusing on key dopaminergic (Nacc, VTA) and prefrontal regions (DLPFC).

4.1. Neuronal correlates of subjective value and choice

We preregistered two replications for neural effects underlying TD. As predicted, and in line with previous work, activity in vmPFC, striatum, and cingulate cortex tracked subjective discounted value (SV) of LL-options (Bartra et al., 2013; Clitero & Rangel, 2014; Lee et al., 2021; Levy & Glimcher, 2012; Peters & Büchel, 2009; Sescousse et al., 2013). This effect was generally

observed in most subjects and similarly evident following neutral and erotic cue exposure (at least for VMPFC and striatum). We found no evidence for condition differences in any of the reported clusters. This observation is inconsistent with the idea that upregulated activity levels, for example, in (dopaminergic) striatal regions following erotic cue exposure might disrupt subjective value encoding, which, in turn, might promote impulsive responding (Miedl et al., 2014).

We then focused on (left) dorsolateral prefrontal cortex (DLPFC), a region frequently implicated in TD (Guo & Feng, 2015; Hare et al., 2014) and self-control more generally (Hare et al., 2009). As preregistered, we observed increased decision-related left DLPFC activity for LL vs. SS choices. This pattern was observed across both experimental conditions (neutral, erotic), with no evidence for condition differences. Elevated DLPFC activity during LL choices (Smith et al., 2018) might be due to increased cognitive control during LL selections. This is supported by (1) increased TD following DLPFC disruption (Figner et al., 2010) and (2) fatigue effects manifested in increased TD that were associated with reduced DLPFC excitability (Blain et al., 2016). Our preregistered analyses therefore confirm an involvement of DLPFC, specifically in LL choices.

On the whole-brain level, two additional areas, right insular cortex and a cerebellar cluster showed increased activity for LL vs. SS choices. Whereas cerebellum has been observed in a wide range of tasks involving cognitive control and inhibition processes (Bellebaum & Daum, 2007; D'Mello et al., 2020; Stoodley & Schmahmann, 2009), insula activity was found to be specifically activated in LL-reward decisions and to depict a critical brain area involved in delaying gratification (Wittmann et al., 2007). This also resonates with findings from previous studies, reporting changes in insular activation in people with deficient foresight (Tsurumi et al., 2014), or reduced bilateral insula volumes in pathological gamblers compared with healthy controls (Mohammadi et al., 2016).

4.2. Appetitive cues affect neuronal reward circuitry

Exposure to appetitive visual cues, presented in a *block-wise* manner, can increase impulsive choice in subsequent TD tasks (Kim & Zauberman, 2013; Van den Bergh et al., 2007; Wilson & Daly, 2004). We reasoned such cue effects on TD to be at least in part driven by upregulated reward circuitry (Li, 2008; Stark et al., 2019; Yeomans & Brace, 2015), an account not directly tested before. We focused on predefined ROIs previously associated with erotic stimulus processing (Stark et al., 2019) and presented participants with 40 intact experimental (neutral, erotic) and 20 scrambled control images. A comparison of intact vs. scrambled visual image processing confirmed highly plausible activation patterns, including large clusters across occipital cortices and the entire visual stream (Margalit et al., 2017).

Exposure to (intact) erotic compared to (intact) neutral stimuli revealed increased activity in widespread cortical and subcortical brain areas. Preregistered ROI analysis ($FWE_{SVC} < 0.05$) yielded strong posterior occipital and temporal clusters showing increased cortical responses to erotic vs. neutral cues. However, subcortical effects in reward-related circuits (e.g., ventral striatum, vmPFC) in our data in many cases fell just beyond the ROI mask constructed from the Stark et al. (2019) data, which mainly contained more dorsal striatal effects. We therefore followed up with an additional ROI analysis that used the same reward mask that we used (and preregistered) for the subjective value analysis (bilateral striatum, vmPFC, PCC, and ACC) based on two meta-analyses (Bartra et al., 2013; Clitero & Rangel, 2014). This confirmed significant bilateral activations in ventral striatum and VMPFC.

Our results are consistent with previously reported erotic cue responses across stimulus types (images or videos) and sexes (Ferretti et al., 2005; Mitricheva et al., 2019; Stark et al., 2019). While effects in parietal and occipital cortices might reflect attentional orientation towards erotic vs. neutral stimuli, striatal and anterior cingulate effects might reflect the intrinsic value of erotic vs. neutral cues (Georgiadis & Kringelbach, 2012; Kuehn & Gallinat, 2011; Poeppl et al., 2016; Stark et al., 2019; Stoléru et al., 2012).

Neuronal cue-reactivity responses in visual regions largely overlapped with our preregistered ROI (based on group-level results (t-map) for the contrast erotic>neutral provided by Stark and colleagues (2019)). However, subcortical effects (e.g., in striatal regions) fell beyond the effects in the Stark et al. mask, and were instead located more ventrally, overlapping with the reward mask provided by the Rangel lab that we also used for the subjective value effects. We applied a binarization threshold (t-value = 6) to the entire T-map provided by Stark et al., to extract target voxels showing increased responsiveness to visual erotic stimuli. However Stark et al. (2019) used a somewhat longer stimulus duration (8 s vs. 6 s) and presented participants with both pictures and video clips to compare erotic vs. neutral cue reactivity responses. In their statistical analysis, they did not differentiate

between both stimulus types to increase generalizability. Stark et al. also used an expectation/anticipation phase prior to image/video onset which cued the nature of the upcoming stimulus (erotic or neutral). These differences might have contributed to the somewhat more ventral striatal effects that we observed compared to Stark et al. (2019).

4.3. No evidence for temporal discounting changes following blockwise exposure to appetitive cues

We used model-free and model-based approaches to quantify TD. Whereas model-free analyses focused on raw choice proportions, our best-fitting computational model allowed us to separate cue effects on steepness of TD (log(k)) from a delay-independent offset in the discounting curve. H1 was not confirmed—TD measures were not differentially affected by erotic cue exposure. Instead, Bayesian statistics suggested moderate evidence for the null model. This contrasts with earlier findings from similarly design studies, reporting increased TD following blockwise exposure to erotic visual stimuli (Kim & Zauberman, 2013; Van den Bergh et al., 2007; Wilson & Daly, 2004). On the other hand, it is consistent with a recent study from our group (Mathar et al., 2022) that used a similar cue exposure design. In Mathar et al. (2022), we used psychophysiology rather than fMRI. The lack of jitter between trial phases thus allowed us to use comprehensive modeling of RT distributions using diffusion models. Cue exposure led to a robust change in the starting point of the diffusion process towards SS options, but, as in the present study, did not reliably affect log(*k*).

Multiple reasons could account for this discrepancy. First, we used fMRI to assess neuronal correlates of cue-exposure and TD. The scanning environment, including loud noises, narrowness, and movement restrictions, itself might have acted as an external stressor, possibly attenuating behavioral effects. Indeed, neuroendocrine stress parameters (salivary alpha amylase, cortisol) increase at the beginning of an fMRI session (Gosset et al., 2018; Lueken et al., 2012; Muehlhan et al., 2011), irrespective of stimulus presentation, and especially in scanner naïve participants (Tessner et al., 2006). Similarly, behavioral priming studies report smaller effects inside the scanner (Hommel et al., 2012), although such findings need replication. Both aspects might have contributed to an attenuation of behavioral cue effects in the current study. But, as noted above, in our earlier study (Mathar et al., 2022), cue exposure effects on log(k) were similarly largely absent, despite the lack of fMRI environment effects.

Further, our implementation of the cue-exposure phase differed slightly from previous approaches. Our cue phase was prolonged and included more experimental visual stimuli (n = 40) than earlier studies (max n = 25; Kim & Zauberman, 2013; Mathar et al., 2022; Van den Bergh et al., 2007; Wilson & Daly, 2004), although this should arguably have increased behavioral effects. We included additional design changes due to the fMRI design (scrambled control images, attention checks, jitter intervals between stimuli). These aspects could have attenuated the *continuous* blockwise character of cue-exposure, and concomitant rise in tonic dopaminergic tone, which might be required to affect TD (Pine et al., 2010). This resonates with previous studies showing that intermittent exposure to erotic cues is not sufficient to elevate TD (Knauth & Peters, 2022; Simmank et al., 2015).

Participants in our study passively viewed the presented images, rather than performing explicit arousal or valence ratings. However, explicit ratings might have induced deeper processing in earlier studies, which could have exhibited stronger effects on choice behavior (Van den Bergh et al., 2007; Wilson & Daly, 2004). Such attention effects can modulate behavioral (Gawronski et al., 2010) and neural effects (Anderson et al., 2003) of emotional stimuli. However, passive vs. active viewing of emotional images leads to similar physiological arousal effects (Snowden et al., 2016). Furthermore, our observation of increased activity in widespread cortical and subcortical networks in response to erotic vs. neutral control stimuli strongly argues against the idea that these cues were not adequately processed.

Although cue exposure was directly followed by the TD task, it could be argued that cue effects, and upregulated physiological reward circuit activity diminished rapidly over time, which might have also limited behavioral effects. However, we think two aspects speak against such idea. First, as already mentioned, our design largely mirrored previous experimental approaches which consistently detected cue effects on actual choice behavior (e.g., Wilson & Daly, 2004) or on more subtle bias parameters from computational models (Mathar et al., 2022). Moreover, a recent study from our lab (Knauth & Peters, 2022) also showed that trialwise emotional cue exposure (erotic, aversive, neutral visual cues) and associated upregulated arousal signals during the time of intertemporal choice were not sufficient to induce changes in TD.

