

UNIVERSITÄTSKLINIKUM HAMBURG-EPPENDORF

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Psychophysiological investigation of the mechanisms underlying successful cognitive and emotional aging

Dissertation

zur Erlangung des Doktorgrades Dr. rer. biol. hum.
an der Medizinischen Fakultät der Universität Hamburg.

vorgelegt von:

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Hamburg 2016

(wird von der Medizinischen Fakultät ausgefüllt)

**Angenommen von der
Medizinischen Fakultät der Universität Hamburg am: 4.5.2016**

**Veröffentlicht mit Genehmigung der
Medizinischen Fakultät der Universität Hamburg.**

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1. Introduction

As a consequence of decreasing birth rates and an increased life expectancy, western populations are facing tremendous demographic changes. Recent population forecasts for Germany (Statistisches Bundesamt, 2015) predict that despite continuous, high immigration flows, the overall population will shrink about 10% between 2013 and 2060, while the number of individuals over the age of 65 will increase by more than 37%. Serious economic and social implications are arising from the rapidly aging population. For instance, while aging involves an increased risk for developing physical diseases, changes in cognitive and emotional functioning are also affecting healthy elderly individuals (Grady, 2012; Mather, 2016). These changes need to be well-characterized so that strategies and intervention programs can be planned which can help older people to participate in the society's social and professional life as long as possible. Such participation will be essential in order to maintain economic stability and to further enhance integration and prevent conflicts between the different generations.

The present thesis aimed to further characterize age-related changes in the processing of affective information and how these changes may be modulated by the perseverance of fundamental cognitive abilities. Specifically, the thesis focused on changes in attention to emotional information and on impulsive decision-making. Since elderly people are progressively confronted with negative information related to limitations and losses in cognitive, physical and social domains, it is crucial to investigate how elderly people might cope successfully with such information. Another central issue in old age is the loss of autonomy, which is critically determined by the ability to remain capable of making rational decisions. Making rational decision, in turn, depends on the ability to control emotional impulses that may be disadvantageous in

the long run. Consequently, it seems important to investigate potential alterations of impulsive decision-making across the lifespan as well as modulatory factors that may diminish such unfavourable choice tendencies in aging.

To study these topics, a multimodal approach was used in which specific behavioural paradigms were designed and investigated with different psychophysiological techniques, including functional magnetic resonance imaging (fMRI) and eye-tracking. Ample evidence indicates that age-associated changes in cognitive functions are paralleled by changes in task-related brain activity that may be addressed with fMRI (for a detailed description of this method, see 3.3.). At the same time, eye-tracking can be helpful to characterize age-related changes in the distribution of attention towards emotional information (see 3.2.). In the following sections, the current state of research on age-related changes in affective processing and potential modulators will be reviewed.

1.1. Age-related changes in emotional well-being

In light of physical changes, alterations in cognitive performance, limited time-horizons and the loss of close friends and partners, it could be speculated that older adults increasingly experience negative emotions in their daily lives. Surprisingly, however, studies report that the frequency of experiencing negative affect actually decreases in healthy aging (Carstensen, Pasupathi, Mayr, & Nesselroade, 2000). Moreover, evidence from large telephone-surveys in the United States indicates that well-being shows a u-shaped profile with an increase after the age of 50, while anger shows a steady decline across the lifespan (Stone, Schwartz, Broderick, & Deaton, 2010). Interestingly, recent trends of increasing well-being after middle age onwards have even been observed in non-human primates, possibly pointing to a more generalized phenomenon associated with aging (Weiss, King, Inoue-Murayama, Matsu-

zawa, & Oswald, 2012). Despite such general trends, individual courses of well-being may strongly vary depending on the country of residence (Steptoe, Deaton, & Stone, 2015), health and socioeconomic status, social roles and behaviours (Read, Grundy, & Foverskov, 2015; Ryff, 2014) and possibly on cognitive resources that are needed to implement strategies to maintain well-being.

Lifespan theories have provided several possible reasons for a change in affect across the lifespan: According to the *Socioemotional Selectivity Theory* (Carstensen, 2006; Carstensen, Isaacowitz, & Charles, 1999), increases in well-being along with greater preferences for emotional meaningful social contacts (Charles & Carstensen, 2010) may be caused by increased perceptions of a limited life-time perspective in old age. Specifically, the theory argues that when lifetime is perceived to be running out, a shift occurs in motivational priorities away from future-orientated goals towards the maintenance of emotional meaning and well-being (Carstensen, 2006). In contrast, when the end of life seems farther away in young adulthood, goals are more likely to be preparatory and more strongly emphasize gathering information, experiencing novelty and expanding knowledge. Supporting this idea, primed fragility of lifetime in the face of life-threatening events (Fung & Carstensen, 2006) or disease (Carstensen & Fredrickson, 1998) has been found to increase the focus on emotional meaning even in younger age. Another discussed reason for increases in well-being and socioemotional selectivity might be a greater long-term experience in dealing with emotional situations that may increase older adults' effectiveness in handling emotional situations and the anticipation of feeling states (Blanchard-Fields, 2007). Moreover, age-associated inabilities in exerting control on external circumstances might lead older adults to adapt and focus more on the regulation of internal emotional states, thus causing less frustration and greater emotional stability (Haase, Heckhausen, & Wrosch, 2013).

1.2. Age-related changes in emotional selectivity

While providing different reasons for a change in motivational preferences, lifespan theories commonly assume that successful aging goes along with an optimization of emotional processing and an increased focus on emotion regulation. Interestingly, a growing body of research suggests that the ability to regulate emotion remains stable and may even improve across the adult life span (e.g. Carstensen et al., 2011). Along those lines, older adults recover more quickly from negative emotional states and maintain positive states longer than younger adults (e.g. Charles & Carstensen, 2008).

At the same time, numerous studies using a variety of experimental methods have provided fairly consistent evidence for a so-called *positivity effect* in older adults' emotional information processing (for a discussion on the reliability of the effect see Reed & Carstensen, 2012). The positivity effect refers to a heightened processing of positive relative to negative information in older as compared to younger adults. For instance, when presented with pairs of an emotional and a neutral image, older versus younger adults devote relatively more attentional resources to positive over neutral items (Brassen, Gamer, & Büchel, 2011; Isaacowitz, Wadlinger, Goren, & Wilson, 2006a) and attend comparatively less to negative ones (Isaacowitz, Wadlinger, Goren, & Wilson, 2006b; Knight et al., 2007) even when presented as task-irrelevant (Lee & Knight, 2009; Mather & Carstensen, 2003; Orgeta, 2011). Furthermore, memory studies demonstrated that older adults may construct past and future episodic events with less episodic detail but in more positive terms than younger adults (Gallo, Foster, & Johnson, 2009; Kennedy, Mather, & Carstensen, 2004; Schlagman, Schulz, & Kvavilashvili, 2006; Szpunar, Addis, & Schacter, 2012). In fact, despite age-related memory decline for neutral and negative information, older adults'

memory for positive information may sometimes be restored to the level of younger adults (Charles, Mather, & Carstensen, 2003; Mather & Knight, 2005). In the context of decision-making, it was found that older adults increasingly rely on positive choice attributes at the time of the decision and when recalling them later (Kim, Healey, Goldstein, Hasher, & Wiprzycka, 2008; Löckenhoff & Carstensen, 2008; Mather & Johnson, 2000). In addition, they tend to show significant reductions in their post-decisional regret responsiveness (Brassen, Gamer, Peters, Gluth, & Büchel, 2012).

1.3. Modulators of emotional selectivity

It has been speculated that the positivity effect might be an expression of increased emotion regulation in aging as postulated in aforementioned lifespan theories. In detail, according to the *cognitive control hypothesis* (Mather, 2012; Mather & Carstensen, 2005), older in comparison with younger adults might increasingly engage top-down control to focus on positive and to disengage from negative information in order to protect well-being. Arguing from a different perspective, the *aging brain model* states that the positivity effect may instead reflect a greater insensitivity towards negative information due to detrimental age-effects on amygdala functioning (Cacioppo, Berntson, Bechara, Tranel, & Hawkley, 2011), which is a key structure involved in emotional information processing.

Inconsistent with the aging brain model, there is broad evidence that the structure of the amygdala remains relatively well preserved in aging (Mather, 2016). In addition, functional imaging studies have demonstrated that although the amygdala may respond less to negative stimuli in older as compared to younger adults, it tends to respond more strongly to positive stimuli (Mather, 2016). These findings advocate a shift in amygdala responding rather than a detrimental change. At the same time, other neuroimaging studies have found the positivity effect to be paralleled by en-

hanced activity in key nodes of the emotion regulation network in older adults, including the ventromedial prefrontal cortex (VMPFC) and the anterior cingulate cortex (ACC) (Brassen et al., 2011, 2012). Further support for the cognitive control hypothesis has been provided by some behavioural studies, which have linked higher levels of cognitive functioning with an amplified positivity effect in memory (Mather & Knight, 2005; Petrican, Moscovitch, & Schimmack, 2008; Simón, Suengas, Ruiz-Gallego-Largo, & Bandrés, 2013; but see Rösler et al., 2005). Moreover, studies have indicated that the effect may be diminished when cognitive resources are exhausted by a secondary task (Brassen et al., 2011; Knight et al., 2007; Mather & Knight, 2005; for conflicting results see Allard & Isaacowitz, 2008).

Yet, the assumption that elderly individuals spontaneously exercise more cognitive control than younger adults to disengage from negative and to focus on positive information seems quite paradoxical, given that in a non-emotional context, such function typically shows decline in aging. Along those lines, findings suggest that while elderly people are generally capable of applying top-down knowledge to guide attentional processing (Madden, 2007), they often show age-associated impairments in executing attentional control to override distraction from unwanted, salient stimuli (e.g. Kramer, Hahn, Irwin, & Theeuwes, 2000; Madden et al., 2014; Tsvetanov, Mevorach, Allen, & Humphreys, 2013; Whiting, Madden, & Babcock, 2007a; for conflicting findings see e.g. Colcombe et al., 2003; Costello, Madden, Shepler, Mitroff, & Leber, 2010; Lien, Gemperle, & Ruthruff, 2011). Moreover, very consistent decline has been reported when attentional control needs to be engaged in a flexible manner in tasks that require simultaneous information processing and where attention needs to be flexibly disengaged and reallocated from one information to the other (Clapp, Rubens, Sabharwal, & Gazzaley, 2011; Verhaeghen & Cerella, 2002; Verhaeghen, Steitz, Sliwinski, & Cerella, 2003). Such function is particularly crucial when

information becomes more complex. Neural evidence indicates that these deficits in attentional control are associated with decreased coherence (Campbell, Grady, Ng, & Hasher, 2012) and functional efficiency in frontal and fronto-parietal networks (Chadick, Zanto, & Gazzaley, 2014; Madden et al., 2007, 2014). Yet, it should be noted that there is usually substantial variability in the decline of executive control functions, including attentional control, and in the underlying neural networks (Glisky, 2007; Zanto & Gazzaley, 2014). These findings advocate that some elderly people might be better than other at mobilizing attentional control resources for their emotional goals and suggest that there may possibly be crucial differences in the positivity effect between older individuals.

Another potential modulator of the degree to which elderly people are willing to exert control over emotional processing may be the self-relevance of the stimulus material. Specifically, emotional material that confronts elderly people with negative information that is more strongly referred to the self might increase the need for emotion regulation to protect well-being. Such self-relevance manipulations may, for instance, be operationalized by the use of emotional images depicting people of the same age in age-relevant emotional scenarios (e.g. older people at a funeral vs. younger people in a brawl). It has previously been demonstrated that images depicting individuals of the same age group tend to be preferentially processed (e.g. Ebner, He, & Johnson, 2011; Ebner & Johnson, 2010; He, Ebner, & Johnson, 2011) and in a more self-referential fashion (Ebner et al., 2013; Ebner, Gluth, et al., 2011) in younger and older age. Moreover, there is broad evidence that as a consequence of heightened self-referential processing, emotional situations happening to people that are more similar to the self typically attract stronger empathic, emotional reactions in the observer (reviewed by Chiao & Mathur, 2010).

Study I aimed to further investigate the impact of attentional control in the context of the positivity effect and assess the role of a) individual attentional control abilities and b) self-relevance of the stimulus material as potential modulators of the effect. The specific hypotheses will be presented in the following chapter (2).

1.4. Impulsive choice

Cognitive control over affective processing is also fundamental in the context of decision-making when emotional impulses need to be inhibited that may lead to undesirable consequences. In fact, impulsive behaviours are a characteristic feature of various psychiatric disorders with marked deficits in self-control, such as addictive disorders (Bickel, Koffarnus, Moody, & Wilson, 2014; MacKillop et al., 2011), borderline personality disorder (Barker et al., 2015), bipolar disorder and schizophrenia (Ahn et al., 2011). Impulsive behaviour can be broadly defined as behavioural actions without adequate forethought and is often assessed in so-called intertemporal choice scenarios. Respective scenarios require participants to choose between a smaller immediate reward versus experiencing a delay for a larger reward. Such choices are often investigated with monetary sums, e.g. 20 € now versus 25 € in two weeks. Yet, intertemporal choices are encountered in various domains in life, including health, education and everyday choices for food. For example, imagine you are hungry and looking for a place to eat: Would you rather go to a restaurant with an open table now and acceptable food or wait for another hour to be seated in your favourite restaurant? In this context, it is important to note that the degree to which individuals exhibit impulsive behaviour in one domain tends to be predictive of such behaviour in other domains, thus making intertemporal choice tasks a good measurement for impulsivity (Peters & Büchel, 2011).

The mechanism underlying impulsive intertemporal choices is that the costs associated with reward typically lead to a decay of the subjective value (SV) of the reward over time. Such phenomenon is termed temporal (or delay) discounting (Soman et al., 2005). Many studies suggest that such time-dependent SV decay follows a hyperbolic curve (Mazur, 1987) where the discount factor (k) decreases with the length of the delay. For example, waiting from today to tomorrow involves more loss of value than waiting from twenty days to twenty-one days (two exemplary hyperbolic discounting functions are depicted in Figure 1). The hyperbolic model has been found to be a reliable model to describe individual discounting behaviour in humans and animals, which allows the detection of subtle differences in impulsivity between different individuals and within individuals in specific situations (Peters & Büchel, 2011).

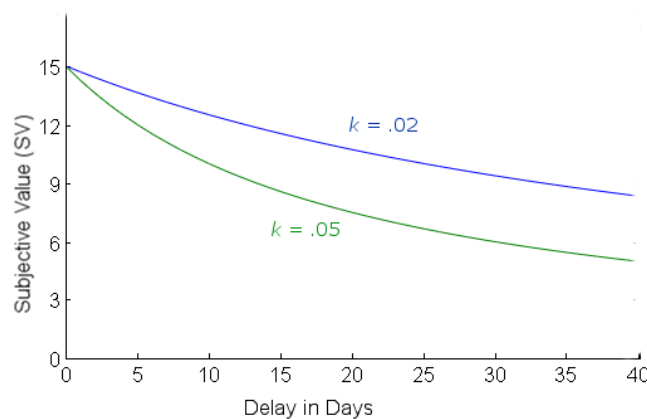


Figure 1. Two hyperbolic discounting curves depicting a higher (green) and a lower (blue) temporal discounting rate.

Individual discounting factors can be used to compute individual SVs for different reward options to investigate how the brain processes such SVs using functional brain imaging. Evidence shows that the SVs of immediate and delayed monetary rewards tend to be tracked by a common value network consisting of the ventral striatum, VMPFC, orbitofrontal (OFC) and posterior cingulate cortex (PCC) (Kable & Glimcher, 2007). In fact, across choice tasks, activity in these regions seems to represent a

“common currency” for choices (Levy & Glimcher, 2012). Thereby, it is assumed that the computation in nodes of such network, particularly the striatum and the VMPFC, are shaped by different neural inputs in the context of choices for immediate versus delayed rewards (Bos, Rodriguez, Schweitzer, & McClure, 2014). Specifically, choosing delayed options depends more on signals from a (self-) control network, consisting of lateral prefrontal regions and the ACC (Peters & Büchel, 2011), while responses to immediate rewards may be triggered by emotional signals in limbic regions, including the amygdala (Bos et al., 2014). Supporting that, individuals were found to choose immediate rewards more often when activation in lateral prefrontal regions was disrupted by transcranial magnetic stimulation (Figner et al., 2010), while, at the same time, steeper discounting in individuals with low levels of self-control tends to be associated with increased connectivity between the striatum and the amygdala (Peters, Miedl, & Büchel, 2013).

1.5. Age-related changes in impulsive choice

In light of a limited lifetime perspective and structural declines in prefrontal and the striatum (Walhovd et al., 2011), it could be speculated that aging might increase older adults tendency to choose smaller immediate over larger later rewards. In fact, one of the first very large studies that compared temporal discounting behaviour among younger and older adults found temporal discounting to be increased in old age (Read & Read, 2004). However, conflicting findings have argued against an age-related increase in impulsive discounting. Specifically, some studies have observed stable rates (Chao, Szrek, Pereira, & Pauly, 2009; Green, Myerson, Lichtman, Rosen, & Fry, 1996; Rieger & Mata, 2015; Roalf, Mitchell, Harbaugh, & Janowsky, 2011; Samanez-Larkin et al., 2011) and others even reported decreases in temporal

discounting with advancing age (Eppinger, Nystrom, & Cohen, 2012; Löckenhoff, O'Donoghue, & Dunning, 2011; Reimers, Maylor, Stewart, & Chater, 2009).

Yet, especially findings of decreases in temporal discounting seem to be difficult to reconcile with aforementioned findings about deficits in cognitive control. A possible explanation for such finding is that the saliency of immediate versus delayed options might decrease with advancing age. For instance, since older adults typically experience time as more compressed and fast-paced than younger adults (Löckenhoff & Rutt, 2015), the costs linked with the reward delay may be reduced in aging and consequently diminish the demands on prefrontal control. In addition, older adults could have gained positive experience with the realization of delayed rewards in the past that possibly led to adaptations in their reward systems (Samanez-Larkin, 2013). In fact, first neuroimaging findings indicate that the ventral striatum in older as compared with younger adults seems to respond less to immediate rewards (Eppinger et al., 2012; Samanez-Larkin et al., 2011). In sum, so far, evidence about age-related changes in temporal discounting is very heterogeneous and explanations are rather speculative, suggesting that further work is needed to specify age-related changes in temporal discounting. In this regard, it may be fruitful to consider inter-individual differences among older adults and further investigate modulatory cognitive factors that may account for such differences.

1.6. Modulators of impulsive choice

There is evidence that decision-making in older age becomes increasingly heterogeneous (Samanez-Larkin & Knutson, 2015). In line with that, it could be demonstrated that older adults who tend to perform worse on other decision-making tasks (e.g. the Iowa Gambling Task, measuring probabilistic learning from rewards and punishments) tend to have steeper discounting rates during intertemporal choices (Half-

mann, Hedgcock, & Denburg, 2013). Other studies have found temporal discounting in older adults to be increased as a function of age-related decline in fundamental cognitive functions, including processing speed and working memory (Boyle et al., 2012; James, Boyle, Yu, Han, & Bennett, 2015). Along similar lines, temporal discounting tends to be increased in patients with mild cognitive impairment (Lindbergh, Puente, Gray, Mackillop, & Miller, 2014). Together with findings from younger adults (Bickel, Yi, Landes, Hill, & Baxter, 2011; Shamosh et al., 2008), existing studies suggest that cognitive control may be an important predictor of temporal discounting behaviour. At the same time, independent neural findings suggest that greater tendencies to pick delayed options in older adults tend to be linked with higher grey matter volumes (Drobetz et al., 2014) and higher functional engagement (Halfmann, Hedgcock, Kable, & Denburg, 2015) in the striatum and prefrontal cortex. As noted earlier, these regions might be involved in the integration of control and other mental considerations during value assessment (Peters & Büchel, 2011).

Yet, work is missing that investigates these factors in combination to get an actual understanding about predictors of temporal discounting among older adults, i.e. by taking into account a) the function of underlying neural choice networks, b) individual levels of cognitive control and c) another factor that has not been systematically controlled in existing studies but may be similarly crucial: the degree to which older adults integrate mental representations associated with the delayed reward options (episodic simulations) in their choices.

One possible way to investigate the impact of episodic simulation on temporal discounting systematically is to compare conditions in which episodic future thinking is experimentally increased to standard monetary conditions. Respective studies have recently been conducted in younger adults. For instance, in a study by Peters and

Büchel (2010), participants performed an intertemporal choice task consisting of a range of choices between a smaller immediate and larger later reward (e.g. 20€ now or 35€ in two weeks). In the episodic condition, keywords related to forthcoming life events (e.g. Mum's birthday), individually assessed before the experiment, were 'tagged' to roughly matched delays. Comparisons of discounting behaviour in the tag condition to a condition without tags indicated that individuals were more likely to choose delayed over immediate rewards in the episodic conditions (i.e. the so-called *tag-effect*; for similar findings see Daniel, Stanton, & Epstein, 2013a, 2013b; Kwan et al., 2015; Peters & Büchel, 2010). On the neural level, discounting in the episodic condition was associated with increased neural activation in an extended episodic prospection network and increased functional connectivity between memory (i.e. the hippocampus and amygdala) and valuation regions (i.e. the anterior cingulate cortex). These findings indicate that episodic prospection linked with future rewards seems to crucially predict discounting behaviour. Yet, it is not clear whether episodic prospection might have similar beneficial effects on temporal discounting in older age and whether there might be inter-individual differences related to a) differences in future thinking ability or b) the ability to integrate such representations with choices.

In detail, there is increasing evidence that older adults show substantial decline in their capacities to simulate past and future events, which has been linked with reduced efficiency in future thinking networks (Addis, Roberts, & Schacter, 2011; Schacter, Gaesser, & Addis, 2013). However, there is typically substantial variability between older adults in their ability to remember past (Nyberg, Lövdén, Riklund, Lindenberger, & Bäckman, 2012) and imagine future events (e.g. Cole, Morrison, & Conway, 2013). In addition, the ability to imagine future events may strongly depend on prior experience with the to-be-simulated event. Specifically, unfamiliar, contextual reward settings that have to be fully constructed may be more difficult to imagine as

they place higher demands on constructive operations in the memory system. For instance, while imagining going to work (where conditions have not changed in the last four years) may largely draw on pre-experience and elements with strong associations, imagining your first day at a new job requires greater combination effort to integrate information from more disparate mnemonic sources into novel representations (Anderson, 2012; Schacter et al., 2012). Several lines of evidence suggest that the hippocampus is crucially involved in such constructive processing (Addis, Cheng, Roberts, & Schacter, 2011; Addis & Schacter, 2012). Such notion fits with its role in recombining single memory elements into novel representations (Duff, Kurczek, Rubin, Cohen, & Tranel, 2013; Rubin, Watson, Duff, & Cohen, 2014) and significant responding of the hippocampus to increased construction effort in the context of future event simulation (Benoit & Schacter, 2015; Gaesser, Spreng, McLelland, Addis, & Schacter, 2013; Okuda et al., 2003; Weiler, Suchan, & Daum, 2010). Yet, the hippocampus tends to be affected by substantial structural and functional alterations in aging (Nyberg et al., 2012; Raz et al., 2005). Consequently, it could be speculated whether older adults may be especially impaired when imagining unfamiliar future scenarios that place higher demands on hippocampal constructive processing. So far, a distinction between familiar and unfamiliar events has not been controlled in previous studies investigating the tag-effect. Yet, in line with aforementioned findings, such factor might crucially modulate the neural correlates of the effect and possibly account for observations of a tag-effect in individuals with hippocampal lesions (Kwan et al., 2015).

At the same time, elderly individuals might differ significantly in their capacity to process value and episodic information simultaneously and to integrate them both in the decision process. Specifically, it has recently been postulated that impairments in decision performance in aging might largely depend on the degree to which decisions

require the simultaneous processing of multiple information and how well control functions that enable such processing are individually preserved (Samanez-Larkin & Knutson, 2015). In a similar vein, the prominent inhibitory control hypothesis (Hasher & Zacks, 1988) has highlighted the preservation of attentional control to be particularly crucial for the dynamic processing of simultaneous information. In detail, the theory argues that when attentional control is low and individuals have difficulties to suppress unwanted information, their working memory is easily over-occupied with one type of information and unable to process other information simultaneously. Supporting that, attentional control ability was found to predict working memory functioning (Darowski, Helder, Zacks, Hasher, & Hambrick, 2008; Gazzaley, Cooney, Rissman, & D'Esposito, 2005) as well as performance in various higher-order tasks (Weeks & Hasher, 2014). As mentioned earlier, several studies have suggested that executive control functions constitute a significant modulator of intertemporal choice behaviour in old age (e.g. Bickel et al., 2011; Boyle et al., 2012; James et al., 2015; Shamosh et al., 2008). It could thus be speculated that individuals with high executive control abilities might have been better at integrating previously uncontrolled mental representations about future rewards in their choices.

In sum, there seems to be substantial variability between older adults' behaviour in intertemporal choice tasks. Studies in younger adults have highlighted the impact of episodic prospection on individual discounting behaviour but these effects have so far been neglected in studies with older adults. Yet, there might be crucial differences between older adults depending on the extent to which older adults engage in episodic prospection during the valuation of future rewards and how well they can imagine these contextual reward setting. The ability to imagine future scenarios might in turn depend on the related construction effort and on the individual preservation of relevant neural structure. In addition, perseverance of executive control functions in

aging, particularly attentional control, might crucially mediate the ability to incorporate episodic signals with intertemporal choices. **Study II** and **III** aimed to further investigate these effects and their neural basis. The specific hypotheses for the studies will be presented in the following sections.

2. Summary and hypotheses

In the previous sections, the current state of research regarding age-effects on emotional information processing and impulsive decision-making was reviewed. It was demonstrated that older in comparison with younger adults seem to prioritize emotional goals more and show an increased preference for positive over negative emotional information. It has been postulated that this positivity effect is resulting from an increased voluntary use of attentional control to focus on positive and avoid distressing information but this assumption requires further investigation. At the same time, there is rather inconsistent evidence regarding age-effects on impulsive choice behaviour and recent studies highlight that there may be substantial variability between older adults. The studies of the present Phd project aimed to further characterize age-effects on emotional selectivity and impulsive choice by considering the impact of potential modulatory cognitive and motivational factors.

In detail, **Study I** was conducted to further address the role of attentional control and the impact of personal relevance of the presented information on the positivity effect in aging. To this aim, attentional preferences were compared between younger and older adults via eye-tracking in a set-up in which attention across positive, negative and neutral stimuli, presented in triads, could be voluntarily distributed. Such set-up requires cognitive control to focus on preferred and ignore unwanted information.

Self-relevance of the depicted material was varied to test whether this would increase motivated, selective processing in aging. Precisely, material that tends to be more strongly referred to the self might increase the need to disengage from negative material to protect a positive view on the self and one's well-being. Consequently, it was hypothesized that if the positivity effect indeed reflects voluntary, controlled preferences, the effect should be a) increased for self-relevant material and b) more strongly pronounced in individuals with higher ability to focus attention in the face of distracting information (as measured by the singleton task, see 3.1.).

The second part of the Phd project focused on impulsive decision-making and the modulatory role of cognitive factors, including episodic prospection and executive control, on individual discounting rates in young and older age.

