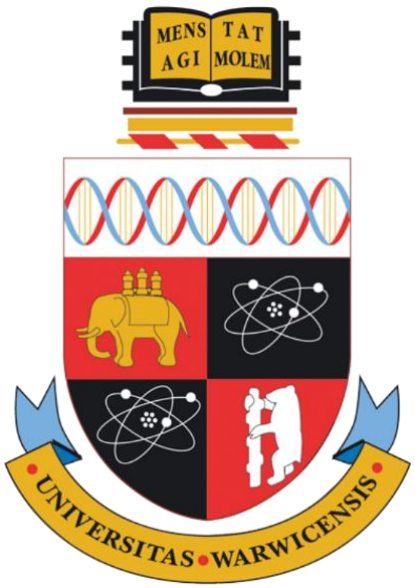

Psychobiology of Emotion-Cognition Interactions in Ageing

By

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List of Abbreviations

Ageing Brain Model	-	ABM
Autonomic Nervous System	-	ANS
Carbohydrate	-	CHO
Cardiovascular	-	CV
Digit Symbol Substitution task	-	DSST
Heart rate	-	HR
Heart rate variability	-	HRV
Mill Hill vocabulary test	-	MHVT
Oral glucose tolerance test	-	OGTT
Parasympathetic Nervous System	-	PSNS
Prefrontal cortex	-	PFC
Positivity Effect	-	PE
Reaction time	-	RT
Socioemotional Selectivity Theory	-	SST
Sympathetic Nervous System	-	SNS

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Declaration

I hereby confirm that I completed this thesis independently, that I have not heretofore presented this thesis to another department or university, and that I have listed all references used, and have given credit to all additional sources of assistance.

Note on Inclusion of Published Work

Parts of this thesis have been published or submitted for publication. Chapters 2 and 3 have been published during the period of my PhD registration, and the copyright of these papers resides with the publishers. The reproduction of the published papers in this thesis is permitted under the terms of the copyright agreement.

Mantantzis, K., Schlaghecken, F., & Maylor, E. A. (2017). Food for happy thought: Glucose protects age-related positivity effects under cognitive load. *Psychology and Aging, 32,* 203–209.

Mantantzis, K., Maylor E. A., & Schlaghecken, F. (2018). Gain without pain: Glucose promotes cognitive engagement and protects positive affect in older adults. *Psychology and Aging, 33,* 789-797.

Mantantzis, K., Schlaghecken, F., & Maylor, E. A. (in press). Heart rate variability predicts older adults' avoidance of negativity. *The Journals of Gerontology, Series B: Psychological Sciences and Social Sciences*.

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Abstract

Despite the cognitive and physiological decrements observed in old age, older adults are emotionally resilient, even showing improved emotion regulation capacity compared with their young counterparts. This age-related improvement in emotion regulation translates into a preference for positive and avoidance of negative information in cognition, known as the positivity effect (PE). The thesis focuses on investigating the physiological underpinnings of emotion-cognition interactions in ageing and, specifically, the role of glucose availability and overall Autonomic Nervous System (ANS) functionality. Experiments 1a and 1b found that although the age-related PE disappeared under high cognitive load, glucose allowed older adults to retain their positivity preference. Whereas young adults used the extra glucose resources to improve their overall performance when cognitive load was high, older adults preferentially allocated them to the encoding/recall of positive over negative material. Experiment 2 showed that glucose availability can increase both young and older adults' ability to engage in demanding cognitive tasks. However, whereas young adults did not experience any additional cognitive or affective facilitation, glucose improved cognitive performance and increased positive affect in older adults while mitigating their subjective effort perceptions. Experiment 3 found that ANS functionality is related to the magnitude of older adults' PE. Specifically, higher ANS capacity was associated with stronger negativity avoidance in older, but not young, adults. Finally, a meta-analysis revealed that carbohydrate (CHO) administration does not lead to any improvements in mood. Instead, CHO ingestion was associated with higher fatigue and decreased alertness within the first hour post-CHO consumption. In summary, the thesis presents important evidence of an association between aspects of physiological functioning and emotion-cognition interactions in ageing, and provides answers to heavily debated topics such as the CHO-mood relationship. Uncovering the physiological profile of emotion-cognition interactions could allow researchers and clinicians to create interventions to improve well-being in older age.

Chapter 1: General Introduction

This chapter provides a general overview of emotional ageing and discusses the theoretical frameworks behind age-related changes in emotion-cognition interactions, which is the primary focus of the thesis. The relationship between physiological functionality and emotional ageing will be outlined and, more specifically, the role of glycaemic regulation, energy availability, and the overall influence of the Autonomic Nervous System (ANS). At the end of this chapter an overview of the studies comprising this thesis will be introduced, and their importance in delineating the psychobiological underpinnings of emotion-cognition interactions will be discussed.

The Paradox of Emotional Ageing

Early assumptions from emotional ageing models posit that emotion regulation and overall emotionality, not unlike biological and cognitive functioning (for reviews, see Drag & Bieliauskas, 2010; Salthouse, 2010), are subject to decline in efficiency with progressing age. Changes in bodily functions, chronic health issues and complaints about cognitive deterioration with advanced age theoretically support the argument of a reduction in quality of life and difficulties in regulating emotions. While it makes intuitive sense to speculate that physiological and cognitive changes due to advancing age lead to a steep decrease in quality of life and emotional stability, research into the affective state of older adults has revealed an interesting account of the relationship between ageing and emotionality.

Despite ageing being a period of social, cognitive and physical losses, older adults appear to be well adjusted and emotionally resilient throughout the ageing process (Carstensen, Pasupathi, Mayr, & Nesselroade, 2000), even showing improved emotion

regulation capacity compared with young adults (Charles & Carstensen, 2007). Studies have demonstrated that older individuals report higher levels of positive affect (Carstensen et al., 2011; Mroczek & Kolarz, 1998) and less negative emotional experiences compared with young adults (Charles, Reynolds, & Gatz, 2001; Kunzmann, Little, & Smith, 2000; Mroczek & Kolarz, 1998). Additionally, older adults tend to show better management of their emotional states (Gross et al., 1997; Lawton, Kleban, Rajagopal, & Dean, 1992; Phillips, Henry, Hosie, & Milne, 2006; Röcke, Li, & Smith, 2009; Tsai, Levenson, & Carstensen, 2000), which potentially allows them to selectively downregulate the emotional influence of negative affective situations while upregulating the positives.

This age-related emotion regulation advantage is thought to be one of the contributing factors behind older adults' reports of higher satisfaction with life and their more positive outlook on interpersonal relationships, when compared with their younger counterparts (Carstensen, Mikels, & Mather, 2006). Furthermore, older individuals tend to show greater ability to deal with emotionally distressing situations, implementing complex emotional coping strategies (for a review, see Blanchard-Fields, 2007), as well as managing interpersonal tensions, arguments and psychosocial stress in response to negative everyday situations (Birditt & Fingerman, 2005; Birditt, Fingerman, & Almeida, 2005).

Positivity Effect

Older adults' improved emotion regulation has also been found to spill-over onto cognition and, more specifically, the way valenced information is processed. Charles, Mather, and Carstensen (2003) were the first to observe an age-related reversal in

emotional memory. They asked young, middle-aged and older adults to memorise positive, negative and neutral pictures. As expected, all age groups showed better memory for emotional rather than neutral pictures (for a review of the emotion enhancement effect, see LaBar & Cabeza, 2006). However, whereas young and middle-aged adults' ability to remember positive and negative information was comparable, older adults showed a strong preference for positive information. Not only did older adults remember significantly more positive than negative pictures, but their ability to remember the negatives was on a par with their memory for neutral pictures.

As such, it has been argued that memory in ageing is selectively enhanced by positive, but not negative, information, which stands in sharp contrast to the memory-boosting effect of negativity found in young adults (see Baumeister, Bratslavsky, Finkenauer, & Vohs, 2001). This age-related preference for positive information, coined the 'Positivity Effect' (PE; Mather & Carstensen, 2005), has been subsequently replicated in studies assessing episodic memory (e.g., Grühn, Scheibe, & Baltes, 2007; Elizabeth A. Kensinger, 2008; Leigland, Schulz, & Janowsky, 2004; Mather & Carstensen, 2003; Mather & Knight, 2005; Tomaszczyk & Fernandes, 2013) and autobiographical memory (Gallo, Korthauer, Mcdonough, Teshale, & Johnson, 2011; Q. Kennedy, Mather, & Carstensen, 2004; Schlagman, Kliegel, Schulz, & Kvavilashvili, 2009; Schlagman, Schulz, & Kvavilashvili, 2006).

Attention is similarly susceptible to the age-related PE, with older but not young adults showing an attentional bias towards positive information. In the first study to observe this attentional bias, researchers presented participants with pairs of emotional and neutral faces in a dot-probe paradigm (Mather & Carstensen, 2003). After a short

delay, the faces disappeared and a single dot appeared behind one of the faces to which participants had to respond by pressing one of two keys corresponding to the side where the dot was presented. Older adults were faster to respond to the dot appearing behind the positive faces when positive-neutral face pairs were presented. Additionally, older adults produced faster responses when the dot appeared behind the neutral face if negative-neutral faces were displayed immediately before, suggesting that older adults have a bias towards positive and away from negative material (also see Isaacowitz, Wadlinger, Goren, & Wilson, 2006a). Over the years, more evidence in favour of an age-related positivity preference in attention has started to accumulate using eye tracking studies. Similar to the results obtained from the dot-probe study (Mather & Carstensen, 2003), eye tracking paradigms have successfully replicated the attentional preference of older adults towards positive and away from negative information through the assessment of gaze preference patterns in participants' fixations (Allard & Isaacowitz, 2008; Isaacowitz, Toner, Goren, & Wilson, 2008; Isaacowitz, Wadlinger, Goren, & Wilson, 2006b; Knight et al., 2007).

The evidence emerging from the attentional cognitive domain highlights an important aspect of the PE. Specifically, older adults' bias in the processing of emotional information does not necessarily emerge as a preference for positive information but can also appear as an avoidance of negative information. In fact, some studies have failed to identify a preference for positive information but have instead found evidence of a reliable negativity avoidance in older age (e.g., Grühn et al., 2007). Although the validity of the age-related PE has been challenged by researchers that have failed to replicate the phenomenon (e.g., Grühn, Smith, & Baltes, 2005; Leclerc &

Kensinger, 2008), a recent meta-analysis of 100 studies has suggested that the PE is a highly reliable effect, irrespective of the cognitive domain investigated (Reed, Chan, & Mikels, 2014). Furthermore, the authors of the meta-analysis argued that the PE is stronger in studies that allow participants to process information in an unconstrained/natural manner (i.e., with no instructions on how to engage with the material) and, therefore, such methodological decisions should be carefully considered when assessing the PE.

Explaining the Positivity Effect

Ageing Brain Model (ABM)

The paradoxical nature of findings of increased positivity and improved emotionality with increasing age has led to theoretical frameworks being formulated to systematically examine the underlying mechanisms of this phenomenon. Researchers have attempted to explain this age-related positivity from a neurobiological perspective. The Ageing Brain Model (ABM; Cacioppo, Berntson, Bechara, Tranel, & Hawkley, 2011) suggests that the amygdala, a central component of the brain's emotion regulation network, is subject to age-related decrements in efficiency. It is argued that, similar to the functional and anatomical deterioration found in other brain areas as a consequence of typical ageing (e.g., prefrontal cortex, PFC; for a review, see Sugiura, 2016), the amygdala becomes less responsive to negative information with increasing age. Therefore, findings of improved well-being and higher positivity in cognition are posited to be serendipitous by-products of the amygdala's decreased ability to selectively respond to negative stimuli.

The ABM's postulates are based on evidence that patients with lesions in the amygdala exhibit impairments in the recognition of negative emotions (Adolphs & Tranel, 2004), and tend to rate negative pictures as less arousing than positive pictures when compared with patients with damage in brain centres unrelated to emotion regulation (Berntson, Bechara, Damasio, Tranel, & Cacioppo, 2007). As these findings are consistent with behavioural outcomes found in typical ageing (i.e., the PE), the ABM posits that amygdala deterioration must be the driving force behind older adults' increased positivity and reduced negativity. However, in response to the ABM's assertion that age-related changes in the amygdala underlie older adults' improved emotional well-being, a number of neuroimaging, longitudinal and post-mortem studies have found that the amygdala's functional and structural integrity is not particularly affected by ageing, challenging the validity of the ABM's principle tenet (for a review, see Mather, 2016). Furthermore, cognitive studies have found older adults to be as responsive as young adults when presented with highly aversive or threatening stimuli, suggesting that older adults' ability to detect strong negative information is impervious to age-related decrements (e.g., Knight et al., 2007; Leclerc & Kensinger, 2008; Mather & Knight, 2006). Additionally, evidence from studies assessing emotion processing patterns in the brains of patients with Alzheimer's disease, a condition known to significantly affect the integrity of the amygdala (Liu et al., 2010), have found that Alzheimer's patients' amygdalae are more responsive to both neutral and fearful faces compared with healthy older adults, contesting the notion that the PE in healthy ageing is a sign of age-related decrements in brain areas involved in emotion regulation (C. I. Wright, Dickerson, Feczko, Negeira, & Williams, 2007).

Socioemotional Selectivity Theory (SST)

The Socioemotional Selectivity Theory (SST; Carstensen, 1995; Carstensen, Isaacowitz, & Charles, 1999) posits that older adults' improved emotion regulation is a result of their limited future time perspective and the realisation that the future is not open-ended (i.e., mortality salience). With increasing age, people perceive their time horizon to be more constrained and, as a result, they begin to focus on short-term emotionally-driven goals that are easy to fulfil and would lead to more emotional gratification, rather than pursuing expansive goals (e.g., expanding their social circles) and long-term future payoffs (Carstensen, Fung, & Charles, 2003; Fung, Carstensen, & Lutz, 1999). To that end, older adults start to prioritise positive life experiences and activities aimed at optimising their emotional well-being, including spending more time with a small group of social or intimate partners, and engaging in more emotionally meaningful interactions (for a review, see Lang, 2001).

It is particularly interesting that when young adults are asked to imagine their time perspective to be limited (e.g., shortened life expectancy scenarios), they tend to show patterns of increased positivity in their memory for emotional material, similar to the PE observed in older adults (Barber, Opitz, Martins, Sakaki, & Mather, 2016). Furthermore, young adults with terminal conditions (Carstensen & Fredrickson, 1998) and young adults facing 'social endings', such as moving to a new location away from their established social circle (Fredrickson & Carstensen, 1990), tend to prioritise emotionally gratifying goals and spending time with their immediate social circle and family members. Conversely, when older adults are asked to think of a more open-ended future, a shift is observed from positive emotional and social experiences to the

prioritisation of more expansive goals and the acquisition of knowledge (e.g., Fung & Carstensen, 2003), providing further evidence for the role of time perspective in young and older adults' choice goal setting.

Cognitive control hypothesis

Older adults' preference for positive and avoidance of negative information in cognition has also been explained through the SST. The 'cognitive control' extension of the SST suggests that older adults' prioritisation of emotional well-being translates into improved memory and greater attention towards positive and away from negative stimuli, and this preference constitutes an emotion regulation attempt (for a review, see Mather & Carstensen, 2005). In sharp contrast to the ABM (Cacioppo et al., 2011), this theoretical framework suggests that older adults' PE is not a result of changes in automatic bottom-up processes stemming from age-related deterioration of the brain's emotion regulation centres, but is rather a controlled top-down mechanism which older adults employ to upregulate positive information and minimise exposure to negative material that could affect their emotional well-being (Kryla-Lighthall & Mather, 2009).

Evidence in support of the 'cognitive control' model has been rapidly accumulating over recent years. Neuroimaging studies have shown that the prefrontal cortex (PFC), an area responsible for adjusting the amygdala's activity during emotion regulation, shows different activation patterns in young and older adults when presented with valenced stimuli. Specifically, it has been found that presenting older adults with negative material leads to significantly higher PFC activation (Murty et al., 2009) and decreased amygdala activity compared with young adults (Fischer et al., 2005; St. Jacques, Dolcos, & Cabeza, 2010; Tessitore et al., 2005), which researchers have

interpreted as an age-related attempt at downregulating the affective impact of negative information (for a review, see St. Jacques, Bessette-Symons, & Cabeza, 2009). It is interesting that, with increasing age, the amygdala starts responding more strongly to positive than to negative information, a phenomenon not evident in young adults' amygdala activation patterns (Kehoe, Toomey, Balsters, & Bokde, 2013; Leclerc & Kensinger, 2011; Mather et al., 2004). When presented with positive material, older adults also show higher PFC activation than young adults, particularly when task instructions require participants to engage deeply with the material (i.e., semantic elaboration; Ritchey, Bessette-Symons, Hayes, & Cabeza, 2011), suggesting that older adults additionally recruit the PFC to upregulate positive influences and not just to downregulate the negatives (for reviews, see Mather, 2012; Nashiro, Sakaki, & Mather, 2012). Further stressing the importance of PFC's modulation of the amygdala with regards to older adults' PE, recent work has shown that the magnitude of older adults' PE is directly related to the strength of the PFC-amygdala functional connectivity at rest, with stronger resting state connectivity translating into a more pronounced PE in cognition (Sakaki, Nga, & Mather, 2013).