Taken together, behavioral effects of erotic cue exposure on TD might not be as unequivocal as previously thought (Kim & Zauberman, 2013; Van den Bergh et al., 2007; Wilson & Daly, 2004). Recent studies utilizing

trialwise erotic cue exposure failed to find changes in TD (Simmank et al., 2015). More critically, cue-evoked physiological arousal did not predict changes in discounting behavior (Knauth & Peters, 2022), casting doubt on the idea of an upregulated internal arousal state, that drives approach behavior towards immediate reward (Knauth & Peters, 2022). Also, recent *blockwise* studies question simple main effects of erotic cue exposure on impulsivity. Some studies find that cue exposure effects only occur under specific motivational or metabolic conditions (e.g., hunger; Otterbring & Sela, 2020). A noted above, we recently observed a robust change in the starting point of the evidence accumulation process towards SS rewards, which was revealed by extensive drift diffusion modeling of response time distributions (Mathar et al., 2022), whereas log(k) was largely unchanged. It is thus possible that the detection of cue exposure effects might require modeling of choices *and* response times. However, our fMRI-based experimental design separated option presentation responses, thereby precluding us from using comprehensive diffusion modeling of response times.

4.4. Elevated activity levels in dopaminergic brain areas cannot account for behavioral changes in temporal discounting

A major strength of the current study is its ability to empirically test the theoretical assumption of a cue-evoked upregulation in neural reward circuits, which might reflect increased dopaminergic activity (O'Sullivan et al., 2011; Redouté et al., 2000). Such effects might facilitate reward approach across domains (Van den Bergh et al., 2007). This idea is supported by pharmacological modulations of central dopamine transmission that affect TD (Arrondo et al., 2015; Cools, 2008; de Wit, 2002; Hamidovic et al., 2008; Kayser et al., 2012; Petzold et al., 2019; Pine et al., 2010; Wagner et al., 2020; Weber et al., 2016).

Here, we directly examined associations between neuronal cue-reactivity-responses towards erotic cues within key dopaminergic (Nacc, VTA) and prefrontal (DLPFC) areas and subject-specific condition effects on TD (SERO(k), SERO(ω)). However, if anything we found rather small evidence for our (preregistered) hypothesized association.

We first identified peak voxels from the group-level contrast erotic(intact)>neutral(intact) within all three above-mentioned ROIs and then correlated extracted beta-values with subject-specific shift parameters (SERO(ω), SERO(k)), as preregistered. This revealed no significant brain-behavior-associations. Based on feedback from a reviewer, we then ran an additional (exploratory) analysis, where we repeated above-mentioned analysis but now used average beta-values from the respective ROIs (DLPFC, VTA, ventral striatal sub-cluster within the preregistered reward mask). This confirmed non-significant association between SERO(k) and brain activity across ROIs. Further, we observed a small to moderate positive correlation between higher erotic cue-reactivity in VS and DLPFC and preference for immediate (SS-) rewards (corresponding to a more pronounced negative shift of the discounting curve offset). This association was numerically similar in the initial analysis, but now appeared more pronounced. However, these results should be cautiously interpreted for at least two reasons. First, while a positive correlation between myopic choice behavior and increased dopaminergic neurotransmission in the VS appears plausible, increased activity in DLPFC is harder to reconcile with this effect. DLPFC activity is often associated with cognitive control (Blain et al., 2016; Figner et al., 2010). Although cue-exposure phases did not entail any task requiring inhibition of prepotent impulsive responding, if anything, one would have expected decreased frontal activity to be related to SS-reward bias on the subject level. Further, the discrepancy between both approaches suggests that these brain-behavior correlations are susceptible to specific methodological details, which highlights that caution is warranted in their interpretation.

While a general dopaminergic impact on TD is well established, direction of reported effects in human studies appears somewhat inconsistent. Pine et al. (2010) observed increased TD following administration of the catecholamine precursor L-DOPA vs. placebo in a small sample of n = 14. In contrast, Petzold and colleagues (2019) observed no overall effect of L-DOPA administration on TD. Instead, effects depended on baseline impulsivity, supporting the view of an inverted-U-model of dopamine effects on cognitive control (Cools & D'Esposito, 2011). We recently observed (Wagner et al., 2020) reduced TD after a single low dose of the D2 receptor antagonist haloperidol, which is thought to increase striatal dopamine. The current study complements these previous findings and attempted to link (dopaminergic) reward system activity—which pharmacological approaches aim to evoke—to behavioral effects. However, upregulated reward system activity appears to be not sufficient to evoke *behavioral* cue effects (see previous section).

In the light of these contradictory findings, future studies should consider additional factors possibly involved in previously reported effects on TD. On the physiological

level, arousal-related enhancement of noradrenaline (NE) release may be one possible mechanism (Ventura et al., 2008). Previous studies, indeed, found increased pupil dilation following highly arousing cues (Aston-Jones & Cohen, 2005; Finke et al., 2017; Kinner et al., 2017; Knauth & Peters, 2022; Murphy et al., 2014). NE agonists have been found to affect several forms of impulsivity (Robinson et al., 2008) and to directly increase the preference for LL rewards (Bizot et al., 2011). Further, Yohimbine, an α_2-adrenergic receptor antagonist that increases NE release, reduced discounting in humans (Herman et al., 2019; Schippers et al., 2016). It appears highly plausible that (appetitive) cue-exposure will always affect both, noradrenergic and dopaminergic neurotransmitter systems.

4.5. Implications for addiction research

Appetitive cue effects on TD in healthy individuals might potentially also provide insights into mechanisms underlying maladaptive behaviors in clinical groups. Specifically, erotic cue effects on impulsive choice may partly resemble cue-reactivity processes in addiction. Drug cues trigger increased subjective, physiological, and neural responses which are associated with increased cravings, impulsive choice, and higher relapse rates (Preston et al., 2018; Vafaie & Kober, 2022). We initially hypothesized two potential routes through which erotic cues could have impacted TD. First, cue exposure could have interfered with (sub-) cortical value coding, thereby diminishing subjective perception of objective reward differences, promoting SS-option preferences. Similar findings have been reported in gambling disorder, when highly arousing gambling cues were presented (Miedl et al., 2014). Second, erotic cues could have impaired executive (cognitive) control over short-sighted choice behavior. Models such as the Interaction of Person-Affect-Cognition-Execution (I-PACE; Brand, Young, et al., 2016) model suggest an imbalance between executive control and reward networks in addicted individuals, which may be further exacerbated by cue exposure and contribute to disadvantageous decision-making. Our findings contribute to these considerations by demonstrating largely unaltered value coding and largely intact prefrontal executive control following exposure to non-drug-related erotic cues.

Notably, the analogy between erotic (appetitive) cue effects in healthy participants and addiction-related cue effects in addiction is complicated by several potential differences. Specifically, evoked cue-reactivity in the two cases might differ both quantitatively and qualitatively. While erotic cues in healthy participants might signal the upcoming occurrence of a pleasurable stimulus (learned via positive reinforcement), addiction-related cues might act via both positive *and* negative reinforcement routes. Over the course of addiction, cue exposure might be associated not only with rewarding (mesolimbic) effects but also with reductions of subjective craving and withdrawal symptoms. Similarly, recent evidence on the development of addiction-like, pathological use of sexual erotic material (SEM) also suggested that escalated impulsive or addictive behavior towards sexual material (compared to recreational use) might be fostered by both, negative and positive reinforcement processes (Brand et al., 2019; Brand, 2022; Stark et al., 2022). Resonating with this idea, Stark et al. (2022) found that elevated stress (indicated by cortisol responses) enhanced the neural reward activation to erotic material, suggesting that the behavioral relevance of reward cues might be strongly affected by the specific expectation (e.g., pleasure vs. stress reduction). Such expectation effects likely differ substantially between healthy subjects and those suffering from addiction. Future studies on erotic cue effects might therefore assess the motivation for the use of erotic stimulus material, as this might moderate potential cue effects and might highlight driving factors of a dysfunctional cue-reactivity response.

4.6. Limitations

Our study has a few limitations that need to be acknowledged. First, we only tested male heterosexual participants. Men and women might differ in neuronal responses to affective stimulus material and emotional processing (Bradley et al., 2001; Lithari et al., 2010; Wrase et al., 2003), although a recent meta-analysis found at most negligible sex differences in neural correlates of sexual arousal (Mitricheva et al., 2019). However, to extend generalizability of results, future studies should include participants from both sexes and different sexual orientations.

Second, we did not include an image rating task, capturing arousal, valence, or related dimensions. Therefore, we cannot directly quantify subjective arousal-associated individual cues. However, fMRI revealed substantial differences in neural responses to erotic vs. neutral cues in plausible brain regions implicated in attention and reward. Further, a pilot study in an independent sample confirmed that the applied stimulus material clearly modulated subjective arousal. Still, future studies might complement fMRI and task-based measures with self-reported arousal.

Third, we did not include an additional aversive cue condition to control for unspecific arousal effects. Previously reported erotic cue effects on TD might be at least partly attributable to increased arousal, although aversive cue effects on TD likewise appear mixed (Cai et al., 2019; Guan et al., 2015; Knauth & Peters, 2022). Nonetheless, it would be interesting to assess whether neuronal measures of aversive cue processing are predictive for choices.