Study II was conducted to study neurobehavioral effects of episodic prospection on impulsive choice in a sample of younger adults to validate whether respective experimental manipulations may be a suitable tool to study such effects in older age (Study III). The discounting paradigm manipulated episodic prospection by linking future monetary rewards to prospective episodic events. It was hypothesized that the neurobehavioral integration of mental simulations linked with delayed rewards would lead to reductions in temporal discounting (tag-effect). Moreover, it was speculated that the degree to which the prospective event relies on prior experience might significantly impact on the size of the tag-effect and its neural basis. Specifically, the hippocampus might critically mediate the construction of unfamiliar future events and the valuation of associated rewards, while neural networks related to autobiographical memory retrieval might have a larger impact on the tag-effect when events are closely linked with prior experience.

In **Study III** the paradigm of Study II was applied in a sample of older adults to systematically study previously uncontrolled effects of episodic prospection on their discounting behaviour. Individual levels of attentional control ability (assessed with the singleton task, see 3.1.) and imagination richness were investigated as potential modulators of the tag-effect in older age. The main hypothesis was that the impact of episodic prospection on choice behaviour would be more heterogeneous in the older compared to the younger group. Yet, variability in the size and in the neural manifestation of the tag-effect in old age may be explained by a) the fluency of episodic simulation and/or b) individual levels of attentional control. Specifically, perseverance of such function in aging is known to be an important modulator of complex cognition and might significantly facilitate the simultaneous processing episodic and value information.

In the following methods section, a description of the singleton task used to assess individual levels of attentional control in **Study I** and **III** as well as a brief overview of the applied methods (i.e. eye-tracking, fMRI and computations modelling) and analyses will be provided. Afterwards, the specific task designs of **Study I, II** and **III** are briefly described together with individual summaries of the study results (see 4., 5., 6.).

3. Methods

For the three studies, participants were recruited via online announcements and from an existing database. Younger participants were between 18 and 30 years of age and elderly participants were aged between 60 and 78 years. All elderly participants lived independently. Moreover, participants had normal or corrected-to-normal vision

(including colour vision) and no present or previous neurological or psychiatric disorders. Older adults were screened with the neuropsychological battery of the Consortium to Establish a Registry for Alzheimer's Disease (Welsh, Butters, Hughes, Mohs, & Heyman, 1991) including the Mini-Mental State Examination (all participants > 28). In addition, all participants received screenings with the Beck's Depression Inventory and Eyesenk Personality Questionnaire to rule out the presence of relevant depressive symptoms. Participants were financially compensated for their participation.

In the following sections, the main techniques used to acquire and analyse the data will be described. The experimental paradigms used in the three studies are briefly summarized in the next chapter and described in more detail in the respective papers. Experiments were all computer-based presented with the Presentation software (Neurobehavioral Systems©), except the singleton task, which was presented with Cogent 2000 stimulus presentation software (Wellcome Department of Imaging Neuroscience, London, UK) in MATLAB (Mathworks©). For the behavioral analyses, MATLAB and SPSS (IBM©) were used. Analysis of the eye-tracking data was conducted in R (www.r-project.org). fMRI data were pre-processed and analyzed using statistical parametric mapping (SPM8; Wellcome Department of Imaging Neuroscience, London, UK).

3.1. Attentional control (singleton) task

In **Study I** and **III**, the influence older adults' attentional control ability was examined as a potential modulating factor of emotional selectivity and the tag-effect in aging. In the following, I will briefly describe the intentions for using a specific computerized singleton task for this purpose and how a single score can be derived from this task. A more detailed description can be found in the published manuscript of **Study I** (Sasse, Gamer, Büchel, & Brassens, 2014).

The singleton task is a well-established visual search task requiring participants to search for a visual target stimulus (e.g. a green circle displayed against a black background) that is surrounded by non-targets differing in a specific dimension, such as shape, from the target (e.g. green squares) (Theeuwes & Burger, 1998). The non-targets may contain a singleton stimulus (e.g. a red square), which differs from the target and the non-targets with one unique feature that consequently stands out from the other stimuli, i.e. having a different colour than the target and non-targets but the same shape as the non-targets. In order to respond accurately to the target, participants may use top-down knowledge about the defining target feature (i.e. searching for a circle) and strategically blank out the singleton dimension (i.e. focusing only on the shape dimension and blank out the colour dimension) so that the demands on flexible attentional control remain relatively low. In fact, in comparison with younger adults, elderly individuals sometimes increasingly rely on such strategic top-down attentional guidance (i.e. focusing extremely on only one dimension) during visual search to counteract their deficits in flexible attentional control abilities (Madden, 2007).

However, in line with the inhibitory control hypothesis (Gazzaley, Knight, & Stuss, 2013; Hasher & Zacks, 1988) age-related impairments in the ability to flexibly disengage attention from information, once it has been captured, may be particularly critical for performance in more complex and naturalistic tasks. To address such function, the singleton task has recently been modified by Costello and colleagues (Costello et al., 2010). The authors introduced a condition in which the singleton distractor could not be strategically ignored and attentional control needed to be actively applied on a trial-by-trial basis. Specifically, in this condition the singleton distractor possessed a potential task-relevance so that it had to be processed first before being actively suppressed. In order to derive a pure score of flexible attentional control abil-

ity, a distraction score was computed that measured the amount of distraction from the singleton stimuli in the flexible condition, which was then set in relation to distractibility in the baseline condition (i.e. the amount of distraction from the singleton in the condition where the singleton could simply be blanked out). The computation of this score is further illustrated in the published manuscript of **Study I** (Sasse et al., 2014).

Crucially, such computation makes it unlikely that the score is confounded by age-related declines in processing speed (Salthouse, 1996). It has been argued that declines in processing speed may be the main reason behind age-deficits in attentional control and higher cognitive functions. Yet, it should be noted that although this factor has been found to mediate some cognitive functions in aging (Salthouse, 2000, 2010), several studies have provided evidence for persistent age-related impairments in the attentional control that were independent of changes in processing speed (Zanto & Gazzaley, 2014).

3.2. Eye-tracking

During the inspection of scenes, objects or words, eye-movements are constantly performed (every 200-350 ms) to move the fovea (the high resolution part of the retina) to specific areas of interest or greater saliency (Rayner, 1998). During the actual eye movement (or saccade), vision is suppressed and new information is processed only during the time when the eyes remain relatively still on a certain spot (fixation) (Rayner, 1998). Although fixations are only indexes of overt attention (Posner, 1980), overt and covert attention (attentional shifts occurring independent of head or eye-movements) tend to be tightly linked, especially during the viewing of scenes (de Haan, Morgan, & Rorden, 2008; Henderson, 2003). Thus, number and duration of fixations on specific positions in the visual field can be helpful to reveal information

about the distribution of visuospatial attention in respect to specific visual information (e.g. images of positive negative and neutral social scenes in Study I).

The best established method to measure visuospatial attention is eye-tracking via the pupil-and-corneal-reflection method (Holmqvist et al., 2011). For instance, within a stable eye-tracking system used in **Study I** (EyeLink 1000, SR Research, Ontario, Canada), the head location is fixed through a chin rest and a forehead bar while the participant watches stimuli through a tilted, semi-transparent mirror on a computer screen in front of him. The mirror is transparent from the viewing position of the participant but functions as a mirror from another angle. The mirror reflects the light from an infrared source and illuminates the participants' eye. At the same time, the mirror image of the eye is being video-based recorded by an infrared sensitive camera. The infrared light produces a solid contrast between pupil and the surrounding iris that enables the identification of the pupil in the video recordings. In addition, the infrared light tends to be reflected in a very bright, condensed light spot on the cornea (the corneal reflection), which offers an additional reference point to the pupil (Holmqvist et al., 2011). The relation between the centre of the pupil and the corneal reflection can be used for a more robust calculation of the gaze position (i.e. the relation is different depending on gaze positions in the screen).

In order to get valid information, the eye-tracker needs several examples how spatially distributed points in the to-be-tracked area correspond to specific pupil-corneal-reflection relations (Holmqvist et al., 2011). This step is typically done in a calibration procedure right before the experiment. Recorded gaze directions are transferred to a coordinate system, so that they can later be analysed with respect to specific regions of interest in the visual field (e.g. the area where a specific image was presented on the screen). In order to account for time-dependent drifts in horizontal and vertical

coordinates during an experiment, the coordinate system can be adjusted to a reference point of the coordinate system before each trial (e.g. average gaze position one a fixation cross before the trial onset). If such reference point is unavailable or invalid (e.g. due to blinks or because participants looks away), a drift correction procedure can be applied for adjustment.

Fixation points and intervening saccades can be defined using a set of heuristics. According to default configurations, an eye movement is classified as a saccade when it exceeds $30^\circ/\text{sec}$ velocity or $8000^\circ/\text{sec}^2$ acceleration. The intervening episodes are defined as fixation events. In **Study I**, the number of fixations as well as the cumulative fixation duration on three regions of interest on the screen was analysed (i.e. the position of the positive, negative and neutral image). The number of fixations was divided by the total number of fixations and the durations were divided by the total fixation time (excluding blinks and saccades) to exclude potential age-effects on these measures.

3.3. FMRI

3.3.1. Physiological background

FMRI is a non-invasive brain imaging technique that has matured as the most prominent research modality in cognitive neuroscience (Singleton, 2009). The following section will only provide a condensed account of the main underlying mechanisms. A more detailed description can be found in the work of Huettel and colleagues (Huettel, Song, & McCarthy, 2008).

FMRI builds on the fact that when an area in the brain gets activated, energy is consumed, which increases the blood flow to that area. Haemoglobin is a protein in the red blood cells that binds oxygen. Thus, an increased blood flow indirectly causes an

increased oxygenation of the blood according to the following time-course (the so called haemodynamic response function, HRF): After an initial dip in the blood oxygen level shortly after stimulation, the hemodynamic response increases after about 2 seconds, reaching its plateau approximately 6-12 seconds later. As the signal then returns to baseline, a short post-stimulus undershoot is often obtained (Logothetis, 2002; Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001). The haemodynamic response is modelled by the *Blood oxygen level dependent* (BOLD) contrast, which is based on the fact that oxygenated and desoxygenated blood have different magnetic properties that differentially interfere with the surrounding magnetic field present in the MR scanner. The physical mechanism is described in the following.

The MR scanner generates a static external magnetic field (B_0) oriented in the z-direction. Hydrogen nuclei in the human tissue have a so-called spin, which is oriented in the presence of the static magnetic field, either in parallel or in antiparallel direction (towards the z-direction). There is a slight imbalance in the population towards the parallel orientation, which has a lower energy state. In particular, the degree of imbalance is dependent on the external magnetic field (here: 3T magnet). This imbalance induces a net magnetization of the sample. An external radiofrequency (RF) pulse can manipulate this net magnetization to change from a longitudinal magnetization into a transverse magnetization (in x-y direction). Specifically, the pulse causes the nuclei to spin in a coherent phase, which causes a transverse magnetization, and their precession movement induces a measurable electric current in the receiver coil (the MR Signal). Spatially variable magnetic fields in the three principle directions (magnetic gradient fields or gradients) are used to locate the signal according to its spatial origin. Three mechanisms can cause the MR signal to decay over time: a) a quick decay of transverse magnetization due to inhomogeneity in the magnetization of the atoms, b) a slightly slower decay of transverse magnetization due to spin-spin

interactions (interference with the background magnetic fields of neighbouring atoms) and c) a slow recovery of the longitudinal magnetization component. Differences in the signal strength due to inhomogeneity are detectable after a relatively short time ($T2^*$) and are strongly influenced by the oxygenation of the environment. Pulse sequences can be optimized to detect differences in the decay of the MR signal in different areas that are mainly resulting from oxygenic differences. The most commonly and widely used type of $T2^*$ -weighted MR sequences is Echo Planar Imaging (EPI), which is a very high frequent sequence optimized for event-related designs as used in **Study II** and **III**.

Furthermore, nuclei in the different types of brain tissue (grey, white matter and liquor) show substantial differences in the longitudinal recovery component of the MR signal ($T1$ describes the time point when 65% of the longitudinal magnetization is build up after the pulse). Such signal differences can be detected with longer repetition times between pulses ($T1$ optimized sequences). $T1$ weighted images thus provide much higher anatomical resolution than EPI images ($T1$ often has a spatial resolution of $1\text{mm} \times 1\text{mm} \times 1\text{mm}$, while the resolution of EPIs is typically between 2 or 3 mm^3). At the same time, $T1$ images are insensitive to changes in oxygenation of the blood. A typical fMRI scanning session as conducted in the context of this dissertation includes a $T1$ structural image and an EPI series. The three-dimensional structural $T1$ image can be used to transfer the EPI time series into a normalized space (as will be described in the following).

3.3.2. Image processing

Raw EPI time series have to be “pre-processed” to increase the signal to noise ratio in the data before statistical analyses can be performed. The typical steps, which were applied to the studies of the present dissertation, include temporal and spatial

realignment of the functional images, co-registration of a T1 weighted image with the EPIs, normalization of all images to MNI space and smoothing of the images. The single steps will be briefly described in the following.

Slice-timing is based on the fact that a whole brain volume is not acquired at the same time, but in horizontal slices within the time between two pulses (e.g. in the present study, the repetition time, TR, was 2.46 seconds). Consequently, the BOLD signal at different layers is sampled at slightly different time points. To correct for such temporal offset, an interpolation procedure is used to align the slices to the time point of the reference slice based on “activity” in these volumes adjacent in time. Such procedure is particularly important in so-called event-related study designs, in which the timing of specific events is very important.

After having realigned the different slices in time, the EPI time series has to be realigned in space. Although participants are instructed to remain still in the scanner, slight head movements are practically inevitable and even the smallest displacements can substantially impair the results. A rigid body transformation can help to map (or co-register) all volumes of the EPI series to a reference volume (usually the first or the middle volume) in six possible movement directions (pitch, roll, yaw). EPIs may be spatially distorted around air filled cavities that can cause inhomogeneity in the magnetic field. Movement may lead to an expansion of these distortions. To attenuate this effect, an “unwarping” procedure can be applied that may be particularly advantageous when ventromedial prefrontal regions are of interest as in **Study II** and **III**.

As mentioned earlier, a high-resolution T1 weighted image can help to improve the normalization of the EPIs to a standard Montreal Neurological Institute (MNI) space. Therefore, the T1 image first needs to be spatially co-registered to the EPI images

using rigid body transformation. The co-registered T1-image can be segmented into grey matter, white matter and cerebrospinal fluid based on probability maps. The grey matter segments of each participant are then mapped or to a standardized brain template. In the present studies, this normalization step was done by using a Diffeomorphic Anatomical Registration Through Exponentiated Lie Algebra (DARTEL, Ashburner 2007) procedure, which is a high dimensional warping process that considers more warping parameters than traditional 12-parameter normalization procedures and uses a normalization (the MNI template from the VBM8 toolbox) that is built on a large sample of healthy individuals (n = 590, age =20-85). The individually extracted transformation parameters are used to bring the EPI images into the normalized space. Simultaneously, a so-called “smoothing” procedure can be applied to the data in order to improve the signal-to-noise ratio and achieve more normally distributed intensity maps. In this process, a Gaussian filter of a specific width (six millimetres full width at half maximum in Study II and III) is laid over the intensity maps.

3.3.3. Statistical analysis of fMRI data

The statistical analysis of fMRI data is split up into two levels: On the first level, a single-subject fixed effects analysis is computed on the pre-processed EPI time series. Resulting variances and parameter estimates are incorporated into a second-level random effects group analysis that allows inferences on the respective population.

fMRI designs can have event or block designs. Block designs are used when neural activity during a whole block is of interest. Instead, event related designs allow inferences about activity during specific events in a block. In the design of **Study II** and **III**, experimental conditions were parsed into blocks, but specific events rather than the whole time span of the block was of interest (i.e. only the time between the option presentation and the choice was of interest). In order to conduct a first level analysis

for such an event-related design, onsets of the events that are of interest for a certain condition have to be extracted for the EPI time-series. Resulting vectors are entered as regressors into a general linear model (GLM) on the single-subject level. Based on the aforementioned theoretical model of the BOLD signal, the stick or box car function (depending on whether the onset is assumed to have a certain duration or not) is convolved with the HRF.

In order to test whether the BOLD signal in the adjacent onset regressor co-varies with a time-varying variable, it is possible to specify a parametric modulator for a specific onset regressor (i.e. a vector with different values for each onset) and include it in the GLM. For instance, in the context of temporal discounting such technique can be applied to investigate whether the subjective value (SV) of the delayed reward option, varying from trial to trial, co-varies with the BOLD signal in a certain condition (i.e. to investigate neural value processing). The computation of the SV for each trial is further explained in 3.4.

During the estimation of the first-level GLM, procedures are applied that account for temporal autocorrelation between the EPIS. Moreover, regressors are computed separately for different sessions and a session constant is included in the GLM to statistically control for altered average BOLD responses in different sessions. The estimated single-subject GLM is then used to compute individual contrast images for the conditions of interest (e.g. by contrasting one condition regressor with another one). There are two types of contrasts that can be computed on the first and later also on the second level GLM: t-contrasts and F-contrasts. The F-contrast is a two-tailed test that informs about whether a significant effect is present or not, while directionality (one-tailed hypotheses) can only be tested using t-contrasts. After the contrasts are estimated on the single-subject level, they can be taken to the second level

to be inserted into a random-effects analysis that allows inferences about significance of the contrasts across the whole group. Correlations between individual contrasts and between-subject measures (e.g. with the singleton control score in Study III) can be performed by including such measure as a covariate at the second level.

In order to test the significance of effects on the second level, tests are performed on a voxel-by-voxel basis. This results in a huge number of statistical tests that need to be accounted for by multiple comparison corrections. A prominent approach is the family-wise error correction (FWE) on the voxel-level as implemented in SPM8. This approach is well suited to correct the significance in studies in which the whole brain is investigated. However, often a priori hypotheses exist concerning the involvement of specific regions based on previous evidence and correction can be limited to these areas. Regions of interest can thereby be anatomically defined by using specific brain atlases or as a sphere (or box) around peak activations reported in previous studies.

3.3.4. Psychophysiological interaction (PPI) and neural coupling

Apart from the investigation of how individual brain areas are independently involved in a task, it is also possible to analyse how connectivity between brain areas changes in response to certain task conditions (O'Reilly, Woolrich, Behrens, Smith, & Johansen-Berg, 2012). Precisely, it may be interesting to investigate whether activity in a predefined seed region of interest is correlated with activity in another region in the brain (neural coupling). In addition, it could be of interest to test whether such connectivity is dependent on the value of a task-related psychological variable (PPI; Friston et al., 1997). For a PPI analysis, three regressors have to be estimated in first-level GLM: (1) a regressor for the time course of the activity in the seed region (deconvolved from the HRF), (2) the psychological variable of interest, which is folded

with the haemodynamic response function, and (3) the product of the former two regressors (the PPI regressor). When entering only the time course regressor into a GLM analysis, the analysis will identify voxels across the brain that show a significant correlation with the seed ROI time course (neural coupling) (O'Reilly et al., 2012). Such information may be useful to compare such general neural coupling in one session to another session on the second level if, for instance, the sessions themselves constitute different conditions (as in the discounting task of Study II and III). Yet, in event-related designs it may additionally be interesting to identify only voxels that show a higher correlation to the seed region when a certain psychological variable takes on a certain value (O'Reilly et al., 2012), e.g. a nominal, "on-off" variable, or when a metric variable, such as the SV in intertemporal choice tasks takes on higher values. In this case, all three regressors are estimated in the first-level GLM and the main interest lies on the third (interaction) regressor. Respective first-level contrasts can be taken to the 2nd-level to be investigated in a random-effects analysis on the group level.

3.4. Computational modelling

During the intertemporal choice task that was applied in **Study II** and **III**, participants were presented with different delayed options with variable delay and amount, while the immediate reward was always fixed (20€ now). The aim of the studies was to compare standard discounting to discounting in the context of episodic prospection. As mentioned before, participants tend to devalue rewards as a function of time (temporal discounting). Traditional economic models assume such decay to follow an exponential course, i.e. that the proportional decay of a value is time-insensitive. For example, if a value of 40 € is subjectively divided in half in 20 days, it is equally divided by half during the following 20 days or from any other time point with the same

time span. However, ample evidence argues more in favour of the hyperbolic discounting function described in 1.4. The hyperbolic function has the form:

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

with A being the objective amount, D the delay and k an inter-individually variable discounting rate, describing how impulsive an individual discounts delayed rewards.

A computational modelling approach was used to estimate the k parameter for each participant and each condition separately so that it could be compared between different conditions. Furthermore, based on the individual k parameter, the SV of the delayed option in each trial could be estimated to be included it as a parametric modulator of the delayed option presentation in the fMRI analysis.

To find the best-fitting value for k , a maximum likelihood estimation procedure was applied in combination with a softmax choice rule on the trial data of each individual participant (Peters, Miedl, & Büchel, 2012). The softmax rule computes the probability of choosing the selected option in a trial by inserting the SVs for both options (see above), as well as the so-called temperature parameters, reflecting the degree of choice incoherence with respect to model predictions. Precisely, on each trial, participants are assumed to make their choices largely based on the comparison of the SV of the immediate option (in our experiment always 20€) and the SV of the delayed option. The temperature parameter reflects the degree how much their choices deviate from that prediction based on subjective influences. The softmax function is formalised as (Peters et al., 2012):

$$P(\text{chosen}) = \frac{\exp(SV_{\text{chosen}}/\beta)}{\sum_i \exp(SV_i/\beta)}$$

The softmax rule is applied to several parameter sets θ , i.e. different combinations of k and β . `fminsearch`, a build-in MATLAB function, was used to iteratively test parameters, gaining a parameter set that maximises the log-likelihood (LL) of the choice probabilities (i.e. $P(\text{chosen})$) for the given set, summing across all trials (t) for each subject:

$$LL = \sum_t \log (P_{\text{chosen}}(t) | \theta)$$

4. Study 1: Attentional control during emotional selectivity in aging

4.1. Background

Life-span theories have argued that the positivity effect in older adults' emotional information processing may reflect an age-specific use of cognitive control to protect emotional well-being in the face of various aging-associated limitations. **Study I** aimed to address this assumption further and investigated whether attentional selectivity for positive over negative information in old age may a) be increased by greater self-relevance of the emotional information and b) depend on individual attentional control ability.

4.2. Experimental design

Eye-movements of younger ($n = 25$, aged 18-30, 10 men) and older adults ($n = 25$, aged 62-78, 12 men) were recorded during the voluntary allocation of attention in a set-up, in which a positive, a negative and a neutral image were presented together in triads for an unconstrained viewing period of 10 seconds. Between trials, self-relevance was manipulated by the use of images depicting naturalistic scenes of so-

cial interactions involving at least two elderly people in aging-relevant scenarios (e.g. elderly people playing with grandchildren) or younger people in scenarios more relevant in young adulthood (e.g. a young couple at their wedding). Photos were taken from IAPS and internet databases and were distinct regarding valence and age relevance. Arrangement and order of the stimuli were randomized in 40 trials. Out of a total of 240 images, two sets of 120 stimuli were created. Participants were randomly assigned to one of the two sets in the eye-tracking task, while the remaining set served as lures in the recognition memory task on the next day. The singleton task was used to assess participants' ability to exert attention control over salient visual distraction in a non-emotional context.

4.3. Results

Results showed that older participants preferentially attended to positive over negative stimuli (i.e. showed a positivity effect), which was particularly pronounced when the scenes were age-relevant. In contrast, younger participants equally attended to positive and negative stimuli independent of their age-relevance. A similar pattern of a selective positivity effect emerged in memory for the material on the following day. While younger subjects showed a general emotional memory enhancement in both relevance conditions (positive and negative), the emotional memory enhancement in the group of older participants was restricted to positive age-relevant images. Finally, higher selective attentional preferences for positive over negative information were predicted by older adults' individual level of attentional control ability. The data clearly strengthen assumptions about an age-specific, motivated engagement of attentional control to selectively focus attention in the context of emotional information. The data will be further discussed in 7.1.

5. Study 2: Episodic simulation and temporal discounting in young adulthood

5.1. Background

Recent studies in younger adults suggest that linking future reward options with prospective episodic events can attenuate temporal discounting (tag-effect), probably through a greater integration of episodic signals with value processing. **Study II** investigated this effect further in younger adults and established whether respective experimental manipulations may be a suitable tool to study effects of episodic prospection on intertemporal choice systematically in older age (Study III). Moreover, previously uncontrolled effects related to the extent to which future scenarios are linked with prior experience were investigated as potential modulators of the neuro-behavioral manifestation of the tag-effect.

5.2. Experimental design

FMRI was combined with a modified intertemporal choice task in a sample of younger adults ($n = 23$, aged 21-30; 12 men). Participants were required to make choices between a fixed amount of 20 € now and a variable, larger but delayed reward (e.g. 25€ in 13 days). The delayed options were either purely monetary (control condition), or linked with a social event, which participants were instructed to imagine (episodic conditions). The social event was either familiar and related to autobiographical experiences (e.g. meeting a close, familiar person in a café) or unfamiliar and needed to be fully constructed (e.g. meeting Angela Merkel in a café). To this aim, four social contacts (two for each condition) were identified with a standardized interview before the experiment. In the control condition, participants were explicitly instructed to refrain from imagery. The delayed choice option together with a visual tag including the

name of the social partner or placeholder strings in the control condition were presented for six seconds before participants indicated their choice. The three conditions were presented in a randomized block order, each consisting of $n = 72$ trials. Post-scan standardized interviews were conducted to assess the quality of imagination for each of the four events.

5.3. Results

The behavioural data replicated previous findings about the tag effect by showing that in both episodic conditions discounting rates were significantly lower than in the control condition. The familiarity of the simulated event neither modulated the behavioural size of the tag-effect nor episodic specificity of the imaginations. However, important condition differences emerged in the neural activation patterns underlying the tag-effect. In the context of unfamiliar events, the hippocampus was particularly involved in the simulation of unfamiliar future scenarios, probably reflecting enhanced construction processes when personal experience with similar past events is lacking. Moreover, valuation of delayed rewards was increasingly predicted by functional coupling between the hippocampus and the ACC. In contrast, valuation of rewards in a familiar context was predicted by activation in key nodes of emotional and autobiographical memory retrieval and associated with enhanced functional coupling between the ACC and the ventral striatum, probably reflecting a greater impact of emotional, autobiographical features on the tag-effect as further discussed in 7.2.

6. Study 3: Episodic simulation and temporal discounting in old adulthood

6.1. Background

Results of **Study II** highlight the role of episodic prospection in the tag-effect in younger adults, thus making it a suitable tool to investigate effects of episodic prospection on temporal discounting in old age. Theories have postulated that perseverance of fundamental cognitive control functions in aging may be a crucial modulator of complex cognition (Gazzaley et al., 2013; Hasher & Zacks, 1988) and the successful integration of multiple information during decision-making (Samanez-Larkin & Knutson, 2015). In line with that, individual levels of attentional control as well as the quality of event simulation were investigated as potential modulators of the tag-effect in older age.

6.2. Experimental design

The identical fMRI paradigm applied in study 2 was now used in a sample of healthy elderly adults (n = 22, aged 60 -74, 9 men). Participants' attention control ability was assessed with the singleton task and investigated as covariate of the tag-effect. Moreover following procedures of Study II, post-scan standardized interviews were conducted to assess the quality of imagination for the different events.