In the cognitive domain, Mather and Knight (2005, Experiment 2) uncovered an association between cognitive control capabilities and the magnitude of the PE, such that older adults with better performance in cognitive control tasks are more likely to show a preference for positive and an avoidance of negative pictures. Additional studies have replicated this finding in the attentional domain, showing that older adults who perform better at baseline executive control tasks are more likely to generate fixations towards positive and away from negative information (Isaacowitz, Toner, & Neupert,

2009; Sasse, Gamer, Büchel, & Brassen, 2014). Mather and Knight (2005, Experiment 3) also asked participants to memorise emotional pictures under both full and divided attention (i.e., dual task) conditions. Results showed that whereas older adults exhibited the expected PE under full attention, their preference for positive information disappeared when they were asked to concurrently perform a dual task during the encoding stage. Similar findings have also been obtained from attentional PE paradigms. Knight et al. (2007) asked young and older adults to view emotional and neutral material (e.g., pictures and faces) under single and dual task conditions while their eye movements were being recorded. Under single task conditions, older adults generated fixations away from negative material (i.e., negativity avoidance). However, this negativity avoidance disappeared when participants had to perform a distracting secondary task. Thus, although older adults show the expected PE when their cognitive resources are focused on a single task, increasing cognitive load through the introduction of a demanding secondary task diminishes the PE. This evidence suggests that the PE is tied to cognitive control capabilities. Disrupting older adults' ability to employ all available cognitive resources towards fulfilling their emotion regulation goals can significantly affect their processing patterns and decrease positivity and/or anti-negativity.

Furthermore, the time-course of the PE in older adults' attention provides additional evidence for the 'cognitive control' model. When older adults are presented with pairs of emotional and neutral stimuli, the PE does not emerge automatically but rather after cognitive control mechanisms have had a chance to influence participants' attention. Specifically, using an eye tracking PE paradigm, researchers found that the

preference for positive material does not appear until after 500 ms following stimulus onset, while avoidance of negative stimuli is established at around 3 s post-stimuli presentation (Isaacowitz, Allard, Murphy, & Schlangel, 2009). The fact that older adults do not show a preference early in their fixations suggests that the PE (both positivity preference and negativity avoidance) reflects the deployment of top-down processes, with older adults actively choosing to divert their attention towards positive and away from negative stimuli only after cognitive control mechanisms have been employed (also see Knight et al., 2007).

Kensinger (2008) presented young and older adults with positive and negative words to memorise, both high and low in arousal. Both young and older adults showed better memory for high- rather than low-arousal words, suggesting that older adults' ability to detect and remember highly arousing information is not impaired as a result of increasing age (see Mather & Knight, 2006). More importantly, whereas older adults showed the PE for material low in arousal, they did not show the same preference when high-arousal words were considered, a finding replicated by Streubel and Kunzmann (2011). Previous studies have shown that in contrast to high-arousal information which is processed automatically, low-arousal material requires the engagement of cognitive control mechanisms to be effectively memorised (Kensinger, 2004). The fact that older adults showed a positivity preference solely for low-arousal material provides further evidence for the need to employ cognitive control resources for the PE to emerge. Neuroimaging findings have reported similar patterns: whereas no age-related differences exist in brain activation patterns in response to high-arousal stimuli, older adults tend to show higher PFC activation during presentation of low-arousal material

compared with their younger counterparts, and this predicts stronger negativity avoidance in the older group (Dolcos, Katsumi, & Dixon, 2014).

Criticism of the SST and cognitive control hypothesis

Although the evidence favouring the SST and its 'cognitive control' extension seem particularly strong, criticisms have been articulated by researchers over the years. With regards to the SST, evidence has suggested that a limited time perspective cannot always explain older adults' positivity. In fact, whereas chronological age is often associated with a stronger emotional profile and higher positivity, a limited future time perspective has been shown to relate to lower ratings of subjective well-being, more negative affect, lower life satisfaction and higher rates of depression (see Grühn, Sharifian, & Chu, 2016; Hoppmann, Infurna, Ram, & Gerstorf, 2017). Researchers have argued that the association between time perspective and positivity could be mediated by other factors, including self-regulatory fatigue (Segerstrom, Geiger, Combs, & Boggero, 2016), awareness of age-related gains (Brothers, Gabrian, Wahl, & Diehl, 2016), and older adults' expectations regarding future health (Tasdemir-Ozdes, Strickland-Hughes, Bluck, & Ebner, 2016; for a review, see Fung & Isaacowitz, 2016).

With regards to the 'cognitive control' extension of the SST, it has been argued that the PE might not necessarily be dependent on cognitive control resources. Allard and Isaacowitz (2008) found that increasing cognitive load by introducing a dual task during an eye-tracking PE paradigm does not diminish older adults' PE when compared to a full-attention condition. It should be noted that the lack of dual-task effects on the PE could be attributed to the relatively easy nature of the distractor task employed and the low number of participants recruited. Thomas and Hasher (2006) reported similar

sparing of the age-related PE, despite emotional material being presented under dual-task conditions. Allard, Wadlinger, and Isaacowitz (2010) found that the generation of fixations towards positive information is not effortful enough to cause significant changes in pupil dilation, a physiological measure known to fluctuate based on different levels of effortful cognitive exertion. This could suggest that no particular cognitive investment is needed by older adults in order to produce the PE. These studies pose important questions regarding the nature of the underlying mechanisms of older adults' PE that require careful and systematic examination.

Positivity Effect and Mood

It is generally assumed that older adults' PE does not simply reflect a cognitive mechanism but it constitutes an active attempt at emotion regulation, with older adults selecting to pay more attention to and remember positive information while ignoring negative material in order to upregulate positive and downregulate negative influences, respectively (for reviews, see Mather & Carstensen, 2005; Scheibe & Carstensen, 2010). The discovery of the age-related PE coincided with the formulation of the SST's tenets and findings of increased positive and reduced negative affect in older adults. As such, researchers have conceptualised the PE as an emotion regulation tool and have speculated that it is related to affective outcomes (e.g., Carstensen et al., 2006; Isaacowitz et al., 2006b; Kryla-Lighthall & Mather, 2009).

In one of the first studies to address the PE-mood relationship, 300 nuns were asked to recall events they reported 14 years before the experiment took place. Participants who were instructed to focus on their emotions during retrieval recalled the past in a more positive manner and reported better mood compared to those who were

told to focus on retrieval accuracy (Q. Kennedy et al., 2004). Isaacowitz et al. (2008) assigned young and older adults to a positive, neutral or negative mood manipulation condition, and subsequently presented them with positive-neutral and negative-neutral face pairs while recording their eye movements. Whereas young adults' fixations were congruent with the mood manipulation that preceded the task (i.e., more negative fixations in the negative mood group), older adults with experimentally-induced negative mood showed a strong preference towards positive and away from negative faces. Interestingly, the PE did not emerge for the older-positive or the older-neutral mood groups. Although no direct measurements of mood were taken after the eye-tracking task, the authors hypothesised that older adults could, potentially, use the PE as a tool to decrease levels of negativity and increase positivity in an effort to improve mood. In a follow-up study, it was found that, at the end of a long eye-tracking task, older adults with higher levels of executive functioning at baseline were better at resisting task-related declines in mood (which they would otherwise experience because of the task) by generating fixations towards positive material (Isaacowitz, Toner, & Neupert, 2009). In a similar vein, higher negativity avoidance in older adults (i.e., looking away from negative information) has also been associated with a smaller performance-related mood decline (Noh, Lohani, & Isaacowitz, 2011; for reviews, see Isaacowitz, 2012; Isaacowitz & Noh, 2011).

It should be noted that the relationship between the PE and mood is not clear and the association between these two constructs is still under investigation. It could be argued that the PE paradigms used in this line of research are not directly related to emotionality and are not intended to be indicative of emotional states. As such, the

cognitive patterns observed in older adults might not necessarily translate into affective outcomes. The tasks used to investigate the PE assess the cognitive changes that emotional material elicit and do not necessarily reflect changes in emotionality (see Isaacowitz & Blanchard-Fields, 2012). Although positive and negative material could cause small fluctuations in transient emotionality, these changes are potentially too weak to affect overall mood and can dissipate by the time mood is assessed following a PE task. The association between the PE and mood is not a consistent finding and researchers have not always uncovered an association between the two (e.g., Kappes, Streubel, Droste, & Folta-Schoofs, 2017; Livingstone & Isaacowitz, 2018). It has been proposed that the PE should be considered a cognitive by-product guided or shaped by older adults' emotion gratification goals (SST; Carstensen et al., 1999) rather than a deliberate age-related strategy to manage emotionality (Carstensen & Deliema, 2018). Further studies are needed to assess the role of the age-related PE in shaping older adults' affective experiences.

Summary

This section has provided an overview of emotional ageing and age-related emotion-cognition interactions. Despite the popular 'doom and gloom' perception of ageing, older adults appear to experience more positive and less negative affect than young adults, and they are better at emotion regulation and dealing with interpersonal tension. This age-related improvement in emotional well-being is posited to be related to older adults' increased prioritisation of emotionality-driven rather than expansive goals, which also affects their processing patterns and makes them show a preference for positive over negative information in cognition. It is generally assumed that this

mechanism is related to cognitive control, with older adults employing their processing resources to prioritise positive and ignore negative information, an assertion which has been challenged by some researchers. Although it is thought that the PE reflects an emotion regulation mechanism serving older adults' motivation to remain positive and avoid negativity, evidence is scarce and no consensus has been reached.

Nevertheless, the ongoing debate with regards to the nature of the PE and its role in older adults' emotionality has provided many fruitful avenues for research. To that end, the role of this thesis is to further examine age-related changes in emotionality and emotion-related cognitive processing by systematically deconstructing the role of cognitive resources in older adults' PE and the relationship between the PE and emotionality. We attempted to understand this ageing paradox through the exploration of its underlying physiological mechanisms. The role of physiological functioning in emotionality will be discussed in the following section.

Emotional Ageing and Physiology

Autonomic Nervous System and Emotion

Although the exact nature of emotions is a topic heavily debated across disciplines, it is widely acknowledged that they are complex processes requiring the coordination of multiple physiological systems (both central and peripheral), behaviour, subjective experience and cognition (Levenson, 2014). To generate appropriate emotional responses to external (e.g., environmental) or internal cues, these systems have to work together to ensure the timely recruitment of resources relevant to emotions (Appelhans & Luecken, 2006). In order to upregulate a positive or downregulate a

negative emotion, individuals have to adjust both their subjective experience and the physiological arousal that accompanies emotion elicitation (Gross, 1998).

As such, the Autonomic Nervous System (ANS) is particularly relevant to the study of emotion. Generally, the ANS innervates all the organs in the human body and is responsible for regulating automatic functions such as heart rate (HR), respiration, glucose metabolism and digestion, amongst others. It consists of two main branches: the Sympathetic Nervous System (SNS) which increases physiological arousal to meet emerging demands ('fight or flight' response), and the Parasympathetic Nervous System (PSNS) which is responsible for decreasing physiological arousal ('rest and digest' function). The purpose of the ANS is to maintain homeostasis, increase physiological arousal by mobilising available resources in response to threats and challenges through the SNS, and decrease arousal via the PSNS during periods of safety to maintain energy and resources (for a review, see Levenson, 2003). It has been reliably shown that the ANS is sensitive to emotionality, with different emotions inducing different levels of physiological arousal (for a review, see Kreibig, 2010). When strong emotional information is encountered, the SNS is responsible for swiftly preparing the body for action by allocating the appropriate level of resources to relevant physiological systems (e.g., increasing HR) at the appropriate time to ensure that the individual is prepared to act. After the source of the arousal disappears, the PSNS is responsible for helping the body return to its baseline function (e.g., decreasing HR).

The polyvagal theory (Porges, 1995) was one of the first frameworks to present a model addressing the connection between physiological arousal and neural circuits relevant to emotion. The theory suggests that fluctuations in physiological arousal are a

result of neuroception, a process that allows individuals to distinguish between situations and environmental cues signifying safety and threat, adjusting physiological activity as appropriate (Porges, 2003). The main point of the theory is that physiological arousal is regulated through the activity of the vagus nerve, which is the main nerve through which the PSNS exerts its influence. The polyvagal theory conceptualises vagal activity as a 'brake': under normal circumstances (safety and stability), the vagal brake maintains low arousal levels (e.g., decreased HR) to promote social behaviours and visceral homeostasis. In the presence of strong emotional information requiring the immediate mobilisation of resources (e.g., danger), the vagal restraint on physiological arousal is withdrawn to support the fight/flight response (Porges, 2007).

Further refining this idea, Thayer and Lane (2000, 2009) outlined the Neurovisceral Integration Model, a comprehensive framework addressing the relationship between cognition, emotion and autonomic regulation of physiological arousal. Similar to the polyvagal perspective, the Neurovisceral Integration Model sees emotion as a self-regulatory mechanism that guides physiological arousal and behaviour, allowing the individual to adapt to demands. An important aspect of this is the ability of the organism to pay selective attention to meaningful information that is important for survival while ignoring irrelevant distractions. As attention is guided by motivational (approach vs. avoidance motivation) and affective influences (positive vs. negative and high intensity vs. low intensity; for a review, see Braver et al., 2014), the theory suggests that cognition and emotionality represent a single integrated system that modulates behaviour and contributes to individual differences in adaptability. Indeed, researchers have identified a network of brain areas supporting behavioural adaptation

and self-regulation that, among other structures, contains the PFC and the amygdala, areas responsible for cognitive control and affective regulation (Benarroch, 1993). As conceptualised by the Neurovisceral Integration Model, the amygdala is under the tonic inhibitory control of the PFC and, as a result, fluctuations in PFC activation lead to modulations in amygdala activity (Thayer & Brosschot, 2005). Interestingly, the amygdala is one of the main brain areas the activity of which affects the PSNS/SNS balance of the ANS through its connections with the vagus nerve (for a review, see Thayer & Lane, 2009). As such, the output of the PFC-amygdala network elicits changes in physiological arousal through the vagus nerve and has observable effects on ANS-controlled organs such as the heart (Benarroch, 1993, 1997). Therefore, the activity of the network could be indexed by markers of vagus nerve activity (also known as vagal tone; Appelhans & Luecken, 2006).

It has been argued that vagal tone is a measure of the strength of the PFC-amygdala functional connectivity, and it has been shown to be directly related to self-regulatory capacity (e.g., Segerstrom & Nes, 2007) and the ability of the individual to generate situation-appropriate responses to emotional and social cues (e.g., Muhtadie, Koslov, Akinola, & Mendes, 2015). As the heart's rhythm is determined by the activity of the vagus nerve on the sinoatrial node (the heart's pacemaker), vagal tone can be reliably assessed through cardiovascular (CV) measures. In particular, heart rate variability (HRV), an index of the variation of the interval between successive heartbeats (Task Force, 1996), has been shown to be a highly valuable marker of vagal tone (for reviews, see Balzarotti, Biassoni, Colombo, & Ciceri, 2017; Laborde, Mosley, & Thayer, 2017). Indeed, HRV levels have been found to be highly correlated with the

strength of the emotion regulation neural network (i.e., PFC-amygdala functional connectivity; Jennings, Sheu, Kuan, Manuck, & Gianaros, 2016; Sakaki et al., 2016; for a meta-analysis, see Thayer, Åhs, Fredrikson, Sollers, & Wager, 2012) and the cortical thickness of prefrontal areas that are responsible for the up- and down-regulation of the amygdala (e.g., medial PFC; Winkelmann et al., 2017; Yoo et al., 2018).