Lastly, on each trial, participants only viewed the LL option, whereas the SS reward was fixed and never shown on the screen, as done in numerous earlier studies (Kable & Glimcher, 2007; Peters & Büchel, 2009). However, additionally displaying the smaller sooner reward (separated by a further jitter interval) could be interesting for two reasons. First, although we showed that value computations for LL rewards were largely unaffected by cue condition, neuronal representations of an *immediate* reward might have been affected by cue condition. Second, elevated dopamine tone might foster approach behavior towards rewards that appear spatially near or available. Only presenting one of two possible choice options instead of both (Guan et al., 2015) might have biased or even compensated cue effects.

4.7. Conclusion

Previous studies indicated that highly appetitive stimuli might increase TD behavior (Kim & Zauberman, 2013; Otterbring & Sela, 2020; Wilson & Daly, 2004). Cue-reactivity in reward-related circuits was suspected as a potential mechanism underlying these effects (Van den Bergh et al., 2007). Here, we leveraged combined fMRI during both cue exposure and decision-making to link activity in reward circuits to changes in TD. We first replicated core neural effects underlying TD (value coding in vmPFC, striatum, and posterior cingulate, LL-choice-related activity in DLPFC) (Bartra et al., 2013; Clitero & Rangel, 2014; Kable & Glimcher, 2007; Peters & Büchel, 2009; Smith et al., 2018). Further, we confirmed increased (sub-) cortical processing during erotic vs. neutral cue exposure in core regions of the reward circuit. However, our preregistered hypothesis of increased TD following erotic cue exposure was not confirmed. This resonates with recent findings from our lab, where such effects were only observed for the bias parameter in the drift diffusion model, and not for choice behavior per se (Mathar et al., 2022). Importantly, and in contrast to our preregistered hypothesis, activity in key reward regions (Nacc, VTA) did not predict changes in behavior. Our results cast doubt on the hypothesis that upregulated activity in the reward system is sufficient to drive myopic approach behavior towards immediately available rewards.

DATA AND CODE AVAILABILITY

T-maps of 2nd-level contrasts as well as STAN model code and raw behavioral data are available on the Open Science Framework (T-maps: https://osf.io/9uzm8/; Stan model code: Base-Model: osf.io/6uz8g; Offset-Model: osf.io/mgjx5; Raw data: https://osf.io/nxcas).

AUTHOR CONTRIBUTIONS

Kilian Knauth: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data Curation, Writing—Original Draft, Writing—Review & Editing, and Visualization. David Mathar: Conceptualization, Methodology, Software, Validation, and Writing—Review & Editing. Bojana Kuzmanovic: Software, Resources, and Writing—Review & Editing. Marc Tittgemeyer: Resources, Writing—Review & Editing. Jan Peters: Conceptualization, Methodology, Validation, Resources, Writing—Review & Editing, and Supervision.

DECLARATION OF COMPETING INTEREST

The authors declare no competing interests.

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SUPPLEMENTARY MATERIALS

Supplementary material for this article is available with the online version here: https://doi.org/10.1162/imag_a_00008.

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Supplementary Information

(*Study 2: Erotic cue exposure increases neural reward responses without modulating temporal discounting*)

Supplementary Table S1. Peak voxels and SVC corrected *p*-values for condition-wise SV-coding (erotic, neutral)

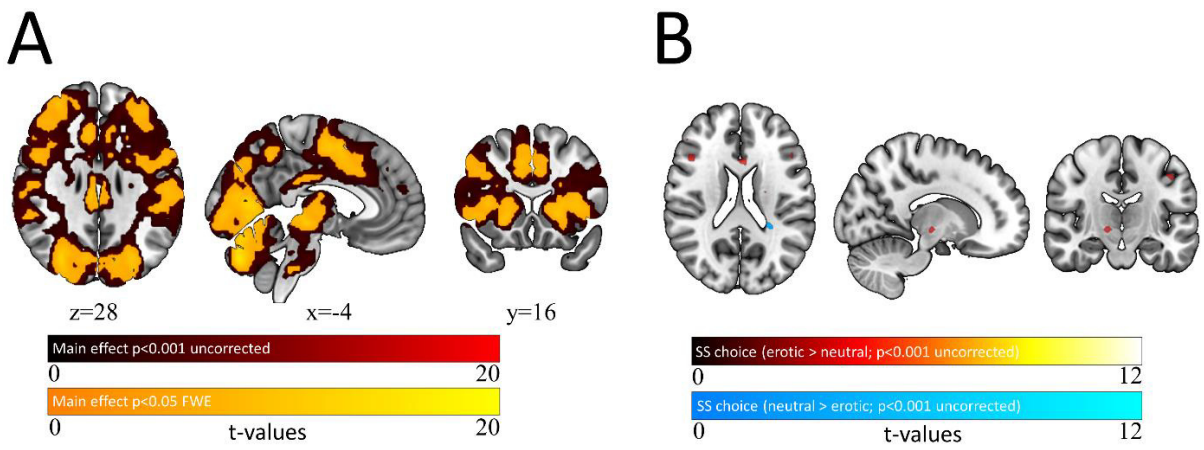
Exp. Condition	Area	Peak Voxel	z-value	p_{SVC}
Neutral	VMPFC	-8/54/-8	5.35	**<0.001***
	Striatum	-8/14/-6	3.61	0.075
	PCC	-8/-32/40	3.27	0.196
Erotic	VMPFC	-6/44/-4	5.13	**<0.001***
	Striatum	-8/10/6	3.96	**0.023***
	PCC	-8/-34/38	3.84	**0.035***

Note: Asterisks denote significant effects after small volume correction (SVC); VMPFC = ventromedial prefrontal cortex; PCC = posterior cingulate cortex.

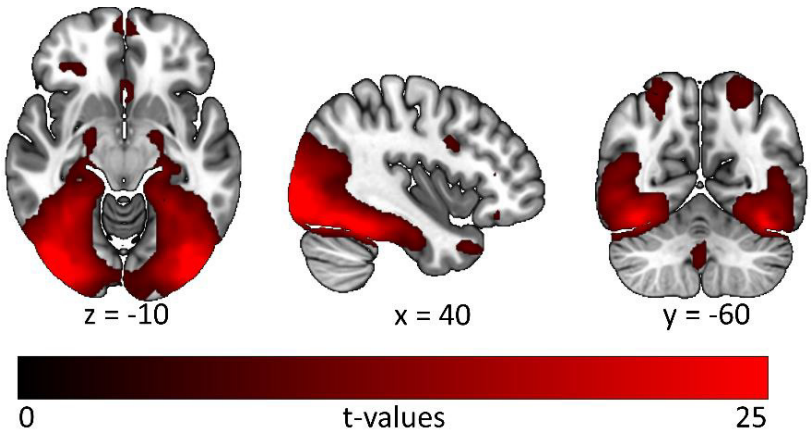
Supplementary Table S2. Peak voxels and SVC corrected *p*-values for condition-wise LL-choice coding (erotic, neutral)

Exp. Condition	Area	Peak Voxel	z-value	p_{SVC}
Neutral	left DLPFC	-44/44/6	3.98	**0.009***
Erotic	left DLPFC	-40/46/2	3.68	**0.025***

Note: Asterisks denote significant activations after small volume correction (SVC); DLPFC = dorsolateral prefrontal



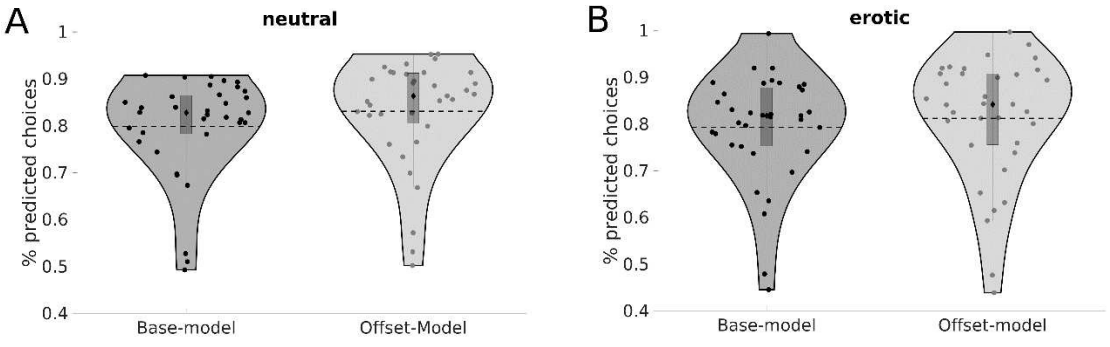
Supplementary Figure S1. Neuronal correlates of smaller-sooner choices. **A**: Display of the parametric (SS-) choice-regressor (mean across conditions); red, $p<0.001$ (uncorrected); yellow, whole-brain FWE corrected $p < 0.05$; **B**: Condition contrasts, erotic > neutral (red/yellow) and neutral > erotic (light blue), p<0.001 uncorrected (whole brain analysis).