6.3. Results

The behavioural data indicated that reductions in temporal discounting demonstrated in younger adults were absent across older adults in both, the familiar and unfamiliar condition. Yet, attentional control ability was found to be a significant predictor of the tag-effect across episodic conditions. In line with that, older adults with high atten-

tional control were more likely to show reduced discounting in the episodic conditions. At the same time, the tag-effect was even reversed in elderly individuals with low attentional control. Presence of the tag-effect in older adults showing high attentional control was paralleled by increased value processing in the hippocampus and the anterior cingulate cortex in the episodic compared to the control condition. Moreover, similar positive correlations emerged between attentional control ability and neural coupling between the hippocampus and the striatum in the context of episodic simulations. Importantly, imagination scores from the post-scan interview and activation in established nodes of episodic prospection network were not correlated with the singleton score. Similarly, basic SV coding seemed to be preserved across all elderly individuals, which underlined that variance in the tag-effect was unlikely resulting from differences in episodic prospection or value coding per se. Instead, findings highlight that attentional control ability seems to be critical in old age for the successful neurobehavioral integration of episodic information into value processing probably by enabling simultaneous processing of different information as further discussed in 7.2.

7. Discussion

In my PhD thesis, specific behavioural paradigms were designed and combined with multimodal techniques in order to characterize age-related changes in the processing of affective information and how these changes are modulated by the perseverance of relevant cognitive functions and motivational factors. Findings highlight the crucial role of attentional control in the context of a) age-specific preferences for positive over negative emotional information and b) for the integration of episodic information

to overcome impulsive choice behaviour. In addition, age-relevance was found to be a crucial modulator of emotional processing in aging. In the following, I will further discuss findings from the three studies in the context of the relevant existing literature, describe their implications and provide an outlook for future research.

7.1. Attentional control and emotional selectivity in aging

Findings of increased preferences for positive information in older adults' attention and memory, observed in **Study I**, are adding to a growing literature about the positivity effect in aging. Yet, several studies in the past have failed to observe a positivity effect (for a related discussion see Reed & Carstensen, 2012) and the only study that investigated voluntary attention in a set-up where positive and negative emotional information were directly presented together failed to detect an effect in this condition (Knight et al., 2007). The present findings might help to conciliate inconsistent findings regarding the positivity effect and strongly emphasize that a) the contextual setting, including restrictions on the exhibition of voluntary preferences, b) motivational factors, such as the degree to which information initiates self-referential processing, as well as c) the perseverance of attentional control abilities, seem to be key modulators of the positivity effect in aging.

Yet, it could be argued that instead of reflecting voluntary preferences, the positivity effect might have resulted from a greater initial insensitivity to negative information in older adults, possibly due to changes in amygdala functioning (Cacioppo et al., 2011). However, such explanation is rather unlikely, given that the amygdala (Mather, 2016) and the initial sensitivity to negative and threatening information (Leclerc & Kensinger, 2008; Mather & Knight, 2006) remain relatively well preserved in aging. In addition, such account has difficulties to explain why the positivity effect was boosted when negative information was made more salient by using images of

elderly people in aging-relevant scenarios. Previous findings have shown that own-age stimuli initially capture attention more than other-age stimuli (He et al., 2011), which similarly holds for positive as well as for negative material (Ebner & Johnson, 2010). Moreover, such own-age stimuli are typically more strongly referred to the self (Ebner et al., 2013; Ebner, Gluth, et al., 2011). Intriguingly, it has been demonstrated that when elderly individuals are forced to process negative scenarios in a more elaborated fashion and without being able to redirect their attention, greater own-age relevance might even decrease the positivity effect in subsequent memory (Tomaszczyk, Fernandes, & MacLeod, 2008). These findings further highlight the saliency signalled by self-relevant negative images and suggest that the present findings were unlikely resulting from initial differences in the sensitivity to positive versus negative information. Instead, together with the observed correlation between the singleton score and the positivity effect, findings clearly emphasize the role of voluntary attentional control in the context of the positivity effect.

The most plausible explanation for the boosting effect of self-relevance on the positivity effect is that the need for attentional control to secure emotional well-being may be greater when confronting elderly people with information that deals with relevant threats and limitations related to their own stage in life (Carstensen, 2006; Haase et al., 2013; Mather, 2012). In fact, previous studies have linked older adults' attentional preferences for positive information with higher general levels of emotional well-being (Brassen et al., 2011) and with acute improvements in mood states (Isaacowitz, Toner, Goren, & Wilson, 2008; Isaacowitz, Toner, & Neupert, 2009). A preference for selective attention over reappraisal (i.e. the reinterpretation of a situation) as an emotion regulation strategy is thereby two-fold: On the one hand, such strategy may be more suitable for a frequent every-day use as it promises quicker emotional relief than more complex reappraisal strategies (Charles, 2010; Paul, Simon, Kniesche,

Kathmann, & Endrass, 2013). On the other hand, a preference for selective attention may be promoted by differences in the preservation of underlying neural emotion regulation circuits: While active coping like reappraisal tends to draw more on lateral prefrontal areas, selective attention is linked with more medial prefrontal regions (Golkar et al., 2012; Kalisch, 2009). Medial prefrontal regions are comparatively less affected by age related atrophy (Fjell et al., 2009) and have previously linked with the positivity effect in functional neuroimaging studies (Brassen et al., 2011, 2012). Interestingly, evidence suggests that while older adults are typically worse than younger adults when instructed to use reappraisal (Opitz, Rauch, Terry, & Urry, 2012), they tend to be better at using strategies relying on the refocusing of attention (Phillips, Henry, Hosie, & Milne, 2008). Moreover, a greater spontaneous use of selective attention in comparison with reappraisal tends to be linked to higher levels of well-being in aging (Scheibe, Sheppes, & Staudinger, 2015). At the same time, deficits in attentional control have been directly linked with late-life depression (Katz et al., 2010; Price, Eldreth, & Mohlman, 2011), which is known to have devastating consequences on cognitive functioning and premature mortality (Naismith, Norrie, Mowszowski, & Hickie, 2012; Steptoe & Wardle, 2011). Thus, it could be speculated whether interventions aimed at improving attentional control ability, as discussed in 7.3., might have beneficial effects on emotional stability in aging. Moreover, interventional approaches promoting emotional well-being might consider self-referential processing as a boosting factor in aging.

Nevertheless, while on the one hand, increased emotional selectivity may be beneficial for emotional stability and related behaviours, excessive suppression of negative information can also be maladaptive in everyday life. Specifically, the processing of negative, self-relevant information can be crucial when assessing risks and negative consequences. In fact, previous research has demonstrated that during the assess-

ment of risks of adverse future life events, older adults more strongly tend to displace important negative information that might compromise a positive view on their future (Chowdhury, Sharot, Wolfe, Düzel, & Dolan, 2014; Sharot, 2011). Moreover, when making health care choices for themselves or people of similar age, older in comparison with younger adults tend to base their choices overly on positive decision attributes (Löckenhoff & Carstensen, 2008). The present findings indicate that such effects are likely resulting from the fact that older adults actively engage attentional control to disengage from negative self-relevant information in these contexts. Thus, when preparing highly relevant negative information for elderly recipients, such information might have to be highlighted more strongly so that it is difficult to ignore and can be adequately considered.

It should be noted that although findings of **Study I** highlight the role of attentional control in emotional selectivity in aging, emotional preferences might also be pursued on more implicit levels when negative information is less salient or self-relevant (Dijksterhuis & Aarts, 2010). Previous studies have found positivity effects under conditions in which the availability of cognitive resources was rather limited (Allard & Isaacowitz, 2008; Johnson & Whiting, 2013; Leclerc & Kensinger, 2010; Rösler et al., 2005). Yet, it seems intriguing that older in comparison with younger individuals exhibit more strategic attentional control in the context of emotional information, given that they often show greater difficulties in controlling interference from distracting information in non-emotional contexts (e.g. Kramer, Hahn, Irwin, & Theeuwes, 2000; Madden et al., 2014; Tsvetanov, Mevorach, Allen, & Humphreys, 2013; Whiting, Madden, & Babcock, 2007a). Such findings are in line with theories about heightened cognitive selectivity in aging (Baltes & Baltes, 1993) and findings reporting an age-related increased sensitivity to the motivational impact of age-relevance on cognition in non-emotional contexts (Freund, Kourilova, & Kuhl, 2011; Germain & Hess, 2007).

To summarize, although older in comparison with younger adults often demonstrate difficulties in controlling interference from distracting information in non-emotional contexts, they tend to increasingly apply attentional control to disengage from negative and to focus on positive information. Moreover, such emotional selectivity seems to be boosted by greater self-relevance of the information and is likely to reflect heightened emotion regulation attempts in aging. It is therefore not surprising that the individual perseverance of underlying attentional control functions is crucially predictive for the degree of emotional selectivity. Overall, findings critically highlight attentional selectivity and the related ability of cognitive control for emotional goal pursuit and possibly emotional stability in aging.

7.2. Cognitive modulators of impulsive choice across the lifespan

The second part of my Phd project focused on impulsive choice and investigated cognitive factors that predict impulsive discounting tendencies in young and older age. Results revealed that in younger age, temporal discounting of future rewards is significantly modulated by the degree of future-thinking during decision-making and that such effect become much more heterogeneous as people age. These findings will be further elaborated in the following.

Study II provides striking evidence that younger adults integrate episodic signals with value computations for delayed rewards, leading to reductions in temporal discounting. These findings replicate previous observations of a tag-effect (see Benoit, Gilbert, & Burgess, 2011; Kwan et al., 2015; Palombo, Keane, & Verfaellie, 2015; Peters & Büchel, 2010) and crucially extend these observations by providing new insights into the neural processes that contribute to the effect.

A possible mechanism underlying the tag-effect is that the integration of episodic signals may diminish the negative impact of temporal distance during SV computations

(Mazur, 1987) by rendering the concreteness of the delayed option. Specifically, it has been argued that the impact of time on intertemporal choices may result from a greater initial de-contextualization of delayed compared with immediate reward representations (Lempert & Phelps, 2016). Such assumption is based on the *construal level theory* (Trope & Liberman, 2010), which states that temporal distance decreases the concreteness and contextualization of mental representations, i.e. making them appear less “within reach”. In fact such assumptions are supported by the *episodic construction hypothesis* (Schacter & Addis, 2009) and findings about a substantial impact of temporal distance on contextual detail and construction demands during episodic simulations (Addis & Schacter, 2008; D’Argembeau & Van der Linden, 2004).

The role of episodic prospection in the tag-effect in younger age was highlighted by characteristic effects of event familiarity on the neural correlates. Specifically, while both, the imagination of familiar and unfamiliar episodes, was associated with increased activity in an established network of brain regions involved in the recollection of previous events and in the construction of novel future scenarios (Schacter et al., 2012), important differences emerged between the two conditions. Along those lines, when imaging events that were closely linked with autobiographical experiences (i.e. meeting a close, familiar social partner in café), affective limbic brain regions were more strongly involved in episodic prospection. In contrast, when events involved a personally unfamiliar partner and could not rely on autobiographical experience, the hippocampus tended to be more strongly involved. Most interestingly, familiarity also directly modulated the degree to which limbic regions versus the hippocampus functionally interacted with SV processing in the ACC. Activity in limbic regions, including the amygdala and the ventral striatum, is likely caused by a greater emotional value of events with a familiar partner (Buchanan, 2007; Speer, Bhanji, & Delgado, 2014).

At the same time, the additional hippocampal involvement in the unfamiliar condition may be best explained by an amplified construction effort when events could not rely on pre-experience. In addition to its general involvement in the construction of future episodes (Hassabis et al., 2007; Race et al., 2011; Palombo et al., 2014), the hippocampus has previously been linked with enhanced construction demands during future event simulation (e.g. Gaesser et al., 2013). These findings indicate that specific episodic information seems to be integrated with the valuation of associated rewards during the tag-effect, which substantially enriches the understanding of the underlying mechanisms. In addition, highlighting the role of episodic prospection, these findings largely rule out alternative explanations for the tag-effect, e.g. that the effect may simply arise from greater attention to delayed rewards.

Results from **Study III** revealed reduced beneficial effects of episodic prospection on temporal discounting in older age in both, the familiar and the unfamiliar condition. Yet, when looking at such impact in detail, episodic prospection seemed to have very divergent effects on discounting between older adults. More specifically, reductions in temporal discounting were only evident among elderly individuals with high attentional control ability, indexed by the singleton score. At the same time, elderly individuals showing low attentional control tended to discount future rewards even more in the episodic condition.

It has been postulated that age-related deficits in attentional control may increase erroneous processing of simultaneous information in old age. The reason for that is that cognitive resources are easily occupied by one type of information from which individuals with low attentional control have difficulties to flexibly disengage (Gazzaley et al., 2013; Hasher & Zacks, 1988). Along those lines, older adults showing low attentional control might have been unable to flexibly disengage from episodic pro-

spection, thus impairing their ability to process value information adequately and to integrate both types of information. Such interpretation fits nicely with recent theoretical assumptions arguing that decision performance in older adults may crucially depend on the extent to which decisions require the integration of multiple information and how well relevant, executive control abilities are persevered (Samanez-Larkin & Knutson, 2015).

Interestingly, the tag-effect in older adults with high attentional control was paralleled by increased neural SV coding in the ACC and the hippocampus and greater hippocampal-striatal coupling in the episodic conditions. All three regions were linked with SV processing in the episodic conditions in **Study II** as well as in the study by Peters and Büchel (Peters & Büchel, 2010). The ACC (Apps & Ramnani, 2014; Croxson, Walton, O'Reilly, Behrens, & Rushworth, 2009; Economides, Guitart-Masip, Kurth-Nelson, & Dolan, 2014; Hillman & Bilkey, 2010) and the ventral striatum (Meer, Ito, Lansink, & Pennartz, 2014; van den Bos, Rodriguez, Schweitzer, & McClure, 2014) have well-established roles in the integration of information during value computation. Moreover, it has previously been argued that the hippocampus with its dense anatomical connections to valuation regions (Haber, 2011) may play a crucial role in updating and constructing value representation in the ACC and in the striatum based on mnemonic representation of past and future experiences (Lebreton et al., 2013; Palombo et al., 2015). Thus, the neural data in **Study III** further highlight that elderly individuals with high attentional control successfully integrated episodic signals with value computation.

The ACC and the ventral striatum have also been implicated in controlling interference from resource competing information (di Pellegrino, Ciaramelli, & Làdavas, 2007; Dreher & Grafman, 2003; Haeger, Lee, Fell, & Axmacher, 2015; Scimeca &

Badre, 2012). Hence, it could be speculated whether these structures in younger adults and in older adults with high attentional control might additionally have served functions related to the control of episodic information processing to enable simultaneous value processing. Yet, further work is needed to shed light on the precise neural mechanisms underlying attentional control during value integration.

The most plausible explanation for the absence of familiarity effects on episodic prospection in older adults is that their imaginations consisted of too little details to reveal such fine-grained differences. In detail, in line with previous evidence (Addis, Roberts, et al., 2011; Addis, Wong, & Schacter, 2008; Schacter et al., 2013; Viard et al., 2011), elderly individuals reported significantly less episodic details than younger adults and activated a largely, though not fully, overlapping episodic prospection network. In fact, it seems plausible that representations of future familiar and unfamiliar events consisted of more schematic representations and could therefore not be well distinguished. For instance, elderly individuals might have had more abstract representations of 'having a coffee' or more schematic representations of the partners without imaging very specific details about the events. It has repeatedly been shown that reduced episodic specificity often goes along with greater semantic/ more abstract representations of past and future events in aging (Addis, Musicaro, Pan, & Schacter, 2010; Cole et al., 2013; Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002; Schacter et al., 2013). Yet, these more abstract representations may still be sufficient to render the concreteness of delayed rewards, provided that individuals are able to integrate them with their choices. It has recently been demonstrated that patients with lesions in the hippocampus, who show deficits in episodic memory but preserved semantic memory, may still be able to demonstrate a tag-effect (Kwan et al., 2015). In order to investigate the impact of episodic specificity on the tag-effect more explicitly, trial-wise imagination ratings and a greater variety of events may be

useful. In addition, it could be speculated that modulatory effects of event familiarity on episodic prospection and temporal discounting may be more pronounced when using completely unfamiliar events or partners (rather than famous individuals from the media).

In summary, when making choices between smaller immediate and larger later rewards, mental representations linked with delayed rewards may be integrated with their valuation and make them more likely to be chosen. In old age, the success of such integrative processing seems to be critically dependent on the individual perseverance of attentional control function. Such function possibly facilitates the simultaneous processing of episodic and value information. These data potentially specify the mechanism underlying previously observed correlations between discounting rates and executive control abilities in discounting studies with older adults where episodic simulation was uncontrolled (Boyle et al., 2012; Halfmann et al., 2013; James et al., 2015; Lindbergh et al., 2014). In these studies, individuals with high executive control might be better at integrating contextual representations of delayed rewards with their choices, thus promoting more patient choice behaviour. Further implications of the findings will be discussed in the following.

7.3. Implications and outlook

Findings of the present Phd project critically highlight that deficits in attentional control may have important negative consequences for emotional functioning and decision-making in late life. Specifically, although an excessive use of attentional control to suppress negative information may bear the risk of overlooking important information, such functions seem to be an efficient emotion regulation tool in aging. It may help to maintain emotional stability in the face of age-related limitations (Carstensen, 2006; Haase et al., 2013) and possibly constitute a resilience factor against

depression in late life (Katz et al., 2010; Price et al., 2011). Attentional control capacity also seems to be important for the integration of multiple aspects with decisions that is essential for autonomous decisions. In fact, the finding that older adults with low attentional control abilities tend to become more impulsive in the face of additional contextual information is particularly worrisome given that impulsive discounting may increase the susceptibility to frauds and has previously been linked with poor health conditions in old age (Boyle, Yu, Gamble, & Bennett, 2013; Dombrovski et al., 2012).

It thus seems important to investigate resilience factors against age-related decline in attentional control and related executive functions. In this context, several studies have begun to evaluate beneficial effects of computerized cognitive trainings and physical exercise interventions. For instance, beneficial long-term effects on behavioural and neural top-down control in aging have recently been reported for adaptive auditory distraction control trainings (Mishra, de Villers-Sidani, Merzenich, & Gazzaley, 2014), 3D video game trainings (Anguera et al., 2013) and other computerized trainings (e.g. Bherer et al., 2005, 2008; Mayas, Parmentier, Andrés, & Ballesteros, 2014). Yet, moderating effects related to training duration and personal factors have been highlighted in a recent meta-analysis (Toril, Reales, & Ballesteros, 2014). Parallel to such effects from cognitive trainings, there is some evidence that cardiovascular fitness trainings with aerobic components may have beneficial neurobehavioral effects on executive functions, including attentional control (S. J. Colcombe et al., 2004; S. Colcombe & Kramer, 2003; Erickson & Kramer, 2009; Predovan, Fraser, Renaud, Ianié, & Bherer, 2012; Renaud, Maquestiaux, Joncas, Kergoat, & Bherer, 2010). It could be speculated whether a multifactorial interventional approach combining physical and cognitive trainings may be most beneficial for the training of attention control in aging. In addition, it may be fruitful to categorize elderly people

based on their initial level of attentional control functioning to investigate the generalization of these effects. Similarly, although transfer effects have been shown for closely related executive functions, it has yet not been established whether beneficial effects can transfer to higher order cognitive and emotional processing as investigated in the present Phd project.

In addition to implications for interventions, the mutual role of attentional control in emotional and incentive information processing may stimulate further research regarding common neural substrates underlying such processes. For instance, it has been noted earlier that the ACC and adjacent medial prefrontal areas play a crucial role in emotion regulation (Etkin, Egner, & Kalisch, 2011) and have been linked with the positivity effect in aging (Brassen et al., 2011, 2012). At the same time, the ACC has been implicated in value computation in **Study II, III** and previous work (Apps & Ramnani, 2014; Economides et al., 2014; Hillman & Bilkey, 2010; Peters & Büchel, 2010). In addition, the ACC tends to be involved in cognitive control and resolving interference during competitive processing (di Pellegrino et al., 2007; Dreher & Grafman, 2003; Newman, Creer, & McGaughy, 2015; Silton et al., 2010; Weissman, Gopalakrishnan, Hazlett, & Woldorff, 2005). Such multiple functions fit nicely with the unique location of the ACC, connecting to emotion and valuation regions within the limbic system and with cognitive control regions in the prefrontal cortex (Stevens et al., 2011). Thus, it could be speculated whether the power of flexible attention control for emotional and incentive processing observed in **Study I** and **III** may reflect differences in functional and structural preservation of task overlapping neural networks. However, such notion is only speculative at present and requires further research.

In a similar vein, it would be interesting to investigate and compare the predictive power of other fundamental cognitive abilities in the context of complex cognitive and

emotional processing in aging. Specifically, the singleton measure used in the present thesis indexed the ability to flexibly exert attentional control over potentially relevant, though distracting information. Importantly, the score was corrected for modes of more strategic and less dynamic forms of attentional selectivity, i.e. when attention is strictly limited to specific dimensions, while other information is simply blanked out. Moreover, it has been argued that elderly people may increasingly rely on such “strategic” top-down guidance to compensate for deficits in the flexible disengagement from information (Madden, 2007). Yet, such mode may not be useful in more naturalistic and dynamic contexts where information has a potential relevance and can therefore not be fully ignored. Consequently, the differentiation between strategic versus flexible top-down attention may possibly be crucial to consider when judging individual attention control capacities and investigating them with respect to higher cognitive functions. It may be interesting to further disentangle both functions with functional and structural imaging in elderly individuals.

9. List of abbreviations

ACC	Anterior cingulate cortex
BOLD	Blood oxygenation level dependent
DARTEL	Diffeomorphic anatomical registration
DLPFC	Dorsolateral prefrontal cortex
EPI	Echo-planar imaging
fMRI	Functional magnetic resonance im-
GLM	General linear model
HRF	Hemodynamic response function
LL	Log likelihood
MNI	Montreal Neurological Institute
OFC	Orbitofrontal cortex
PCC	Posterior cingulate cortex
PPI	Psychophysiological interaction
RF	Radiofrequency pulse
SPM	Statistical Parametric Mapping
SV	Subjective value
TR	Repetition time
VBM	Voxel-based morphometry
VMPFC	Ventromedial prefrontal cortex

10. References

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11. List of included articles

1. **Sasse**, L.K., Gamer, M., Büchel, C., & Brassens, S. (2014). Selective Control of Attention Supports the Positivity Effect in Aging. *PLoS ONE*, 9(8), e104180.
2. **Sasse**, L.K., Peters, J., Büchel, C., & Brassens, S. (2015). Effects of prospective thinking on intertemporal choice: The role of familiarity. *Human Brain Mapping*, 36, 4210–4221.
3. **Sasse**, L.K., Peters, J., & Brassens, S. (submitted). Effects of Executive Control and Episodic Simulation on Intertemporal Choice in Aging.



Selective Control of Attention Supports the Positivity Effect in Aging

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Abstract

There is emerging evidence for a positivity effect in healthy aging, which describes an age-specific increased focus on positive compared to negative information. Life-span researchers have attributed this effect to the selective allocation of cognitive resources in the service of prioritized emotional goals. We explored the basic principles of this assumption by assessing selective attention and memory for visual stimuli, differing in emotional content and self-relevance, in young and old participants. To specifically address the impact of cognitive control, voluntary attentional selection during the presentation of multiple-item displays was analyzed and linked to participants' general ability of cognitive control. Results revealed a positivity effect in older adults' selective attention and memory, which was particularly pronounced for self-relevant stimuli. Focusing on positive and ignoring negative information was most evident in older participants with a generally higher ability to exert top-down control during visual search. Our findings highlight the role of controlled selectivity in the occurrence of a positivity effect in aging. Since the effect has been related to well-being in later life, we suggest that the ability to selectively allocate top-down control might represent a resilience factor for emotional health in aging.

Citation: Sasse LK, Gamer M, Büchel C, Brassen S (2014) Selective Control of Attention Supports the Positivity Effect in Aging. *PLoS ONE* 9(8): e104180. doi:10.1371/journal.pone.0104180

Editor: Jan de Fockert, Goldsmiths, University of London, UK, United Kingdom

Received: March 12, 2014; **Accepted:** July 11, 2014; **Published:** August 5, 2014

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Data Availability: The authors confirm that all data underlying the findings are fully available without restriction. The data underlying the main findings are available in a public repository under <http://dx.doi.org/10.6084/m9.figshare.1027503>.

Funding: This work was supported by the German research foundation (DFG, BR2877/2-2) to SB. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

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Introduction

Over the past 10 years, a great amount of studies has been dedicated to explore the phenomenon of a positivity effect (PE) in older adults' information processing [1]. The PE describes an age-related increase in the ratio of positive relative to negative information processing, which can either be driven by a heightened processing of positive information, or a diminished processing of negative information [2]. For instance, older versus younger participants were found to be less distracted when responding to a dot target appearing after a negative relative to a neutral item [3–5] and to attend relatively more on positive [6–8] and less on negative items [9,10]. Moreover, some studies demonstrated that in relation to their overall memory performance, elderly people recall a larger proportion of positive items and a lower proportion of negative items than younger adults [11,12]. Motivated by theoretical assumptions, recent work has now begun to investigate the boundary conditions of this effect. In particular, it could be demonstrated that the occurrence of the PE depends on the degree of natural information processing permitted by the paradigm and substantially relies on cognitive resources (for reviews see [1,2]).

The most prominent theoretical framework for the PE is provided by the Socio-emotional Selectivity Theory [13,14]. The theory attributes the effect to a systematic shift in goal-setting behavior, occurring in the context of a limited life-time perspective. More specifically, narrowed time horizons in late life

lead to a greater priority of goals about emotional meaning and well-being, which direct the allocation of cognitive resources during the processing of emotional information. In contrast, younger people, who normally perceive their lifetime as more open-ended, prioritize future-oriented goals, such as expanding knowledge and making new experiences, and consequently focus less on their emotional state. Supporting this notion, a PE can be observed also in younger adults when instructed to focus on their current emotional state [15]. In addition, the prominence of emotional aspects for younger adults appears to increase when being confronted with a limited life-time perspective [16].

It has been speculated that the shift towards emotional goals in aging is closely linked with an age-related increased engagement of emotion regulation [17–19]. This speculation is supported by self-reports of healthy older adults, indicating a greater access to emotion regulation strategies as well as a stronger ability to engage in goal-directed behavior [20,21]. Moreover, experimental studies have repeatedly documented reduced distractibility by negative information [3–5,22,23] and preferred processing of positive distractors and information in older as compared to younger adults [6,7], which was directly associated with emotional well-being [6]. More support comes from recent neuroimaging studies, demonstrating an increased engagement of ventromedial brain regions during the generation of a PE in older adults [6,24,25]. Ventromedial brain regions, including the anterior cingulate cortex, are assumed to be key nodes of the “emotion regulation

network' [26–28]. In addition, medial prefrontal brain regions have been associated with self-referential processing [29], one of the discussed mechanisms facilitating a boost in attention and memory for positive items in older adults [25,30–32].

There is also evidence for an age-related shift in the choice of prioritized emotion-regulation strategies for maintaining well-being. According to self-reports and experimental findings, older adults seem to specifically exert self-directed attention-control strategies involving selective attention and withdrawal from distressing situations when being confronted with emotional information [19,33]. Interestingly, in contrast to younger age, such suppression strategies are not associated with enhanced psychological distress (i.e. depression, stress or anxiety) but, instead, may be an effective emotion regulation tool against the stressors experienced in later life [34].

Both selectively focusing on positive information and ignoring negative distraction probably rely on cognitive resources and the general ability of top-down control [18,19]. In line with that, the “cognitive control hypothesis” states that elderly people selectively invest cognitive control to pursue their emotional goals [35]. Consistent with this assumption, the PE can be diminished when attentional resources are exhausted by a secondary task [6,10,12], and a PE in memory is reduced in older people with lower degrees of executive control [12]. On the other hand, executive control is frequently affected by an age-related decline [36]. In fact, older adults often show worse performance than younger adults during interference tasks with neutral distractors [37]. Moreover, the “aging brain model” [38] has argued that reduced responses to negative stimuli in older adults result from a decline in arousal-sensitive brain circuits, including the amygdala (see [39] for a critical discussion). As described above, there is emerging evidence speaking against such a deficit-oriented approach. However, it is still rather unclear whether and which preserved cognitive ability might facilitate a PE in aging.