In line with the conceptualisation of vagal tone as a marker of individual differences in the capacity of emotion regulation brain networks, high levels of HRV have been associated with better emotion regulation. Across two studies, it has been observed that resting HRV levels are negatively associated with self-reported difficulties in emotion regulation, such that higher levels of HRV predicted lower difficulty in regulating emotions (Visted et al., 2017), as well as improved impulse control and higher emotional clarity (Williams et al., 2015). Similarly, researchers have also uncovered a positive association between HRV and ratings of self-compassion, a trait that has been shown to predict psychological well-being (Svendsen et al., 2016). Interestingly, low HRV has been associated not only with difficulties in emotion regulation but also with the presence of psychopathological conditions such as depression and high levels of anxiety (for reviews, see Chalmers, Quintana, Abbott, & Kemp, 2014; Kemp et al., 2010). Although the clearest relationship between HRV and behaviour is found in the domain of emotion regulation (for reviews, see Appelhans & Luecken, 2006; Thayer & Lane, 2000, 2009), studies have also found HRV to be related to cognitive control capacity. Gillie, Vasey, and Thayer (2014) found that high-HRV participants have better ability to suppress unwanted memories and employ inhibitory control mechanisms in a think/no-think paradigm. High levels of HRV also appear to be

associated with improved inhibition of prepotent responses and superior action cascading capacity (Colzato & Steenbergen, 2017), as well as improved performance in tasks requiring executive control (Hansen, Johnsen, & Thayer, 2003).

It should be noted that findings of an association between ANS functionality, emotion regulation and cognition are limited to young adults. The paucity of ageing data is particularly surprising considering the age-related changes in emotion regulation and older adults' preference towards positive and away from negative information. One of the few relevant ageing studies assessing the relationship between vagal tone and emotion regulation neural networks has found the association between PFC-amygdala connectivity and HRV to remain intact across the adult lifespan (Sakaki et al., 2016). However, there exists a large gap in our knowledge of how these neuroimaging findings translate into emotion-cognition outcomes in late adulthood. This is of particular importance to the age-related PE. Although research has suggested that the PE reflects an emotion regulation mechanism (e.g., Isaacowitz et al., 2009; Noh et al., 2011), there is not enough evidence to unequivocally support that assertion (see Isaacowitz & Blanchard-Fields, 2012). Understanding whether ANS functionality, as measured by ANS-related emotion regulation indices (e.g., vagal tone and HRV), relates to older adults' PE could provide further evidence of the purpose of the age-related positivity preference and the underlying physiological mechanisms that might contribute to its emergence. The idea of an association between overall ANS functionality and older adults' PE is further explored and elaborated on in Chapter 4.

Glycaemic Regulation and Ageing

It is evident that the ANS and emotionality are intrinsically related. However, our knowledge of how ANS functionality relates to emotion-cognition interactions in ageing is surprisingly limited. This could also relate to the fact that the ANS encompasses a vast number of biological functions that could plausibly contribute to the cognitive and emotional outcomes observed in older age. Therefore, more research is needed to explore the underlying mechanisms of older adults' positivity preference and how they are influenced by ANS-controlled functions.

A physiological system that might be implicated in emotion-cognition interactions is glucose regulation and metabolism. Glucose is the main energy fuel underlying all biological functions. The brain, in particular, has the highest energy demands of all the organs in the human body and requires continuous energy influx to support neuronal activity (Mergenthaler, Lindauer, Dienel, & Meisel, 2013). Despite accounting for approximately 2% of an individual's weight, the brain is metabolically 'expensive' and consumes at least 20% of the body's total glycaemic resources on a typical day (Dunbar, 1998), a number that can reach 55% when fasted (Amiel, 1995; Wang & Mariman, 2008). Unsurprisingly, studies assessing the behavioural and physiological effects of varying glucose levels have found low or excessively high levels of circulating glucose to be associated with compromised neurocognitive processes and cognitive deficits (Amiel et al., 1991; Mortby, Janke, Anstey, Sachdev, & Cherbuin, 2013; for a review, see Sünram-Lea & Owen, 2017), supporting the idea that healthy glucoregulation is a prerequisite for normal cognition.

It is well known that glucose metabolism is particularly affected by ageing, with studies suggesting the presence of pronounced age-related difficulties in metabolising and using energy resources (for a review, see Davidson, 1979). Such decrements have been implicated in the aetiology of metabolic disorders, evidenced by the high prevalence of metabolic conditions such as diabetes mellitus in older adults (Wild, Roglic, Green, Sicree, & King, 2004). It has been suggested that older adults' blood glucose levels following a meal tend to remain abnormally high for longer periods of time compared with young adults who are able to manage their glucoregulatory responses more effectively, indicating an age-related reduction in insulin sensitivity (Melanson et al., 1998). Similar difficulties in regulating glucose levels have also been found in hypoglycaemia, with older adults showing impaired ability to produce counterregulatory responses to low glucose levels, a trend not moderated by factors such as levels of physical activity/fitness (Marker, Cryer, & Clutter, 1992). Additionally, it has been argued that older adults have reduced subjective awareness of the physical symptomatology of low blood glucose concentrations (Meneilly, Cheung, & Tuokko, 1994).

Normal ageing is also accompanied by a marked decrease in glucose metabolism in the brain (8% decrease/decade), with limbic structures pertaining to memory (e.g., the hippocampus) being more prominently affected by this trend (Blesa et al., 1997). Significant metabolic declines have also been observed in sub-areas within the frontal cortex that are responsible for cognitive control processes (Kuhl, Metter, Riege, & Hawkins, 1984). Interestingly, animal studies have suggested that compared with young rats, aged rats also tend to show higher rates of extracellular glucose depletion in brain

areas supporting memory when performing demanding tasks (McNay, Fries, & Gold, 2000). Furthermore, this depletion has been shown to have longer-lasting effects on aged rats' cognitive performance, as replenishing energy resources takes considerably longer to achieve compared with their younger counterparts (McNay & Gold, 2001). In light of such findings, researchers have considered the possibility that impairments in glucose metabolism, both centrally and in the periphery, could be one of the main factors underlying the cognitive decrements observed in older age (for a review, see Gold, 2005). Considering the real-life applicability of these findings and the relative safe nature of manipulating glycaemic resources through glucose administration in experimental settings, research has focused on understanding how the availability of energy/glucose resources can potentially facilitate cognitive performance in both young and older adults.

Glucose and cognition

The majority of studies assessing the effects of glucose administration on cognition have been conducted with young adults and have generally reported positive effects of glucose ingestion on a wide range of cognitive outcomes. These effects have been shown to be more consistent for verbal declarative memory, with glucose leading to significant improvements in long-term memory (J. K. Foster, Lidder, & Sünram, 1998; Owen, Finnegan, Hu, Scholey, & Sünram-Lea, 2010; Sünram-Lea, Foster, Durlach, & Perez, 2001; Sünram-Lea, Foster, Durlach, & Perez, 2002). Studies assessing the effects of glucose on short-term memory recall also report performance improvements from increases in glucose availability (D. O. Kennedy & Scholey, 2000; Sünram-Lea et al., 2002), but the effects appear to be less reliable than those observed

for long-term memory processes (for reviews, see Hoyland, Lawton, & Dye, 2008; Messier, 2004; Riby, 2004; M. A. Smith, Riby, van Eekelen, & Foster, 2011). This phenomenon has been attributed to the hippocampus, an area strongly related to long-term memory retention (Aggleton & Brown, 1999), being densely populated by insulin receptors and, thus, sensitive to glucose manipulations (Unger et al., 1989). Other hippocampus-dependent functions have been shown to be affected by glucose manipulations, including performance on recognition tasks (Owen, Scholey, Finnegan, & Sünram-Lea, 2013; Sünram-Lea, Owen, Finnegan, & Hu, 2011), and visuospatial memory (Sünram-Lea, Foster, Durlach, & Perez, 2002b). This preferential glucose targeting of the hippocampus has led researchers to consider that glucose effects are cognitive domain-dependent, with memory being the cognitive domain that benefits the most from glucose consumption (for a review, see Messier, 2004). However, it should be noted that the glucose facilitation effect in young adults has also been observed for domains other than memory, with a glucose drink increasing speed of recognition during a memory task (Owen et al., 2013), as well as improving reaction times (RTs) and accuracy in attention tasks (Jones, Sünram-Lea, & Wesnes, 2012; Owens & Benton, 1994), and enhancing event related potentials relating to attentional processes (L. A. Brown & Riby, 2013).

Research into the effects of glucose administration on older adults' cognition has produced results that largely mirror the ones obtained from young adults. Glucose has been found to improve verbal episodic memory (Craft, Murphy, & Wemstrom, 1994; Manning, Hall, & Gold, 1990; Parsons & Gold, 1992; Riby et al., 2006; Riby, Meikle, & Glover, 2004), even when retrieval occurs after a relatively long period of retention

(e.g., 24 hours; Manning, Parsons, & Gold, 1992; Manning, Stone, Korol, & Gold, 1998). In line with findings of larger glucoregulatory deficits in ageing (for a review, see Korol & Gold, 1998), researchers have hypothesised that older adults might experience a more pronounced cognitive boost compared with young adults. Indeed, it has been observed that providing the same dose of glucose to young and older adults prior to cognitive performance leads to stronger memory benefits in older individuals compared with young (Hall, Gonder-Frederick, Chewning, Silveira, & Gold, 1989), while other studies have even uncovered selective glucose-related cognitive improvements in older but not young adults (Macpherson et al., 2015; Manning, Parsons, Cotter, & Gold, 1997). The importance of glucose regulation in cognitive ageing has also been highlighted by studies showing that glucose tolerance and levels of glucoregulatory capacity are strong predictors of cognitive performance in older adults (Hall et al., 1989; Messier, Gagnon, & Knott, 1997; Messier, Tsiakas, Gagnon, Desrochers, & Awad, 2010; for a review, see Messier, 2004).

What is particularly interesting about the glucose facilitation effect is its sensitivity to cognitive demands. It has been suggested that the effects of glucose on cognition are entirely dependent on the difficulty of the cognitive task, with the facilitation being more robust under conditions where participants are asked to perform two tasks simultaneously (i.e., dual tasks) rather than a single task. Sünram-Lea et al. (2002a) found that glucose improves young adults' memory for word lists only when participants are asked to concurrently perform a demanding secondary task, and not when the memory task is performed alone (single task; also see Scholey, Harper, & Kennedy, 2001; Scholey & Kennedy, 2004) or when manipulating its difficulty by

increasing the number of the to-be-remembered items (high-difficulty single task; but see D. O. Kennedy & Scholey, 2000). Similarly, it has been found that glucose can improve attention solely under dual-task conditions (Scholey, Sünram-Lea, Greer, Elliott, & Kennedy, 2009), suggesting that cognitive performance might be limited by the availability of energy resources and that glucose can offer the necessary resources to perform demanding tasks. As studies have found both memory and attention benefiting from glucose ingestion under high cognitive load, it has been hypothesised that the glucose facilitation effect is not necessarily domain-dependent as initially suggested (i.e., glucose advantage for hippocampus-mediated tasks) but rather difficulty-dependent.

If a task requires the recruitment of high levels of cognitive control resources and multitasking, glucose administration provides individuals with the necessary resources to support their cognitive performance by improving their ability to successfully divide their attention across two or more tasks (Scholey et al., 2013). On the other hand, if a task is relatively easy, glucose does not seem to have a strong effect on cognitive capability as the task does not require a lot of resources to be adequately performed by participants (e.g., Scholey et al., 2009; Sünram-Lea et al., 2002a). This theory is supported by findings of marked decreases in peripheral blood glucose levels following performance of cognitively demanding, but not easy, tasks (Fairclough & Houston, 2004; Scholey et al., 2001; Scholey et al., 2006). Glucose administration is posited to support cognitive functioning under high-load conditions by preventing a drop-off in resource availability (Gold, 2005; Macpherson et al., 2015; Scholey et al., 2001).

The relationship between glucose and performance in cognitively demanding tasks has not received much attention in ageing. The few ageing studies that have used dual-task paradigms have observed findings resembling the ones obtained from young adults, with glucose promoting improved cognitive performance in older adults under dual-task conditions. Glucose administration prior to a demanding dual task has been shown to improve older adults' accuracy (Macpherson et al., 2015), but this facilitation was not found for performance under single-task conditions. Further supporting these findings, neuroimaging studies have suggested that glucose administration during strenuous performance on a dual-task paradigm increases activation in brain areas supporting cognitive control exertion (e.g., sub-areas within the PFC) and can enhance older adults' ability to deal with multiple task demands simultaneously (Gagnon et al., 2012).

These results, however, have not been successfully replicated across all studies, with some researchers arguing that glucose can improve older adults' memory performance irrespective of task load (Riby et al., 2004), or that cognitive facilitation in older age is seen only for single- and not for dual-task conditions (Riby et al., 2006). As mentioned earlier, it is believed that, because of the glucoregulatory decrements observed in ageing, older adults might be more sensitive to glucose manipulations and experience a glucose facilitation effect of higher magnitude compared with their younger counterparts (Korol & Gold, 1998). Therefore, it is possible that older adults require the additional energy resources even when a task is of relatively low difficulty and not only when cognitive load is high. As this is only a speculation, more research is needed to address the role of age and cognitive load in the glucose facilitation effect.

Glucose and emotion-cognition interactions

Although glucose appears to consistently improve cognitive performance, the relationship between energy availability and emotion-cognition interactions is unclear. Studies conducted with young adults have uncovered a pattern of increased blood glucose levels and better memory when participants are presented with emotional, but not neutral, narratives (Parent, Varnhagen, & Gold, 1999), pictures (Blake, Varnhagen, & Parent, 2001), and words (C. E. Ford, Scholey, Ayre, & Wesnes, 2002; Scholey, Laing, & Kennedy, 2006). Although it is well established that positive and negative material is better remembered than neutral due to its emotionally salient nature (for reviews, see Baumeister et al., 2001; LaBar & Cabeza, 2006), researchers have suggested that the accompanying increase in blood glucose levels could be an important part of the mechanism that allows participants to prioritise emotional over neutral information in memory (Blake et al., 2001). However, not all studies have found an association between circulating glucose levels and the emotion enhancement effect (i.e., prioritisation of emotional over neutral material), challenging the notion that the emotion-related increase in glucose contributes to this phenomenon (Scholey et al., 2006).

The effect of glucose on emotional memory has also been examined to assess whether manipulating energy availability can further boost the emotion enhancement phenomenon in young adults. In these experiments, increasing glucose levels did not appear to alter or enhance the prioritisation of negative information compared with placebo (Brandt, Sünram-Lea, & Qualtrough, 2006). With studies suggesting that glucose effects are stronger under high cognitive load, researchers have also examined

the emotion enhancement effect using a dual-task paradigm, but have failed to uncover convincing evidence of further glucose facilitation in young individuals (Brandt, Sünram-Lea, Jenkinson, & Jones, 2010).

Considering our knowledge of how emotion-cognition interactions change in late adulthood, it is surprising that researchers have not examined the role of glucose in older adults' preference for positive over negative information. Although glucose administration in young adults does not appear to modulate the processing of emotional information, there is reason to believe that older adults are more sensitive to glucose manipulations. Because of the glucoregulatory decrements observed in ageing (for a review, see Gold, 2005) and the stronger magnitude of the glucose facilitation effect in older age (e.g., Macpherson et al., 2015), the PE could be subject to manipulations in glycaemic resources. More importantly, as discussed in an earlier section, the PE is posited to be a cognitive mechanism, with older adults recruiting cognitive control resources to prioritise positive and ignore negative material (Mather & Carstensen, 2005). Indeed, research has found the PE to be constrained by the availability of resources, such that when resources are spread across a number of tasks the PE tends to disappear (Knight et al., 2007; Mather & Knight, 2005; but see Allard & Isaacowitz, 2008). This phenomenon has been attributed to older adults not having the necessary resources to manage multiple tasks simultaneously, minimising their ability to allocate all available resources towards achieving positivity-related goals.

However, research has shown that older adults' multitasking capacity can be reliably improved via glucose administration (e.g., Gagnon et al., 2012, 2010; Macpherson et al., 2015). Increasing energy resources prior to a dual task could allow

older adults to perform both tasks at their highest capacity while, at the same time, providing them with enough resources to support their preference for positive and avoidance of negative information. Investigating this possibility could provide further evidence regarding the role of cognitive control resources in older adults' positivity preference and, potentially, ways through which the age-related PE could be protected under high-load conditions. Furthermore, if the PE is related to mood outcomes, findings of a connection between glucose and the PE could have practical implications for improving older adults' affective states. To that end, Chapter 2 presents two experiments in which the relationship between glucose availability and the age-related PE is further explored.

Glucose and cognitive engagement

The importance of uncovering methods for improving cognitive performance (e.g., glucose manipulations) in older adults cannot be overstated. Recent reviews have highlighted the importance of actively engaging with cognitively demanding and intellectually challenging tasks as a way of promoting cognitive health and maintenance, particularly in late adulthood (Hertzog, Kramer, Wilson, & Lindenberger, 2008). Therefore, it is imperative to investigate and delineate the circumstances under which older adults are more likely to actively engage with cognitive tasks and use their processing resources to perform at their highest capacity.