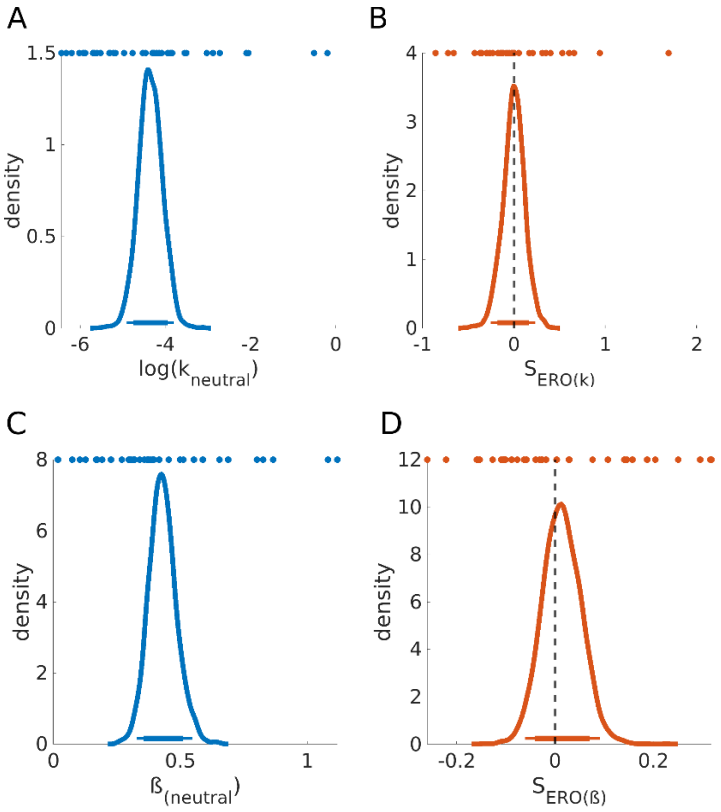
Supplementary Figure S2. Neuronal correlates intact vs. scrambled image processing irrespective of experimental condition. Red, whole-brain FWE corrected $p < 0.05$ (whole brain analysis).

Supplemental Table S3. Proportions of correctly predicted binary choices (mean [CIs]) for both included TD models (Base-Model, Offset-Model) split by experimental condition (see also Supplementary Figure S3).

Model	Neutral	Erotic
Base-Model	0.799 [0.762-0.836]	0.793 [0.753-0.833]
Offset-Model	0.831 [0.791-0.870]	0.812 [0.766-0.858]



Supplementary Figure S3. Proportions of correctly predicted binary choices for the Base-Model and the Offset-model (including an SV-offset parameter ω) split by experimental condition (A: neutral, B: erotic); Dots = single subjects; Dashed lines = group means; Black diamonds = group medians.

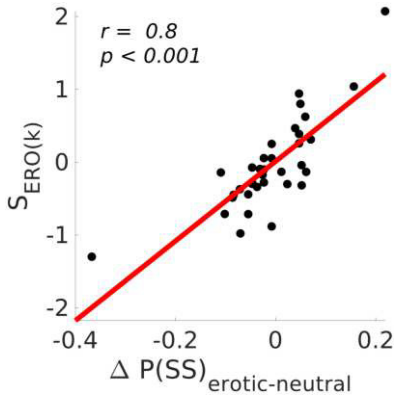


Supplementary Figure S4. Posterior distributions for log($k_{neutral}$) (A), ß$_{(neutral)}$ (C) and associated erotic shift parameters (B & D; Base-Model); Colored dots depict single subject means. Thick and thin horizontal lines indicate 85% and 95% highest density intervals.

Supplementary Table S4. Summary statistics of the posterior distributions of computational shift-parameters (Base-Model)

Parameter	Mean	SD	dBF	BF_{01}
SEro(k)	-0.004	0.484	1.030	5.810
SEro(ß)	0.014	0.154	0.530	30.807

Note. Abbreviations: BF_{01}, undirected Bayes factor in favor of null model; dBF, directional Bayes factor; *SD*, standard deviation.



Supplementary Figure S5. Associations between model-free (SS-choice proportions) and model-based measures ($S_{Ero(k)}$) of temporal discounting behavior (Offset-model); *r* = Pearson's correlation coefficient.

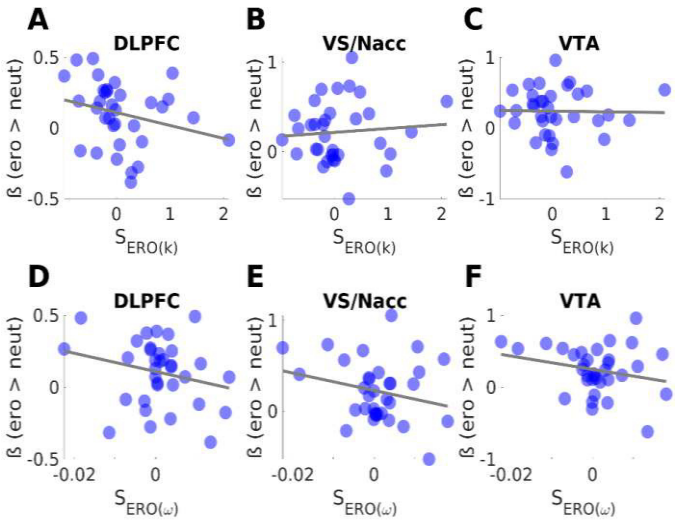


Figure S6. Associations between neuronal cue-reactivity-responses within key dopaminergic (VS/Nacc, VTA) and prefrontal (DLPFC) areas and subject-specific shift-parameters ($S_{Ero(k)}$, $S_{Ero(\omega)}$). Neuronal cue-reactivity within ROIs was quantified by extracting peak-voxel activity.

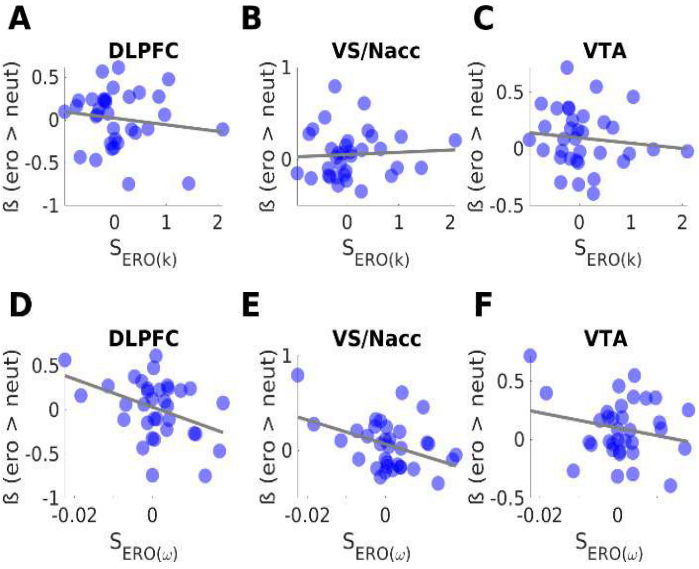


Figure S7. Associations between neuronal cue-reactivity-responses within key dopaminergic (VS/Nacc, VTA) and prefrontal (DLPFC) areas and subject-specific shift-parameters ($S_{Ero(k)}$, $S_{Ero(\omega)}$). Neuronal cue-reactivity within ROIs was quantified by extracting average voxel activity across the ROI.

General Discussion

At the end of the day, we have faced countless decisions. Chances are high, many of them entailed a tradeoff between small immediate pleasures and larger long-term benefits. Chances are likewise high, we did not always resist the temptation. Similar to many animals, humans tend to discount the value of future rewards as a function of time, resulting in an increased preference for immediate rewards (temporal discounting; TD; Kalenscher & Pennertz, 2008; Peters & Büchel, 2011). Although, such a behavior is common and to a certain degree rather rational, excessive manifestations of such a tendency appear problematic and maladaptive. Many psychiatric disorders and clinical conditions have been characterized by robust alterations in TD (Bickel, 2015), rendering it a transdiagnostic process (Bickel, 2019; Lempert et al., 2019), that might also play a role for the Research Domain Criteria (RDoC), a framework for investigating mental disorders, which aims to foster new research approaches that will enable better diagnosis, prevention, intervention, and treatment.

If altered TD is considered a maladaptive, clinically relevant feature evident across disorders, exploring factors *influencing* such behavior is of particular importance. Emotional stimuli of either valence (e.g., appetitive (erotic), aversive) have been identified as one such influencing factor, that can induce short-term changes to otherwise highly stable TD. However, to date findings still appear mixed and precise mechanisms driving these (partly contradictory) effects still remain elusive.

Bodily reactions accompanying emotional responses to external cues might be considered a valuable and rich source of information here. While processing of positively valenced, highly arousing cues (e.g., erotic images) will likely upregulate (dopaminergic) reward circuits (Stark et al., 2019), appetitive and aversive cues will both trigger more general phasic fluctuations of autonomous nervous system (ANS) activity (Bradley et al., 2008; Finke et al., 2017; Kinner et al., 2017). These bodily reactions or "internal signals" might contribute to previously observed cue-evoked choice biases in TD tasks, often in favor of available immediate rewards (Kim & Zauberman, 2013; van den Bergh et al., 2008; Wilson & Daly, 2004). However, this was never explicitly tested before.