In the present study, we aimed to shed more light on the conditions and mechanisms underlying a PE in aging. To investigate the impact of voluntary selective attention on the occurrence of the effect, we analyzed young and older participants' fixation profile during a novel free-viewing eye-tracking paradigm in which images of positive, negative and neutral social scenes were pitted directly against one another in triads. As demonstrated in a recent meta-analysis, the magnitude of the PE is significantly reduced in studies that constrain elderly people's natural information processing through specific experimental instructions [1]. By presenting different emotional stimuli simultaneously, we maximized the need to engage cognitive control in order to selectively process information. To evaluate the depth of (selective) information processing, we also assessed participants' subsequent memory performance in a recognition paradigm on the following day. As described above, it has been speculated that the selective depth of information processing in older adults might be modulated by an increased tendency to process positive information in relation to oneself [31]. To follow up on this idea, we varied the attractiveness for self-referential processes in our paradigm by including images that display younger versus older adults in age-typical social scenarios (e.g. a wedding versus playing with grandchildren). Both older and younger adults have been found to be more distracted by own-age compared to other-age faces [7] and to show a preference for faces of the own age in attention [40,41] and memory [42], all of which points to an enhanced self-referential processing [43,44]. Finally, in order to investigate the impact of participants' general cognitive ability to exert attentional top-down control over salient distraction on the occurrence of a PE, we measured participants' performance in a visual search task.

Overall, our study was designed to further illuminate the main hypotheses on the basic mechanisms underlying the PE in aging.

Materials and Methods

Participants

Twenty-five younger (18–30 years; $M = 24.28$; $SD = 3.20$; 10 men) and 25 older (62–78 years; $M = 67.56$; $SD = 4.43$; 12 men) adults participated in the present study. Three additional participants were excluded prior to the analyses due to difficulties in obtaining stable eye tracking data (<70% valid data in more than half of the trials). All participants had normal or corrected-to-normal vision (including color vision), and no present or previous neurological or psychiatric disorders like depression or dementia. Older participants successfully completed the neuropsychological battery of the Consortium to Establish a Registry for Alzheimer's Disease (CERAD [45]) including the Mini-Mental State Examination (MMSE, all participants >28). Participants were recruited via an online-announcement and from an existing database and were paid 10 Euro per hour for participation. The study was approved by the local ethics committee of the Medical Association, Hamburg, Germany, and all participants gave written informed consent before participating.

Study design and tasks

There were two consecutive study days. On the first day, selective visual attention to emotional and neutral social scenes was assessed using an eye-tracking paradigm. Afterwards, participants' general ability to exert top-down control over salient distraction was measured with a visual search task. Twenty-four hours post eye-tracking, memory performance for the material was tested in a recognition paradigm. This was followed by emotional ratings of each image. Measurements were conducted in a sound-attenuated, air-conditioned and shaded room with constant illumination. The recording and programming equipment was located outside the room. Participants were tested individually while the experimenter stayed outside the room.

Eye-tracking paradigm. Stimuli of the eye-tracking paradigm consisted of 240 color photographs selected from the internet as well as from the International Affective Picture System (IAPS; [46]). All pictures had a size of 600×450 pixels. Pictures featured social situations, involving at least two persons in distinct positive, negative or neutral social interactions. Half of those pictures depicted elderly people in social situations that were thematically more relevant for their respective age (e.g. playing with grandchildren, funeral; see Figure 1) and the other half of the images showed younger people in social situations more typical for young adulthood (e.g. wedding, brawl). Affiliation of the images to the emotion and relevance categories was based on the consensual classification by three independent raters from our laboratory. Moreover, picture categories were confirmed by an independent sample of 20 young participants, who rated all images on a valence scale (ranging from 1 = very negative to 6 = very positive) and classified them according to their relevance for people around 30 years versus 65 years of age. In this sample, the average valence ratings were $M = 1.73$, $SD = 0.16$ for negative, $M = 3.18$, $SD = 0.24$ for neutral and $M = 4.08$, $SD = 0.20$ for positive images. The classified age-relevance of the stimuli was in accordance with the a priori grouping for 91% of the negative stimuli, for 86% of the neutral stimuli and for 87% of the positive stimuli.

Out of the 240 images, two sets of 120 stimuli were created. Participants were randomly assigned to one of the two sets in the eye-tracking task, while the remaining set served as lures in the



Figure 1. Outline of the eye-tracking paradigm. Two consecutive trials are presented, each starting with a fixation cross, followed by a display of a positive, negative and neutral social scene. The first trial includes social scenes that depict young adults in age-typical scenes, while images of the second example trial belong to the old-age category.
doi:10.1371/journal.pone.0104180.g001

recognition memory task. Eye-movements were recorded during the computer-based presentation of slides, showing three images at a time on a grey-scaled background (Figure 1). In each of the 40 trials, two images were presented at the upper half of the screen and one in the center of the lower half of the screen. Each trial contained one positive, one negative and one neutral image of the same age-category.

Arrangement and order of stimuli were pseudo-randomized. More specifically, it was assured that each type of valence would occur equally often in the three positions. Moreover, the three images presented together were selected so that differences in the average picture salience were minimized to control for differences in low-level image features [47]. Finally, trials were arranged in a way that not more than three succeeding slides belonged to the same age category. Each trial started with a central fixation cross for a jittered interval of 3–6 s. Subsequently, the three images were presented for 10 s (see Figure 1). Participants were instructed to look naturally at the pictures as if they were watching them on TV. After 20 of the 40 trials, a short break was provided to prevent drops in attention. A practice phase of four trials preceded the experiment. The whole procedure took approximately 20 minutes.

Eye movement data were continuously recorded with a sampling rate of 1000 Hz using an infrared pupil-corneal reflection technique (EyeLink 1000, SR Research Ltd., Ottawa, Canada). The head location was fixed using a chin rest and a forehead bar. The software Presentation (Neurobehavioral Systems) was used to present the picture stimuli on a 20-inch LCD monitor (Samsung SyncMaster 204B; display dimension = 40.64 cm × 30.48 cm; resolution = 1600 × 1200 pixels; refresh rate = 60 Hz). Participants viewed the screen from a distance of 47 cm.

For the analysis, eye movement data were parsed into saccades and fixations using EyeLink's standard parser configuration, which classifies an eye movement as a saccade when it exceeds 30°/sec velocity or 8000°/sec² acceleration. Subsequently, horizontal and vertical coordinates of fixations were drift corrected with reference to the central fixation cross at trial start. The baseline consisted of the average gaze position during the last 300 ms before stimulus onset. If the baseline was unavailable (e.g. due to blinks) or invalid (horizontal or vertical deviation of more than 100 pixels or 3 *SDs*

from the average of all baselines in one session), it was replaced by the average baseline of all valid trials within the session. Such adjustment was necessary in 193 of all 2000 trials across participants. Finally, two measures were derived from the eye movement recordings: the number of fixations as well as the cumulative fixation duration on positive, negative and neutral pictures. The numbers of fixations were divided by the total number of fixations and the durations were divided by the total fixation time (excluding blinks and saccades) in each trial.

Singleton task. After the eye-tracking task, participants performed a visual search task. This singleton distraction paradigm was adopted from Costello and colleagues [48] and implemented using Cogent 2000 stimulus presentation software (Wellcome Department of Imaging Neuroscience, London, UK) in MATLAB (Mathworks Inc). Most importantly, this procedure allows for the assessment of participants' general ability to recruit top-down control trial-by-trial in order to focus on or to ignore salient visual stimuli ("singleton-detection mode"). In detail, participants had to indicate as quickly as possible whether a target-shape (circle) contained either the symbol "+" or "-" by pressing the left or right arrow key on a standard computer keyboard with the index and ring finger of the dominant hand. Key assignment was counterbalanced across participants. The target shape was surrounded by 3 or 11 distractors (squares). Please note that we focused our analyses on the 12-items-trials since we were mainly interested in control ability under high cognitive demands [48]. The 4-items-trials were left in the design to prevent participants from fatigue.

In the baseline blocks, 50% of the trials contained no particularly salient item (all green, i.e. no singleton), while in the other 50% of trials, one distractor was printed in red (singleton distractor). Baseline blocks started with the information that the target-circle is always green. Thus, participants could completely concentrate on one color, thereby minimizing the effect of the singleton distractor. In contrast, in the interesting singleton-detection blocks, participants were informed that in some cases (~8%) the color singleton could also be the target. In other words, in addition to trials with no singleton and singleton distractors, there were also some trials in which the target-shape was printed in red (singleton target). Now, the color singleton could not be easily

ignored but became highly salient because it might include the target relevant feature.

The whole task comprised eight blocks of 48 trials each. Baseline blocks ($n = 4$) were alternated with singleton-detection blocks ($n = 4$). Trials within the blocks were randomized with respect to display size (4 versus 12 items) and with targets and singletons appearing equally often in each quadrant of the visual field, while distances between singleton and target were balanced. Before and after half of the trials in each block, a break of 5000 ms was provided. Within this break, a note appeared on the screen for 3000 ms instructing/reminding the participant which type of block would follow (“Which symbol is displayed in the circle? The circle is always green” or “Which symbol is displayed in the circle? The circle can sometimes be red”).

The diameter of the circle was 1.2° and the sides of the squares were each 1.2° . All shapes were presented as color outlines against a black background on a 20-inch LCD monitor (Samsung SyncMaster 204B) with a viewing distance of approximately 60 cm. The shapes were presented in an invisible 2×2 grid ($8.5^\circ \times 8.5^\circ$) for balancing spatial locations of display items. In each trial, half of the shapes framed a plus and the other half an equal symbol. Shapes were separated by at least 0.61° . If participants did not respond within three seconds or responded incorrectly, a note appeared on the screen for 1000 ms, telling them to either “press quicker” or denoting “error”. The note was followed by a random delay of 200–800 ms. Following a correct response, a black screen was displayed for a random time interval between 1200–1600 ms before the next trial was initiated.

32 practice trials preceded the experiment. Completion of the task took approximately 20 minutes. One older participant was excluded from this particular analysis due to technical problems.

For the analysis of the singleton task, all trials in which participants missed a trial, responded inaccurately or faster than 200 ms were excluded. Trials in which the singleton corresponded to the target were also excluded due to specific response patterns induced by such trials (see [48] for details). In accordance with Costello et al. [48], we then calculated a distraction by singleton score for each participant for each condition (singleton detection vs. baseline). More specifically, mean reaction time in trials without singleton was subtracted from mean reaction time in trials with singleton distractor. In the next step, we estimated the ability to flexibly exert top-down control in the context of salient stimuli (which could be targets or distractors) by calculating the difference between singleton-detection and baseline distraction scores (adapted from Costello et al. [48]). Figure 2 provides an overview of the different task conditions and illustrates the calculation of the singleton score.

Recognition Memory and Affective Rating Task. In the recognition paradigm applied on the second day, the 120 stimuli presented on the first day were randomly intermixed with the 120 new stimuli from the second stimulus set. In a self-paced manner, participants had to respond to each image individually and indicate whether they had seen it on the previous day by pressing the corresponding button for “sure yes”, “probably yes”, “probably no”, or “sure no”. Such detailed response categories (instead of simple old/new ratings) were offered to reduce response bias and to maintain deep elaboration throughout the recognition task. Participants had five practice trials before the actual recognition test started and the whole test lasted approximately 40 minutes.

For the analysis of the recognition data, we collapsed across probable and sure responses because of the low and variable number of trials in each category. Subsequently, we calculated corrected hit rates by subtracting the proportion of false alarms

from the proportion of hits. These values were computed for each stimulus category (valence by age-content) separately.

Finally, participants rated the affective quality of all stimuli with a computerized version of the Self-Assessment Manikin (SAM; [49]). The SAM is a non-verbal self-report measure, consisting of two bipolar five-point scales, which represent the affective dimensions of valence (ranging from unpleasant to pleasant) and arousal (ranging from calm to excited). Picture sequence was randomized for each participant and again five practice trials were provided, amounting to an overall duration of 45 minutes.

The recognition as well as the affective rating task were implemented using the software Presentation (Neurobehavioral Systems). Stimuli were presented on a 20-inch LCD monitor (Samsung SyncMaster 204B) with a viewing distance of approximately 60 cm.

Data processing

All statistical analyses were accomplished with R, an open-source language for statistical computing (www.r-project.org). Fixation and recognition memory data were analyzed in $2 \times 3 \times 2$ repeated measures analyses of variance (ANOVA), including the factors age-group (young/old), emotion (positive/negative/neutral) and image category (own-age/other-age). Where appropriate, degrees of freedom were adjusted using the Greenhouse-Geisser procedure [50] to correct for potential violations of the sphericity assumption. Two sample *t*-tests were applied in post-hoc comparisons between groups and paired *t*-tests for comparisons within groups. Pearson product moment correlations were used to calculate correlations between fixation data and the singleton score. Cohen's *d* and partial eta squared η_p^2 are depicted as effect sizes for pair wise comparisons and ANOVAs, respectively.

Results

Ratings

As expected, ANOVAs for the SAM ratings including the factors emotion (positive/negative/neutral) and age-category of the image (young-age/old-age) as within-subject factors and group (young/old) as a between-subjects factor revealed significant main effects of emotion for the valence, $F(2,96) = 203.54$, $\epsilon = .61$, $p < .001$, $\eta_p^2 = .81$ as well as for the arousal scale, $F(2,96) = 118.65$, $\epsilon = .95$, $p < .001$, $\eta_p^2 = .71$. Post-hoc analysis indicated that these effects were driven by the following rankings for the valence scale: positive > neutral > negative and for the arousal scale: negative > positive > neutral (all $p < .01$). Results of interactions between emotion and age-category of the image revealed no significant group differences for none of the two SAM-scales (all $p > .29$).

Eye-tracking

For the analysis of the eye-tracking data, the relative number of fixations (Figure 3A) and the relative fixation durations (Figure 3B) were analyzed in separate repeated measures ANOVAs with emotion (positive/negative/neutral) and image category (own-age/other-age) as within-subject factors and group (young/old) as a between-subjects factor. For both models, a significant main effect of emotion was found (fixation number: $F(2,96) = 7.19$, $\epsilon = .87$, $p < .01$, $\eta_p^2 = .13$; fixation duration: $F(2, 96) = 7.11$, $\epsilon = .87$, $p < .01$, $\eta_p^2 = .13$), as well as a significant emotion \times group interaction (fixation number: $F(2,96) = 4.11$, $\epsilon = .87$, $p < .05$, $\eta_p^2 = .08$; fixation duration: $F(2,96) = 3.53$, $\epsilon = .87$, $p < .05$, $\eta_p^2 = .07$). Moreover, for the number of fixations, a trend was observed for the emotion \times image category interaction, $F(2,96) = 2.96$, $\epsilon = .97$, $p = .06$, $\eta_p^2 = .06$, as well as the three-way interaction of all factors, $F(2,96) = 2.49$, $\epsilon = .97$, $p = .09$, $\eta_p^2 = .05$.

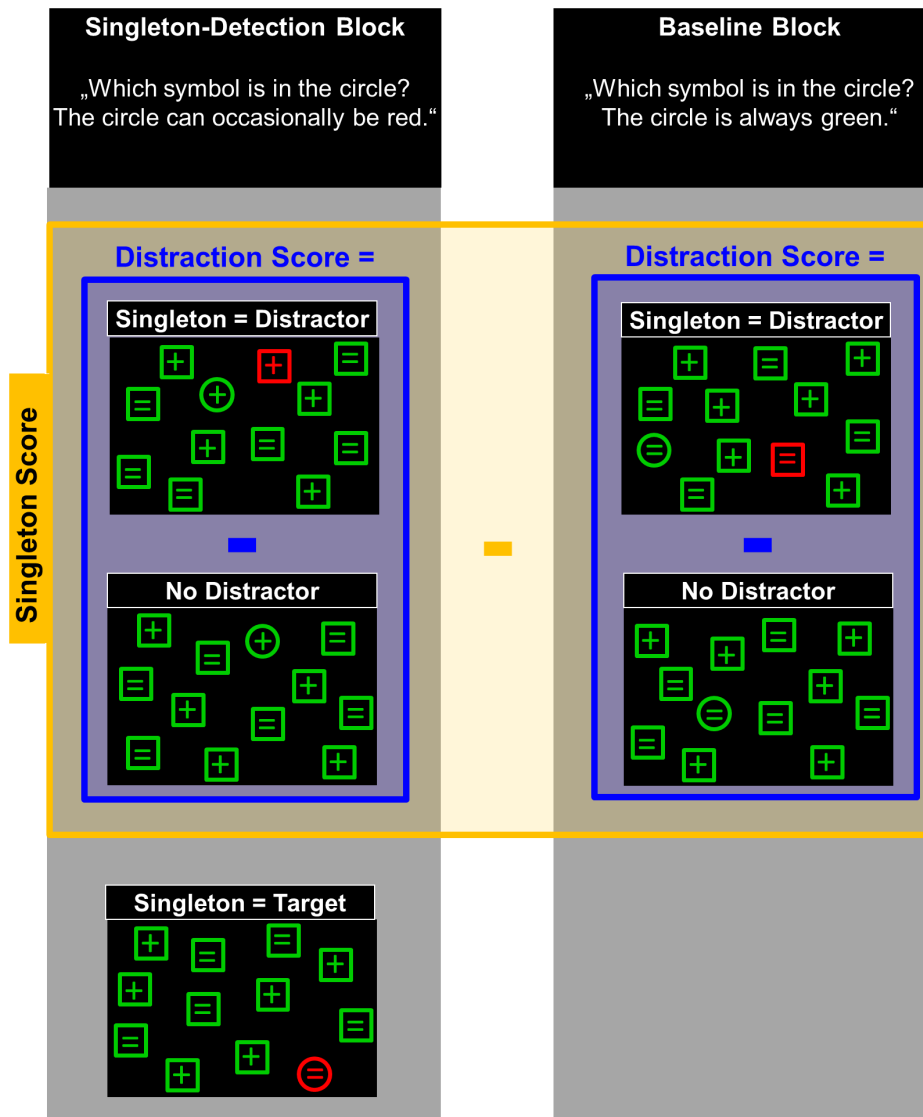


Figure 2. Illustration of the possible singleton-task conditions and of the score calculation. The left panel exemplifies the singleton-detection condition, in which the singleton distractor (red shape) can occasionally correspond to the target (circle). In the baseline condition, demonstrated in the right panel, the distractor never appears as the target. For both conditions, a distraction score (illustrated in blue) was calculated as the difference in reaction times between trials with singleton distractor and trials without distractor. Subtraction of these scores formed the singleton score (illustrated in yellow).

doi:10.1371/journal.pone.0104180.g002

Post-hoc comparisons for the number of fixations across both age-categories (Figure 4a) indicated that older adults fixated positive stimuli significantly more than negative, $t(24) = 2.31$, $p < .05$, $d = 0.46$, and neutral ones, $t(24) = 2.97$, $p < .01$, $d = 0.59$, while in contrast, younger adults showed significant preferences for positive over neutral, $t(24) = 3.68$, $p < .01$, $d = 0.74$, and negative over neutral stimuli, $t(24) = 3.91$, $p < .001$, $d = 0.78$. The same pattern was observed for fixation durations across both age-categories (see Figure 4B): Older adults fixated positive stimuli significantly longer than negative, $t(24) = 2.09$, $p < .05$, $d = 0.42$, and neutral, $t(24) = 2.80$, $p < .01$, $d = 0.56$, stimuli, while younger adults significantly preferred positive, $t(24) = 3.58$, $p < .01$, $d = 0.72$, and negative, $t(24) = 3.99$, $p < .001$, $d = 0.80$, over neutral images. Moreover, direct group comparisons of these preferences revealed that for both, fixation numbers and fixation durations, the difference in negative versus neutral stimuli was significantly lower

in older than in younger participants: $t(48) = 2.50$, $p < .05$, $d = 0.71$ (fixation numbers), $t(48) = 2.40$, $p < .05$; $d = 0.68$ (fixation durations). Additionally, the older adults' preference in their number of fixations for positive over negative stimuli was significantly greater than in younger participants, $t(48) = 2.07$, $p < .05$, $d = 0.58$.

Regarding the marginally significant 3-way interaction for fixation number, post-hoc comparisons revealed that this trend was mainly driven by group x image category effects for positive versus negative stimuli. More specifically, older participants' focus on positive versus negative stimuli was significantly stronger for stimuli of the own-age compared with the other age-category, $t(24) = 2.60$, $p < .05$, $d = 0.52$, and this effect was significantly stronger than in younger participants, $t(48) = 2.10$, $p < .05$, $d = 0.59$ (Figure 5).

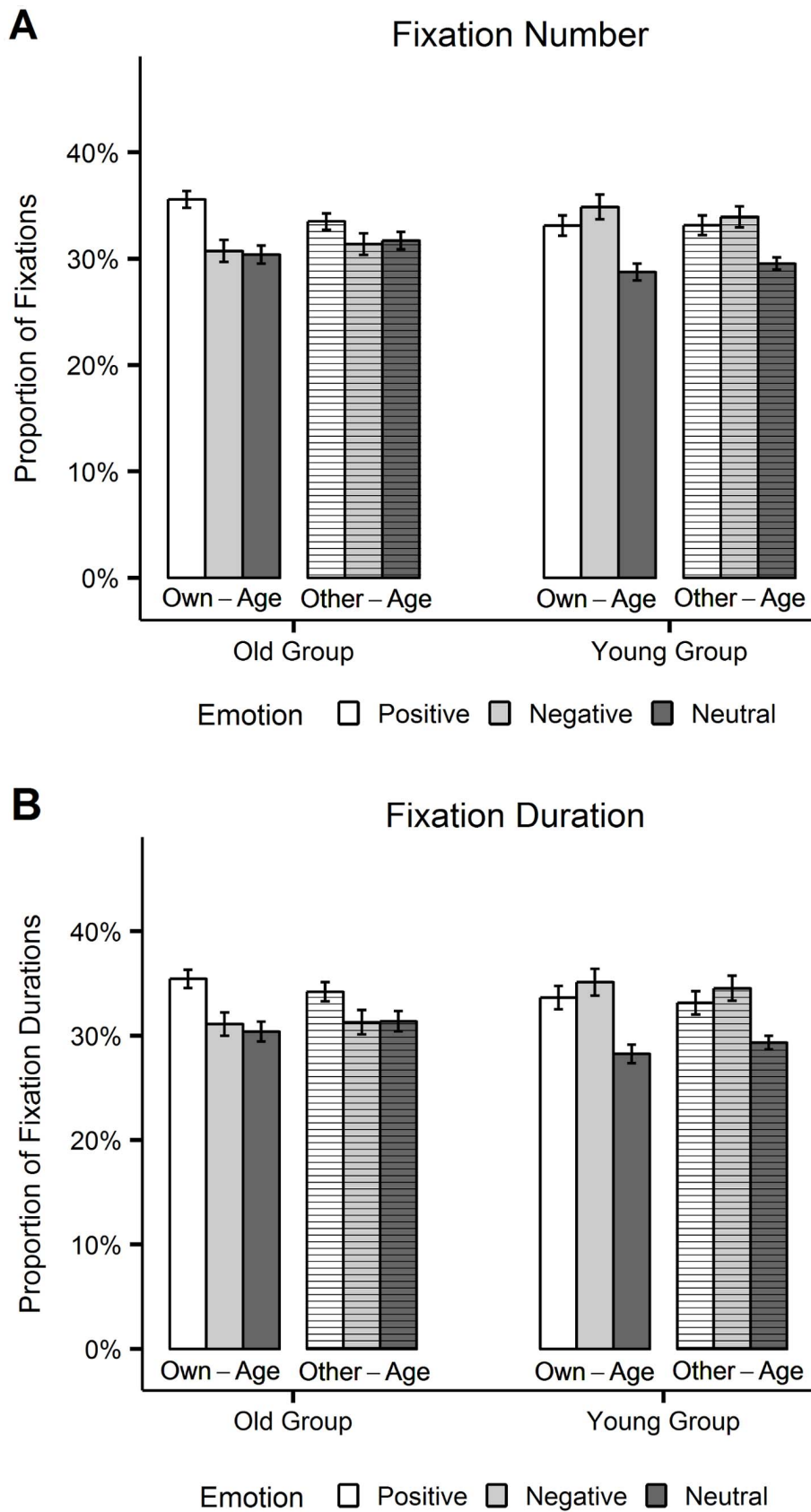


Figure 3. Eyetracking data. Proportions of fixations (A) and fixation durations (B) on positive, negative and neutral own-age and other-age stimuli, plotted separately for each age-group. Error bars represent standard errors of the mean. doi:10.1371/journal.pone.0104180.g003

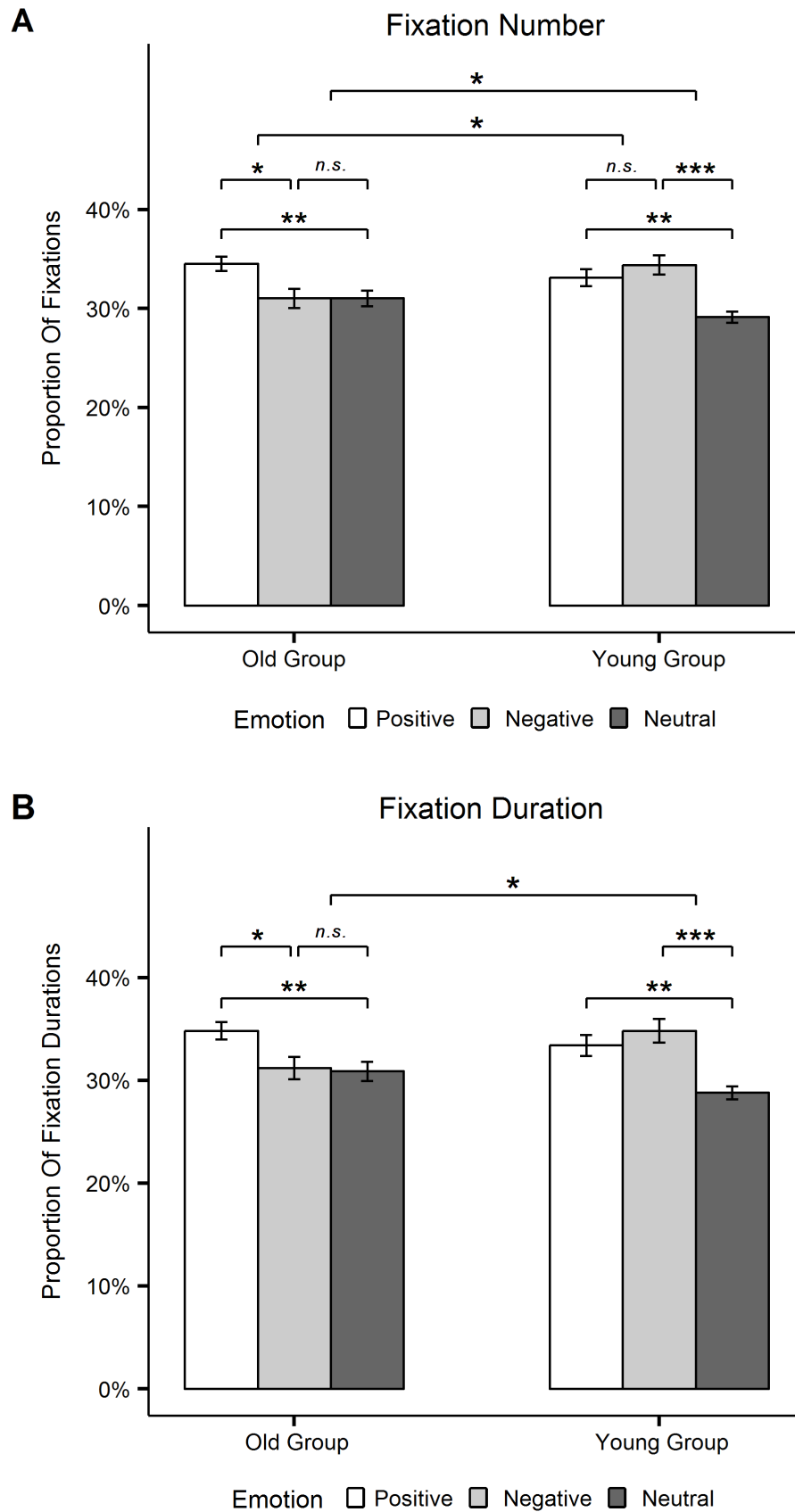


Figure 4. Post-hoc eyetracking results of emotion and emotion x group effects. Proportions of fixations (A) and fixation durations (B) on positive, negative and neutral stimuli aggregated across own-age and other-age stimuli, plotted separately for each age-group; Error bars represent standard errors of the mean. * $p < .05$, ** $p < .01$, *** $p < .001$, *n.s.* = not significant.
doi:10.1371/journal.pone.0104180.g004

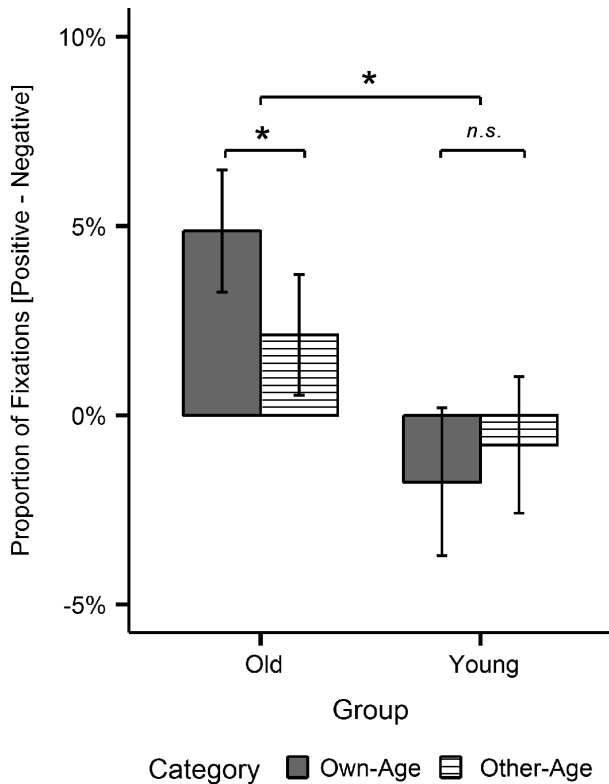


Figure 5. Post-hoc test results for interactions with image category. Difference between proportions of fixations for positive minus negative images in the two image categories (own-age vs. other-age), plotted separately for each age-group. Error bars represent standard errors of the mean. * $p < .05$, n.s. = not significant. doi:10.1371/journal.pone.0104180.g005

The ability of top-down control and associations with the positivity effect in attention

Only few trials had to be discarded from the singleton analysis due to errors or missing responses (old group: $M = 1.14\%$, $SD = 1.09\%$; young group: $M = 2.39\%$, $SD = 2.02\%$).