A number of studies have suggested that one of the factors that determines older adults' ability to exert effort in a cognitive task (i.e., cognitive engagement) is task difficulty (Ennis, Hess, & Smith, 2013; Hess & Ennis, 2012; Hess, Smith, & Sharifian, 2016). Ennis et al. (2013) asked young and older adults to perform tasks of varied

difficulty while measuring their levels of engagement through changes in CV reactivity. Both young and older adults showed high CV reactivity during performance of the easy and moderate difficulty tasks (indicative of higher engagement; for reviews, see Hess, 2014; Richter, Gendolla, & Wright, 2016). However, whereas young adults retained relatively high levels of engagement even when difficulty was high, older adults showed reduced CV reactivity (i.e., lower effort) compared to when difficulty was moderate, which was construed by the authors as an indication that older adults engage less with a task if demands are high. Additionally, it has been suggested that the reason behind older adults' disengagement is participants' subjective perceptions of difficulty. Simply perceiving a task to be difficult can decrease older adults' ability to exert effort, irrespective of the task's objective level of difficulty (Hess et al., 2016). Researchers have argued that when a task is of high difficulty and, therefore, success seems unlikely, older adults withdraw effort and show lower levels of engagement (Hess et al., 2016; B. T. Smith & Hess, 2015). Therefore, it would be particularly interesting to examine ways of changing older adults' engagement patterns, in a way that would motivate them to exert higher levels of effort even when difficulty is high.

The Selective Engagement Theory (SET; Hess, 2014) posits that the pattern of cognitive engagement observed in older adults' performance might be a result of resources being limited in ageing: if processing resources are scarce, older adults have to be more selective in terms of how these resources should be spent. Indeed, as discussed in a previous section of this introduction, older adults' selective recruitment of resources is evident in many aspects of their performance, including the prioritisation of positive over negative information in memory and attention (for a review, see Mather &

Carstensen, 2005). If a task is particularly difficult to perform and success seems unlikely, older adults might preserve these resources and selectively employ them only if they think that the cost of engaging with the task (i.e., resource usage) is smaller than the benefit of performing it (e.g., success or heightened feeling of self-efficacy).

However, the SET does not specify what these resources might be or how researchers can manipulate them to increase older adults' ability to perform a task. In light of the age-related decrements observed in the regulation of glucose, the higher rates of depletion and slower replenishing of energy in late adulthood (Gold, 2005; Korol & Gold, 1998), it is possible that the resource described in the SET is related to energy/glycaemic resources. Although a large number of studies have investigated the effects of glucose on cognitive performance, research has yet to examine how energy availability relates to cognitive engagement. If the resource underlying engagement pertains to energy, glucose administration and the increase in energy availability that accompanies it could increase older adults' ability to engage in cognitively demanding tasks. If older adults feel that they have an abundance of resources and that cognitive exertion even in difficult tasks will not deplete them, that might enable them to exert more effort in a task.

Additionally, as glucose has been shown to improve cognitive performance during both easy (Riby et al., 2004) and more difficult tasks (Macpherson et al., 2015), the glucose-related boost in cognition could further increase older adults' ability to engage with a cognitively demanding task by increasing their sense of self-efficacy and the probability of successfully completing the task. Researchers have also suggested that glucose administration can lead to significant improvements in mood (e.g., Benton &

Owens, 1993; but see van der Zwaluw, van de Rest, Kessels, & de Groot, 2014), an effect which could plausibly contribute to older adults' ability to perform a demanding task (the relationship between glucose and mood is discussed in detail in the following section). Therefore, it would be interesting to explore the effect of glucose availability on cognitive engagement, performance and affect in older adults. Is glucose one of the resources underlying cognitive engagement and, if so, would its consumption be accompanied by improved cognitive performance and higher positive or lower negative affect?

The possibility of glucose being able to not only improve performance but also increase older adults' ability to engage in cognitive tasks presents an exciting opportunity to further our understanding of the physiological underpinnings of older adults' cognitive engagement patterns. This would provide fruitful avenues for future research in exploring ways of enabling older adults to exert effort in tasks that might seem impossible to perform. In turn, this could have important implications for cognitive health and maintenance in old age. The idea of a connection between glucose availability, cognitive engagement and affect is further explored in Chapter 3.

Carbohydrates (CHOs) and mood

As mentioned in the previous section, it is possible that the facilitative effects of glucose could stem from (or be accompanied by) a general glucose-related mood-boosting effect. Considering that the purpose of this thesis is to explore the contribution of physiological processes to emotion-cognition interactions, understanding how increases in energy resources as a result of carbohydrate (CHO) administration affect emotionality is particularly important. Numerous studies have addressed the CHO-mood

relationship through studies of the neurobiological and behavioural consequences of CHO consumption. Surprisingly, whereas the effects of glucose on both young and older adults' cognitive performance are undisputed, results from studies investigating the relationship between CHO consumption and mood outcomes are not as clear.

The idea of CHO-mood interactions is based on early studies reporting a CHO-related increase in serotoninergic activity (Fernstrom & Wurtman, 1971), a neurotransmitter that has been consistently found to be implicated in the regulation of mood aspects such as depression, anxiety and anger/aggression (Chaouloff, Berton, & Mormède, 1999; Jenkins, Nguyen, Polglaze, & Bertrand, 2016; S. N. Young & Leyton, 2002). This effect has been attributed to an increase in tryptophan, the amino-acid precursor to serotonin. CHO consumption facilitates tryptophan influx in the brain by increasing the ratio of tryptophan-to-other-amino acids in the plasma, allowing tryptophan to overtake the blood brain barrier transport molecules and enter the brain more readily. Therefore, larger concentrations of tryptophan in the brain are able to increase serotonin synthesis (for a review, see Spring, Chiodo, & Bowen, 1987). As serotonin has been reliably shown to moderate mood, it has been argued that findings of increased tryptophan/serotoninergic activity following CHO consumption could also translate into significant improvements in mood. This hypothesis has motivated a large number of studies being conducted to assess the impact of CHO ingestion on different aspects of mood.

Indeed, CHO consumption has been found to be associated with positive mood outcomes. Studies have suggested that CHOs can decrease levels of fatigue after bouts of effortful cognitive processing (David Benton & Owens, 1993; Owens, Parker, &

Benton, 1997; Smit, Cotton, Hughes, & Rogers, 2004). Similar findings have been observed after periods of physical exercise performed at maximum effort (Ali, Moss, Yoo, Wilkinson, & Breier, 2017; Lieberman, Falco, & Slade, 2002; Welsh, Davis, Burke, & Williams, 2002) as well as following experimental procedures aimed at increasing levels of stress (e.g., cold pressor task; Markus, 2007). At the same time, CHO ingestion has been shown to increase arousal and alertness (Backhouse, Bishop, Biddle, & Williams, 2005; Owen, Scholey, Finnegan, Hu, & Sünram-Lea, 2012), lower tension (Benton & Owens, 1993) and confusion following performance on demanding physical tasks (Lieberman et al., 2002), and even induce a higher sense of calmness after performing a series of cognitive tasks (Owen et al., 2012), compared to an inert placebo. It is particularly interesting that most studies that have observed a facilitative effect of CHO administration ask participants to perform cognitively or physically demanding tasks prior to mood assessment. Therefore, researchers have argued that the mood facilitation effect of CHOs might be dependent on the difficulty of the task preceding the assessment of mood, similar to the glucose facilitation effect observed in the cognitive domain (for a review, see Benton, 2002).

On the other hand, an ever-growing number of studies have largely failed to replicate the findings discussed above. Reid and Hammersley (1995, 1998) have found trends of reduced levels of calmness as well as patterns of increased fatigue within the first hour post-CHO ingestion. Although trends of increased contentedness were identified across their two studies, these results were not significant. In a similar manner, other studies have found no effects of CHO consumption on alertness (Green, Taylor, Elliman, & Rhodes, 2001; Jones et al., 2012; Scholey et al., 2014; Sünram-Lea

et al., 2011), depression (Brody & Wolitzky, 1983; G. E. Giles et al., 2012; O'Neal, Poulos, Wingo, Richardson, & Bishop, 2013), levels of fatigue/tiredness (Miller, Bourrasseau, & Blampain, 2013; Scholey et al., 2014; Ullrich et al., 2015), and tension (Brody & Wolitzky, 1983; Markus, 2007; Scholey et al., 2014).

Of note, the vast majority of studies examining the relationship between CHOs and mood have been conducted with samples of young adults. One could expect that, similar to findings from studies investigating CHO effects on cognition (e.g., Macpherson et al., 2015), older adults' mood would potentially be more sensitive to CHO administration and manipulations of energy availability. However, the studies investigating this possibility have not found any aspects of older adults' mood to be positively affected by CHO ingestion (van der Zwaluw et al., 2014), and have even observed patterns of decreased arousal as a result of CHO ingestion in older individuals (Riby et al., 2004).

Reviewing these studies, it is apparent that no definitive conclusions can be drawn regarding the association between CHOs and mood outcomes. A number of reviews have been published over the years in an effort to understand the exact nature of CHO effects on mood, most of them suggesting that CHO-mood interactions are not particularly strong (for recent reviews, see Bernard, Lawton, & Dye, 2018; van de Rest, van der Zwaluw, & de Groot, 2017). Others have suggested that, when examining CHO-mood interactions, it is important to systematically assess and deconstruct the role of methodological differences in explaining the highly discrepant findings reported across different studies (see Benton, 2002). This is an important observation as studies investigating CHO-mood interactions follow vastly different methodological

approaches. For example, studies tend to use different types of CHOs (e.g., glucose, sucrose and fructose), doses (e.g., 25, 50, and 100 g), fasting intervals (e.g., no fasting, 2 hours or 12 hours) as well as a number of different cognitive and physical tasks before the assessment of mood. Furthermore, as the increase in serotonin synthesis has been found to occur beyond the first hour post-CHO ingestion (for a review, see Markus, 2008), researchers have suggested that the timeframe of CHO consumption and assessment should also be carefully considered. All these factors could plausibly affect how CHO effects on mood might emerge.

To that end, it is imperative to systematically examine all these factors and the influence they might have on CHO-mood interactions. It should be noted that although reviews attempt to bring together results from all available studies, the conclusions they reach are not necessarily reliable as they are based on observation rather than the implementation of statistical methods that would provide a quantifiable index of the true effect. Similarly, single experiments examining the influence of each potential moderator variable would be time-consuming and expensive given the complicated nature of the research question. However, the use of synthesis methods (i.e., meta-analysis) could provide robust statistical results that would allow us to evaluate the true nature of the CHO-mood relationship by grouping results from all available studies and systematically examining the effect of moderating variables. For a more in-depth discussion of how CHOs affect mood and a meta-analysis, see Chapter 5.

Summary

The purpose of this section was to provide an overview of the relationship between emotional ageing and different aspects of autonomic functionality. Overall, the

ability to express and regulate emotions is dependent on the functionality of the ANS. Recent advances in psychophysiological methodologies and assessment techniques have facilitated the assessment of ANS strength through simple measures of HRV. Studies assessing the association between HRV and emotion regulation have primarily focused on young adults and have found a strong relationship between the two. No research has assessed how ANS functionality relates to older adults' emotion regulation and, specifically, the age-related PE that is supposed to be an emotion regulation mechanism.

This review also focused on glycaemic regulation and energy availability, processes regulated by the ANS. Older age is associated with decrements in glucose regulation both centrally and in the periphery, higher rates of depletion and slower rates of replenishing, as well as higher insulin resistance compared to young adults, findings which are posited to contribute to the presence of cognitive decrements in typical ageing. Interestingly, glucose administration has been shown to improve cognitive performance in young and especially in older adults. The facilitation effects of glucose appear to be stronger for high cognitive load tasks, including dual-task paradigms that require participants to manage multiple task demands simultaneously. Although research has not found glucose to affect memory for emotional words in young adults, no research has been conducted to investigate the same question from an ageing perspective. As the PE is posited to be sensitive to cognitive demands and can disappear under high load conditions, glucose could potentially increase older adults' capacity to retain their PE when demands are high.

Additionally, this section examined the possibility that energy availability could be manipulated to not only improve cognitive functioning but to also increase older

adults' ability to exert effort in a cognitively demanding task. Researchers have found that older adults tend to disengage from a task when difficulty is high. This finding has been attributed to older adults having limited resources. These resources might represent a functional energy resource such as glucose, which could be limited because of the glucoregulatory decrements that accompany typical ageing. It is possible that glucose administration could increase cognitive engagement in older adults by providing more available resources to be used in a task while, at the same time, improving cognitive performance and mood through an increase in older adults' sense of self-efficacy.

The relationship between CHO ingestion (e.g., glucose) and mood has also been examined over the years yielding highly conflicting findings of both mood improvements and decrements following CHO administration. These discrepant results could be a result of methodological differences across studies. A systematic deconstruction of CHO-mood interactions using synthesis methods could provide a more reliable and robust index of the true nature of this relationship.

Thesis Overview

The overarching goal of this thesis is to investigate the mechanisms underlying emotion-cognition interactions in ageing. Specifically, the present work focused on assessing the role of ANS functionality as well as the influence of ANS-related physiological systems (e.g., glucose availability) in older adults' positivity preference, cognitive engagement patterns and overall mood. A convergent operations approach was employed combining the implementation of placebo-controlled, double-blind interventions (i.e., glucose administration), and the evaluation of behavioural outcomes and concomitant changes in physiological functioning. Additionally, synthesis methods

(i.e., meta-analysis) were used to deconstruct complicated concepts and controversial effects, namely the supposed relationship between CHO consumption and mood, to provide a deeper understanding of the physiological mechanisms supporting emotion-cognition interactions in young and older adults.

Chapter 2 examined the relationship between energy availability and the age-related PE. The purpose of this chapter is to test the theory that the age-related PE is dependent on cognitive control resources, and the idea that increasing such resources could protect older adults' PE even under high cognitive load conditions. Across two experiments, young and older adults were presented with word-lists consisting of positive, negative and neutral material, both high and low arousal, that participants had to memorise. At the end of each list, participants were asked to recall as many words as possible to assess the age-related PE. These word-lists were presented under both low- and high-load conditions (i.e., single and dual tasks, respectively) to assess whether the PE disappears when cognitive demands are exceedingly high. Prior to commencing these tasks, participants were provided with either a glucose or a placebo drink to investigate the possibility that energy resources would allow older adults to retain their PE despite having to perform a resource-demanding task. We predicted that glucose would provide older adults with the necessary resources to retain their PE even under high cognitive load conditions. The aim of this study was to provide further evidence for the exact role of cognitive control in older adults' PE, through the manipulation of resources that are known to influence cognitive control capacity.

Chapter 3 investigated ways of increasing older adults' cognitive engagement. Similar to Chapter 2, young and older adults ingested either a glucose or a placebo drink

and were asked to perform a memory search task of varied levels of difficulty. Cognitive engagement was assessed through changes in CV reactivity during task performance compared to an inactive rest period. The purpose of this study was also to assess age-related differences in the glucose facilitation effect. Would an increase in engagement be followed by improved cognitive performance and higher positive or lower negative affect? If so, would there be any differences in the way young and older adults use their available resources? Considering that older adults appear to be more sensitive to glucose manipulations and might need the extra energy boost even when a task is relatively easy, it was expected that glucose would increase cognitive engagement, cognitive performance and affect specifically in older, but not necessarily in young, adults. Therefore, the goal of this chapter was to examine the possibility that energy resources might be one of the factors underlying older adults' ability to exert effort in cognitively demanding tasks, and whether glucose can improve cognitive performance and affect.

Chapter 4 investigated the potential association between overall ANS functionality and older adults' PE. As ANS functionality is associated with emotion regulation capabilities, and the PE is posited to reflect an emotion regulation mechanism, we wanted to examine whether older adults' PE can be indexed by markers of ANS functionality. Young and older adults' levels of HRV were measured during rest and were used as an index of their ANS capacity. Following that, participants' gaze preferences for emotional versus neutral faces were assessed using an eye tracking paradigm, under both single and dual task conditions. At the end of each eye-tracking block, participants also completed affective judgment tasks to assess their levels of positive and negative affect. With studies suggesting that the PE and HRV are related to

emotion regulation, we wanted to examine whether older adults' PE and levels of ANS functionality are associated with affective outcomes. As the PE is a phenomenon found only in older adults, we predicted that HRV levels would predict gaze preferences specifically in older, but not necessarily in young, adults. It was also expected that the PE and HRV levels might be related to affect ratings, a finding which would offer further evidence for the role of the PE as an emotion regulation mechanism and the conceptualisation of HRV as an index of emotion-regulatory capacity.