Examination of emotional cue effects in healthy individuals as well as potential associations between cue-evoked, neurophysiological arousal responses and alterations in choice impulsivity might also inform *cue-reactivity* phenomena in different psychopathologies like addiction. In addiction various sorts of stimuli (e.g., people, places or objects) will be repeatedly paired with the pleasurable effects of drug consumption. Multiple studies revealed that such stimuli or cues evoke strong craving responses (Volkow et al., 2019), which have been associated with elevated VS BOLD signaling (Breiter et al., 1997) and accompanying (striatal) DA release (Volkow et al., 2011; Wong et al., 2006). However, evidence on a direct association of neurophysiological responsivity to external cues and changes in myopic choice behavior is still scarce. Moreover, whether such potential (brain-behavior/arousal-behavior) coupling can also be observed in healthy individuals when confronted with non-drug natural rewards like erotic pictures is likewise unclear, but would point to a more basic mechanism.

This dissertation project therefore aimed to contribute to a better understanding of these mechanisms, focusing on associations between cue-evoked short-term arousal responses (study 1) or neuronal reward circuit (re-) activity (study 2) and changes in TD behavior as proxy for choice impulsivity. The upcoming chapters will briefly recapitulate key findings from both studies. Further, these findings will be discussed with regard to the current state of research and placed in a wider context of emotional cue effects.

Trial-wise Emotional Cue Effects on Temporal Discounting

Emotional processing is closely linked to physiological arousal (Herman et al., 2018). Although such interconnection is well established, prior studies did not adequately control for alterations in autonomic signaling following or during cue exposure (e.g., Guan et al., 2015; Luo et al., 2014; Simmank et al., 2015). Such short-term changes of the physiological arousal state might shed light on previous contradictory results of trial-wise cue effects on TD.

Study 1 ("*Trial-wise exposure to visual emotional cues increases physiological arousal but not temporal discounting*") therefore directly tested trial-wise effects of erotic, aversive and neutral visual cues on TD, while measures of autonomic arousal were closely monitored. Results confirmed, that arousal was indeed substantially increased following erotic and aversive visual stimuli (compared to neutral). Importantly, this was mirrored by both, mainly SNS- (late pupil dilation; Finke et al., 2017; Marumo & Nakano, 2021) and PNS-moderated (early heart rate (HR) deceleration; Gordan et al., 2015; Vila et al., 2007) psychophysiological indices. However, computational modeling as well as model-agnostic analyses revealed that TD remained mostly unaffected by emotional cue exposure. Although parameter estimates indicated a small decreasing effect of erotic cues on steepness of TD (log(k) parameter), these results were largely compatible with a null model, assuming no condition effects. In two additional computational models we assessed whether momentary arousal fluctuations (approximated via pupil size, HR and electrodermal activity (EDA)) could explain variance proportions in TD behavior *over and above* condition effects or whether there were any pure arousal effects on choice, irrespective of the experimental manipulation. If anything, results indicated small but non-significant negative effects of pupil size and HR regressors on TD, which were likewise both highly compatible with a null model.

In summary, these findings speak against a general effect of trial-wise physiological arousal on TD.

Block-wise Appetitive Cue Effects on Temporal Discounting

In study 2 "*Erotic cue exposure increases neural reward responses without modulating temporal discounting*", we investigated candidate neuronal mechanisms, assumed to play a role in previously observed *block-wise* erotic cue exposure effects on TD (Kim & Zauberman, 2013; Mathar et al., 2022a; van den Bergh et al., 2008; Wilson & Daly, 2004). We therefore closely aligned our experimental design to preceding studies (e.g., Kim & Zauberman, 2013). On two different testing days, healthy male participants either viewed a series of highly arousing erotic or neutral visual stimuli, before they performed a classical TD task. FMRI was applied during both experimental phases.

On the neuronal level we first replicated a number of important results from prior TD studies. These comprise subjective value (SV) coding of depicted LL reward options in ventromedial prefrontal cortices (vmPFC), ventral striatum (VS) and cingulate cortex (Peters & Büchel, 2009), as well as increased lateral prefrontal cortex (lPFC) activity during choices of delayed rewards, a finding that is often interpreted in terms of increased cognitive control (Smith et al., 2018). Regarding cue exposure, erotic compared to neutral stimuli increased activity in multiple subcortical (e.g., bilateral striatum) and cortical ROIs (e.g., vmPFC, PCC, lateral occipital cortices). While effects in parietal and occipital cortices possibly reflected increased attention allocation towards erotic vs. neutral stimuli, upregulated BOLD activity in striatal or vmPFC regions might be attributed to differences in their respective intrinsic values (Georgiadis & Kringelbach, 2012; Kuehn & Gallinat, 2011; Poeppl et al., 2016a; Stark et al., 2019; Stoléru et al., 2012). On the behavioral level, we found no evidence for TD changes following block-wise exposure to appetitive (erotic) cues. Computational parameters that quantified cue-evoked alterations in steepness of discounting (S_{Ero_k}), offset of the discounting curve as a whole (S_{Ero_ω}), as well as decision noise (S_{Ero_β}) all largely overlapped with zero. Furthermore, and similar to study 1, we directly assessed the link between (neuro-) physiological cue-reactivity and changes in TD. Physiological cue-reactivity was now quantified via BOLD alterations in key (dopaminergic) mesolimbic (NAc, VTA) and prefrontal (lPFC) areas. Elevated neuronal (re-) activity in VS and dlPFC in response to erotic>neutral cues showed small to medium sized positive associations with a general bias towards SS rewards. However, this finding appeared highly dependent on the precise voxel selection procedures (see study 2 manuscript for details).

To sum up, these results indicate that block-wise effects of erotic cue exposure on TD might not be as unequivocal as previously thought. Moreover, they raise doubt on the hypothesis of a *specific dopaminergic* mechanism, that might support myopic approach behavior towards immediate rewards.

The results from the two studies add to the current state of research on emotional cue effects on TD. Prior results from *trial-wise* studies, presenting cues of either valence alongside intertemporal choice options appeared highly mixed (e.g., Guan et al., 2015; Luo et al., 2014; Simmank et al., 2015). Whereas some studies observed increased (Guan et al., 2015; Sohn et al., 2015) or decreased (Luo et al., 2014) discounting following negative primes, others reported increased (Sohn et al., 2015) or unaltered (Simmank et al., 2015) discounting in response to erotic cues.

Interpretation of such contradictory findings was at least partly hampered by the use of small sample sizes (n <= 20-26) or trial numbers per condition (n <= 30; Guan et al., 2015; Luo et al., 2014; Sohn et al., 2015). More critically, studies often could not disentangle valence and arousal effects on TD, as they included emotional stimulus material, that differed with respect to both dimensions. In these cases, experimental images for example depicted "happy" (e.g., older couples) and aversive (e.g., bodily, mutilation or fearful faces) visual scenes (Guan et al., 2015; Luo et al., 2014). Other approaches included stimuli, with high ratings on both, valence and arousal (e.g., erotic cues vs. palatable food cues), which makes it equally difficult to differentiate their relative contributions to changes in TD (Simmank et al., 2015). Study 1 can therefore inform the discussion on trial-wise cue effects on TD, by showing that emotional stimuli of opposing valence, but carefully matched according to subjective arousal levels, are not per se sufficient to induce changes in impulsive choice. Moreover, the study was well powered and included approximately hundred trials per cue condition, enabling model-free evaluation but also extensive computational modeling of behavior. This way, we were able to provide additional evidence, that subprocesses contributing to intertemporal choice (steepness of discounting, decision noise) were likewise not substantially affected by trial-wise cue exposure or arousal, respectively.

At first glance, results from previous *block-wise* studies appeared far more converging. Early findings indicated that passive viewing or rating of highly arousing opposite-sex faces or erotica prior to a TD task might increase preference of SS rewards (e.g., Kim & Zauberman, 2013; van den Bergh et al., 2008; Wilson & Daly, 2004). Results from study 2 however, stand in contrast to these findings, showing unaltered TD following block-wise exposure to highly arousing pre-rated erotic stimuli. Reasons for this disparity, including (minor) adaptations of the experimental design as well as specifics of the testing environment (fMRI vs. laboratory) have been discussed extensively in the discussion section of the respective manuscript.

However, more recent study findings also indicated that block-wise cue effects on TD might not be as unequivocal as previously thought (Cai et al., 2019; Mathar et al., 2022a; Otterbring & Sela, 2020). For example, Cai and colleagues (2019) classified a student sample based on schizotypy questionnaire scores. Especially low-scoring (healthy) participants did not differ in TD following block-wise exposure to highly arousing negative or highly arousing positive images. Similarly, results from a more recent study from our own lab (Mathar et al., 2022a) showed that cue exposure effects on TD might be far

more subtle. Using comprehensive modeling of reaction time (RT) distributions employing drift diffusion models (DDMs), we observed a bias-like change in the starting point of the evidence accumulation process towards SS options. However, here as well steepness of discounting (log(k)) was not reliably affected by cue exposure. Related findings support a more fine-graded association between visual appetitive stimulus processing and impulsivity, possibly moderated by internal homeostatic or motivational conditions. For example, Otterbring and Sela (2020) reported more impatient financial decisions following sexually arousing ads compared to neutral ones – but only in hungry male individuals. In satiated participants, cue exposure had no effect. Similarly, Chiou and colleagues (2015) found that a *mating mindset* mediated the association between viewing pictures of attractive women and greater TD in men. Study 2 of this dissertation project contributes to and extents these recent ambiguous findings, by showing unaffected TD following an extended block-wise cue exposure phase of highly arousing (pre-rated) erotic stimuli. Unaffected TD following cue-exposure was confirmed by our comprehensive computational modeling approach, which showed little to no change in parameters quantifying steepness and offset of the TD functions.