First of all, we compared the singleton score between young and old adults. A two-sample t-test revealed no significant difference, $t(47) = 1.44$, $p = .16$.

In the next step, we investigated whether there is a relationship between older participants’ attentional PE (i.e. focusing on positive while ignoring negative stimuli) and their ability to flexibly exert top-down control. Pearson product moment correlations were calculated between older adults’ singleton score and the number and duration of fixations on positive minus negative stimuli. Results revealed significant correlations with both eye-tracking measurements: $r = -.44$, $n = 24$, $p < .05$ for number of fixations and $r = -.46$, $n = 24$, $p < .05$ for fixation duration. As visualized in Figure 6, older participants who were more able to adaptively control their attention in the context of salient stimuli, showed a larger positivity effect.

Recognition memory

Corrected hit rates were subjected to an ANOVA with the factors emotion (positive/negative/neutral), image category (own-age/other-age) and group (young/old). The analysis revealed significant main effects of emotion, $F(2,96) = 8.12$, $\epsilon = .97$, $p < .01$, $\eta_p^2 = .15$, and group, $F(1,48) = 12.16$, $p < .01$, $\eta_p^2 = .20$, a significant interaction between emotion and group, $F(2,96) = 4.07$,

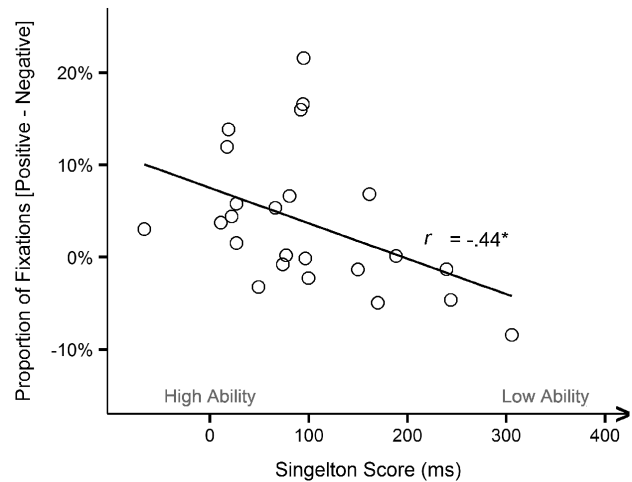


Figure 6. Correlation between the positivity effect and the singleton score. Illustrated for the number of fixations, but similar results were obtained for the fixation duration. * $p < .05$. doi:10.1371/journal.pone.0104180.g006

$\epsilon = .97$, $p < .05$, $\eta_p^2 = .08$ as well as a significant interaction between emotion, image-category and group, $F(2,96) = 3.29$, $\epsilon = .98$, $p < .05$, $\eta_p^2 = .06$.

As evident in Figure 7, younger participants showed a general emotional memory enhancement for positive, $t(24) = 3.40$, $p < .01$, $d = 0.69$, and negative, $t(24) = 4.23$, $p < .001$, $d = 0.83$, over neutral items across both age-relevance conditions. In contrast, the emotional memory enhancement in the old group was restricted to positive over neutral own-age stimuli, $t(24) = 3.19$, $p < .01$, $d = 0.65$. Moreover, post-hoc analyses revealed that the latter effect was also the main reason for the significant 3-way-interaction between emotion, image category and group: the enhancement of positive over neutral memory for own-age versus other-age stimuli was significantly stronger in old compared to young adults, $t(48) = 2.62$, $p < .05$, $d = 0.74$ (see Figure 8).

Discussion

Our study could demonstrate that older adults engage in selective attention to produce an age-specific positivity effect (PE) in attention. The selective depth of stimulus elaboration was also reflected in an analogical positivity preference in memory on the next day. Moreover, focusing on positive and ignoring negative stimuli was strongest in older adults with a generally higher ability of attentional control in the context of highly salient information. Finally, the observed PE was boosted for stimuli with higher own-age relevance, which further underlines older adults’ selectivity to allocate cognitive resources in the service of prioritized emotional goals.

The main aim of the present approach was to further illuminate the most frequently discussed conditions and mechanisms underlying the PE in older adults’ emotional attention and memory. In this context, one of the main hypotheses we tested was that the PE results from an age-related increased emphasis on selective attention as a tool to control emotional information processing. To study this question, we established an eye-tracking paradigm in which participants were simultaneously presented with positive, negative and neutral stimuli. Thus, participants needed to engage in selective attention in order to focus on a preferred emotion and to ignore non-target emotions respectively. Replicating and strengthening previous results (for a recent meta-analysis on the

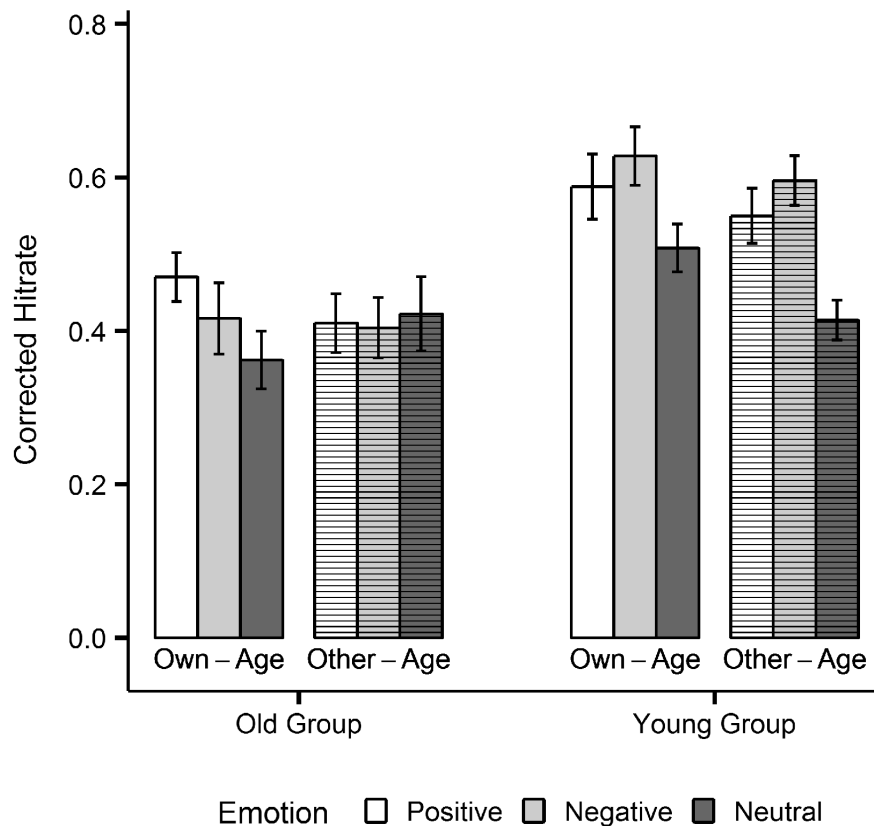


Figure 7. Memory data. Corrected hit rates for positive, negative and neutral own-age and other-age stimuli, plotted separately for each age-group. Error bars represent standard errors of the mean.
doi:10.1371/journal.pone.0104180.g007

reliability of the effect see [1]), we found that older adults exhibited a PE, i.e. significantly focused their attention on positive and away from negative stimuli compared with young adults. In detail, while young adults showed a general boost in attention by emotional stimuli, older adults showed such a boost only for positive pictures, but seemed to ignore the saliency of negative stimuli. Intriguingly, a similar pattern was observed in memory for the presented stimuli on the next day, thus emphasizing the impact of selective processing on the depth of encoding. Life-span theorists have proposed that the occurrence of a PE is triggered by an increased resource allocation in the service of emotional goals to maintain emotional well-being in aging. In line with that, an increased focus on the positive has only been found in emotionally healthy older adults, but not in adults with late-life depression [24], and has been directly related to emotional well-being [6]. It has been argued that the prioritization of selective attention among different emotion regulation strategies is promoted by the age-related availability of underlying brain resources. In particular, there is evidence that while dorsolateral frontal brain regions are typically affected by an age-related decline, ventromedial circuits, including the anterior cingulate cortex (ACC), remain relatively preserved in late-life [51]. Thus, it could be speculated that elderly people focus on those strategies that are easiest to implement. Consistent with this idea, healthy older adults are often worse than younger adults [52] when instructed to use higher-order, rather dorsolaterally mediated regulation strategies, such as reappraisal [53,54]. In contrast, they often demonstrate unimpaired or even better performance than younger adults when they get the opportunity to use selective inhibition and enhancement [55], which are

thought to rely more on ventromedial brain regions [26]. In line with that, in our previous work we found an age-specific increase of ventromedial brain activity when healthy older adults selectively focused on positive stimuli [6] or inhibited negative information [24].

In contrast to most existing eye-tracking studies [8,9,33,56], participants in our study were free to shift their attention towards preferred and away from unfavored emotional stimuli. Previous findings on instructed emotion regulation in older adults indicate that the PE in aging most likely occurs when attentional deployment is not controlled or instructed, and when there is an alternative stimulus on which older adults can focus their attention while ignoring negative information [19]. The lack of one or both of these aspects may account for the failure to observe age-specific emotional preferences in some previous studies [57] and their presence in our study might have maximized the effect.

Despite the aforementioned speculations on the role of preserved brain circuits in aging, it is still surprising that older adults are able to voluntarily shift their attention in the context of highly salient distraction as in our paradigm. There is ample evidence that cognitive functions including executive control are typically affected by an age-related decline [36]. However, most of these findings are limited to non-emotional distractors, while ignoring negative distractors is frequently maintained and associated with lower cognitive costs in older as compared to younger adults [5,22,23,58,59]. One discussed reason for this phenomenon is that older adults may be less sensitive to negative stimuli, for instance due to changes in amygdala functioning [38], and are consequently less challenged by ignoring salient (negative)

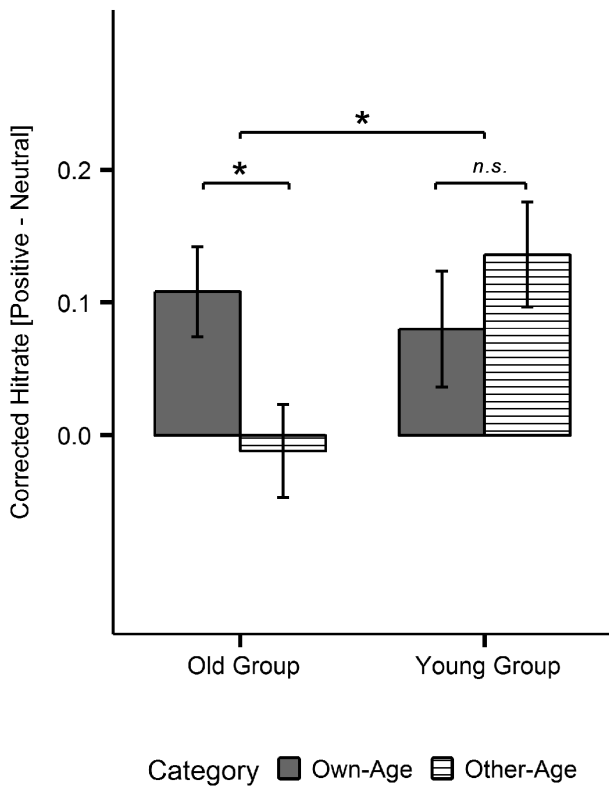


Figure 8. Post-hoc memory results for the three-way interaction between emotion, image category and age-group. Difference between corrected hit rates for positive minus neutral own-age and other-age stimuli, plotted separately for each age-group. Error bars represent standard errors of the mean. * $p < .05$, n.s. = not significant. doi:10.1371/journal.pone.0104180.g008

information. This argument, however, cannot explain findings regarding a selectively increased distractibility by positive stimuli [6,7] and the reported lack of age-effects in initial emotional experiences [10,56]. A probably more convincing explanation is provided by the Socio-emotional Selectivity Theory, which proposes that the maintenance of well-being becomes a major goal in late-life and that cognitive resources are selectively recruited in the service of this goal. More specifically, when older people are confronted with emotional stimuli and have enough freely available cognitive resources, they predominantly activate emotion regulation in a goal-consistent manner, even when it is not required by the setting [6]. Following this assumption, older people with more cognitive resources should be particularly capable to produce a PE. In line with this hypothesis, we investigated whether there is a direct relationship between elderly peoples’ selective attention ability and their tendency to exhibit a corresponding PE. Results revealed a significant correlation between older adults’ attentional focus on positive compared to negative stimuli and their general ability to ignore highly salient distractors in a cognitively demanding setup. The ability to exert top-down control was measured with an established visual search task [48]. This task is able to assess the specific function of spontaneously focusing on target information in the context of salient distraction, which is probably involved when people voluntarily control their attention in an emotional context. The observed correlation in our study strongly supports this assumption and extends previous findings on links between cognitive ability and a PE in memory [12,60].

Interestingly, emotionally healthy older adults in our study did not differ from young adults in their ability to manage distraction by highly salient stimuli. Although this finding is consistent with some previous findings [48,61–63], it is not yet clear whether it reflects preservation, compensation, or even decline in older adults. For instance, it could again be speculated that a reduction in the responsiveness to arousing stimuli because of age-related limbic brain decline might facilitate the disengagement from salient but irrelevant stimuli [38]. While this might hold for our observed singleton findings, it cannot explain older adults’ increased focus on highly salient, positive stimuli. In addition, and as discussed in the next section, the amplification of the PE through stimulus relevance rather supports assumptions from the “cognitive control hypothesis” [35] than from the “aging brain model” [38].

We further explored the idea that healthy older adults actively apply cognitive resources for emotional means by manipulating the personal relevance of the stimulus material. In fact, there is evidence that the selective allocation of cognitive resources in aging can be facilitated by self-referential processes and that older people predominantly engage in self-referential processing to compensate for age-related cognitive decline [25,64–66]. Along these lines, we expected an amplification of the PE when older participants are presented with stimulus material that depicts social scenes with a higher degree of own-age relevance. Consistent with this expectation, we could show that elderly participants’ emotional selectivity in attention and memory was enhanced for images of higher own-age relevance. Thus, our results fit with previous neuroimaging studies, demonstrating more engagement of the “emotion-regulation” brain network in older adults when the emotional material was processed under conditions of stronger in-depth elaboration [39], such as self-referent processing [29] and semantic elaboration [66].

Some previous studies that manipulated self-relevance by introducing own- and other age face stimuli in young and old adults did not demonstrate an enhanced PE for relevant stimuli [7,40,67]. One main reason for these results may be the comparatively lower degree of socioemotional relevance conveyed by decontextualized emotional faces as compared to more natural social scenes [68,69]. Social emotional stimuli have a strong impact on self-referential processing as people try to understand the mental state of the other [70]. This is particularly pronounced the more similar the person is to the self [43,44]. Other findings that are controversial to our results come from Tomaszczyk and colleagues [71]. More consistent with us, they used complex IAPS images but presented them in a single-stimulus encoding paradigm. The authors observed a reduction of the PE in memory under conditions of high compared to low personal relevance, suggesting that, here, the saliency signalled by the self-relevant negative stimuli interfered with emotional goals in the elderly. As mentioned above, the PE in aging most likely occurs when attentional deployment is not controlled and when there is an alternative stimulus on which older adults can focus their attention while ignoring negative information [19]. Both factors were lacking in the previous study, but present in our one, which suggests that they constitute significant modulators of the PE in aging.

The selection and categorization of our stimulus material was based on independent raters and validated by a sample of young adults. Thus, we cannot exclude the possibility that older adults’ relevance ratings would differ from those of younger adults. In the same vein, to investigate the impact of personal relevance on participants’ information processing in more detail, it seems desirable to consider individual relevance ratings. The fact that we

still observed significant effects of the age-relevance, however, supports the assumption that we rather under- than overestimated the effect by this limitation. Furthermore, we only included emotionally healthy young and old adults in our study and can thus only speculate about the clinical role of our findings. Nevertheless, it has consistently been demonstrated that elderly patients with emotional disorders, such as geriatric depression or geriatric anxiety disorder, show marked executive control dysfunctions together with fronto-limbic abnormalities [24,72–74]. Moreover, these patients are typically more strongly distracted by negative stimuli, which is paralleled by decreased prefrontal attention control activity [75,76]. Taking these findings into account, we propose that the ability to selectively recruit cognitive control processes to assist emotional well-being might be an important resilience factor for emotional health in aging. Intervention- and prevention schemes might therefore benefit from including specific trainings of cognitive control and such training might be facilitated through the implementation of self-relevant material.

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Effects of Prospective Thinking on Intertemporal Choice: The Role of Familiarity

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Abstract: Imagining future events while performing an intertemporal choice task can attenuate the devaluation of future rewards. Here, we investigated whether this effect and its neural basis depend on the degree of personal prior experience associated with the simulated future scenarios. Functional magnetic resonance imaging was combined with a modified intertemporal choice task in which the delayed options were either purely monetary, or linked with a social event. Subject-specific events differed regarding familiarity, that is, meeting a close, familiar person or a celebrity in a café. In line with recent hypotheses on episodic construction, the simulation of future familiar and unfamiliar events equally attenuated delay discounting behavior in comparison with the control condition and both were imagined with similar richness. Imaging data, however, indicate that these results rely on differential neural activation patterns. The hippocampus was particularly involved in the simulation of unfamiliar future scenarios, probably reflecting enhanced construction processes when personal experience with similar past events is lacking. Consequently, functional coupling of the hippocampus with neural valuation signals in the anterior cingulate cortex predicted the subjective value only of rewards offered in the unfamiliar context. In contrast, valuation of rewards in a familiar context was predicted by activation in key nodes of emotional and autobiographical memory retrieval and dynamically modulated by frontal-striatal connectivity. The present data emphasize that the mechanisms underlying neural valuation of prospective rewards largely depend on the pre-experience with the context in which they are offered. *Hum Brain Mapp* 36:4210–4221, 2015. © 2015 Wiley Periodicals, Inc.

Key words: decision-making; intertemporal choice; prospection; autobiographical memory; hippocampus

INTRODUCTION

Farsighted decisions are strongly biased by the tendency to devalue rewards as a function of time to delivery [Peters and Büchel, 2011]. The resistance to the temptation of an immediate gratification for the benefit of a larger but delayed payoff can be increased when connecting it to an anticipated future event (“tag-effect”) [Daniel et al., 2013a,b; Kwan et al., 2015; Peters and Büchel, 2010], when the reward consumption itself is simulated [Benoit et al., 2011; Palombo et al., 2015] and when a future-oriented mindset is induced via prospective imagery [Cheng et al., 2012]. Highlighting the impact of episodic prospection on this effect, neural activation in response to episodic tags strongly overlaps with a core network implicated in remembering and imagining

Additional Supporting Information may be found in the online version of this article.

Contract grant sponsor: German Research Foundation (DFG); Contract grant numbers: BR 2877/2-2 and PE 1627/3-1.

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Received for publication 2 April 2015; Revised 11 June 2015; Accepted 12 July 2015.

DOI: 10.1002/hbm.22912

Published online 28 July 2015 in Wiley Online Library (wileyonlinelibrary.com).

events [Race et al., 2011; Schacter et al., 2012], including the ventromedial prefrontal cortex, precuneus, and posterior cingulate cortex [Benoit et al., 2011; Peters and Büchel, 2010]. This fits with suggestions that constructing coherent future scenarios involves the flexible recombination of episodic memories [Schacter and Addis, 2007b, 2009].

The extent to which prospective thinking requires such flexible recombination is certainly affected by the degree to which a particular event relies on self-experience. Along those lines, lacking self-experience during the imagination of unfamiliar future events may be compensated by stronger reliance on episodic information from other sources, such as media and third person experiences [Anderson, 2012]. Findings are mixed whether such additional recombination demands affect the quality of imagination with some studies reporting richer episodic thought when based on prior experience [D'Argembeau and Van der Linden, 2012; Szpunar and McDermott, 2008] and others reporting the quality of imagination to be unaffected by familiarity [Anderson, 2012]. In the same vein, it is unclear whether the neural circuits modulating the tag-effect are different for familiar and unfamiliar future events. It seems likely that the hippocampus is generally involved in the episodic construction of future events [Hassabis et al., 2007; Maguire and Mullally, 2013]. Moreover, there is evidence suggesting that the hippocampus is even stronger engaged when self-experience with simulated events is lacking. Specifically, increased hippocampal activation has been observed during the imagination of novel compared to remembering episodic events [Addis et al., 2011; Okuda et al., 2003; Schacter and Addis, 2007a; Weiler et al., 2010b]. In addition, a recent study that explicitly controlled encoding related processing in the simulation of unfamiliar events demonstrated that activity within the posterior hippocampus was significantly modulated by construction effort [Gaesser et al., 2013]. When construction demands are reduced in the context of familiarity, however, episodic simulation seems to be less dependent on hippocampal processing [Weiler et al., 2010a] and to rely more on posterior parietal regions [Szpunar et al., 2009], which together with occipital and temporal regions are part of the core network implicated in autobiographical memory retrieval [Cabeza and St Jacques, 2007; Martinelli et al., 2013; Svoboda et al., 2006].

In the context of the tag-effect, episodic prospection has so far either been restricted to familiar scenarios [Palombo et al., 2015] or familiarity was not controlled at all [Daniel et al., 2013a,b; Peters and Büchel, 2010]. However, the quality [Lebreton et al., 2013; Palombo et al., 2015; Peters and Büchel, 2010] and emotional valence [Benoit et al., 2011; Liu et al., 2013] of imagination, which might rely on the personal experience with future events, has found to be crucial for the magnitude of the tag-effect. Recent mixed findings about presence [Kwan et al., 2015] or absence [Palombo et al., 2015] of the tag-effect in amnesic patients with hippocampal lesions further indicate a differential impact of future event features on the neurobehavioral manifestation of the

tag-effect. To fill this gap, this study combined functional magnetic resonance imaging (fMRI) with a modified intertemporal choice task in which future rewards were linked to subject-specific social events differing systematically in familiarity. An established hyperbolic model of delay discounting [Mazur, 1987] and extensive interview data were used to explore potential behavioral differences or similarities between episodic conditions. On the neural level, we used factorial and functional coupling analyses to focus on condition dependent interactions between neural decision-making and episodic future-thinking networks. Specifically, the hippocampus might critically mediate the construction of unfamiliar events and consequently impact on neural valuation signals more strongly in the unfamiliar condition. In contrast, neural networks related to autobiographical and emotional memory retrieval might have a larger impact on neural valuation in the context of familiar event simulation.

MATERIALS AND METHODS

Participants

Twenty-three healthy young adults (21–30 years; $M = 24.96$; $SD = 2.79$; 12 men) participated in this study. Participants were recruited via an online-announcement and from an existing database and gave written informed consent before participating. Exclusion criteria were neurological, psychiatric, and other serious physical conditions. Participants were financially compensated with 10 Euros per hour. In addition, one chosen reward from the delay discounting task was randomly selected and paid out with the respective delay. The study was approved by the local ethics committee.

Study Design

Following established procedures [Peters and Büchel, 2009], all participants were invited in on a separate day, prior to testing, to complete a computer-based delay-discounting procedure. This pretest was used to construct subject-specific trials for the main discounting experiment to ensure that participants would choose the delayed option in 50% of the trials. Individual choices from this pretest were fitted via a hyperbolic discounting function of the form

$$SV = \frac{A}{(1+kD)}$$

to estimate the individual discount rate for a reward of 20€ (SV = subjective value; A = amount of the delayed reward; D = delay in days; k = discount rate) [Mazur, 1987]. The discount rate was then used to calculate indifference amounts for six delays, randomly drawn from one of two sets [1, 2], [6, 7], [13, 15], [28, 32], [85, 95], [170, 190]. Next, the six delays were paired with six amounts lying equally above and below the respective indifference point. Monetary amounts ranged from 20.5€ to 79.50€. In

TABLE I. Interindividual variability in the reward ranges at each delay

Delay	<i>M</i> (IQR)	SD
[1, 2]	21.30	3.11
[6, 7]	21.26	3.58
[13, 15]	20.39	3.66
[28, 32]	20.05	5.76
[85, 95]	21.14	9.11
[170, 190]	25.13	10.40

Means (*M*) and standard deviations (SD) of the individual IQR of the delayed rewards from the fMRI experiment are reported separately for each of the six delays. IQRs are computed for each participant by subtracting the 25% percentile of the rewards across all sessions from the 75% percentile.

this fashion, six blocks of 36 trials each were constructed for the fMRI experiment. While minimum and maximum amount for each delay were close to the extreme values for each participants, values varied individually between these extremes. In order to get an impression of such interindividual variability, Table I shows the average interquartile ranges (IQR) computed as the difference between the 75% minus the 25% percentile of the rewards across the six sessions and their standard deviation for each of the six delays (for complete information on the individual IQRs, see Table S1 in the Supporting Information).