Chapter 5 presents a systematic literature review and meta-analysis to elucidate the complex relationship between CHO administration and mood. The purpose of this chapter is to provide an in-depth review of studies investigating CHO-mood interactions, assess the methodological differences between studies reporting conflicting results, and use synthesis methods to group effect sizes from all available studies to assess the validity of claims of mood improvements/decrements following CHO administration. The highly discrepant findings reported across different studies make this research area a prime candidate for using meta-analytic techniques to investigate the true nature of CHO-mood interactions.

Chapter 6 presents an outline of the findings from each study included in the thesis. The implications of the results are discussed as well as the limitations associated with each study. Finally, proposals for future research are also discussed.

Chapter 2: Food for Happy Thought: Glucose Protects Age-Related Positivity Effects Under Cognitive Load

Abstract

Older adults show a preference for positive information, which disappears under high task demands. We examined whether glucose can help older adults preserve their positivity effect (PE) under high cognitive load. One hundred and twenty-two adults (40 young and 42 older in Experiment 1a; 40 older in Experiment 1b) consumed a glucose (25 g) or a taste-matched placebo drink and completed an immediate recall task of emotional word-lists presented under high- and low-load conditions. Older adults showed PEs for low-load lists. Whereas PEs disappeared for older-placebo participants for high-load lists, older-glucose participants retained their positive preference. Providing the brain with extra energy resources can help older adults achieve PEs even under demanding conditions.

Experiment 1a

Introduction

Despite the physiological and neuroanatomical degradations that accompany ageing (Salthouse, 2010), emotional well-being remains impervious to age-related decrements, with older adults appearing to be well-adjusted and emotionally resilient throughout the ageing process (e.g., Carstensen et al., 2000). According to the SST (Carstensen, 1995), as people grow older they experience a motivational shift, favouring emotional stability and positive experiences over ‘expansive’ goals relating to wealth or

social status (Carstensen et al., 1999). This preference extends to a range of cognitive domains and emerges as a cognitive bias towards the processing of positive over negative information in memory and attention, a phenomenon called the PE (for a meta-analysis, see Reed et al., 2014).

The 'cognitive control' extension of the SST (Mather & Carstensen, 2005) posits that PEs are a result of top-down processes employed by older adults in order to downregulate negative affect. Compared with young adults, older individuals show increased functional connectivity between the amygdala and the PFC and a decrease in amygdala-hippocampal coupling during the encoding and retrieval of negative versus neutral information (Murty et al., 2009). It has been suggested that the age-related differences in the recruitment of frontal brain areas during exposure to negative stimuli indicate an emotion regulation attempt (an assumption for which there is as yet only limited evidence; see Isaacowitz & Blanchard-Fields, 2012), with the PFC being employed to minimise amygdala activation and dampen responses to negative stimuli (St. Jacques et al., 2009). The downregulation of negative affect appears to be more successful for material requiring elaborate processing (i.e., low-arousal stimuli; Dolcos et al., 2014; Kensinger, 2008) than for high-arousal stimuli, which are thought to be processed in a more automatic fashion (Kensinger, 2004). Neuroimaging and behavioural studies have shown that the amygdala's activation patterns in response to high-arousal material remain relatively intact throughout ageing, suggesting that the PFC cannot suppress strong activations triggered by highly aversive stimuli (Leclerc & Kensinger, 2008; Mather & Knight, 2006). Interestingly, although the amygdala does not seem to be particularly sensitive to age-related structural and functional degradations

(for a review, see Mather, 2016), ageing is accompanied by a shift in the valence to which the amygdala is more responsive. Specifically, whereas the amygdala of young adults is more responsive to negative information, the reverse is true for older adults, who exhibit stronger amygdala activation when presented with positive compared with negative stimuli (Kehoe et al., 2013; Mather et al., 2004).

If PEs do indeed depend on cognitive control (a finding challenged by some studies; see Allard & Isaacowitz, 2008; Petrican, Moscovitch, & Schimmack, 2008), then this poses constraints on the circumstances under which the phenomenon emerges. Increasing cognitive load by introducing a cognitively demanding secondary task during encoding of emotional words (Mather & Knight, 2005) or during a visual attention task with emotional material (Knight et al., 2007) attenuates or even reverses PEs (i.e., negativity bias). In situations where high task demands limit the availability of cognitive resources, the PFC can no longer suppress the encoding of negative stimuli which gain an advantage due to their affective salience (Baumeister et al., 2001). It should be noted that the mere introduction of a divided attention task is not always sufficient to hinder the age-related positivity preference (e.g., Allard & Isaacowitz, 2008). The secondary task must place considerable strain on cognitive control resources to successfully diminish the PE in older adults (e.g., Knight et al., 2007; Mather & Knight, 2005). In view of the evidence for the role of cognitive control in the emergence of PEs, an interesting question arises: If PEs are dependent on cognitive resources, could increasing the availability of these resources help older adults retain their preference for positive material when cognitive demands are high?

A number of studies have demonstrated that orally administered glucose can lead to significant improvement in cognitive processes in both young and older adults (for a review, see Riby, 2004). In young adults, glucose is thought to primarily target the hippocampus, leading to a facilitation of memory processes (for reviews, see Hoyland et al., 2008; Messier, 2004). The beneficial effects of glucose administration have been shown to be particularly sensitive to task difficulty (D. O. Kennedy & Scholey, 2000; Scholey et al., 2001). Specifically, the magnitude of cognitive improvement seems to be proportional to the amount of effort that the task requires, with the facilitation being more reliable under high than low cognitive load (Scholey et al., 2009; Sünram-Lea et al., 2002a). Consistent with findings from young adults, glucose has been shown to enhance memory processes in older adults (Riby et al., 2006; Riby et al., 2004). In addition to memory improvement, recent studies have also found that glucose administration in older adults can improve attention and minimise the cognitive cost associated with task-switching – a cost arising from participants' difficulty in effectively splitting available cognitive resources between two tasks (Gagnon et al., 2010; Macpherson et al., 2015). Similarly to young adults, this facilitation effect is only observed when processing load is high (i.e., dual-task conditions). According to these studies, glucose can equip older adults with the necessary metabolic and cognitive resources to successfully coordinate different cognitive strategies and manage the processing demands of a challenging dual task (Gagnon et al., 2010). Although it is difficult to pinpoint the cognitive domain benefiting the most from moderate increases in blood glucose levels, it is possible that, under high cognitive load, glucose administration has the potential to enhance both hippocampal- (memory) and PFC-

mediated (attentional) processes in older adults (Donohoe & Benton, 1999). Irrespective of whether glucose effects are domain-specific or context-dependent, task difficulty appears to be an important determinant of the glucose facilitation effect, with the cognitive enhancement being more robust when cognitive demands are high and attentional resources are split across a number of tasks (for reviews, see Messier, 2004; M. A. Smith et al., 2011).

With the recent controversy surrounding the glucose model of ego depletion (for a review, see Vadillo, Gold, & Osman, 2016), it is important to distinguish between the self-control tasks used in the ego depletion line of research and dual-task paradigms. Whereas studies investigating self-control have adopted a sequential task presentation (i.e., two single tasks presented in succession; see Gailliot et al., 2007), dual-task experiments require participants to perform two cognitively demanding tasks concurrently. Thus, successful performance in dual-task paradigms is more cognitively demanding (e.g., requiring more complex attentional or strategic processes; Pashler, 1994) than self-control tasks, which allow participants to direct all available resources towards a single task. If glucose effects are mostly evident for tasks that tap into multiple cognitive functions simultaneously (Scholey et al., 2013), ego depletion should be unaffected by glucose administration (e.g., Carter, Kofler, Forster, & McCullough, 2015), whereas dual-task performance should show a systematic modulation.

Considering the role of cognitive control in PEs, the idea of attentional resources being sensitive to manipulations in glucose availability can be of particular interest when examining failures in retaining the positivity preference under high cognitive demands. To date, the effects of glucose on emotional memory have been examined

only in young adults, where no selective glucose facilitation of either positive or negative material under single- (Brandt et al., 2006) or dual-task conditions (Brandt et al., 2010) has been observed. Surprisingly, no studies have addressed the same question from an ageing perspective. In view of findings suggesting that the age-related PEs disappear under high cognitive load and that glucose can improve attentional resources in the presence of a demanding secondary task, our goal was to investigate whether glucose administration prior to a difficult task would allow older adults to preserve their preference for positive material.

In the present study, we asked young and older adults to memorise emotionally valenced words (both high- and low-arousal) under high versus low cognitive load conditions. Half of the participants in each age group were given a glucose drink, and half a placebo drink. Young adults were expected to show a preference for negative material regardless of drink or cognitive load. Older adults were expected to show PEs (irrespective of drink), under low-load conditions. Our central prediction was that under high-load conditions, older adults in the placebo group would exhibit a negativity bias, whereas older adults in the glucose group would retain their PEs. Furthermore, as previous research has indicated that PEs are more evident for material that is low in arousal (e.g., Kensinger, 2008), we expected PEs to emerge for low- rather than high-arousal stimuli.

Method

Design and Drinks. A between-subjects 2 (Age: young, older) × 2 (Drink: glucose, placebo) randomised, placebo-controlled design was employed. Participants were randomly assigned to ingest a drink containing either 25 g of glucose or an

artificial sweetener (five aspartame tablets), dissolved in 300 ml of water. To improve palatability, 25 ml of sugar-free orange cordial was added to both drinks. Past research has identified a 25-g glucose dose to be effective for cognitive facilitation in young and older populations (Parsons & Gold, 1992; Sünram-Lea et al., 2011).

Participants. A total of 41 young adults (age range 18-30) and 44 community-dwelling older adults (age range 65-82) with no recent history of neurological, psychiatric, or endocrine disorders participated in the study. Sample size was based on past research showing that for glucose intervention studies in ageing, a total of 20-25 participants per experimental group is sufficient to identify potential glucose effects on cognition (e.g., Gagnon et al., 2010; Macpherson et al., 2015). Young adults received course credits as part of their course requirements. Older adults received £10 for their participation. One young adult was excluded from the sample for not being familiar with the words presented, and two older adults were excluded for failing to perform the secondary task, resulting in a final sample of 40 young and 42 older adults (see Table 1 for characteristics). Participants completed the Digit Symbol Substitution task (DSST; Wechsler, 1981) and the Mill Hill vocabulary test (MHVT; Raven, Raven, & Court, 1988) to assess processing speed and crystallised intelligence, respectively. Young adults had higher processing speed scores, $t(80) = 4.70$, $p < .001$, but lower performance on the vocabulary test, $t(80) = -10.66$, $p < .001$, and fewer years of full-time education, $t(80) = -5.86$, $p < .001$, compared with older adults. No differences in age or in DSST and MHVT scores were identified between participants assigned to glucose and placebo within each age group (all ps > .24). The only significant intergroup difference was that young glucose adults had a few months more formal education than their placebo

counterparts, $t(38) = 3.38$, $p = .002$. The study was approved by the Psychology Department's Research Ethics Committee at the University of Warwick. Written consent was obtained from all participants prior to beginning the study.

Table 1

Characteristics of the Sample and Performance on the Secondary Task as a Function of Age and Drink in Experiment 1a

	Experiment 1a			
	Young		Older	
Measure	Glucose	Placebo	Glucose	Placebo
Characteristics				
N (M/F)[1]	20 (2/18)	20 (2/18)	21 (9/12)	21 (9/12)
Age	19.50 (2.54)	18.80 (0.77)	72.19 (3.43)	71.38 (4.78)
Years of education	14.20 (0.41)	13.60 (0.68)	16.62 (2.80)	17.00 (3.39)
Speed[2]	69.55 (9.12)	66.55 (11.36)	57.67 (14.26)	54.43 (10.91)
Vocabulary[3]	16.35 (2.46)	15.40 (2.95)	23.52 (3.01)	23.71 (4.44)
Secondary task				
Reaction time[4]	732.91 (93.71)	735.80 (92.50)	729.77 (90.90)	772.54 (79.34)
Accuracy[5]	83.52 (12.51)	83.29 (10.45)	90.58 (7.99)	87.88 (10.45)

Note. All values except for *N* (M/F) are given as means (with standard deviations).

[1]Number of participants in each age and drink group (male/female). [2]Processing speed as measured by the DSST (Wechsler, 1981). [3]Vocabulary score as measured by the multiple-choice section of the MHVT out of a maximum of 33 (Raven et al., 1988). [4]Reaction time in milliseconds. [5]Percentage accuracy calculated as 100 × ((Number of correct hits ÷ Number of 1-back matches) – (Number of false alarms ÷ Number of non-matches)).

Cognitive tasks. Participants were presented with four 25-word lists, each with 10 positive (valence ratings: 6-9), 10 negative (1-3.99) and five neutral (4-5.99) words. In each list, five positive and five negative words were low arousal (arousal ratings: 1-4.99), and the remaining five from each valence category were high arousal (5-9). All neutral words were low arousal. Valence and arousal ratings were obtained from

Warriner, Kuperman, and Brysbaert (2013). Two buffer words were added at the beginning and two at the end of each list. Words were presented on a 15.6-inch laptop screen for 3 s, with a 1-s interstimulus interval. They appeared in black lowercase letters on a white background, with a letter height of approximately 3.4^{o} at a 60-cm viewing distance. Word-lists were matched for frequency (Coltheart, 1981), imagery (Cortese & Fugett, 2004; Schock, Cortese, & Khanna, 2012) and concreteness (Brysbaert, Warriner, & Kuperman, 2014). The lists contained one- and two-syllable words with no more than two words from the same valence category being presented consecutively (see Appendix A for word lists). Two of the lists were presented under low cognitive load and two under high cognitive load conditions. The allocation of the lists to the conditions was randomised (each list was used under low-load conditions as often as under high-load conditions) and the condition order was counterbalanced. Memory performance was measured with an immediate free recall task at the end of each list.

During the encoding of the high-load word-lists, participants were asked to simultaneously perform an auditory 1-back task. A sequence of single-digit numbers was presented through headphones, with each number played for 1 s followed by an interstimulus interval of 1 s. Participants had to press a key each time the number they heard matched the one that immediately preceded it. Before the presentation of the lists, participants were reminded that they should pay equal attention to the two tasks and not prioritise one over the other. Numbers were presented in a pseudorandom order to ensure that the possibility of a 1-back match occurring during the presentation of positive or negative words was equal. Participants' RTs and accuracy were measured.

Procedure. Participants were asked to refrain from any food and drink for two hours before the testing session. Those who did not abide by that condition (n = 1) were asked to reschedule their visit. Participants consumed a glucose or placebo drink and completed a short practice block consisting of one low- and one high-load list (eight words each, not presented in the actual experiment) to familiarise themselves with the tasks. After a 10-minute waiting period, participants were presented with two low-load followed by two high-load lists, or vice-versa. At the end of each list, they were asked to verbally recall the words. Next, participants provided demographic information and completed the DSST. Then ten minutes from the end of the last recall task, participants completed a delayed recall task of all the words; performance was very poor, hence results from delayed recall are not reported here. Finally, participants completed the MHVT, after which they were debriefed and compensated for their participation.

Results

Word recall. A five-way mixed analysis of variance (ANOVA) was performed on words correctly recalled, with age (young, older) and drink (glucose, placebo) as between-subjects factors, and valence (negative, positive), load (low, high) and arousal (low, high) as within-subjects factors. As there was no main effect or interaction involving arousal (all Fs < 2.31, all ps > .1), Figure 1 displays the number of correctly recalled words collapsed across this factor. Young adults recalled more words than did older adults, $F(1, 78) = 60.50$, $p < .001$, $\eta_p^2 = .437$. Recall was greater with glucose than with placebo, $F(1, 78) = 6.92$, $p = .010$, $\eta_p^2 = .081$, and greater under low-load than high-load conditions, $F(1, 78) = 83.66$, $p < .001$, $\eta_p^2 = .518$. There were two significant two-way interactions: Drink × Valence, $F(1, 78) = 4.72$, $p = .033$, $\eta_p^2 = .057$, and

Valence × Load, $F(1, 78) = 4.31$, $p = .041$, $\eta_p^2 = .052$, and a marginal Age × Valence interaction, $F(1, 78) = 3.90$, $p = .052$, $\eta_p^2 = .048$. There were two three-way interactions: Age × Drink × Valence, $F(1, 78) = 5.73$ $p = .019$, $\eta_p^2 = .068$, and Age × Drink × Load, $F(1, 78) = 4.79$, $p = .032$, $\eta_p^2 = .058$.