Neurophysiological Contributions to (Intertemporal) Decision-making

Most importantly, study 1 and 2 can inform the debate on emotional cue effects on intertemporal choice by directly testing whether increased physiological arousal and/or reward system (re-) activity contribute to emotional cue effects on TD. This is of particular importance as perception of emotional stimuli causes multifaceted reactions in the individual, and neurophysiological changes might be considered the most basic ones.

Multiple theoretical approaches previously emphasized that emotion might bias choice. Many of them can be classified as dual-system models (Inzlicht et al., 2021), which propose a rather simplified dichotomy of two distinct sub-systems, representing opposing decision-making strategies. While the "cool" or self-controlled System II acts more slowly, prudently and rational, necessary to prioritize long-term goals, the impulsive, "hot" System I stands for fast and reflexive action and appears more bottom-up driven by external or internal stimuli (Metcalf & Mischel, 1999). According to such classes of theories, myopic choice behavior might be fostered by an imbalance of these antagonizing agents. An overactive hot-system, related to various internal states (e.g., hunger, sexual desire, moods or emotions) would affect relative desirability of proximal goods, thereby increasing behavioral tendency of impulsive responding (Loewenstein, 1996).

Previous studies, observing increased TD following appetitive cue exposure interpreted their results as confirmation of a such dual-system idea (e.g., Li et al., 2008; van den Bergh et al., 2008), arguing that exposure to 'hot stimuli' or primary reward cues would evoke a general motivational state, narrowing attention to the proximate environment. Such generality would give rise to non-specific effects, explaining (out-of-domain) increased immediate reward preference following appetitive food

cues (Li et al., 2008) or erotic stimuli (van den Bergh et al., 2008). Similarly, it could also be argued that above-mentioned mediated erotic cue effects on TD (Chiou et al., 2015; Otterbring et al., 2020) would also resonate with these considerations, as cue effects were dependent on an actual balance of homeostatic (e.g., hunger; Otterbring et al., 2020) or motivational (e.g., mating mindsets; Chiou et al., 2015) systems.

In study 1 and 2 we equally observed strong evidence for a successful cue-induced "overactivation" or upregulation of the "hot" System I. In study 1 this was mirrored in complementary proxies of ANS activity. Moreover, increased pupil dilation that has been associated with elevated phasic firing of locus coeruleus (LC) neurons and widespread cortical norepinephrine (NE) release (Reimer et al., 2016) indicated a cue-induced state of heightened alertness and attentiveness (Cole & Robbins, 1992; Holland et al., 2021). In study 2, erotic cues elevated BOLD activity in mesolimbic reward areas (e.g., VS), value-coding- (e.g., vmPFC) and attention-related cortices (e.g., PCC), ROIs that largely overlapped with results from previous studies (Ferretti et al., 2005; Mitricheva et al., 2019; Stark et al., 2019). Despite this clearly visible "overactivation", TD was unaffected - speaking against classical dual-system imbalance theories (at least for the observed *magnitude* of cue-induced arousal/reward system upregulation).

However, the complementary experimental designs of the two conducted studies (trial-wise vs. block-wise) as well as the included methodologies (psychophysiology vs. fMRI) enabled us to systematically assess neurophysiological underpinnings of emotional cue effects in more detail:

In study 1, mean estimates of psychophysiological indices were fed into computational TD models, allowing us to directly test whether short-term emotional arousal predicted intertemporal choice on the trial level. Moreover, this approach enabled us to delineate possible pre-decision ANS activity effects on parameters related to reward devaluation and choice stochasticity, respectively. A previous study found increased passive pupil-related arousal to be associated with more patient choices in a TD task (Lempert et al., 2016). However, in this study value effects were not adequately controlled for, although pupil size is known to reliably track option values (Cash-Padgett et al., 2018; van Sloten et al., 2018). Moreover, the study (Lempert et al., 2016) did not include any cue exposure phase. Here, we inform this discussion, by showing that cue-evoked *physiological arousal* does not explain variance proportions over and above emotional cue effects on valuation and decision noise/stochasticity. Such findings might also be interesting with regard to other domains of value-based decision-making. Specifically, evidence from early risky choice research found that trial-wise arousal might be used to approximate the degree of uncertainty or risk associated with available choice options (Bechara, 2004; Bechara & Damasio, 2005; Bechara et al., 1997). Moreover, physiological arousal (measured via EDA) *prior* to the decision was found to be negatively related to risk-taking, suggesting that high arousal might possibly signal a sort of "situational ambiguity" to the individual, which could foster approach behavior towards more certain choice options (FeldmannHall et al., 2016). Following this idea, it may be suggested that uncertainty-signaling physiological arousal during intertemporal decisions would

promote choice of immediately available options, which might also be considered as *more certain* compared to delayed choice options. However, this seems not to be the case. Exploiting our design, future studies might assess emotional cue effects on subprocesses of risky choice (valuation, choice stochasticity) and actively control for trial-wise physiological arousal. To our knowledge this has not been examined before.

In study 2, we tested whether block-wise exposure to highly erotic stimuli systematically interacted with key cognitive subprocesses implicated in TD, that is valuation and cognitive control and related neuronal activation (Lempert et al., 2018). Instead of simply inducing unspecific approach behavior towards proximate rewards following reward system upregulation, appetitive cue exposure may directly interfere with SV representations. Thereby, perceived objective value differences would diminish and immediate reward preference might be fostered. Similar findings in people suffering from problem gambling support this idea (Miedl et al., 2014). Alternatively, appetitive cues may downregulate activity in lateral prefrontal cortex (LPFC), a region often implicated in cognitive control (Smith et al., 2018) and with this increase myopic choice behavior following erotic cues (e.g., Kim & Zauberman, 2013; Wilson & Daly, 2004). DlPFC contributions to far- vs- short-sighted choice are supported by (1) fatigue effects manifested in increased TD that were associated with reduced dlPFC excitability (Blain et al., 2016) and (2) increased TD following dlPFC disruption (Figner et al., 2010). Our results provide evidence that, although erotic vs. neutral cue exposure increased activity in multiple cortical as well as subcortical brain areas, both SV coding and cognitive control (indicated by dlPFC activity) in a subsequent TD task were not impaired.

Crucially, using brain-behavior correlation analyses we found that (re-) activity to erotic vs. neutral cues in key mesolimbic (dopaminergic) reward areas (e.g., VS, VTA) showed if anything only minor associations with TD. Moreover, such an association was only apparent in an exploratory analysis using a different voxel selection procedure and was not specific to dopaminergic brain areas. Instead, reactivity in frontal areas (e.g., dlPFC) showed comparable results. These findings contradict the idea, that a cue-evoked upregulation of (dopaminergic) reward systems results in increased choice impulsivity. As such, they more closely resonate with results from study 1, where we found no significant associations between arousal-related pupillary cue-reactivity indices and changes in TD.

Implications for Clinical Research

The above-mentioned lacking associations between cue-evoked neurophysiological reactivity and changes in choice impulsivity as measured by TD are also of interest for clinical research. People suffering from addictions (Reynolds & Monti, 2013) but also other psychiatric disorders (e.g., binge eating disorder; Arend et al., 2022) show specific responses when they are exposed to disease-related stimuli or cues. Such responses, subsumed under the term *cue-reactivity*, can be observed on subjective, psychophysiological and neural levels (Starcke et al., 2018). On the subjective level, consumption- or

drug-related cues usually evoke craving, a strong desire to approach and consume the drug or the desired object (Vafaie & Kober, 2022). The subjective experience of craving might be accompanied by peripheral nervous system responses, like increased heart rate, sweat gland activity or skin temperature. On the neural level, it has been suggested that an over-sensitized mesolimbic reward system may play a crucial role in cue-reactivity (Robinson & Berridge, 1993, 2008).

Cue-reactivity responses comprise highly important phenomena as they are closely associated with addiction severity, treatment success and relapse probability (Allenby et al., 2020; Dieterich & Endrass, 2022; Vollstädt-Klein et al., 2010). Drug-related cue-reactivity responses towards drug cues are learned. They evolve over time as various sorts of stimuli or cues become associated with the rewarding properties of the drug and/or predict drug occurrence, respectively (Starcke et al., 2018).

In experimental contexts, cue-reactivity responses in addiction have been well documented on all levels (subjective (craving), psychophysiological, neuronal) and there is ample evidence for close interactions between them (e.g., between subjective craving and neuronal cue-reactivity in cortical (Miedl et al., 2014) and mesolimbic brain areas (Limbrick-Oldfield et al., 2017)). On the behavioral level, presence of drug cues can increase measures of choice impulsivity (e.g., Dixon et al., 2006, Genauck et al., 2020; Miedl et al., 2014; Wagner et al., 2020).

However, evidence on a direct association between neurophysiological cue-reactivity in addiction and changes in behavior is still limited (Bruder et al., 2021; Brunette et al., 2019). Moreover, it is unclear whether a potential association between multi-level cue-reactivity and choice impulsivity in addiction resembles a more general (dopaminergic) mechanism that can also be provoked by cues predicting primary reinforcers in healthy controls (e.g., erotic stimuli). This dissertation project as a whole, but especially study 2, informs this debate by showing that this seems not to be the case per se. The degree of neuronal cue-reactivity to highly arousing erotic vs. neutral cues in mesolimbic reward areas did not predict changes in impulsive choice.