Two of these six blocks served as the control condition, which involved standard delay discounting without episodic prospecting, while the remaining four blocks were assigned to the episodic tag conditions. In each of these four blocks, participants were instructed to imagine meeting a person in a café for the day of delayed reward delivery. To ensure not only temporal but also spatial specificity of the imaginations, participants were familiarized with five images depicting scenes of a typical café before the experiment. In two of these blocks, this event was related to prior experiences and involved meeting with a familiar social partner (e.g., Mother). In the two other blocks, the event was unfamiliar and involved meeting with a famous person from the media who had not been met in person before (e.g., Angela Merkel). A standardized interview (adopted from [Carstensen and Fredrickson, 1998]) was used to identify these two familiar and two novel social partners: For the identification of the familiar social partners, participants had to imagine moving to a foreign country on their own and to appoint familiar persons with whom they would like to spend the last hours before their departure. To identify the famous, novel partners, participants imagined conducting an interview for the local newspaper with persons of public interest whom they had never met in person before.

The applied fMRI paradigm was a modified version of the task used by Peters and Büchel [2010] (Fig. 1). The three conditions were presented in six blocks (2 blocks per condition) of 36 trials each. To avoid various types of confounding

sequence effects, the presentation of the three conditions was randomized but the two blocks of each condition were always presented successively. Between blocks, participants were given a five minutes break to relax. In each trial, participants were required to choose between a fixed immediate reward option of 20 € (which was not shown on the screen) and a larger but delayed amount. During episodic conditions, this delayed reward option was presented together with the name of the social partner with whom they had to imagine a meeting in a café for the date of the delayed reward delivery. In the control condition, delayed options were presented together with placeholder strings (“XXXX” or “YYYY”) and participants were explicitly instructed not to imagine anything. Participants were trained on the task before scanning. After the task and without being scanned, participants remained lying in the scanner for approximately ten minutes for an interview about the richness of their imagination for the four events. During this interview, participants were asked to describe their imaginations for the four scenarios as detailed as possible. Answers were recorded and later transliterated.

Outside the scanner, participants were given questionnaires to rate the emotionality and curiosity they associated with the four partners as well as their motivation to meet the partners for each event on scales ranging from 1 to 7.

Data Acquisition

We used Presentation software (Neurobehavioral Systems) for stimulus presentation and recording. FMRI data were acquired on a 3 tesla system (Magnetom Trio, Siemens) equipped with a 32-channel head coil. Each volume comprised 41 transversal slices (2mm thickness, 1mm gap, TR = 2460 ms, TE = 25 ms, FOV = 216 × 216 mm², in-plane resolution 2 × 2 mm², GRAPPA factor 2). After functional imaging, high-resolution anatomical MR images were acquired using a T1-weighted MPRAGE sequence (1 × 1 × 1 mm).

Behavioral Data Analysis

Behavioral data analysis was performed with Matlab (Mathworks). Individual-subject choice data were fitted using maximum likelihood estimation by combining a hyperbolic discounting function with softmax action selection [Peters et al., 2012] separately for each experimental condition. This yielded two free parameters per condition, the hyperbolic discounting constant *k*, where higher values reflect greater impatience, and the inverse temperature parameter β of the softmax choice function, where greater values reflect more decision noise (see Table II for medians and IQRs of the absolute single-subject maximum likelihood parameter estimates, model fit criterion and reaction time data). A square-root transformation was applied to the resulting *k* parameters prior to analyses [Ballard and

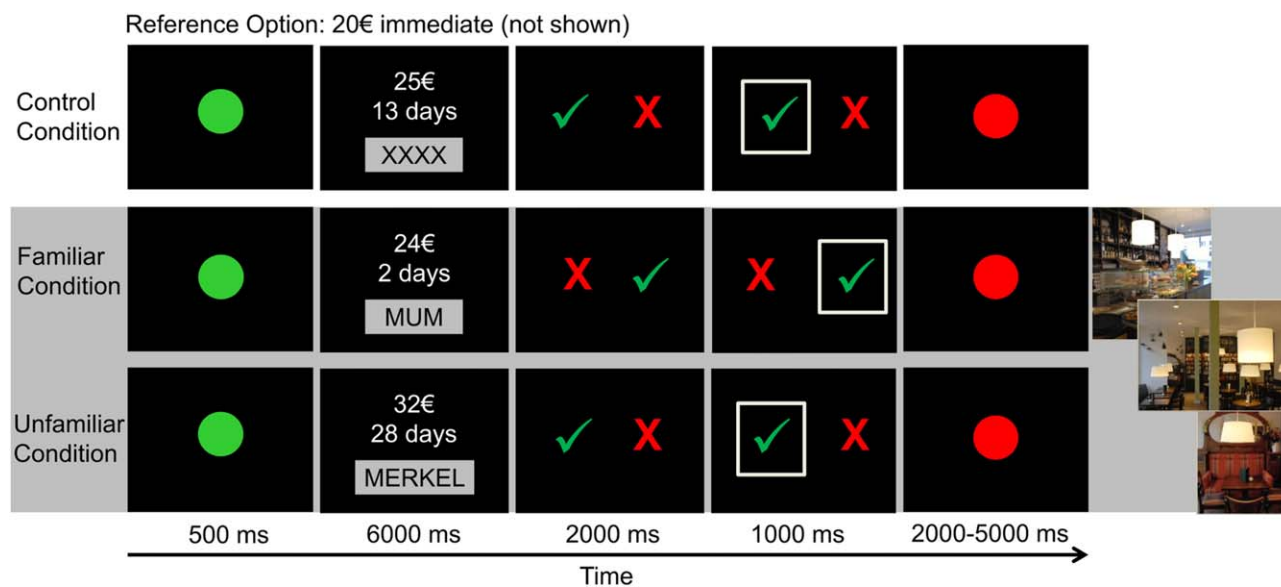


Figure 1.

Outline of the paradigm. Each trial started with a green dot, signaling the start of the trial. Next, the delayed reward option was presented for 6 s. Participants had to indicate their choice by selecting the red cross for the immediate reward (20 € that were not shown) or the green check mark for the delayed reward option. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Knutson, 2009; Peters et al., 2012], accounting for their skewed distributions.

Descriptions of the imaginations for the four events were analyzed with respect to the level of episodic richness using a similar procedure to the Autobiographical Interview Analysis [Levine et al., 2002]. Details were categorized as internal (episodic information relating to the given future event) or external (nonepisodic information). Internal details were categorized further into one of five categories adapted from Levine et al.: time, place, perceptual, emotions/thoughts, and event details (examples of narratives coded into internal and external details are presented in Figure S1 in the Supporting Information). External details comprised semantic details, repetitions and other metacognitive statements. A second independent rater coded details into the same categories, yielding a reliability between the raters of cronbach's alpha = 0.97 for internal details and cronbach's alpha = 0.89 for external details. Where appropriate, degrees of freedom

were adjusted using the Greenhouse-Geisser procedure to correct for potential violations of the sphericity assumption.

FMRI Data Analysis

FMRI data processing and statistical analyses were performed using statistical parametric mapping (SPM8; Wellcome Department of Imaging Neuroscience, London, UK).

Functional data were corrected for slice timing, rigid body motion and susceptibility artefacts ("realign and unwarp"). Next, the individual structural T1 image was coregistered to the mean functional image generated during realignment. Coregistered T1 images were then segmented using the 'New Segment' routine in SPM8. Resulting tissue-class images for gray and white matter were subsequently used for spatial normalization of the functional images using the DARTEL toolbox. Data were smoothed with a 6-mm

TABLE II. Model parameters

	k		β		AIC		RT	
	Median	IQR	Median	IQR	Median	IQR	Median	IQR
Control	0.0086	0.0099	1.30	2.31	40.27	36.17	745.58	96.88
Familiar	0.0060	0.0093	1.12	1.92	38.11	26.40	752.97	191.79
Unfamiliar	0.0066	0.0105	1.60	2.44	37.42	29.51	748	240.35

For each of the three conditions, medians and IQRs are reported for the model estimates of the discounting parameter (k) and temperature parameter (β), the Akaike information criterion (AIC) as a measure of goodness-of-fit, as well as for the reaction times (RT).

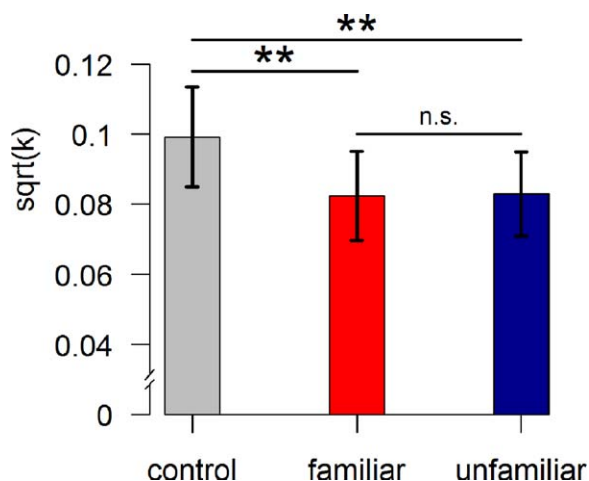


Figure 2.

Behavioral data. Square-root transformed delay discounting rate k , plotted separately for the three conditions. Error bars represent standard errors of the mean. ** $P < 0.01$, n.s.: not significant. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

full-width at half maximum (FWHM) isotropic Gaussian kernel.

Data analysis was performed using the general linear model (GLM) approach as implemented in SPM. Sustained activation during the presentation of the delayed option (i.e., from option onset until button press) was modeled by boxcar regressors that were convolved with the canonical hemodynamic response function. Condition-specific k -parameters from the scanning session were used for the calculation of the subjective value of each delayed option and included as a parametric regressor in the GLM. Error trials (trials in which participants responded too early/late) were modelled separately. All first-level analyses also contained a set of regressors that modelled images contaminated by movement (using an adaptive velocity cutoff with a criterion of 0.4 mm/TR).

For each subject, contrast images for each condition (control/familiar/unfamiliar) and for the respective subjective value regressor were constructed. For differential analyses, these contrast images were entered into a second-level random effects ANOVA model.

Finally, we used psychophysiological interaction analyses (PPI) [Friston et al., 1997] to test for potentially different connectivity patterns of neural valuation regions for the familiar and unfamiliar condition. To this end, we designed first-level models for each participant consisting of the following three regressors: (1) the time course of the seed region; (2) the psychological variable (i.e. the subjective value of the delayed option folded with the haemodynamic response function); and (3) the product of the former two.

To correct for multiple comparisons in the hippocampus, we used anatomical masks obtained from the Harvard-Oxford atlas (probability threshold 50%). In addition,

due to the ventral striatum's role in coding delayed reward signals [Miedl et al., 2014] and emotional aspects of autobiographical memories [Speer et al., 2014], 8mm-spheres were centred around established coordinates: x,y,z : $\pm 14, 8, -8$ mm [O'Doherty et al., 2004; Yacubian et al., 2006]. The threshold of small volume corrections was set to $P < 0.05$ corrected for multiple comparisons using the family wise error rate (FWE < 0.05). Other regions were reported when passing a whole-brain corrected cluster-threshold of FWE < 0.05 (cluster forming threshold $P < 0.005$ uncorrected).

RESULTS

Behavioral Results

The condition specific discounting parameters (transformed k -values) were subjected to a repeated measures ANOVA, yielding a significant main effect of condition (control/familiar/unfamiliar), $F(2,44) = 5.83$, $P < 0.01$. Post-hoc comparisons revealed that participants' discounting behaviour was significantly lower in both episodic conditions compared with the control condition (familiar $>$ control: $t(21) = 2.71$, $P < 0.01$; unfamiliar $>$ control: $t(21) = 2.93$, $P < 0.01$). No significant difference was observed between the conditions ($P = 0.92$; Fig. 2).

Post-Hoc Ratings

Confirming presumed categorization, post-hoc interviews revealed an equal motivation to meet the familiar ($M = 5.96$, $SD = 1.30$) and unfamiliar social partners ($M = 5.96$, $SD = 1.03$), $P > 0.99$. Moreover, familiar partners ($M = 6.65$, $SD = 0.51$) were rated as significantly higher on emotional closeness than the unfamiliar partners ($M = 2.52$, $SD = 1.01$), $t(22) = 15.91$, $P < 0.001$. Analysis of the autobiographical Interview indicated that participants imagined familiar and unfamiliar events with similar amounts of internal, $t(22) = 0.06$, $P > .94$ and external details, $t(22) = 1.31$, $P > .20$ (Table III). Neither for the familiar nor for the unfamiliar condition was the tag-effect directly correlated with the amount of internal details.

FMRI Data

We first analyzed differences in the condition regressors without parametric modulation. The comparison of both episodic conditions versus the control condition was associated with greater BOLD signals in a network consisting of the left medial rostral and ventromedial prefrontal cortex, left middle temporal gyrus, left retrosplenial cortex/posterior cingulate cortex and left lateral parietal cortex (all $P < 0.05$ FWE; Table IV, Fig. 3).

When comparing the familiar with the unfamiliar condition (familiar $>$ unfamiliar), whole-brain analyses revealed a significant increase in the BOLD response in the right

TABLE III. Level of detail and episodic richness of simulations across future event scenarios

	Familiar		Unfamiliar	
	M	SD	M	SD
Internal Details	10.70	4.80	10.74	5.85
Event Details	4.35	2.21	3.70	2.96
Perceptual Details	2.09	2.13	2.26	1.91
Place Details	1.57	0.79	1.52	0.79
Emotion/Thought Details	2.48	1.93	3.30	3.15
External Details	1.09	1.48	0.87	1.33
Semantic Details	0.39	0.84	0.39	0.66
Repetition	0.48	0.79	0.39	0.78
Other	0.22	0.85	0.22	0.67

Means (*M*) and standard deviations (*SD*) are reported for the amount of details imagined for familiar and unfamiliar events with further divisions into subcategories of internal and external detail categories. Due to the link of the imagined scenarios to specific time delays, time details were only rarely reported and are therefore not listed in the table.

extended amygdala, the left thalamus, the left ventral tegmental area, as well as the left middle temporal gyrus (all $P < 0.05$ FWE see Fig. 4A and Table IV). In the reverse contrast (unfamiliar > familiar), a higher BOLD signal was observed in the left posterior hippocampus ($P < 0.05$ FWE, see Fig. 4B). No further regions exhibited significant activation in this contrast on the whole brain level.

In order to investigate whether differences in the neural tag effect could be predicted by interindividual differences in the discounting behavior, we next performed a simple regression analysis including the single-subject contrast images and transformed *k* values. Results revealed that across both episodic conditions there was a significant correlation between individual discounting parameters and the ACC (0,42,0, $z = 4.64$, cluster size = 429, $P < 0.05$ FWE). As demonstrated in Figure 5, this correlation did not differ between episodic conditions.

Next, we were interested in whether the neural substrates of subjective valuation underlying both episodic conditions differ from each other. To this aim, individual contrast images coding for parametric modulation by subjective values were entered into the analysis. The main effect across both conditions revealed significant clusters in the ACC, the right orbitofrontal cortex, the bilateral ventral striatum, left posterior and middle frontal regions, the bilateral middle temporal gyrus, the right mid cingulum and the left hippocampus to be significantly modulated by subjective value (all $P < 0.05$ FWE). Subsequent differential analyses for the contrast familiar > unfamiliar revealed a stronger positive subjective value correlation in a cortical network including inferior and middle frontal gyrus, inferior and middle temporal gyrus, precuneus and the cerebellum (all $P < 0.05$ FWE; Table V, Fig. 6). No significant differences were observed in the reverse contrast (unfamiliar > familiar).

Given our aforementioned findings demonstrating the ACC to be involved in individual discounting behavior and parametric valuation as well as previous evidence for a key role of dynamic ACC-limbic interactions on choice behavior [Peters and Büchel, 2010; Roiser et al., 2009], we next analyzed whether the valuation signals in the ACC are differentially connected with other brain regions in familiar versus unfamiliar trials. In other words, we were interested in whether the contribution of brain regions to the valuation in the ACC changes with the episodic context.

To this end, PPI were conducted using a 4mm sphere around the ACC peak from the SV main effect analysis (−12, 48, 6) as the seed region. Results revealed a stronger coupling between ACC and left hippocampus (−22, −26, −14, $z = 3.56$, $P < 0.05$ FWE) in the unfamiliar compared with the familiar condition. For the reverse contrast (familiar > unfamiliar), stronger coupling was detected between the ACC and the left ventral striatum (−10, 10, −14, $z = 3.50$, $P < 0.05$ FWE; Fig. 7). No further regions showed significant differences in coupling with the ACC between the two conditions.

DISCUSSION

We investigated the role of familiarity in the episodic modulation of delay discounting using fMRI combined with a modified intertemporal choice task. Behaviorally, reward delay discounting was attenuated by episodic future event imagination regardless of the degree of personal prior experience associated with the simulated future scenarios. In the same vein, interview data showed that both familiar and unfamiliar scenarios were imagined with similar richness. The neuroimaging data highlight the hippocampus to be particularly crucial for the construction of unfamiliar events and for triggering frontal valuation signals when rewards are presented in an unfamiliar context. In contrast, the valuation of delayed rewards in a familiar context more strongly relied on key nodes of emotional and autobiographical memory circuits.

Our observation of a behavioral tag-effect further confirms suggestions of an adaptive function of episodic prospective in future decision-making. Both the imagination of familiar and unfamiliar episodes increased activity in a network of brain regions involved in the recollection of previous events and in the construction of potential future scenarios, including the ventromedial PFC (vmPFC), the posterior cingulate cortex and the lateral parietal cortex [Hassabis and Maguire, 2007; Peters and Büchel, 2011; Schacter et al., 2012].

The simulation of unfamiliar future events was specifically mirrored by additional hippocampal engagement. According to the constructive episodic simulation hypothesis, episodic memories of individual events can be flexibly recombined to construct future scenarios [Schacter and Addis, 2007a,b] and such recombination has been related

Episodic > Control

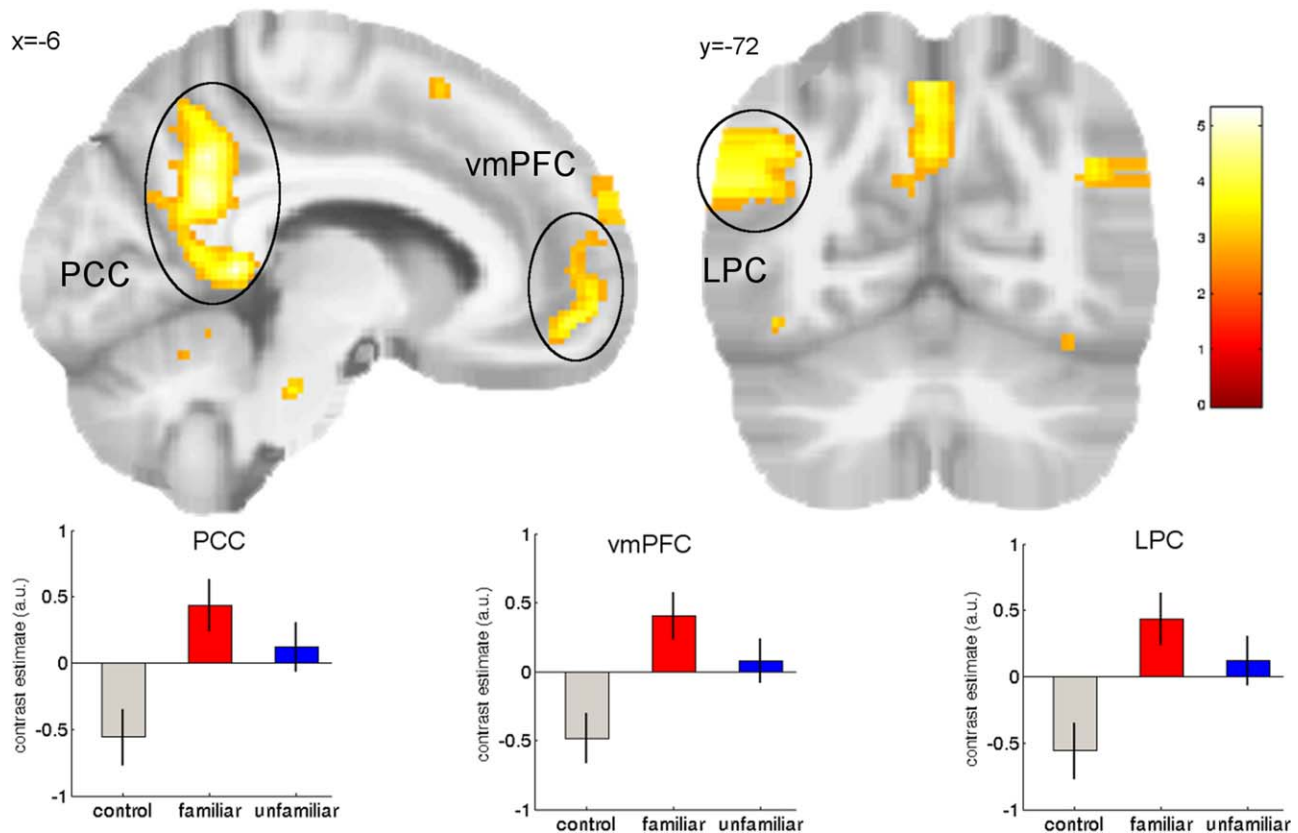


Figure 3.

Greater activation for both episodic (familiar and unfamiliar) conditions compared with the control condition was observed in the left posterior cingulate cortex (PCC), the left ventromedial prefrontal cortex (vmPFC) and the left lateral parietal cor-

tex (LPC) (all $P < 0.05$ FWE). Activations are overlaid on the mean structural image of all participants (display threshold $P < 0.005$ uncorrected). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

to hippocampal activity [Addis and Schacter, 2008, 2011; Schacter and Addis, 2007a]. It is, however, unclear how much the result of such construction processes depends on the availability of self-experienced, similar episodes. While some data demonstrated richer and more detailed simulations when strong personal prior experience of similar previous events was available [Arnold et al., 2011; Szpunar and McDermott, 2008], other findings suggest no impact of personal familiarity on the quality of future event simulations [Anderson, 2012]. The latter findings have been attributed to the cognitive flexibility to recruit alternative sources for future event construction, such as media and third party reports, when personal experience is lacking.

In our paradigm, unfamiliar events, that is, events that have previously not been experienced, consisted of meeting a famous person about whom participants certainly possessed media-sourced information. It seems likely that the cover story used to identify novel contacts specifically

encouraged participants to choose persons about whom they possessed such detailed information. Examples from our post-scan imagination interviews support this assumption: “During our meeting, he [an author] always looked like on this photograph on the back of his new book”; “He [the politician] smoked cigarettes throughout our meeting as he is always doing on TV” (see also Supporting Information Fig. S1 for sample narratives).

Contacts were identified in this way to ensure a similar attractiveness of familiar and unfamiliar events, which was confirmed by our ratings indicating equal motivation towards both events. It is possible, however, that if participants had been asked to imagine personally insignificant and rather unknown persons, results might have been different. In this case, the lack of information might have led to declines of episodic richness and hippocampal engagement [Rabin and Rosenbaum, 2012; Rabin et al., 2012; Westmacott et al., 2004]. In the present study, participants

TABLE IV. Regions in which the BOLD signal was significantly increased in the episodic (familiar + unfamiliar) compared with the control condition and significantly differed between the episodic conditions (familiar > unfamiliar)

Brain Region	Side	MNI (peak)			Cluster size	Z-Score
		x	y	z		
Episodic > Control						
Medial rostral PFC	l	-6	62	22	798	3.87
Ventromedial PFC	l	-6	58	-6	Same Cluster	4.05
Middle Temporal Gyrus	l	-64	-6	-12	346	4.22
Retrosplenial Cortex	l	-10	-44	4	1865	4.65
Posterior Cingulate Cortex	l	-4	-52	36	Same Cluster	4.47
Lateral Parietal Cortex	l	-50	-72	28	943	4.03
Familiar > Unfamiliar						
Amygdala	r	16	-6	-12	661	4.04
Thalamus	l	-8	-12	8	Same Cluster	3.90
Ventral Tegmental Area	l	-10	-22	-8	Same Cluster	3.79
Middle Temporal Gyrus	l	-52	-52	-2	329	3.70
Unfamiliar > Familiar						
Hippocampus	l	-16	-38	2	26	3.51 ^a

Montreal Neurological Institute and Hospital (MNI) coordinates and z values are reported for peak voxels and local maxima within each cluster. All $P < 0.05$ FWE. l: left; r: right.

could not rely on self-experience while simulating the event with the famous person, thus they needed to construct the scenario by combining episodic details from different sources [Anderson, 2012]. They seemed to master this construction successfully since the level of episodic details generated by participants and the impact of future thinking on delay discounting was unaffected by personal experience and plausibility in our study. In sum, we speculate that increased hippocampal engagement during such successful construction of unfamiliar events reflects an increased need or effort to combine information from disparate sources for which no pre-association exist (e.g., categorical memory of “having a coffee” combined with

media-sourced information about the person) [Weiler et al., 2010a].

The simulation of an event including a familiar person, with whom participants described significantly higher emotional closeness than with an unfamiliar person, induced specific activation in affective brain regions, i.e., the extended amygdala and the ventral tegmental area. Hence, these results extend findings of an overlap of brain

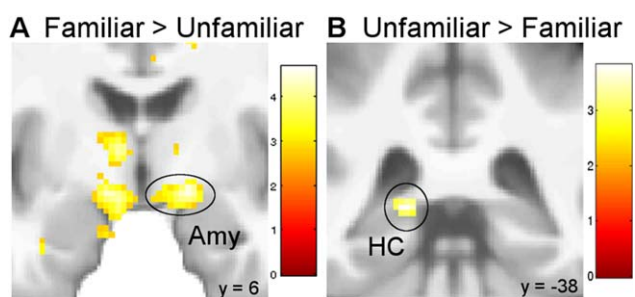


Figure 4.

A: Activation in the right extended amygdala was significantly increased in the familiar compared with the unfamiliar condition ($P < 0.05$ FWE). **B:** The reverse contrast yielded a greater signal in the left posterior hippocampus ($P < 0.05$ FWE). Activations are overlaid on the mean structural image of all participants (display threshold $P < 0.005$ uncorrected). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

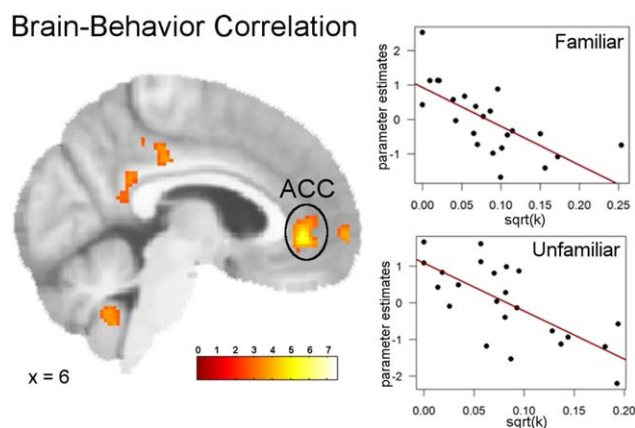


Figure 5.