These interactions were qualified by a four-way interaction between age, drink, valence and load, $F(1, 78) = 4.87$, $p = .030$, $\eta_p^2 = .059$ (see Figure 1). To determine the source of the interaction we conducted two additional three-way mixed ANOVAs with drink, valence and load as factors, one for each age group. Follow-up *t*-tests were used to further examine significant effects. Unsurprisingly, both age groups performed better in the low-load than in the high-load condition (both Fs > 29.28, both ps < .001). Young adults performed better with glucose than with placebo, $F(1, 38) = 7.05$, $p = .012$, $\eta_p^2 = .156$, and this benefit was larger for the high-load than for the low-load lists, $F(1, 38) = 6.55$, $p = .015$, $\eta_p^2 = .147$. Furthermore, young adults showed a preference for negative over positive words, $F(1, 38) = 4.31$, $p = .045$, $\eta_p^2 = .102$, which was not modulated by drink or load (both Fs < 1). In contrast, older adults showed no main effects of either drink or valence (both Fs < 1). However, two two-way interactions were identified: Drink × Valence, $F(1, 40) = 13.95$, $p = .001$, $\eta_p^2 = .259$, and Valence × Load, $F(1, 40) = 7.73$, $p = .008$, $\eta_p^2 = .162$, which were qualified by a three-way interaction between drink, valence and load, $F(1, 40) = 6.29$, $p = .016$, $\eta_p^2 = .136$. Under low-load conditions, older adults showed an overall preference for positive over negative material, $t(41) = 2.33$, $p = .025$. Whereas under high-load conditions, older adults in the placebo group produced a substantial negativity bias, $t(20) = 4.66$, $p < .001$, older adults in the glucose group produced a PE that despite being only marginally significant, $t(20)$

= 1.94, $p = .067$, was indistinguishable from the PE produced under low-load conditions, $t < 1$. No other effects in the two ANOVAs were significant (all other Fs < 1).

Secondary task performance. Two two-way ANOVAs with age and drink as between-subjects factors were conducted on mean correct RTs and accuracy (see Table 1 for means). For RTs, there were no significant effects (all Fs < 1.35, all ps > .25). Older adults were significantly more accurate on the secondary task than were young adults, $F(1, 78) = 6.36$, $p = .014$, $\eta_p^2 = .075$, but there was no effect of drink on accuracy or any interaction between age and drink (both Fs < 1).

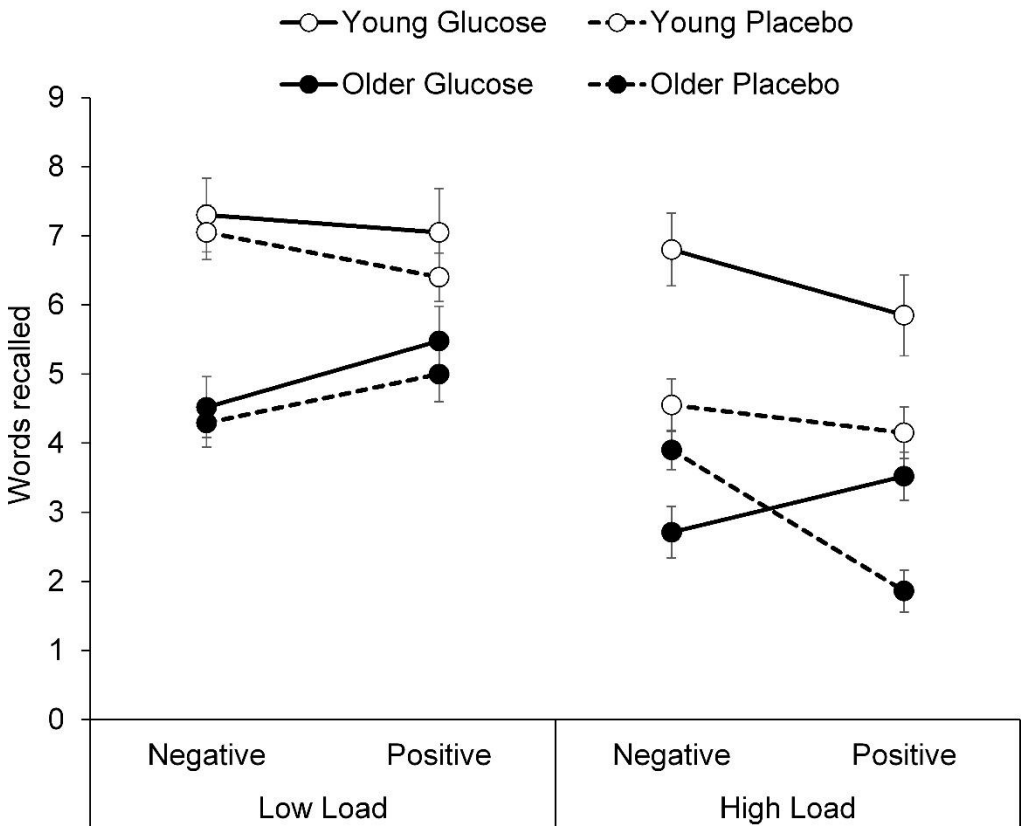

Figure 1. Mean number of words recalled out of 20 (± standard error of mean) as a function of drink (glucose/placebo), valence (negative/positive) and load (low/high) for young and older adults in Experiment 1a.

Experiment 1b

Replication Rationale

Although the results of Experiment 1a were in line with our central prediction (i.e., under high-load conditions, the older placebo group showed a negativity bias, whereas the older glucose group retained their PE), they might have been affected by two factors unrelated to our hypothesis: 1) the experimenter was aware of the experimental conditions (glucose/placebo), and thus might have subconsciously influenced participants during recall, and 2) the palatability of the two drinks, which potentially might bias recall of positive versus negative words, was not assessed.

Therefore, we conducted a replication (Experiment 1b) with a new sample of older adults only, to establish the reproducibility of the new findings, and to rule out these two potential confounding factors.

Table 2

Characteristics of Older Adults and Performance on the Secondary Task as a Function of Drink in Experiment 1b

	Experiment 1b	
	Older	
Measure	Glucose	Placebo
Characteristics		
N (M/F)[1]	20 (8/12)	20 (7/13)
Age	73.05 (3.83)	72.90 (3.84)
Years of education	16.40 (3.27)	15.90 (2.32)
Speed[2]	53.35 (10.49)	54.45 (11.25)
Vocabulary[3]	25.05 (3.40)	24.20 (4.15)
Secondary task		
Reaction time[4]	780.47 (119.92)	764.10 (100.7)
Accuracy[5]	87.86 (13.07)	87.62 (9.26)

Note. All values except for *N* (M/F) are given as means (with standard deviations).

[1]Number of participants in each age and drink group (male/female). [2]Processing speed as measured by the DSST (Wechsler, 1981). [3]Vocabulary score as measured by the multiple-choice section of the MHVT out of a maximum of 33 (Raven et al., 1988). [4]Reaction time in milliseconds. [5]Percentage accuracy calculated as 100 × ((Number of correct hits ÷ Number of 1-back matches) – (Number of false alarms ÷ Number of non-matches)).

Method

We recruited 40 older adults aged 65-79 who had not taken part in Experiment 1a (see Table 2 for characteristics; one additional participant was excluded from the sample for failing to perform the secondary task). As before, the glucose and placebo groups were well matched in terms of background characteristics. The stimulus material was identical to Experiment 1a. The procedure was also identical except that a) the drinks were prepared by assistants, keeping the experimenter blind to the experimental conditions, b) at the end of the experiment, participants were asked to rate how much they enjoyed the drink on a scale ranging from 1 ('not at all') to 10 ('very much'), and c) the delayed recall task was omitted as recall was so low. The number of correctly recalled words was analysed using a three-way mixed ANOVA with drink (glucose, placebo) as the between-subjects factor, and valence (negative, positive) and load (low, high) as within-subjects factors, and follow-up analyses were conducted using *t*-tests.

Results

The pattern of results closely resembled that obtained in Experiment 1a (see Figure 2). Recall was greater under low load than under high load, $F(1, 38) = 66.91$, $p < .001$, $\eta_p^2 = .638$, and greater for positive than for negative words, $F(1, 38) = 10.01$, $p = .003$, $\eta_p^2 = .209$. These two factors interacted, $F(1, 38) = 25.04$, $p < .001$, $\eta_p^2 = .397$, as the overall positivity bias under the low-load condition disappeared under the high-load condition, $t(39) = 6.07$, $p < .001$, and $t(39) = -1.48$, $p = .147$, respectively. There was no main effect of drink, $F < 1$, but there was a significant Drink × Valence interaction, $F(1, 38) = 22.19$, $p < .001$, $\eta_p^2 = .369$, further qualified by a marginal interaction between drink, valence and load, $F(1, 38) = 4.05$, $p = .051$, $\eta_p^2 = .096$. Whereas in the placebo

group older adults' PE turned into a significant negativity bias under high cognitive load, $t(19) = -3.99$, $p < .001$, participants in the glucose group managed to retain a preference for positive words, $t(19) = 1.99$, $p = .030$ (one-tailed), even though this preference was smaller than in the low-load condition, $t(19) = 2.17$, $p = .043$.

Type of drink did not affect RTs or accuracy in the secondary task (both Fs < 1, both ps > .643). Finally, taste ratings for glucose ($M = 4.85$, $SD = 1.04$) and placebo ($M = 4.70$, $SD = 1.42$) drinks did not differ, $t < 1$, $p = .705$. Taken together, the results suggest that the modulation of older adults' memory performance observed in Experiment 1a is a genuine effect of glucose, rather than an artefact of unconscious experimenter bias or differences in palatability between glucose and placebo drinks.

It has to be noted, though, that although glucose significantly altered older adults' recall preference under high cognitive load (Drink x Valence for older adults under high load: $F(1, 40) = 22.24$, $p < .001$, $\eta_p^2 = .357$, in Experiment 1a; $F(1, 38) = 18.87$, $p < .001$, $\eta_p^2 = .332$, in Experiment 1b), the positivity preference it produced was only marginally significant ($p = .067$ in Experiment 1a; $p = .061$, in Experiment 1b). However, when the older adult data from the two experiments were pooled to increase statistical power, the glucose group's ($N = 41$) PE under high cognitive load became highly significant, $t(40) = 2.80$, $p = .008$, and was statistically indistinguishable from the PE found under low cognitive load, $t(40) = 1.49$, $p = .145$.

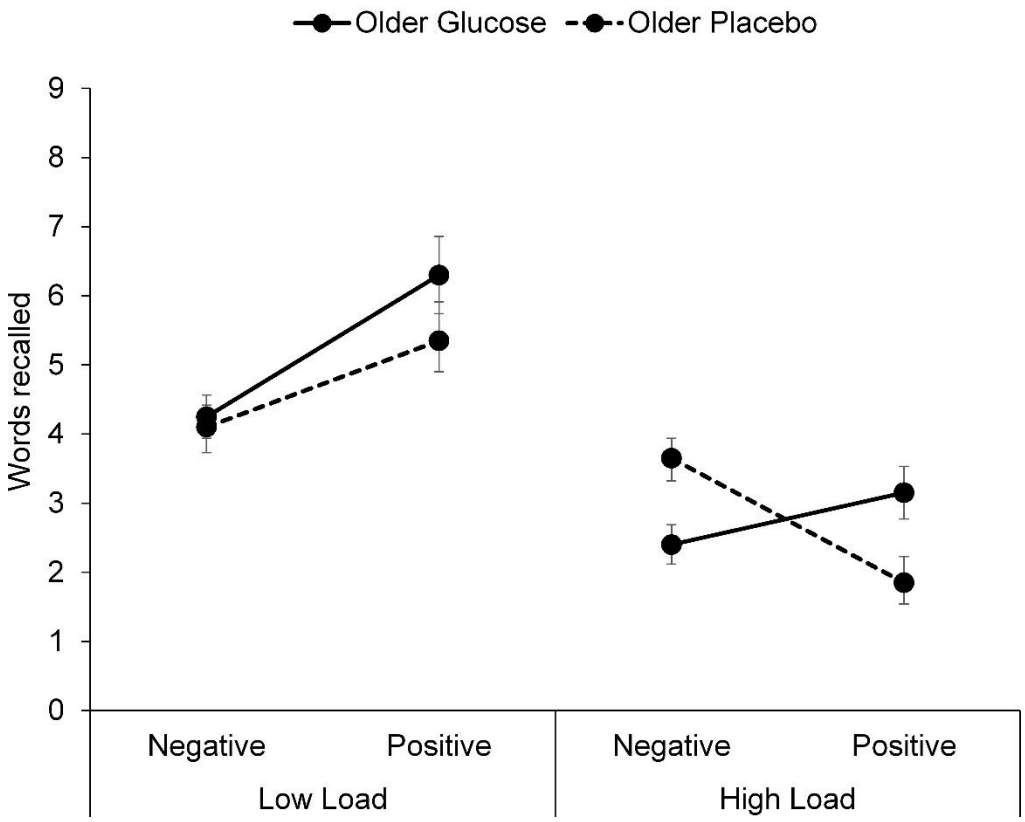

Figure 2. Mean number of words recalled out of 20 (± standard error of mean) as a function of drink (glucose/placebo), valence (negative/positive) and load (low/high) for older adults in Experiment 1b.

Discussion

The aim of this study was to examine whether glucose administration can preserve older adults' PEs when cognitive demands are high. In Experiment 1a, we gave young and older participants 25 g of glucose or a placebo drink and compared their performance on an immediate recall task of emotional word-lists presented under low- and high-load conditions. As predicted, young adults showed a preference for negative over positive words throughout the experiment, irrespective of drink or load condition. Glucose facilitation manifested in this group as generally improved memory for high-

load lists, replicating previous studies showing that glucose facilitation is more reliable when task demands are high (Scholey et al., 2009; Sünram-Lea et al., 2002a). Similarly consistent with previous research (e.g., Brandt et al., 2010, 2006) was the finding that in young adults, glucose facilitated recall irrespective of word valence.

In line with studies describing an age-related advantage for positive material (see Reed et al., 2014), our data showed PEs in the low-load condition, with older adults remembering more positive words when attention was focused solely on the encoding of word-lists. Although some studies have identified PEs mainly for low-arousal stimuli (e.g., Kensinger, 2008), the positivity bias in our experiments did not arise specifically for material low in arousal as initially predicted. Consistent with previous findings indicating that PEs can be observed across high- and low-arousal material (e.g., Mather & Knight, 2005), our results support the possibility that the strength of the positivity phenomenon is not always modulated by arousal conditions. It should be noted that, with the exception of a few studies (e.g., Dolcos et al., 2014; Kensinger, 2008), the role of arousal in PEs has not been systematically examined to date. The importance of arousal intensity has been highlighted by studies showing that memorability for emotional information (and by extension the PE) might be an arousal-driven phenomenon (e.g., Grühn & Scheibe, 2008). Further investigations into the role of arousal might offer interesting insights regarding the parameters influencing the emergence of the positivity preference in ageing.

In both experiments, as hypothesised, PEs turned into a negativity bias for dual-task lists in older adults administered a placebo. When cognitive load was increased, the preference for positive material was eliminated and negative words were prioritised,

possibly due to the inability of the PFC to suppress activity triggered by negative information while managing multiple task demands. The novel finding of our study is that when given a glucose drink, older adults managed to retain their preference for positive material despite the presence of a demanding secondary task. In Experiment 1a, although glucose had to counteract a strong negativity bias – as observed in the older-placebo group – participants in the older-glucose group produced PEs that not only approached statistical significance, but were indistinguishable from those produced under low-load conditions. Experiment 1b succeeded in replicating the negativity reversal in the older-glucose group but, on this occasion, glucose was not able to completely reinstate the positivity preference found under low-load conditions. Interestingly, when we pooled the data from the two experiments, the PE for the older-glucose group became significant even under high task demands. Furthermore, the results mirrored those of Experiment 1a, with the older-glucose group producing a PE of similar magnitude under both low and high cognitive load.

We speculate that even though there was no behavioural enhancement in the traditional view of improved memory (e.g., Riby et al., 2006) or shorter RTs (e.g., Gagnon et al., 2010), the ability of the older-glucose group to preserve the positivity preference under high cognitive load could reflect a glucose-related improvement of PFC-mediated processes and, specifically, an increase of available cognitive resources (e.g., Gagnon et al., 2010; Macpherson et al., 2015). This would, theoretically, allow the PFC to effectively control both task demands, while simultaneously minimising the potential affective impact of negative information. It is important to note that the older group used this attentional advantage not to outperform the placebo group but to retain

their positive preference. In contrast to the widespread memory facilitation of glucose that was observed in young adults under cognitive load, older adults exhibited a more valence-specific glucose enhancement by remembering more positive words compared with the placebo group. Consistent with the idea that this preference for positive information can be a strong moderator of memory and attention processes in older adults' cognition (see Reed et al., 2014), it seems plausible that the positivity-related glucose facilitation effects were driven by older adults' priority to selectively remember more positive than negative information. Our findings seem to be in line with the cognitive control model of PEs showing the relevance of the availability of cognitive resources in the emergence of the phenomenon (Mather & Carstensen, 2005).