Instead, our results might suggest that impulsivity-increasing effects of drug cues on choice behavior could either be addiction-specific and/or dose dependent. Previous studies suggested that people suffering from addiction (relative to healthy controls) display diminished neuronal processing in widespread cortical networks in response to non-drug, natural rewards like erotic pictures (e.g., Costumero et al., 2015). Moreover, addicted individuals compared to controls exhibit lower arousal ratings of highly pleasant non-drug imagery and higher arousal ratings in response to drug cues (Lubman et al., 2009). Therefore, it might be speculated that erotic cues and other naturalistic rewards cannot reliably evoke the same degree of neurophysiological arousal (in control) as compared to drug cues in addiction. However, this is highly speculative and warrants testing in upcoming studies.

Alternatively, one could suggest that drug-related and "natural" cue-reactivity towards primary rewards like erotic stimuli might indeed differ qualitatively. For healthy participants e.g., erotic cues indicate the upcoming availability of a pleasurable stimulus, which was learned via positive reinforcement processes. In contrast, addiction-related or drug cues might take effect through both

positive *and* negative reinforcement routes. During addiction development cue exposure might co-occur with rewarding (mesolimbic) effects but also with reductions of subjective craving and withdrawal symptoms, especially at later developmental stages. Therefore, cue-elicited expectations (e.g., pure pleasure or reward vs. reduction of withdrawal symptoms and negative affect) might indeed differ qualitatively between subgroups suffering from addiction and healthy controls. Such expectations might in turn affect behavioral relevance of external cues. Whether "consumption-related" expectations moderate cue effects in either subgroup remains an open question for future research.

Limitations and Future Directions

This dissertation project and the studies entailed have a number of limitations that have to be acknowledged and that might be addressed in future studies.

First, although we clearly focused on neurophysiological changes associated with emotional cue exposure and their contribution to TD, it could have been beneficial to also evaluate participants' subjective image ratings in terms of valence and arousal. All included images were either taken from established image data bases (e.g., IAPS; Lang et al., 2008) or identified via a google search. Moreover, they were pre-rated by independent samples in separate pilot studies, enabling us to assure that neutral and emotional image categories differed in relevant dimensions as intended. However, image ratings from our participants in study 1 would have allowed us to focus on physiological and behavioral data analyses on the most arousing trials. As already mentioned, Miedl and colleagues (2014) observed that SV representation of objective rewards was impaired in gamblers, but only in response to highly arousing drug cues, that also induced elevated craving and steeper TD. In study 2, image ratings could have been used as a parametric modulator in fMRI analysis of the cue exposure phase. Thereby, brain areas specifically coding for *variation* in subjective (erotic) arousal could have been detected. Reactivity in these areas might also (partly) explain variance in TD changes. Future studies might therefore also include post-hoc image ratings.

It might even be considered to expand image ratings by an additional *approach-avoidance* dimension. It appears plausible that such category entails information that is not completely covered by arousal and valence ratings. For example, one could imagine that different aversive stimuli, equally characterized by low valence and high arousal, might trigger different emotional reactions (e.g., anger vs. fear), that give rise to differences in approach vs. avoidance behaviors. Some more recent databases already entail image ratings of such dimensions (Marchewka et al., 2014).

Further, we did not assess any baseline arousal measures (study 1) or proxies that could be used to estimate baseline dopaminergic activity or neurotransmission, respectively (study 2). For example, previous study results indicated that baseline arousal levels, as indicated by tonic pupil size, might be related to decreased phasic responses, possibly indicating reduced (re-) activity (da Silva Castanheira et al., 2020). Moreover, in a more recent study from our lab, we found that individual eye blink rate at

baseline predicted arousal-related changes in pupil dilation (Mathar et al., 2022b). Spontaneous eye blink rate has been discussed as an estimate for central catecholamine levels (Groman et al., 2014; Kaminer et al., 2011; Sescousse et al., 2018), although most recent evidence challenges such interpretation (van den Bosch et al., 2023). However, given these possible interactions, future studies might characterize the baseline arousal or activation levels prior to cue exposure phases.

Apart from baseline physiological arousal levels, people may generally differ in their subjective responsivity to emotional stimuli and/or differ in their interoceptive awareness of physiological states. This might be especially true for individuals suffering from addiction, who regularly experience craving and therefore potentially exhibit a heightened sensitivity to bodily reactions. Such interindividual differences were not assessed in the current studies and might moderate emotional cue exposure effects. Future experiments could therefore include measures like the Emotional Reactivity Scale (ERS; Nock et al., 2008) or Multidimensional Assessment of Interoceptive Awareness (MAIA) questionnaires (Mehling et al., 2018) to address this issue. In these future experiments, it might also be considered to intersperse queries of the *current* (subjective) emotional arousal level, which could be presented during cue exposure phases or during temporal discounting tasks, respectively. By this means, it could be ensured that subjective arousal of the individual is indeed elevated as intended. This appears of particular importance, as it might be speculated that certain experimental design specifications of the current studies (e.g., trial-wise cue exposure (study 1) or circumstances of the fMRI environment including loud noises, narrowness, restricted movement (study 2)) could have slightly reduced the magnitude of internal arousal or perception thereof, respectively.

Upcoming studies on emotional cue effects on TD might also benefit from a greater use of sequential sampling models like drift diffusion models (DDMs; Forstmann et al., 2016) in which choices emerge from a noisy evidence accumulation process that terminates as soon as the accumulated evidence exceeds one of two decision boundaries (Wagner et al., 2022). More recent experiments indicated that cue effects on TD might appear rather subtle. Mathar and colleagues (2022a), observed a shift in the starting point bias of evidence accumulation towards the immediate choice option, while cue effects on steepness of discounting (log(k) parameter) were largely absent. The specific single-trial sequence prevented the use of DDMs in both of our studies, as the actual choice was only possible with a short delay. This was for example due to jitter intervals, which we included to better disentangle valuation and decision-making phases. Future utilization of DDMs might enable a deepened investigation of the latent processes underlying intertemporal choices. Moreover, variation in physiological arousal and/or neuronal cue-reactivity in response to emotional cues might specifically interact with entailed (more sensitive) DDM model parameters. Importantly, DDM parameters have also been linked to various (sub-) clinical symptoms, and thereby can also contribute to a better understanding of potential disease mechanisms (see e.g., Forstmann et al., 2016; Sripada & Weigard, 2021).

In accordance with upcoming advanced computational modeling approaches, neurophysiological indices of cue-reactivity might also further evolve. Quantification of mean trial-wise

arousal and condition-wise contrasts (erotic > neutral) in fMRI analysis might be considered as too coarse to capture all relevant nuances of cue-evoked responding. Future studies might more heavily rely on a characterization of the specific shapes of recorded response functions (e.g., dilatory pupil responses - including measures like time-to-peak-dilation or dilation rate). Moreover, latent components underlying physiological responses like pupil dilation might be dissociated by temporal principal component analysis (PCA; Finke et al., 2017). It might be exciting to assess potential associations with computational modeling parameters to better characterize the decision-making process. Also, in fMRI analyses, utilization of more sophisticated functional connectivity analyses might reveal a more detailed picture of cue effects on TD. It might be speculated that fronto-striatal signaling could show closer associations with TD (Achterberg et al., 2016; Peper et al., 2013; van den Bos et al., 2015) than mean BOLD activity changes in separate brain clusters.

Future studies might also simultaneously account for alternative mechanisms that have been assumed to contribute to previously reported cue effects on choice. For example, some authors reasoned that erotic cue exposure might alter subjective time perception in a way that future durations are judged to be longer (Kim & Zauberman, 2013; Laube & van den Bos, 2020), thereby fostering impulsive responding. This was not tested in the studies entailed in this dissertation project. Given the lacking main effects of emotional cues on TD in our experiments, it would have been interesting to assess if cue effects on perceived time durations were likewise absent. Moreover, future studies might directly relate neurophysiological changes in cue-reactivity to subjective time judgements.

We reasoned that neurophysiological cue-reactivity responses to highly emotional imagery (e.g., erotic stimuli) in healthy participants might partly resemble cue-reactivity to drug cues in people suffering from addiction, thereby acting as a "arousal-driven" baseline mechanism. However, to directly test this, future studies might include both healthy subjects as well as participants exhibiting maladaptive behaviors, like pathological gambling or substance-use-disorders (SUDs). Using such a "full design", effects of highly arousal erotic, aversive and addiction-related cues on TD could further elucidate the way external environments and stimuli influence choice behavior. Although it has been observed that addicted subjects sometimes show blunted neuronal reactivity to cues predicting non-drug arousing stimuli (e.g., erotic imagery; see Sescousse et al., 2013), it could be confirmed, that previously observed elevated choice impulsivity in people suffering from addiction (e.g., Miedl et al., 2014), is specifically related to the processing of drug cues or "content" and can neither be explained by high arousal states or upregulations of dopaminergic reward circuitry.