Simple regression of the discounting parameter across the two episodic conditions and neural activation during the two episodic conditions yielded a significant correlation in the bilateral ACC ($P < 0.05$ FWE). Separate regression plots of parameter estimates in the peak voxel of the ACC and the individual discounting parameters of the familiar and unfamiliar condition confirm the presence of a correlation in both conditions. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Cortical Network: Familiar > Unfamiliar

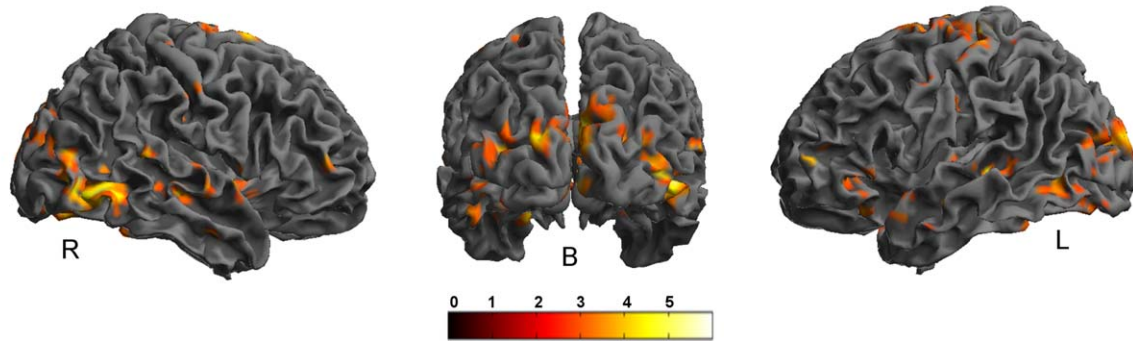


Figure 6.

Cortical activation in middle and inferior frontal gyrus, middle and inferior temporal gyrus, precuneus and the cerebellum was significantly increased during subjective value processing in the familiar compared with the unfamiliar condition ($P < 0.05$ FWE). L, left; R, right; B back. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

networks engaged in remembering events and future memory construction to brain regions relevant for emotional processing [Cabeza and St Jacques, 2007; Scheele et al., 2013]. Such impact of emotional, autobiographical memory on simulating and evaluating future familiar events is further supported by the finding of a direct correlation between a cortical fronto-tempo-parietal network and valuation of future rewards in a familiar context. This cortical network has previously been implicated in representing distributed semantic and visuospatial features

of consolidated autobiographical memories [Cabeza and St Jacques, 2007; Martinelli et al., 2013; Svoboda et al., 2006].

Across both episodic conditions, the ACC signal correlated with subjective values as expected from its role for cost-benefit computations [Hillman and Bilkey, 2012; Hosokawa et al., 2013] and adaptive decision-making [Rushworth and Behrens, 2008]. This function is further highlighted by our finding of a direct correlation between ACC activity and individual discounting rates. The ACC exhibits bidirectional anatomical connections with regions

TABLE V. Regions in which the BOLD signal was significantly modulated by the subjective value of the delayed reward option in the episodic conditions

Brain Region	Side	MNI (peak)			Cluster size	Z-Score
		x	y	z		
SV (familiar + unfamiliar)						
Middle Frontal Gyrus	l	-36	40	32	311	4.24
Anterior Cingulate Cortex	l	-12	48	6	1972	3.69
Orbital Frontal Cortex	l	-6	44	-10	Same Cluster	3.82
Ventral Striatum	r	8	12	-8	78	4.05 ^a
	l	-6	8	-8	70	3.53 ^a
Posterior-Medial Frontal	l	-18	-6	62	1472	4.42
Mid Cingulum	r	10	-16	38	498	3.81
Hippocampus	l	-20	-20	-18	63	3.57 ^a
Middle Temporal Gyrus	r	46	-56	2	1645	4.41
	l	-48	-62	-14	1083	4.44
SV (familiar > unfamiliar)						
Inferior Frontal Gyrus	l	-34	24	-18	351	3.77
Middle Frontal Gyrus	r	10	6	70	1323	3.84
Middle Temporal Gyrus	r	50	-24	-6	406	3.97
Inferior Temporal Gyrus	r	52	-62	-6	2935	4.29
Precuneus	r	8	-72	20	Same Cluster	4.42
Cerebellum	l	-24	-76	-18	618	4.88

Montreal Neurological Institute and Hospital (MNI) coordinates and z values are reported for peak voxels and local maxima within each cluster. All $P < 0.05$ FWE. l: left; r: right.

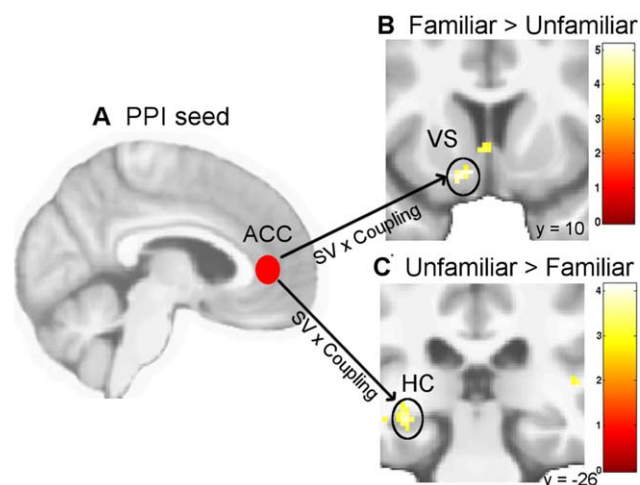


Figure 7.

A: The seed for the PPI analysis was placed in the left anterior cingulate cortex (ACC; $-12,48,6$, with 4 mm sphere). **B:** In comparison to the familiar condition, functional coupling between the ACC and the left hippocampus during subjective value (SV) processing was increased in the unfamiliar condition ($P < 0.05$ FWE). **C:** The reverse contrast revealed increased functional coupling between ACC and left ventral striatum for the familiar compared with the unfamiliar condition ($P < 0.05$ FWE). Activations are overlaid on the mean structural image of all participants (display threshold $P < 0.005$ uncorrected). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

of the reward and memory circuits, including the hippocampal formation and the striatum [Haber and Knutson, 2009]. Since general ACC activation predicted both discounting rates in familiar and unfamiliar conditions, we further investigated whether its modulation by other brain regions differs between the two conditions. Results of psychophysiological interaction analyses revealed a significantly stronger connectivity of the ACC valuation signal with the hippocampus in the unfamiliar condition. The hippocampus has previously been related to subjective value computation [Lebreton et al., 2009, 2013]. Previous data showed an increased ACC-hippocampal coupling to predict decreased discounting rates in the context of future episodic thinking even though these studies did not explicitly control for familiarity of future events [Benoit et al., 2011; Peters and Büchel, 2010]. It has been argued that hippocampal neurons may modulate medial prefrontal information processing through their role in mentally simulating potential future outcomes [Schacter et al., 2012], that is, by providing episodic predictions of decision outcomes [Johnson and Redish, 2007; Lee et al., 2012]. Our results suggest that such modulation of frontal valuation regions might crucially depend on the required construction effort, which was amplified in the unfamiliar condition of the present paradigm. Intriguingly, in a very recent

study by Gaesser et al. [2013] a subregion of the left hippocampus, very similar to the region in our study, was engaged during construction of unfamiliar event stimulation, indicating that the location might play a critical role in this context.

When imagined events were familiar, the ACC valuation signal was specifically mediated by activity in the striatum. Given recent data indicating that positive emotional quality of autobiographical information may be modulated by the striatum [Scheele et al., 2013; Speer et al., 2014], such coupling possibly signals the emotional value of reactivated autobiographical memories.

More generally, our data may contribute to the ongoing debate about the role of the hippocampus in episodic propection [Addis and Schacter, 2011; Schacter et al., 2012]. Controversial findings stem from hippocampal lesion patients who often [Andelman et al., 2010; Hassabis et al., 2007; Race et al., 2011], but not always [Cooper et al., 2011; Maguire et al., 2010; Squire et al., 2010], show impairments in memory construction. Our findings suggest a critical role of familiarity in this context by showing that future events that strongly draw on autobiographical, familiar experiences seem to depend less on hippocampal construction activity but increasingly engage neocortical areas containing already consolidated autobiographical memories. Moreover, due to pre-scan familiarization with the spatial context (café) and participants' strong personal experience with the familiar contact in our study, simulation might have included more generic/semantic memory representations (e.g., Mum always drinks cappuccino), which might be less hippocampus dependent (e.g., as discussed by [Moscovitch et al., 2006]) than scene construction involving the processing of dispersed memories [Maguire and Mullally, 2013]. Since both imagination richness and external details were similar for both conditions, this idea, however, is rather speculative at present [Verfaellie et al., 2014].

It has been shown that reduced delay discounting can rely on shifts of attentional resources to the future [Radu et al., 2011]. These shifts also depend on how distant time is described (e.g., specific date versus unspecific delay) [Read et al., 2005]. Hence, it seems likely that future event construction, as required in our study, additionally binds attentional resources to the delayed option [Marchetti, 2014]. To disentangle incremental effects of attention and episodic propection on temporal discounting, future studies should therefore compare effects of episodic tags with those of other attentional manipulations. Existing findings showing the tag-effect to be parametrically modulated by episodic network activity and imagination quality [Palombo et al., 2015; Peters and Büchel, 2010], however, strongly argue for a specific impact of episodic simulation in the present context. Whereas our neural findings further support this assumption, we did not observe direct correlations between episodic richness and the behavioral tag-effect. The lacking correlation might be caused by individual ceiling effects in imagination quality due to the block-wise presentation of prioritized contacts but also by the

limited sensitivity of a post-scan interview on imagination. Future studies might be able to provide more sensitive insights into relations with imagination quality by assessing trial-wise imagination scores during the task without influencing behavior in the primary intertemporal choice task.

Taken together, our findings strengthen and extend previous assumptions about the impact of episodic prospection on reduced delay discounting. By applying different analytical approaches, we were able to specify a general engagement of the imagination/prospection network in response to episodic tags whose activation strength in some core regions (i.e., ACC) predicted discounting behavior and the subjective value of a reward on a trial-by-trial basis. Depending on episodic construction demands, this neural valuation signal was directly modulated by dynamic interactions with different limbic brain structures. Most importantly, our findings indicate a critical role of the hippocampus when future simulations include scenarios that have not yet been encountered. While healthy young adults, as in our study, were capable to master the construction demands by hippocampal engagement, it could be speculated that patients with hippocampal lesions or older people with hippocampal atrophy might show a reduced tag-effect when unfamiliar future events are included. So far, findings regarding the presence of the tag-effect in amnesic patients are mixed [Kwan et al., 2015; Palombo et al., 2015], thus supporting the notion that additional factors such as prior experience with a prospective event may mediate the impact of hippocampal involvement on intertemporal choice. Our findings may be especially important for future studies in which potentially beneficial consequences of future thinking on decision-making may be used in the context of interventions, e.g. in clinical populations characterized by steep discounting, such as substance abuse or pathological gambling [Bickel et al., 2014].

ACKNOWLEDGMENTS

The authors confirm that they have no financial interests in the subject matter or materials discussed in the manuscript. The manuscript has not been published previously nor is it concurrently submitted for publication elsewhere.

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Effects of Executive Control and Episodic Simulation on Intertemporal Choice in Aging

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Abbreviated Title: Aging and Episodic Discounting

Number of pages: 29

Number of figures: 5

Number of tables: 3

Number of words (Abstract): 186

Number of words (Introduction): 601

Number of words (Discussion): 1213

Conflict of Interest: The authors declare no competing financial interests.

Acknowledgements: The study was supported by the German Research Foundation
(DFG, grant BR 2877/2-2 to S.B. and PE 1627/3-1 to J.P.).

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Abstract

Future thinking and cognitive control ability are discussed as modulators of older adults' temporal discounting behavior. We investigated these hypotheses combining fMRI with an intertemporal choice task that modulates future thinking by episodic cues in healthy older participants with varying abilities to control attention in a highly distracting context. Behavioral findings show that only older adults with high levels of attention control benefitted from episodic cues in their discounting behavior, while episodic prospection seemed to disturb intertemporal decisions in participants with low ability. Imaging results revealed correlations of control capacity with value coding in the hippocampus and the anterior cingulate cortex as well as with hippocampal-striatal coupling when future rewards were combined with episodic cues. Imagination scores and basic activation patterns in episodic neurocircuits did not explain variation in discounting rates or cognitive functioning. Our findings highlight the critical role of cognitive control ability for the successful integration of episodic information into future value processing in aging. The impact of age-related decline in neurobehavioral control function on intertemporal choice might thereby depend on the degree to which episodic and valuation signals have to be processed simultaneously.

Significance Statement

Temporal discounting describes the tendency to devalue rewards as a function of time to their delivery. So far, findings are rather controversial about how such behavior changes in aging. To shed light on the topic, we investigated neurobehavioral mechanisms underlying discounting in older adults while considering a) their individual levels of executive functioning and b) the degree to which they engaged in episodic simulation. Our findings highlight the critical role of executive control for the successful integration of episodic information during the valuation of future rewards in aging.

Introduction

Across the lifespan, measures of delay discounting (i.e. a strong preference for smaller-sooner over larger-later rewards) have been related to executive control ability (Shamosh et al., 2008; Bickel et al., 2011) and health behaviors (Chabris et al., 2008; Reimers et al., 2009) but also problematic decision-making such as gambling and drug use (Bickel et al., 2014). While there is consistent evidence for a decrease of discounting rates until adulthood (Olson et al., 2007; Drobetz et al., 2012), findings about changes in older age are rather inconsistent (Green et al., 1996; Chao et al., 2009; Reimers et al., 2009; Löckenhoff et al., 2011; Roalf et al., 2011; Samanez-Larkin et al., 2011; Eppinger et al., 2012; Rieger and Mata, 2015). High variance in these findings might be due to an uncontrolled, individual impact of age-related changes in episodic future thinking (Seinstra et al., 2015) and in the controlled integration of episodic information with value processing (Samanez-Larkin and Knutson, 2015). A systematic investigation of these interactions, however, is lacking so far.

Studies manipulating future thinking by episodic cues in younger age could show that both functions are crucial for less impulsive intertemporal choice behavior (Peters and Büchel, 2010; Benoit et al., 2011; Palombo et al., 2015; Sasse et al., 2015). In these studies, the combination of future episodic events with delayed options led to reduced discounting rates possibly due to facilitated mental time traveling. The neuroimaging findings further support this assumption by indicating an engagement of episodic memory circuits and the integration of these signals into value signals of prefrontal-limbic reward circuits (Peters and Büchel, 2010; Sasse et al., 2015). Since previous studies were limited to younger participants, it is yet unclear whether older adults equally benefit from this modulation and whether such tag-effect depends on the individual preservation of cognitive key-functions.

Indeed, there is considerable evidence that aging is associated with deficits in the construction of episodic events and prospective thinking (Schacter et al., 2013), even though there is typically high variability in age-related changes in episodic processing (Nyberg et al., 2012).

Observed deficits have been attributed to age-specific decline in key regions of cortical-subcortical episodic memory networks, including the hippocampus, precuneus und prefrontal cortex (Addis et al., 2011; Persson et al., 2011; Pudas et al., 2014). Moreover, older adults have shown impairments in value-based decision making under conditions of high cognitive load (Lighthall et al., 2014) as well as deficits when learned information needed to be integrated in the decision-process (Mata et al., 2011). In line with the inhibitory control hypothesis (Hasher and Zacks, 1988), such deficits in multidimensional information processing might primarily result from age-related impairments in controlling interfering information. Since modulation of delay discounting by episodic prospection requires the simultaneous processing and integration of mnemonic and valuation signals, older adults' ability to exhibit cognitive control might thus be a critical determinant of variability in intertemporal choice behavior.

When assessing neurobehavioral mechanisms of delay discounting in aging, previous studies have not explicitly modulated the impact of episodic prospection nor did they control for participants' cognitive control abilities. In the current study, we filled this gap by investigating older participants' intertemporal choice behavior and related brain correlates combining fMRI with a discounting paradigm that manipulates the influence of episodic prospection (Sasse et al., 2015). Additionally, participants' ability to exhibit cognitive control under conditions of high cognitive load was assessed using an established visual search task (Theeuwes and Burger, 1998; Costello et al., 2010; Sasse et al., 2014). Based on neural findings in younger adults, we focused our factorial and functional connectivity analyses on networks engaged in episodic prospection and reward integration.

Materials and Methods

Participants. Twenty-two healthy older adults ($M = 66.55$; $SD = 4.02$; 60 – 74 years; 9 men) participated in the present study. Participants were recruited from an existing database and gave written informed consent before their participation. It was ensured that all participants had no present or previous neurological or psychiatric disorders like depression or dementia and successfully completed the neuropsychological battery of the Consortium to Establish a Registry for Alzheimer's Disease (CERAD) including the Mini-Mental State Examination (MMSE, all participants > 28). Participants were financially compensated with 10 Euros per hour. In addition, one chosen reward from the delay discounting task was randomly selected and paid out with the respective delay. The study was approved by the local ethics committee.

Study design of the discounting task. The design and procedure of the fMRI discounting task have previously been applied in a group of younger adults (Sasse et al., 2015) (Figure 1). The experiment consisted of three conditions presented in six blocks (2 blocks per condition). Two of these six blocks served as the control condition, which involved standard delay discounting without episodic prospection, while the remaining four blocks were assigned to two episodic tag conditions, requiring participants to imagine meeting a person in a café for the day of delayed reward delivery.

The social event that participants imagined in the episodic conditions was either related to prior experiences, i.e. meeting with a familiar social partner (e.g. Husband) or were personally unfamiliar, i.e. meeting with a famous person from the media who had not been met in person before (e.g. Angela Merkel). On a separate day, prior to scanning, a standardized interview (adopted from Carstensen and Fredrickson, 1998) was carried out to identify these two familiar and two novel social partners: For the identification of the familiar social partners, participants had to imagine moving abroad on their own and to appoint familiar persons with whom they would like to spend the last hours before their departure. To identify the famous,

novel partners, participants imagined conducting an interview for a newspaper with persons of public interest whom they had never met in person.

During each trial, participants were required to choose between a fixed immediate reward option of 20 € (which was not shown on the screen) and a larger but delayed amount. During the episodic conditions, this delayed reward option was presented together with the name of the social partner with whom they had to imagine a meeting in a café for the date of the delayed reward delivery. In the control condition, delayed options were presented together with placeholder strings (“XXXX” or “YYYY”) and participants were explicitly instructed to refrain from imagery.

insert Figure 1 about here

In each block, participants viewed 36 trials involving six different delays that were randomly drawn from one of two sets [1, 2], [6, 7], [13, 15], [28, 32], [85, 95], [170, 190]. Next, the six delays were paired with six amounts lying equally above and below the respective indifference point. Monetary amounts ranged from 20.5€ to 79.5€. While minimum and maximum amount for each delay were close to the extreme values for each participant, values varied individually between these extremes for each participant. More specifically, the values that were presented as delayed rewards were participant-specific constructed based on a computer-based delay-discounting procedure participants completed on the date prior to scanning. This procedure has been done in previous experiments in our lab to ensure that participants would choose the delayed option in 50% of the trials (see Sasse et al. 2015).

In order to avoid sequence effects, the presentation of the three conditions was randomized but the two blocks of each condition were always presented successively. Between blocks, participants were given a short break to relax. Participants were trained on the task and

familiarized with five images depicting scenes of a typical café before the experiment. After the end of the task and without being scanned, participants remained lying in the scanner for approximately ten minutes for an interview about the richness of their imagination for the four events. During this interview, participants were asked to describe their imaginations for each of the four events as detailed as possible. Answers were recorded to be later transliterated.

Outside the scanner participants were asked to rate the emotionality they associated with the four partners as well as their motivation to meet the partners for each event on scales ranging from 1 to 7.

Attention control task. On the separate date prior to scanning, participants also performed a visual search task, which was used to calculate a measure of participants' attention control ability during highly salient distraction as previously described in Sasse et al. (2014). In brief, participants had to focus their attention on a target stimulus (a circle) that was surrounded by non-targets differing in shape from the target (squares). Participants had to respond via button press as quickly (< 3 seconds) and accurately as possible to a "+" or "-" displayed inside of the target shape. In 50% of the trials, non-targets additionally included a singleton distractor that differed in color from the other stimuli (red square). The task involved two conditions presented in blocks (each n = 4 conditions with 48 trials) that manipulated the saliency of this singleton distractor. Baseline blocks required participants to focus on the shape dimension while they could simply ignore the color dimension across trials. In addition, the paradigm also included so-called singleton detection blocks in which the singleton had a potential relevance and needed to be actively ignored on a trial by trial basis to raise demands on flexible attention control. This was achieved by including trials (8% of the trials) in which the singleton could be the target (i.e. target-shape but printed in red) as well as an explicit instruction before each block. Further details on stimulus composition and presentation are provided in Sasse et al. (2014).

Inclusion of the two conditions allowed the computation of an index score of participants ability to flexibly control attention under high cognitive load (see Sasse et al., 2014). Therefore distraction control performance, i.e. reaction time (RT) in singleton present trials (s+) versus RT in singleton absent trials (s-), was computed for baseline blocks (base) and singleton detection blocks (detect) and then subtracted using the following formula:

$$d = [mean(RT_{detect_s+}) - mean(RT_{detect_s-})] - [mean(RT_{base_s+}) - mean(RT_{base_s-})].$$

Data acquisition. Presentation software (Neurobehavioral Systems©) was used for stimulus presentation and recording. fMRI data were acquired on a 3 tesla system (Magnetom Trio, Siemens) equipped with a 32-channel head coil. Each volume comprised 41 transversal slices (2mm thickness, 1mm gap, TR = 2460 ms, TE = 25 ms, FOV = 216x216mm², in-plane resolution 2 x 2mm², GRAPPA factor 2). High-resolution anatomical MR images were acquired after functional imaging using a T1-weighted MPRAGE sequence (1x1x1 mm).

Behavioral data analysis. For the behavioural data analysis, individual choice data were fitted using Maximum Likelihood Estimation (MLE) by combining a hyperbolic discounting function with softmax action selection (Peters et al., 2012) separately for each experimental condition in Matlab (Mathworks©). This yielded two free parameters per condition, the hyperbolic discounting constant k , where higher values reflect greater impatience, and the inverse temperature parameter β of the softmax choice function, where greater values reflect more decision noise. Following Sasse et al. (2015), a square-root transformation was applied to the resulting k parameters prior to analyses, accounting for their skewed distributions. Table 1 depicts model characteristics, such as medians and Inter-Quartile-Ranges (IQRs) of the absolute single-subject maximum likelihood parameter estimates, Akaike Information Criterion (AIC), where smaller values reflect a better model fit, and reaction time data.

insert Table 1 about here

Descriptions of the imagination ratings for the four events were analyzed with respect to the level of episodic richness using a rating procedure based on the Autobiographical Memory Interview (Levine et al., 2002). Details were categorized as internal (episodic information relating to the given future event) or external (non-episodic information). Internal details were categorized further into one of five categories adapted from Levine et al. (2002): time, place, perceptual, emotions/thoughts, and event details. External details comprised semantic details, repetitions and other metacognitive statements, but were combined into a single score since there were only very few external details. A second independent rater coded details into the same categories, yielding a reliability between the raters of cronbach's alpha = .81 for internal details and cronbach's alpha = .81 for external details.

FMRI data analysis. FMRI data were pre-processed and analysed using statistical parametric mapping (SPM8; Wellcome Department of Imaging Neuroscience, London, UK).

Functional data were corrected for slice timing before being realigned and unwarped. Then, the individual structural T1 image was coregistered to the mean functional image generated during realignment. Coregistered T1 images were then segmented using the 'New Segment' routine in SPM8. Resulting tissue-class images for gray and white matter were subsequently used for spatial normalization of the functional images using the DARTEL toolbox. Data were smoothed with a 6-mm full-width at half maximum (FWHM) isotropic Gaussian kernel.

Using the GLM denoise toolbox for Matlab (Kay et al., 2013), the data were then "denoised" by deriving regressors from voxels unrelated to the experimental paradigm and entering these regressors in a general linear model (GLM) analysis. In this GLM, sustained activation during

the presentation of the delayed option (i.e. from option onset until button press) was modelled by boxcar regressors that were convolved with the canonical hemodynamic response function. Condition-specific k -parameters from the scanning session were used for the calculation of the subjective value of each delayed option and included as a parametric regressor in the GLM.

For each subject, contrast images for each condition (control/ familiar/ unfamiliar) and for the respective subjective value regressor were constructed. These contrast images were passed to the second level where group contrasts were computed using one-sample t -tests on the single-subject contrasts. Correlations between individual fMRI-signals and the singleton control score were performed by including the singleton score as a covariate at the second level. All second-level analysis further included gender as covariate of no interest to account for unequal distributions of men and women.

Coupling analyses were performed by extracting the deconvolved, individual time course of the seed region from conditions of interest.

We performed whole brain corrections for multiple comparisons at the cluster level using a cluster-threshold of $FWE < 0.05$ (cluster forming threshold $p < 0.005$ uncorrected). Small volume corrections for multiple comparisons (SVC) were performed for anatomical masks of the hippocampus, (Harvard Oxford atlas, probability threshold of 50%) and for the ventral striatum (8mm- spheres centered on x,y,z : +/- 14, 8, -8 mm (O'Doherty et al., 2004; Yacubian et al., 2006). In addition, we defined 10mm spheres around the coordinates of the episodic prospection network implicated in the tag-effect with the same paradigm in younger adults (Sasse et al., 2015), including the ventromedial prefrontal cortex (vmPFC; x,y,z : -6, 58, -6 mm), the posterior cingulate cortex/ precuneus (x,y,z : -4, -52, 36 mm) and the lateral parietal cortex (x,y,z : -50, -72, 28 mm). The threshold of small volume corrections (SVC) was set to $p < 0.05$ corrected for multiple comparisons using the family-wise error rate ($FWE < 0.05$).

Results

Post-hoc ratings. Confirming presumed categorization, post-hoc interviews revealed an equal motivation to meet the familiar ($M = 6.21$, $SD = 1.02$) and unfamiliar social partners ($M = 5.82$, $SD = 1.41$), $p > 0.28$. Moreover, familiar partners ($M = 6.26$, $SD = 0.54$) were rated as significantly higher on emotional closeness than the unfamiliar partners ($M = 2.93$, $SD = 1.08$), $t(21) = 11.91$, $p < 0.001$. Analysis of the post-scan Autobiographical Memory Interview procedure indicated that participants imagined familiar and unfamiliar events with similar amounts of internal ($t(21) = 1.25$, $p > .22$) and external details ($t(21) = .89$, $p > .38$) (Table 2). Comparison of the number of internal details to our recently published data (Sasse et al., 2015) from younger adults ($n = 23$, mean age: 24.96 years) yielded significant reductions in older adults' internal details sum scores for familiar ($t(43) = 2.60$, $p < .05$) as well as for unfamiliar events ($t(43) = 3.03$, $p < .005$).

insert Table 2 about here

Behavioral results. In a first step, we investigated whether condition specific discounting parameters (square-root transformed k-values) would differ across the whole group using a repeated measures ANOVA. This analysis yielded no significant difference between the three conditions (control/ familiar/ unfamiliar), $F(2,42) = 1.51$, $p > .32$ (see Figure 2A).