In summary, our results provide evidence to support the role of cognitive control as a potential moderator of PEs. If the necessary resources are available, older adults are more likely to recruit them to achieve goals that are consistent with their intrinsic motivation to prioritise positive material, rather than enhancing their overall cognitive performance. Furthermore, our findings can offer interesting insights into how older adults approach/avoid difficult situations. Lifestyle changes are imperative for maintaining good health. However, older adults' resistance to novelty (e.g., Fung et al., 1999) means that initiating such changes requires effortful behavioural strategies. Considering that exerting effort can be inherently aversive (see Kurzban, 2016), failing to implement changes could be attributed to older adults' motivation to avoid unpleasant emotions. Glucose prior to a difficult task could potentially enable ageing individuals to focus on the positive aspect of behavioural change (gains over costs), facilitating the transition to healthier lifestyles. If there is indeed a connection between emotionality

and glucoregulation in ageing, it would be interesting to explore whether motivation is driving the allocation of energy resources toward tasks that are more closely aligned with older adults' positivity preference.

Chapter 3: Gain Without Pain: Glucose Promotes Cognitive Engagement and Protects Positive Affect in Older Adults

Abstract

When faced with a cognitively demanding task, older adults tend to disengage and withdraw effort. At the same time, their usual processing preference for positive information disappears. Providing glucose as an energy resource is known to improve cognitive performance and reinstate older adults' positivity preference. Here, we examined whether glucose can help older adults to exert more effort under high difficulty conditions, and if so, whether such increase is accompanied by a change in positive affect. Fifty-three young and 58 older adults consumed a glucose or a placebo drink and completed a memory-search task at three levels of difficulty. Cognitive engagement was measured through changes in heart rate (HR) and self-reported effort. After each memory-search block, participants completed an implicit emotion-assessment task. In both age groups, glucose produced increased HR (indicating higher task engagement) relative to placebo. In older but not in young adults, glucose also improved cognitive performance and increased positive affect. Subjective effort, in contrast, did not differ between the older-glucose and older-placebo groups. These results suggest that in older adults, glucose improves cognitive performance by promoting higher cognitive engagement while mitigating the subjective costs of effortful exertion.

Experiment 2

Introduction

The ability to initiate effortful behavioural strategies and persist even when success seems unlikely is a fundamental human attribute that has been linked to positive health and social outcomes, especially in ageing (Rowe & Kahn, 1997). Recent evidence suggests that cognitive engagement and participation in intellectually stimulating activities contribute to the maintenance of cognitive skills and the attenuation of age-related cognitive decline (for a review, see Hertzog et al., 2008). However, the neuroanatomical and cognitive changes that occur naturally in the course of healthy ageing (for reviews, see Antonenko & Flöel, 2014; Rossini, Rossi, Babiloni, & Polich, 2007; Salthouse, 2010) pose constraints on older adults' ability to maintain complex cognitive strategies and high levels of task engagement during cognitive exertion. Such age-related processing decrements make cognitive exertion more difficult for older adults (Hess & Ennis, 2012), as evidenced by the sharp decline in older adults' chances of success in high difficulty tasks compared with their young counterparts (for a review, see Drag & Bieliauskas, 2010).

This pattern is observed not only in behavioural but also in physiological indices. Actively engaging in demanding cognitive tasks mobilises the SNS (Wright, 1996) and increases the activity of peripheral physiological mechanisms linked to myocardial sympathetic function (Richter, Friedrich, & Gendolla, 2008). Therefore, CV indices such as HR and systolic blood pressure responsivity during cognitive performance might reflect objective measures of cognitive engagement (for a review, see Richter et al.,

2016).[1] Recent studies measuring young and older adults' CV changes in response to cognitive tasks of increasing difficulty found age-related differences in the effect of task demands on physiological reactivity. In both young and older adults, CV reactivity increases strongly in relatively easy tasks where success seems attainable and within the participants' control, but it increases substantially less in tasks that surpass their cognitive capabilities (i.e., participants exerting submaximal cognitive effort). However, this relative reduction in the increase of CV responsivity during difficult cognitive tasks is more pronounced in old age, suggesting that the threshold for reducing one's task engagement is lower in older than in young adults (Ennis et al., 2013; Hess et al., 2016).

Such lower threshold might reflect an adaptive mechanism aimed at safeguarding energy resources available for cognitive processing (Hess, 2014). The physiological underpinnings of energy availability and utilisation can be traced back to the regulation of glucose, the main energy fuel subserving all biological functions. Supporting the notion that cognitive effort is glucose dependent, moderate increases in peripherally circulating blood glucose have been shown to facilitate cognitive performance (for reviews, see Messier, 2004; Riby, 2004; M. A. Smith et al., 2011), particularly in more demanding tasks (Gagnon et al., 2010; Macpherson et al., 2015; Scholey et al., 2013, 2009; Sünram-Lea et al., 2002a). With increasing age, the efficiency of glucoregulation deteriorates: typical ageing is accompanied by impaired peripheral and cerebral glucose

[1]Although heart rate is considered a less sensitive measure of cognitive engagement compared with systolic blood pressure because its function is modulated both by the sympathetic and the parasympathetic branch of the autonomic nervous system, it has been found to follow similar, albeit weaker, patterns to those observed for systolic blood pressure (e.g., Ennis et al., 2013).

metabolism (Biessels, Bravenboer, & Gispen, 2004; Blesa et al., 1997; Kuhl et al., 1984; Messier & Gagnon, 1996), reduced insulin sensitivity (Chang & Halter, 2003; Melanson et al., 1998), and higher glucose depletion and slower replenishing rates following performance on cognitively challenging tasks (Gold, 2005). Given such inherent age-related difficulties in the mobilisation and restoration of energy resources, it is perhaps not surprising that older adults would be more cautious than young adults about spending energy on activities that would compromise the availability of these valuable resources. If a task requires high energy expenditure but promises little benefit (i.e., costs outweighing potential gains), it makes intuitive sense that older adults would show a more pronounced effort withdrawal than their young counterparts, as evidenced by the steeper reduction of CV responsivity with increased task difficulty in ageing (Ennis et al., 2013; Hess et al., 2016). In view of evidence suggesting that older adults often benefit more from glucose administration than young adults, whose glucoregulatory mechanisms are usually intact and who do not necessarily require external glucose administration to perform at the peak of their cognitive skills (e.g., Hall et al., 1989; Macpherson et al., 2015; Manning et al., 1997), it is likely that older adults' cognitive engagement patterns are modulated by glucose availability.

Although a facilitative effect of glucose on older adults' cognition has been observed in previous studies, recent evidence suggests that glucose does not necessarily lead to improved cognitive performance but can be used by older adults to prioritise other aspects of their performance. For instance, glucose ingestion makes older adults more likely to prioritise positive over negative information (PE; see Mather & Carstensen, 2005; Scheibe & Carstensen, 2010), whereas young adults use it to optimise

their overall performance (see previous chapter). It is possible that the purpose of this positivity bias is to help older adults maintain their positive affect (e.g., Isaacowitz et al., 2009; Kappes et al., 2017), although the relationship between the PE and positive affect has been contested (Isaacowitz & Blanchard-Fields, 2012).

Overall, the picture that emerges is that older adults' performance deficits in cognitively demanding tasks are driven by the dual disadvantage of increased cognitive difficulty (due to age-related neural decline) and decreased efficiency in utilising and replenishing physiological resources, potentially leading older adults to reduce their cognitive engagement in difficult tasks at a lower threshold than young adults. So far, however, this scenario is merely intuitively plausible. No study has yet directly investigated the relationship between not only age, task difficulty, and availability of physiological resources, but also their combined effects on cognitive engagement, task performance, subjective effort and affect. The present experiment aimed to address these issues. We asked young and older adults to consume a glucose or a placebo drink and to perform a memory-search task consisting of three blocks of different levels of difficulty, calibrated so as to be centred on each participant's individual memory span. We measured participants' HR at rest and during task performance, and calculated task-related HR change as a measure of task engagement. At the end of each block, participants rated their effort on a self-report scale and completed an implicit emotion-assessment task to assess their levels of positive or negative affect.

We expected the following pattern of results: first, in view of findings suggesting that older adults prioritise the preservation of processing resources, we expected older adults to perform less well in the memory-search task than young adults despite the

individually calibrated difficulty levels, and to show greater signs of disengagement at high task difficulty. It should be noted that we operationalise cognitive engagement as HR change, assumed to reflect the level of effort exerted in a task, irrespective of whether this results in improved cognitive performance (Hess, 2014). Second, based on the assumption that age-related constraints in neural processing capacity and energy metabolism make cognitive tasks more effortful for older than for young adults, we expected older adults to give higher subjective effort ratings than young adults. Third, in line with evidence showing that task engagement increases with more challenging tasks but decreases when success seems unattainable, we expected HR changes to be largest in the medium difficulty condition and to decrease from the medium to the high difficulty condition, particularly in older adults. The question of interest was how glucose would affect these measures, particularly in older adults. If the scenario outlined above is correct, that is, if additional energy resources enable older adults to increase task engagement without compromising their resource balance, then we should expect older adults in the glucose group to show greater task-related HR change and improved memory-search performance, without feeling that they have exerted more effort. We also expected that older adults' positive affect might be reduced with increasing task difficulty. We hypothesized that glucose could help older adults retain their positive emotionality by increasing their ability to successfully perform the task without compromising resource availability.

Method

Design and Drinks

We employed a between-subjects 2 (Age: young vs. older) × 2 (Drink: glucose vs. placebo) randomised, placebo-controlled, double-blind design. All drinks were prepared and labelled by assistants to ensure that the experimenter was unaware of the composition of the drinks. Participants assigned to the glucose condition were asked to consume a drink containing 25 g of glucose. The placebo groups were given a non-glucose drink of equivalent sweetness (five aspartame tablets). Both drinks were dissolved in 300 ml of water and 25 ml of sugar-free orange-flavoured cordial (to improve palatability). The glucose dose was chosen based on previous studies indicating that 25 g of glucose is sufficient for observing cognitive enhancement in both young and older adults (Parsons & Gold, 1992; Riby, 2004; Sünram-Lea et al., 2011). The drink composition used in the current study does not lead to differences in palatability ratings between glucose and placebo (see previous chapter).

The sample consisted of 54 healthy first-year undergraduate students (age range 18-27) and 58 healthy community-dwelling older adults (age range 65-82). The study was approved by the Psychology Department's Research Ethics Committee at the University of Warwick and all participants provided written consent. Older adults were compensated £10 and young adults were offered course credit in exchange for their participation. Exclusion criteria included self-reported history of recent neurological or psychiatric disorders, diabetes, CV disease and use of medication that could potentially affect CV reactivity (e.g., β-blockers). The sample size was determined based on previous work indicating that age-related differences in task engagement (i.e., changes in CV responses) can be identified with a sample of 50-55 participants per age group (Ennis et al., 2013; Hess & Ennis, 2012; B. T. Smith & Hess, 2015), and glucose studies

requiring approximately 25 participants per drink condition (Gagnon et al., 2010; Macpherson et al., 2015). One young participant failed to complete the testing session, leaving 53 young adults in the final sample. HR data from six older adults (four glucose, two placebo) were excluded from further analysis because of artefacts affecting accurate heart-beat detection,[2] leading to a final sample of 52 older adults for HR analysis. The full sample of 58 older adults was used in all other analyses (see Table 3 for characteristics of the final sample).

Both young and older adults completed background measures of short-term memory (Forward Digit Span; Wechsler, 1981), processing speed (DSST; Wechsler, 1981) and vocabulary knowledge (MHVT; Raven, Raven, & Court, 1988). As expected, older adults had lower speed scores, $t(109) = -8.29$, $p < .001$, higher vocabulary scores, $t(109) = 12.06$, $p < .001$, and more years of formal education, $t(109) = 5.39$, $p < .001$, compared with young adults. Young adults had lower digit span scores compared with older adults, $t(109) = -2.71$, $p = .008$. Further examination of education, digit span, speed, and vocabulary differences between the glucose and placebo groups within each age group revealed that the young-placebo group had marginally higher speed scores compared with the young-glucose group, $t(51) = 1.96$, $p = .056$. No other differences were identified (all ps > .37).

[2]HR data from four older adults were excluded because of movement artifacts affecting the accurate estimation of HR from the ECG signal. Additionally, ECG data from two older adults were discarded because of artifacts relating to heart conditions which participants failed to disclose during the screening stage.

Table 3

Characteristics of the Sample and Performance on Background Cognitive Measures for Each Age and Drink Group in Experiment 2

	Young		Older	
Characteristics	Glucose	Placebo	Glucose	Placebo
N (M/F)[1]	26 (1/25)	27 (4/23)	30 (13/17)	28 (11/17)
Age	18.46 (0.65)	18.93 (1.73)	72.47 (4.06)	72.75 (4.01)
Years of education	14.08 (0.27)	14.19 (0.56)	16.40 (2.99)	16.25 (2.93)
Digit span[2]	8.46 (1.03)	8.26 (0.98)	9.00 (1.66)	9.11 (1.55)
Speed[3]	68.85 (9.45)	73.85 (9.16)	56.50 (10.28)	54.50 (10.84)
Vocabulary[4]	15.65 (3.56)	16.41 (3.19)	24.43 (3.67)	23.86 (3.77)

Note. All values except for *N* (M/F) are given as means (with standard deviations).

[1]Number of participants in each age and drink group (male/female). [2]Digit span score as measured by the forward digit span subscale of the WAIS (Wechsler, 1981). [3]Processing speed as measured by the DSST (Wechsler, 1981). [4]Vocabulary score as measured by the multiple-choice section of the MHVT out of a maximum of 33 (Raven et al., 1988).

Cognitive Tasks and Equipment

CV responsivity. HR was continuously measured throughout the testing session using a standard 3-lead ECG electrode placement configuration. Disposable Ag/AgCl pre-gelled ECG electrodes were placed on the participant's right wrist ('negative'), left wrist ('ground') and left ankle ('positive'), and connected to a BIOPAC MP36 data acquisition system (BIOPAC Systems Inc., Goleta, CA, USA). The ECG signal was digitised at a 1,000 Hz sampling rate and filtered online with a low-pass filter of 35 Hz and a high-pass filter of 0.5 Hz. Stimulus delivery markers were sent to BIOPAC's Acq*Knowledge* recording software (version 4.2) through a parallel port, and saved in digital channels. The analog (ECG signal) and digital channels (event markers) were synchronised and visually displayed on Acq*Knowledge*. The 5-minute baseline and

cognitive block segments were extracted from the raw ECG signal and subsequently entered into Kubios version 2.2 (Tarvainen, Niskanen, Lipponen, Ranta-aho, & Karjalainen, 2014), which allows for automatic detection of heart beats and HR calculations. To ensure that all heart beats were accurately detected, the raw ECG signal was visually inspected. Additionally, Kubios's medium artefact correction level was used to identify and correct potential artefacts. Across both age groups, less than 1% of identified heart beats were marked as artefacts and were corrected before analysis.

Memory search. Participants performed a memory-search task (Sternberg, 1966) consisting of three blocks at different levels of difficulty: low, medium and high. A set of pseudo-randomly selected consonants were presented on a 20-inch screen, with no single consonant appearing more than once in the same trial. White uppercase letters appeared in random positions on the edges of a 150 × 150 pixels square centred on the middle of the screen, and drawn on a black background. Each letter subtended a visual angle of 0.95^{o} at a 60-cm viewing distance. The consonants remained on the screen for 3 s and participants were asked to memorise them. After a 2-s retention period (blank screen), a single target letter appeared at the centre of the screen and participants had to press a key as fast and accurately as possible to indicate whether the target letter was part of the set of consonants presented immediately before. The target remained on the screen for 2.5 s or until a response was made. Participants responded with their left and right index fingers (left 'Z' key for a new target, right 'M' key for a memory set target). After a response was recorded, the target disappeared and the screen remained blank for the rest of the 2.5-s period. All trials were preceded by a 1-s central fixation cross. The probability of the target letter being part of the memory set was 50%. Each block

consisted of 36 trials and lasted for a fixed duration of approximately five minutes (8.5 s per trial) to allow for meaningful comparisons of CV responsivity across difficulty blocks, age and drink groups. The size of the memory sets (i.e., number of letters presented) was based on each participant's individual short-term memory capacity as measured by the Forward Digit Span subscale of the WAIS (Wechsler, 1981). Blocks were created such that the medium difficulty level set size would match each participant's short-term memory capacity. The low difficulty level contained three fewer and the high difficulty level had three more items than each participant's short-term memory capacity. For example, a participant with a forward digit span of seven items was given a low difficulty block of four items, a medium difficulty block of seven items and a high difficulty block of 10 items. The presentation order of the difficulty blocks was counterbalanced.