Given the assumed generality of cue-reactivity responses and neurophysiological mechanisms entailed, future studies should include participants from all sexes by default. For both studies of the current dissertation project, only male participants were recruited as we suggested, men and women might differ in their neurophysiological reactivity to affective stimuli (Bradley et al., 2001; Lithari et al., 2010; Wrase et al., 2003) and we aimed to closely adapt our experimental design to previous cue exposure studies, which consistently reported increased TD in response to erotic cue exposure (Wilson

& Daly, 2004; Kim & Zauberman, 2013; Sohn et al., 2015; van den Bergh et al., 2008). In these studies, cue effects appeared to be most pronounced in male participants. However, more recent studies raise doubt on the fact that neuronal cue-reactivity e.g., to drug cues (Gerhardt et al., 2022) or erotic stimuli (Stark et al., 2019) does majorly differ between male and female participants. Although substance use disorders (SUDs) are characterized by greater prevalence in men (McHugh et al., 2018; Fonesca et al., 2021), which are therefore probably more often confronted with maladaptive cue-reactivity effects, the use of participants of all sexes would extend generalizability of study results to the entire population.

A more unspecific or widely applicable limitation or criticism concerns the possible limited informative value of laboratory-based cue-reactivity studies per se. The purpose of cue exposure phases directly preceding behavioral tasks measuring choice impulsivity or stimuli embedded in single trial sequences might be quite obvious to participant samples (often comprising mainly university students). Moreover, perceived elevation of neurophysiological (and subjective) arousal in such designs is certainly attributable to the cues presented. Cue effects triggered e.g., by drug-paired stimuli and environmental cues in real-world settings (e.g., Wagner et al., 2022) might take effect on choice in more subtle ways, fostered via higher-order conditioning processes. Thereby, people are mostly unaware of any operating cue effect they are targeted by. Ambulatory assessment methods measuring cue-reactivity under naturalistic conditions can at least complement present lab-based approaches by increasing ecological validity and predictive value. Moreover, they enable to directly assess cue-reactivity within real-world conditions in which relapse episodes of people suffering from addiction will likely occur.

The visual (especially erotic) stimuli used in the current studies were selected (and expected) to increase TD (Kim & Zauberman, 2013; van den Bergh et al., 2008; Wilson & Daly, 2004). Simultaneously, we aimed to capture neurophysiological changes that might accompany or even explain such behavioral adaptations. We reasoned, knowledge about such mechanisms driving choice impulsivity might also inform potential interventions. Our results indicated that increased physiological arousal and elevation of neuronal reward circuitry are both not sufficient to elevate TD - at least in the magnitude observed here. Similar approaches found that other types of visual stimuli might be capable to *decrease* rather than *increase* choice impulsivity as measured by TD tasks. Such stimuli are of particular importance as they might more directly inform possible countermeasures that can reduce maladaptive behaviors in both people suffering from addiction and healthy subgroups. Examples for such stimuli entail so-called *episodic* (textual) *future thinking cues* (Rösch et al., 2021) that are presented during the TD task and refer to real subject-specific future events planned for the respective day of LL reward delivery (Peters & Büchel, 2010) or imagery of nature cues and photographs (Berry et al., 2014; Berry et al., 2015; van der Wal et al., 2013). It might be promising for future studies to more strongly focus on potential mechanisms driving the reported medium to large-sized *reductions* in TD following exposure for example to such nature cues (Rung et al., 2018). Interestingly such reductions seem not to be related to alterations in time estimations. An assessment of potential neurophysiological changes that accompany such behavioral adaptations could be exiting.

Conclusion

This dissertation project investigated neurophysiological mechanisms contributing to emotional cue effects on temporal discounting (TD). Due to its high intraindividual stability and its close association with a range of maladaptive behaviors and clinical conditions (including addiction) TD has been considered a transdiagnostic marker and potential (future) indicator of treatment response. Improving our understanding of *how* TD is affected by external factors therefore represents a both vital and extensive endeavor. Our results revealed by the two conducted experimental studies promote these efforts in multiple ways.

First of all, and most critically, our findings raise doubt on the robustness, clarity and generality of cue effects on TD induced by visual emotional stimuli. This is true for effects stemming from both trial-wise and block-wise cue exposure approaches.

Studies applying trial-wise cue exposure designs already revealed somewhat mixed results in the past and it appears plausible that differences in physiological arousal, which is inextricably linked to emotional processing, might explain these differences. Results from study 1 complement these earlier findings, revealing absence of both aversive and erotic cue effects on TD. Importantly, we demonstrated that short-term physiological arousal fluctuations that accompany emotional cue exposure seem not to be sufficient to explain trial-wise alterations in choice behavior. Moreover, extensive computational modeling approaches confirmed that also different subprocesses contributing to actual choice (steepness of TD, decision noise) are not systematically affected by elevated phasic arousal, which was indexed by psychophysiological measures capturing both sympathetic and parasympathetic activation.

Compared to trial-wise designs, past block-wise appetitive cue exposure studies have yielded seemingly more consistent results. However, most recent reports stemming from our own lab (Mathar et al., 2022a) have already suggested that e.g., erotic cue effects might be rather subtle. Our findings fall in line with this notion, showing a lack of (behavioral) erotic cue effects in an fMRI environment. Although we replicated a number of important neuronal TD signatures associated with value computation and cognitive control, both processes were not differentially affected by the preceding erotic cue exposure phase. This is of particular interest, as we simultaneously observed widespread upregulation of neuronal reward and attention circuitry following erotic cues, confirming previous findings. Such a response pattern has also been detected in clinical subgroups suffering from addiction, when visual drug cues were being processed and cue-induced changes in neuronal activation have been associated with an increased desire for drug consumption (craving) and higher choice impulsivity. Therefore, we suggested, that cue-evoked upregulation especially of neuronal reward circuitry by highly (non-drug related) appetitive stimuli in healthy participants could depict a more basic mechanism, that may drive myopic and dysfunctional choice behavior. However, finding at most small associations between BOLD activity in mesolimbic reward areas and TD changes in study 2 contradicts this idea, potentially pointing to a more addiction-specific mechanism.

Future research might benefit from a combined approach of computational choice models (e.g., evidence accumulation models), that enable an even more detailed description of decision-making (sub-) processes and close multi-level monitoring of neurophysiological signatures associated with cue exposure. This might yield an even more sophisticated characterization of the variety of features contributing to the *cue-reactivity phenomenon* and how these features might affect real-world myopic choice behavior, especially in people suffering from addiction.

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List of Figures

Abbreviations

ACC	anterior cingulate cortex
ANS	autonomous nervous system
AUC	area under the curve
BF	bayes factor
BOLD	blood oxygenation level dependent
CI	choice impulsivity
dBF	directional bayes factor
DA	dopamine
dlPFC	dorsolateral prefrontal cortex
EDA	electrodermal activity
fMRI	functional magnetic resonance Imaging
GLM	general linear model
HDI	highest density interval
HR	heart rate
LL	larger later reward
LC	locus coeruleus
MCMC	markov-chain-monte-carlo
NE	norepinephrine
NAc	nucleus accumbens
NMR	nuclear magnetic resonance
OFC	orbitofrontal cortex
PCC	posterior parietal cortex
ROI	region of interest
SCR	skin conductance response
SS	smaller sooner reward
SN	substantia nigra
TSST	trier social stress test
TD	temporal discounting
vmPFC	ventromedial prefrontal cortex
VS	ventral striatum
VTA	ventral tegmental area

Contribution Statement

Study 1: Kilian Knauth and Jan Peters: *Trial-wise exposure to visual emotional cues increases physiological arousal but not temporal discounting* (2022); Psychophysiology

Kilian Knauth: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Software; Validation; Visualization; Writing – original draft; Writing – review & editing

Jan Peters: Conceptualization; Funding acquisition; Methodology; Resources; Software; Supervision; Validation; Writing – review & editing

Study 2: Kilian Knauth, David Mathar, Bojana Kuzmanovic, Marc Tittgemeyer, Jan Peters: *Erotic cue exposure increases neural reward responses without modulating temporal discounting* (2023); Imaging Neuroscience

Kilian Knauth: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data Curation, Writing - Original Draft, Writing - Review & Editing, Visualization

David Mathar: Conceptualization, Methodology, Software, Validation, Writing - Review & Editing

Bojana Kuzmanovic: Software, Resources, Writing - Review & Editing

Marc Tittgemeyer: Resources, Writing - Review & Editing

Jan Peters: Conceptualization, Methodology, Validation, Resources, Writing - Review & Editing, Supervision

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Sprachkenntnisse	Deutsch: Muttersprache Englisch: Verhandlungssicher Spanisch, Französisch: Grundkenntnisse
EDV	Microsoft Office: Sehr gute Kenntnisse Matlab, R: Sehr gute Kenntnisse Python: Grundkenntnisse

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VERÖFFENTLICHUNGEN (Auswahl)

- Knauth, K., & Peters, J. (2022). Trial-wise exposure to visual emotional cues increases physiological arousal but not temporal discounting. Psychophysiology, 00, e13996. https://doi.org/10.1111/psyp.1399
- Kilian Knauth, David Mathar, Bojana Kuzmanovic, Marc Tittgemeyer, Jan Peters; Erotic cue exposure increases neural reward responses without modulating temporal discounting. Imaging Neuroscience 2023; 1 1–25. doi: https://doi.org/10.1162/imag_a_00008
- Smith E, Michalski S, Knauth KHK, Kaspar K, Reiter N, Peters J. Large-Scale Web Scraping for Problem Gambling Research: A Case Study of COVID-19 Lockdown Effects in Germany. J Gambl Stud. 2023 Sep;39(3):1487-1504. doi: 10.1007/s10899-023-10187-1. Epub 2023 Jan 27. PMID: 36707481; PMCID: PMC9882744.

Bonn, 21. Oktober 2023

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