In order to further evaluate age-effects on the tag-effect, we then compared these behavioral data to our recently published data from younger adults using a repeated measures ANOVA. Results revealed a significant condition by group interaction, $F(2,86) = 4.91$, $p < .05$ and no main effects of group ($F(1,43) = 1.52$, $p > .22$) or condition ($F(2,86) = 1.33$, $p > .26$). The interaction effect was driven by a significant effect of experimental condition on discounting rates in the young subjects $F(2,44) = 5.83$, $p < 0.01$ that was absent in the older participants.

Hence, an overall effect of episodic thinking on discounting behavior was observed in younger but not older participants. Age groups did not differ significantly in their discounting rates in the control condition ($p > .54$).

In a next step, we tested whether this absence of the tag-effect in older adults was mediated by attention control ability. Since there was no significant difference between the two episodic conditions, we fitted the discounting rate across both conditions and then built a tag-effect score by subtracting the k value from the control condition from the sampled k value of the episodic conditions. We then correlated the tag-effect score with the singleton score which yielded a significant correlation between both parameters ($r = -.54, p < .05$ (see Figure 2B)) (a comparable result was observed using spearman correlation, $r = -.52, p < .05$). Thus, participants with higher cognitive control ability were more likely to exhibit a tag-effect, i.e. demonstrated reduced discounting in the episodic compared with the control condition. At the same time, neither the tag-effect nor the singleton score was correlated with the amount of internal or external details generated for familiar or unfamiliar events (both $p > .59$).

insert Figure 2 about here

FMRI data. We first analyzed general effects of episodic prospection on brain activity. Here, we observed a significant increase in the BOLD signal across both episodic conditions compared to the control condition in the left vmPFC (-10, 52, -10, $z = 3.97$) and the the left precuneus (-4, -60, 42, $z = 3.76$). In line with previous studies on episodic prospection (Peters and Büchel, 2010; Benoit and Schacter, 2015), we also observed a cluster in more inferior posterior midline regions, i.e. the retrosplenial/ posterior cingulate cortex (see Figure 3). However, this result did not survive our FWE correction procedure (-4, -54, 20, $z = 3.40, p <$

.001). No significant differences emerged when comparing activation patterns between the two episodic conditions.

insert Figure 3 about here

We next investigated whether activation in episodic neural networks was modulated by attention control ability. Results of the simple regression analysis including single-subject contrast images of the tag-effect (onset: episodic > control) and the singleton score revealed no significant impact of attention control ability on the neural prospection network.

In the next sets of analyses, we focused on brain activity modulated by the subjective value (SV) of each trial. Across all conditions, there was a significant modulation by SV in the vmPFC, the orbitofrontal cortex, the posterior cingulate cortex and the bilateral lateral parietal cortex (Table 3). No significant differences in this modulation emerged when comparing the tag and control conditions.

insert Table 3 about here

To elucidate whether the lack of such valuation differences between the tag and control condition depends on variation of attention control ability, we then repeated the differential analyses of parametric modulation (tag x SV > control x SV) but entered the singleton-score as covariate into the analysis. This analysis revealed significant correlations in the right anterior cingulate cortex (18, 46, 4, $z = 4.95$, $p < 0.05$ FWE), the left hippocampus (-20, -18, -

18, $z = 3.77$, $p < 0.05$ FWE) and the left postcentral gyrus (-38, -24, 42, $z = 4.06$, $p < 0.05$ FWE) (Figure 4), i.e. activity in these regions was differentially modulated by value in the tag compared to the control condition depending on participant's attention control ability. That is, these regions showed higher correlations with value in the tag vs. control conditions in subjects with high but not low attention control.

insert Figure 4 about here

Finally, we investigated relations between cognitive control and functional coupling during value integration. Based on our previous findings (Sasse et al., 2015), we therefore extracted the individual time course of the hippocampus peak voxel of the previous analysis (-20, -18, -18). Regression analysis including the singleton score revealed a significant positive correlation with the left ventral striatum (-14, 4, -12, $z = 4.01$, $p < 0.01$ FWE; Figure 5), indicating that coupling between the hippocampus and the ventral striatum was greater for elderly people with higher attention control ability. Figure 5 shows an outlier in the data. Yet, after removing it from the analysis, the observed correlation remained significant.

insert Figure 5 about here

Discussion

We investigated the impact of episodic future thinking and executive control on neurobehavioral correlates of intertemporal choice in healthy aging. To this aim, older adults with varying degrees of executive control ability were examined with fMRI while performing an intertemporal choice task including episodic cues. Behaviorally, only older adults with high cognitive control ability demonstrated a lower discount rate when future options were combined with episodic events. Neuroimaging findings highlight two mechanisms underlying this result: 1) value processing in the hippocampus and the ACC and 2) neural coupling between hippocampus and ventral striatum. In the episodic conditions, both effects were stronger in older adults with high attention control ability. Since there were no correlations with imagination scores from the autobiographical interview and general episodic network activity, observed variance in the “tag-effect” cannot be attributed to differences in episodic future thinking. Instead, our findings indicate that beneficial effects of future thinking on delay discounting in aging strongly depend on participants’ ability to focus attention control in a highly competitive setup. This ability may allow these older participants to more efficiently integrate episodic information during value computation.

Episodic network activation during the episodic conditions across all older participants replicate some but not all previous findings on the neural tag-effect in younger age (Peters and Büchel, 2010; Sasse et al., 2015). For instance, key nodes like the lateral parietal cortex and the hippocampus did not show differential activation during the episodic compared to the control conditions. Moreover, compared with younger adults, tested with the identical paradigm (Sasse et al., 2015), older adults reported fewer imagination details. Such reductions in episodic specificity are likely to account for the absence of differences between familiar and unfamiliar events. Age-related impairments in the construction and elaboration of

episodic simulations have been discussed before (Addis et al., 2011; Schacter et al., 2013) and probably depend on age-specific changes in underlying neural networks (Nyberg et al., 2012).

Post-scan imagination scores as well as observed episodic network activity, however, did not correlate with discounting rates or executive control ability, indicating that the potential reduction in prospection per se did not explain variance in the decision behavior in our sample. In a similar vein, possible deficits in general value processing cannot easily account for differences in the tag-effect: First of all, discounting rates in the control condition were comparable to those of younger adults and secondly, subjective values in elderly adults were robustly coded in well-known neural valuation regions including the vmPFC, the OFC and the PCC (Kable and Glimcher, 2007; Bartra et al., 2013; Clithero and Rangel, 2014). Such preservation of basic value coding in aging has been shown before (Chowdhury et al., 2013; Samanez-Larkin, 2013; Lighthall et al., 2014; Samanez-Larkin and Knutson, 2015) and might account for the lack of age-effects during non-episodic delay discounting in some previous studies (Green et al., 1996; Chao et al., 2009; Roalf et al., 2011; Samanez-Larkin et al., 2011; Rieger and Mata, 2015).

Instead, differences in the tag-effect in the present study emerged as a function of individual attention control ability, indexed by the function of flexibly exerting attention control over salient distracting information. An age-related decline in this ability has been discussed as a critical factor underlying changes in older adults' performance in higher order tasks as it modulates capacities to maintain and integrate information (Hasher and Zacks, 1988; Gazzaley et al., 2013). Our neural findings support and extend these assumptions by demonstrating direct correlations between cognitive control ability and neural signals of episodic value integration. In detail, subjective value coding in the hippocampus and the ACC as well as hippocampal coupling with the VS during episodic conditions were directly related to older participants' general cognitive control ability. The ACC as well as the ventral

striatum are involved in the filtering and controlling of competing and goal-relevant information (Rushworth, 2008; Demanet et al., 2013; Haeger et al., 2015). Moreover, the ventral striatum has been implicated in the structuring of memory encoding and retrieval based on the expected utility of memories (reviewed by Scimeca and Badre, 2012).

In younger adults, findings of subjective value signals in the hippocampus and the ACC have been related to the successful value integration of episodic information during intertemporal choices (Peters and Büchel, 2010; Sasse et al., 2015). The hippocampus is thereby thought to modulate value computation by providing episodic prospection of decision outcomes, leading to a reduction in temporal discounting. In a similar vein, episodic signals from the hippocampus have been shown to modulate reward based decision-making via connections to the ventral striatum in animals (Johnson et al., 2007; Meer et al., 2014) and humans (Wimmer and Shohamy, 2012; Palombo et al., 2015).

Our findings provide empirical evidence for recently postulated assumptions from the ‘Affect-integration-motivation-framework’ (Samanez-Larkin and Knutson, 2015). The authors suggest that while reward anticipation may be preserved in aging, specific deficits in the phase where memory content and other information have to be integrated in the decision-process might critically rely on fluid cognitive abilities in older adults. When delayed reward options were combined with episodic events, value computation and future thinking might have strongly competed for attentional resources in our older participants with reduced control ability. Consequently, episodic thinking may disrupt rather than facilitate value processing during future anticipation in some older people. Consistent with this assumption, episodic prospection negatively impacted on temporal discounting in older participants with low cognitive control ability.

Our findings also fit with previous behavioral studies indicating an impact of cognitive functioning on standard delay discounting, even though these studies did not control for

episodic prospection (e.g. Hinson et al., 2003; Shamosh et al., 2008; Huckans et al., 2011; Boyle et al., 2012; Lindbergh et al., 2014; James et al., 2015). However, episodic future thinking may occur spontaneously during standard discounting tasks (Mitchell et al., 2011; Peters, 2011), thus making previous findings likely to be modulated by individual differences in episodic imagery. In our study, we systematically manipulated such an impact by explicitly instructing participants to either avoid or focus on imagination during the different conditions. The fact that age-effects on temporal discounting only became evident when episodic imagery was induced, argues for a critical impact of the degree to which older participants engage in such processing.

To summarize, our data indicate that in the context of episodic discounting in aging, attention control ability predicts whether imagined episodic content can be successfully integrated into value processing. Since there is high variability in age-related changes of cognitive functioning as well as the functional integrity of key regions like the ACC and the ventral striatum (Bäckman et al., 2010), individual changes in these aspects should be considered when investigating intertemporal choice behavior in older adults.

The induction of episodic imagery has been proposed as a strategy to alleviate impulsive discounting in younger age (Wiehler and Peters, 2015). The present results suggest that this does not necessarily hold for older adults and that a certain level of attention control ability is needed to benefit from the effect in aging. Recent results in aged rats and humans have demonstrated beneficial effects of specific adaptive trainings on attention control ability and its neural correlates (Mishra et al., 2014). It would be interesting to see whether such effects also generalize to performance in higher order tasks like temporal discounting.

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Figure Legends

Figure 1. Outline of the paradigm. Each trial started with a green dot, signaling the start of the trial. Then, the delayed reward option was presented for 6 s and participants had to either imagine the event in the café (episodic conditions) or not imagine anything in the control condition. Subsequently, participants had to indicate their choice by selecting the red cross for the immediate reward (20€ that were not shown) or the green check mark for the delayed reward option.

Figure 2. Behavioral data. A: In comparison to younger adults (Sasse et al., 2015), discounting behavior did not significantly differ between the two episodic conditions and the control condition in older adults. B: Differences between the two conditions in older age were related to individual differences in attentional control ability (singleton score). * $p < .05$.

Figure 3. Activation differences between episodic and control conditions. Greater activation for the episodic conditions compared to the control condition was observed in the left ventromedial prefrontal cortex (vmPFC) and the left precuneus (all $p < 0.05$ FWE). Activations are overlaid on the mean structural image of all participants (display threshold $p < 0.005$ uncorrected).

Figure 4. Correlations between attentional control ability and neural modulation by subjective value (parametric analysis) for the episodic compared to the control condition. Significant correlations were found in the right ACC and the left hippocampus (all $p < 0.05$ FWE). Plots show the separate correlations in the peak voxels of the ACC and hippocampus. Activations are overlaid on the mean structural image of all participants (display threshold $p < 0.005$ uncorrected).

Figure 5. Correlation between attention control ability and hippocampal coupling.

Individual control ability (singleton score) was related to functional coupling between the left hippocampus and the left ventral striatum in the episodic compared to the control condition ($p < 0.05$ FWE). The plot demonstrates the correlation in the peak voxel of the left ventral striatum. Activations are overlaid on the mean structural image of all participants (display threshold $p < 0.005$ uncorrected).

Table Legends

Table 1

For each of the three conditions, medians and inter-quartile ranges (IQR) are reported for the model estimates of the discounting parameter (k) and temperature parameter (β), the Akaike information criterion (AIC) as a measure of goodness-of-fit, as well as for the reaction times (RT).

Table 2

Means (M) and standard deviations (SD) are reported for the amount of details imagined for familiar and unfamiliar events with further divisions into subcategories of internal detail categories. Due to a low number of semantic details, repetitions and other metacognitive statements, we combined them into a single external detail score (see e.g. Addis et al., 2009). Time details were not reported (due to the concrete time reference of the event) and are therefore not listed in the table.

Table 3

MNI coordinates and z values are reported for peak voxels and local maxima within each cluster. All $p < 0.05$ FWE. l, left; r, right; b, bilateral.

Figures

Figure 1

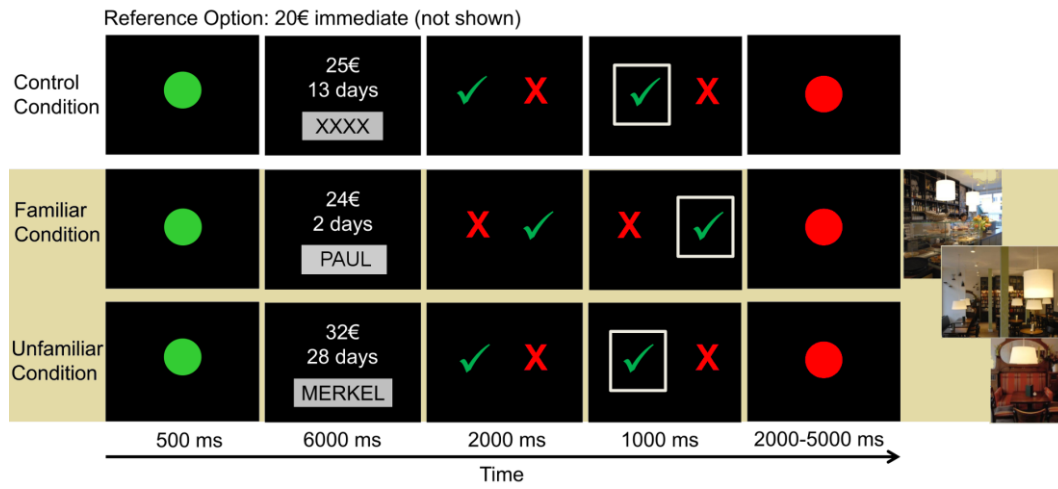


Figure 2

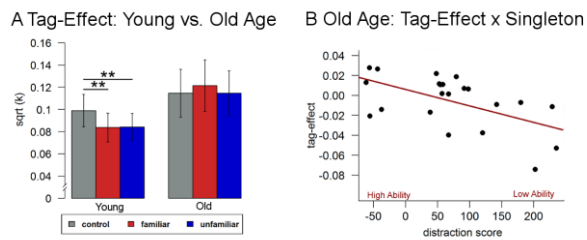


Figure 3

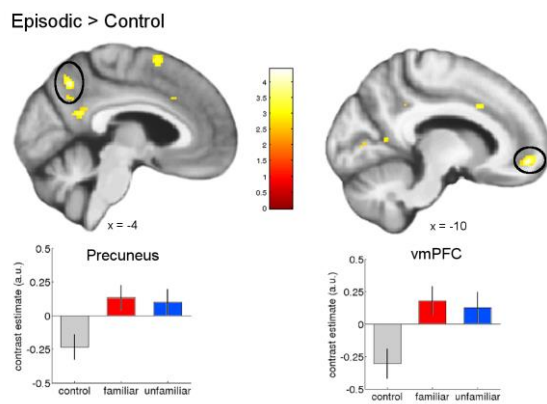


Figure 4

Cognitive Control and Differential Value Processing

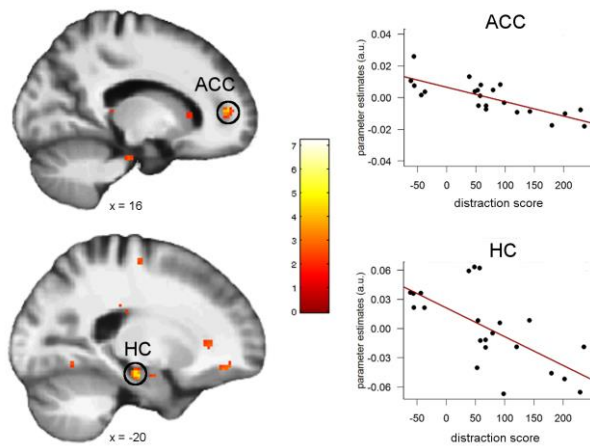
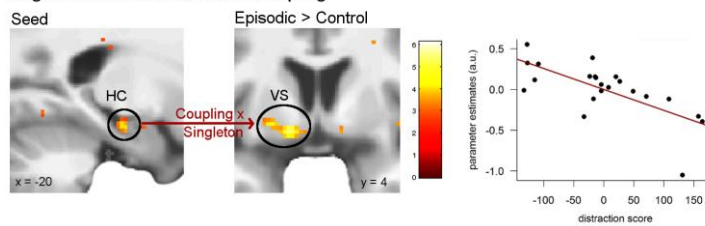


Figure 5

Cognitive Control and Neural Coupling



Tables

Table 1. Model Parameters.

	k		β		AIC		RT	
	Median	IQR	Median	IQR	Median	IQR	Median	IQR
Control	.02	.18	2.50	4.72	44.23	66.66	875.44	399.99
Familiar	.03	.20	3.78	8.25	54.24	51.70	923.35	385.75
Unfamiliar	.02	.19	3.30	10.73	49.89	72.68	919.24	438.59

Table 2. Level of detail and episodic richness of simulations across future event scenarios.

	Familiar		Unfamiliar	
	M	SD	M	SD
Internal Details	6.55	5.86	5.86	4.86
Event Details	2.23	3.10	2.09	2.60
Perceptual Details	1.55	1.85	0.82	1.05
Place Details	1.32	1.09	1.14	0.94
Emotion/Thought Details	1.45	1.34	1.82	1.82
External Details	0.86	1.08	0.68	1.04

Table 3. Regions in which the BOLD signal was significantly modulated by subjective value across all conditions.

Brain Region	Side	MNI (peak)			Cluster size	Z-Score
		x	y	z		
vmPFC	b	0	54	-8	1768	4.71
Orbitofrontal Cortex	l	-26	38	-10	370	5.10
Insula	l	-38	4	-2	1214	4.80
Precentral Gyrus	r	56	2	36	380	4.36
Middle Temporal Gyrus	l	-66	-32	-2	429	4.76
Posterior Cingulate Cortex	l	-8	-34	48	2664	5.39
Lateral Parietal Cortex	r	58	-44	26	792	4.39
	l	-54	-56	22	1937	5.73

I. Summary of the thesis

As the proportion of older adults continues to grow rapidly in western societies, age-related changes in cognition and emotion need to be well-characterized in order to develop approaches that help to preserve these functions as long as possible. Yet, further work is needed to specify the nature of such changes and their underlying (neural) mechanisms. The present Phd project focused on age-related changes in emotional information processing and impulsive choice using a multimodal approach in which specific behavioural paradigms were designed and investigated with multimodal psychophysiological methods.

Study I investigated age-related changes in emotional processing during attention and memory encoding. Results emphasize that older in comparison to younger adults increasingly applied top-down control to direct their attention towards positive and away from negative information, which resulted in a positivity effect in both functions. Underlining the impact of top-down control in this context, the size of this positivity effect was mediated by the individual preservation of relevant attentional control functions and boosted for material with a higher self-relevance. The data emphasize the role of motivation and cognitive control capacity for emotional selectivity and as potential resilience factor for emotional health in aging.

The second part of the thesis focused on neurobehavioral effects of aging and cognitive modulators on impulsive decision-making. In **Study II**, a modified delay-discounting paradigm that manipulates episodic prospection was successfully developed and validated in a young, healthy sample using fMRI. Findings replicate and extend previous assumptions on reduced discounting behaviour due to future-thinking and further specify the neural correlates underlying this effect. Applying this

design in healthy older adults in **Study III** revealed reduced beneficial effects of episodic prospection on temporal discounting. However, behavioural and neural findings indicate that such beneficial effects seemed to be significantly mediated by the degree to which attentional control was individually preserved. Specifically, the data highlight that higher levels of attentional control may help to override impulsive choices by facilitating the neuro-behavioural integration of episodic information with value processing.

Taken together, results from the present Phd project strongly emphasize the heterogeneity of age-effects on cognitive and emotional processing as well as the importance to consider individual levels of fundamental cognitive functions, such as attentional control, in future studies. In addition, the present work highlights attentional control a potential target for interventional approaches in geriatrics.

II. Deutsche Zusammenfassung

Angesichts des wachsenden Anteils älterer Menschen in westlichen Gesellschaften ist es wichtig, altersbedingte Veränderungen in emotionaler und kognitiver Verarbeitung näher zu charakterisieren, um älteren Menschen eine längere aktive Teilhabe im gesellschaftlichen Leben zu ermöglichen. Das vorliegende Promotionsprojekt konzentrierte sich auf die Untersuchung von Alterseffekten in emotionaler Informationsverarbeitung und impulsivem Entscheidungsverhalten. Dazu wurden spezifische Verhaltensparadigmen konzipiert und mit multimodalen psychophysiologischen Methoden, wie fMRI und Eye-tracking, verknüpft.

Studie I beschäftigte sich mit altersbedingten Veränderungen in der Aufmerksamkeit und der Enkodierung emotionaler Informationen. Die gewonnenen Ergebnisse zeigen, dass ältere im Vergleich zu jüngeren Erwachsenen vermehrt (top-down) Kontrolle ausüben, um ihre Aufmerksamkeit stärker auf positive Informationen auszurichten und von negativen Informationen abzuziehen. Dabei war das Ausmaß dieses Positivitätseffekts abhängig vom individuellen Erhalt genereller Aufmerksamkeitskontrolle sowie von der Selbstrelevanz des gezeigten Materials. Die Daten unterstreichen die Rolle von Motivation und kognitiver Kontrolle in emotionaler Selektivität und als mögliche Resilienzfaktoren für emotionale Gesundheit im Alter.

Im zweiten Teil der Arbeit wurden neuronale und kognitive Mechanismen, die impulsivem Entscheidungsverhalten (Belohnungsaufschub) im jungen und höheren Alter zugrunde liegen, näher untersucht. Dazu wurde ein Paradigma konzipiert, welches das Ausmaß von Zukunftsdenken (episodischer Vorstellung) bei der Evaluierung zukünftiger Belohnungsoptionen systematisch manipuliert.

In **Studie II** wurde das Paradigma zunächst in einer Gruppe junger Erwachsener getestet. Die dabei gewonnenen Ergebnisse replizieren frühere Befunde und unterstreichen, dass vermehrtes Zukunftsdenken impulsive Entscheidungsmuster entscheidend abschwächen kann. Außerdem erweitern sie bestehende Befunde um spezifische neuronale Mechanismen, die diesem Effekt zugrunde liegen.

In **Studie III** wurde das erfolgreich validierte Paradigma schließlich in einer Gruppe gesunder älterer Erwachsener angewendet. Es zeigte sich, dass vermehrtes Zukunftsdenken zunächst nicht den gleichen abschwächenden Effekt auf impulsives Entscheidungsverhalten hat und dass ein solcher Effekt im Alter entscheidend dadurch bedingt wird, wie gut Aufmerksamkeitskontrolle erhalten ist. Ein hohes Maß an Aufmerksamkeitskontrolle scheint dabei das gleichzeitige, integrative Verarbeiten von episodischen und Belohnungsinformation entscheidend zu begünstigen.

Die Ergebnisse der vorliegenden Arbeit betonen die Heterogenität von Alterseffekten auf die emotionale und kognitive Verarbeitung sowie die Wichtigkeit, den individuellen Erhalt fundamentaler Funktionen, wie Aufmerksamkeitskontrolle, bei der Untersuchung solcher Effekte zu berücksichtigen. Weiterhin hebt die Arbeit Aufmerksamkeitskontrolle als mögliches Ziel für strategische Interventionen im geriatrischen Bereich hervor.

III. Personal contributions

Study I

The design of Study I was conceptualized by Laura Karim and Stefanie Brassens. Laura Karim was responsible for the acquisition, analysis and interpretation of the data. During the analysis and interpretation of the data, she was supported by Stefanie Brassens and Matthias Gamer. Laura Karim was responsible for the drafting of the published manuscript.

Study II and III

The design of Study II and III was mainly conceptualized by Stefanie Brassens. In both studies, Laura Karim was responsible for the acquisition, analysis and interpretation of the data. Stefanie Brassens and Jan Peters supported her during the analysis and interpretation of the data. Laura Karim drafted both manuscripts for publication.

IV. Acknowledgments

First of all, I want to thank my supervisor PD Dr. Stefanie Brassens for giving me the opportunity to write my thesis within her working group, for her close supervision and scientific support during all my studies. Moreover, I want to thank the co-authors, Prof. Dr. Matthias Gamer, Dr. Jan Peters and Prof. Christian Büchel for their contributions to the studies. I would also like to thank Prof. Dr. Bernd Löwe and PD Dr. Götz Thomalla for their willingness to assess my thesis.

I am grateful for the support I received from my colleagues at the Department of Systems Neuroscience during the last four years. In particular, I would like to thank Eva Bauch for proof-reading this dissertation and for being such a wonderful friend. I would also like to thank Heidrun Schultz, Martin Hebart, Sabrina Boll, Antonius Wiehler and Johann Kim for many helpful discussions. Moreover, my thanks go to Missanga van de Sand for being a great office-mate along the way.

I thank my family and my close friends for their loving support, interest and encouragement. Finally, my special thanks belong to my husband, Arian Karim, for backing me up in every situation.

V. Curriculum Vitae

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- **February – July 2009:** Studies of Psychology, Université du Luxembourg
- **October 2007 – August 2010:** Studies of Psychology, Westfälische Wilhelms-Universität Münster; Thesis Title: "*The relationship between semantic interference and distractor frequency in the Picture - Word Interference Paradigm*"; Supervisor: Prof. Dr. Pienie Zwitserlood

VI. Eidesstattliche Versicherung

Ich versichere ausdrücklich, dass ich die Arbeit selbständig und ohne fremde Hilfe verfasst, andere als die von mir angegebenen Quellen und Hilfsmittel nicht benutzt und die aus den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen einzeln nach Ausgabe (Auflage und Jahr des Erscheinens), Band und Seite des benutzten Werkes kenntlich gemacht habe.

Ferner versichere ich, dass ich die Dissertation bisher nicht einem Fachvertreter an einer anderen Hochschule zur Überprüfung vorgelegt oder mich anderweitig um Zulassung zur Promotion beworben habe.

Ich erkläre mich einverstanden, dass meine Dissertation vom Dekanat der Medizinischen Fakultät mit einer gängigen Software zur Erkennung von Plagiaten überprüft werden kann.

Unterschrift:

A handwritten signature in blue ink, appearing to read 'Dunkin', written over a light blue horizontal line.