Effort ratings. The 'Effort' subscale of the NASA Task Load Index (NASA-TLX; Hart & Staveland, 1988) was used to evaluate subjective perception of effort expended in the task (question: 'how hard did you have to work to accomplish your level of performance?'). At the end of each block, participants were asked to give their rating by using the computer mouse to place the cursor on one field of a 10-point scale, displayed horizontally in the middle of the screen and ranging from 1 ('very low') to 10 ('very high').

Affective judgment. Affect was measured through an affective judgment task based on Bartoszek and Cervone's (2017) implicit emotion-assessment task. This task has been shown to accurately detect changes in affect following mood manipulation and exposure to emotional material (e.g., fear-inducing stimuli), and can be assumed to be

more sensitive to small changes in emotionality compared with self-report/explicit affect-assessment tools (Abercrombie, Kalin, & Davidson, 2005; Quirin, Kazén, Rohrmann, & Kuhl, 2009).

At the end of each memory-search block, participants were asked to rate 10 abstract expressionist artworks. Participants were required to give a response by using the computer mouse to place the cursor on one field of a 7-point scale (displayed horizontally below the painting) ranging from -3 (‘very negative’) to 3 (‘very positive’). A set of 10 new paintings were presented after each block. Each painting remained on the screen until a rating was given. We opted for paintings depicting ambiguous abstract patterns and excluded paintings containing figures (e.g., human faces) or items that could influence emotional states because of familiarity. Paintings were retrieved from the internet. All stimuli were grey-scaled and resized to 500 × 400 pixels, and were presented one at a time at the centre of the screen. A 1-s central fixation cross preceded each trial. Participants were asked to rely on their first impression of the painting and give their ratings immediately. This was done to ensure that their affect ratings were based on heuristic processes, which have been shown to accurately reflect participants’ affective state, rather than controlled processes, which could introduce processing biases, such as social desirability and situation-related beliefs about emotion, that can influence explicit measures of affect (Quirin, Kazén, & Kuhl, 2009).

Procedure

Participants were instructed to avoid consuming any food or drink for two hours before coming to the lab. All participants reported to have adhered to that condition.

Upon arrival, participants signed a consent form, provided demographic information and completed the digit span test. After that, they were connected to the ECG equipment and given instructions on optimal testing conditions (e.g., avoid excessive movement). This was followed by a 7-minute period during which participants were asked to sit back and relax. The final five minutes of the 7-minute resting period were used as the HR baseline for each participant. At the end of the resting period, participants were given instructions on how to perform the cognitive tasks and were asked to consume the glucose or placebo drink within five minutes. After the drink, participants completed a short practice to familiarise themselves with the procedure and timings. The practice phase consisted of four memory-search trials per difficulty block (two target matches and two non-matches per block). At the end of each memory-search practice block, they completed the effort self-report scale and rated two paintings (different from the ones presented in the actual task). Following the end of the practice and 10 minutes after drink ingestion, participants were given the full cognitive task. At the end of the testing session, young participants completed the processing speed and vocabulary tests (older participants completed these during an earlier session). Finally, they were compensated for their participation and debriefed.

Results

Cognitive Performance

Two separate three-way mixed ANOVAs were conducted on mean correct RTs and error rates (Figures 3A and 3B, respectively), with age (young, older) and drink (glucose, placebo) as the between-subjects factors, and difficulty (low, medium, high) as

the within-subjects factor. Follow-up *t*-tests were used to further examine significant interactions between factors.

Overall, young adults were faster and more accurate than older adults ($F(1, 107) = 107.60$, $p < .001$, $\eta_p^2 = .501$, and $F(1, 107) = 13.55$, $p < .001$, $\eta_p^2 = .112$, for RTs and error rates, respectively). Responses were both slower and less accurate with increasing task difficulty (RTs: $F(2, 214) = 133.56$, $p < .001$, $\eta_p^2 = .555$; error rates: $F(2, 214) = 390.34$, $p < .001$, $\eta_p^2 = .785$), and this performance decline was steeper in older than in young adults, as reflected in Age × Difficulty interactions (RTs: $F(2, 214) = 25.58$, $p < .001$, $\eta_p^2 = .193$; error rates: $F(2, 214) = 8.49$, $p < .001$, $\eta_p^2 = .074$). RTs were shorter with glucose than with placebo, $F(1, 107) = 3.96$, $p = .049$, $\eta_p^2 = .036$, though the corresponding effect for error rates was not significant, $F(1, 107) = 1.88$, $p = .17$. However, the Age × Drink interaction was significant for both RTs, $F(1, 107) = 6.21$, $p = .014$, $\eta_p^2 = .055$, and error rates, $F(1, 107) = 5.70$, $p = .019$, $\eta_p^2 = .051$: whereas older adults in the glucose group were overall significantly faster ($t(56) = -3.64$, $p = .001$) and more accurate ($t(56) = 2.81$, $p = .007$) than those in the placebo group, no glucose effect was found in young adults (both *p*s > .50).

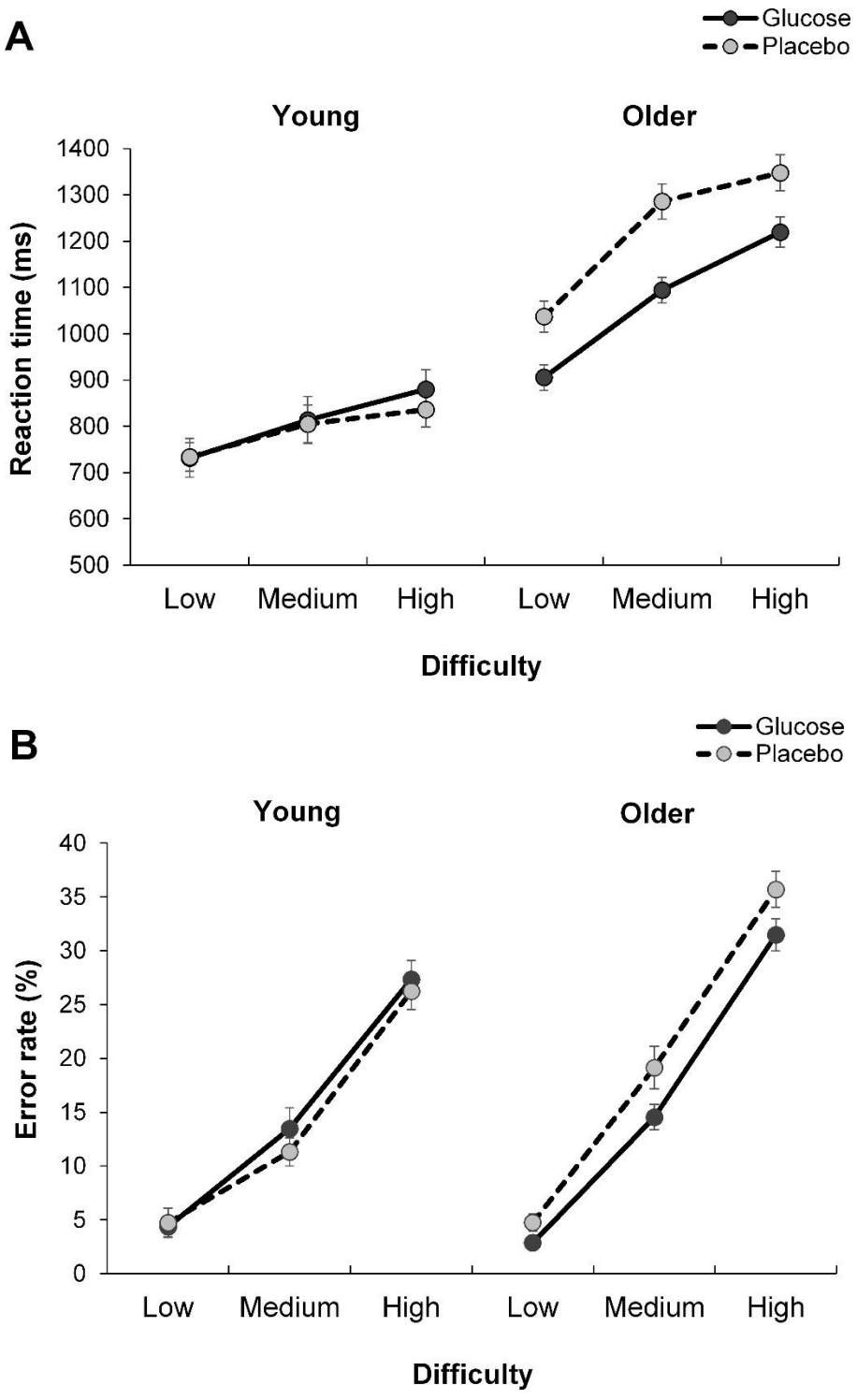

Figure 3. Performance on the memory-search task: (A) mean correct RTs in milliseconds, and (B) mean percentage error rates, as a function of age (young/older), drink (glucose/placebo) and difficulty level (low/medium/high) in Experiment 2. Error bars denote ±1 standard error of the mean.

CV Responsivity and Subjective Effort

HR. Percentage HR change from baseline was used as the physiological index of effortful exertion/task engagement in the memory-search task (see Figure 4A). Thus, change scores for the cognitive blocks were calculated individually for each participant as ([Raw HR during cognitive block / Raw HR during baseline] – 1) × 100.

Compared with young adults, older adults showed higher HR change, $F(1, 101) = 12.87$, $p = .001$, $\eta_p^2 = .113$. HR change varied with difficulty, $F(2, 202) = 13.49$, $p < .001$, $\eta_p^2 = .118$, being greatest in the medium difficulty block and smallest in the low difficulty block. Pairwise comparisons between difficulty conditions confirmed that they all were significantly different from each other, all *t*s > 2.6, all *p*s < .01. However, whereas young adults' HR change was comparable between medium and high difficulty, $t(52) = -0.97$, $p = .339$, HR reactivity in older adults was significantly smaller in the high than medium difficulty level, $t(51) = -2.85$, $p = .006$. Finally, glucose led to higher HR change during the cognitive task than did placebo, $F(1, 101) = 11.82$, $p = .001$, $\eta_p^2 = .105$. This was true for both age groups: $t(51) = 2.76$, $p = .008$, and $t(50) = 2.06$, $p = .045$, for young and older adults, respectively. There were no interactions (all *F*s < 2.08, all *p*s > .12).

Subjective effort. Subjective effort ratings (see Figure 4B) rose with increasing difficulty, $F(2, 214) = 293.39$, $p < .001$, $\eta_p^2 = .733$, and older adults rated their cognitive exertion as being more effortful compared with young adults, $F(1, 107) = 3.99$, $p = .048$, $\eta_p^2 = .036$. Glucose did not affect subjective effort perception, $F < 1$, nor were there any interactions between age, difficulty, and drink (all *F*s < 1.69, all *p*s > .18).

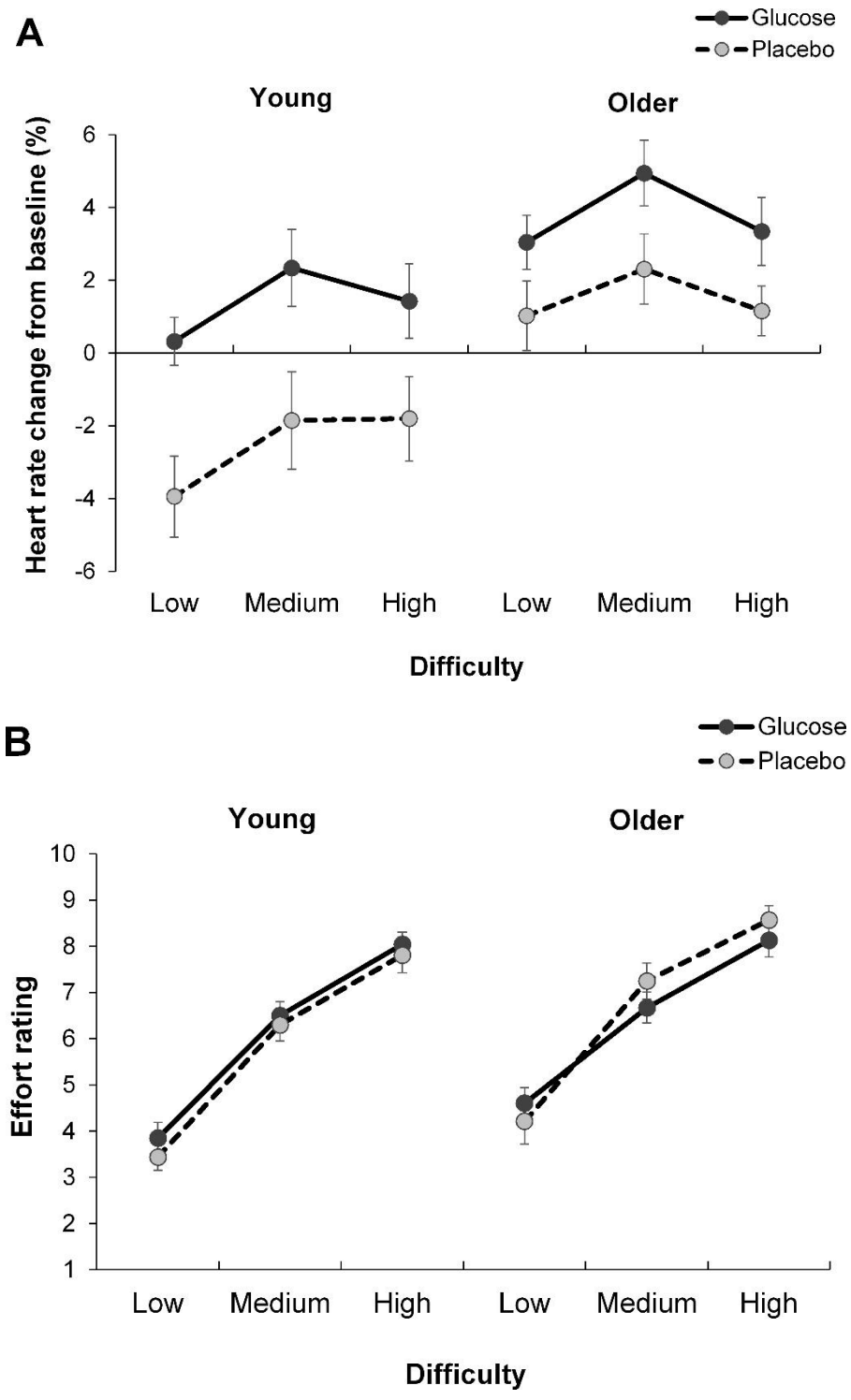

Figure 4. Participants' scores on measures of task engagement and effortful exertion: (A) mean percentage HR change from baseline, and (B) mean self-report effort scores on the NASA-TLX effort subscale, as a function of age (young/older), drink

(glucose/placebo) and difficulty level (low/medium/high) in Experiment 2. Error bars denote ±1 standard error of the mean.

Affective Judgment

Figures 5A and 5B display participants' mean affect ratings and RTs, respectively. Older adults took longer than young adults to rate each painting, $F(1, 107) = 94.15$, $p < .001$, $\eta_p^2 = .468$. No other main effects or interactions were significant for RTs (all Fs < 2, all ps > .16). Importantly, older adults rated the pictures more positively than did young adults, $F(1, 107) = 9.96$, $p = .002$, $\eta_p^2 = .085$. Moreover, this effect of age was qualified by an Age × Drink interaction, $F(1, 107) = 5.01$, $p = .027$, $\eta_p^2 = .045$: whereas young adults' ratings were not affected by drink, $t < 1$, older adults in the glucose group gave significantly more positive ratings compared with their placebo counterparts, $t(56) = 2.53$, $p = .014$. There were no other main effects or interactions for ratings (all Fs < 2.53, all ps > .11).[3]

[3]With the exception of CV responsivity, all analyses presented in the results section were conducted using the full sample of older adults ($n = 58$). Repeating the cognitive performance, subjective effort, and affective judgment analyses with the sample of older adults whose CV data were included in the HR analysis ($n = 52$) did not alter the significance of the main effects and the interactions reported in the results section. The only difference found was for the main effect of age on subjective effort ratings, with the effect being only marginally significant, $F(1, 101) = 3.32$, $p = .072$, $\eta_p^2 = .032$.

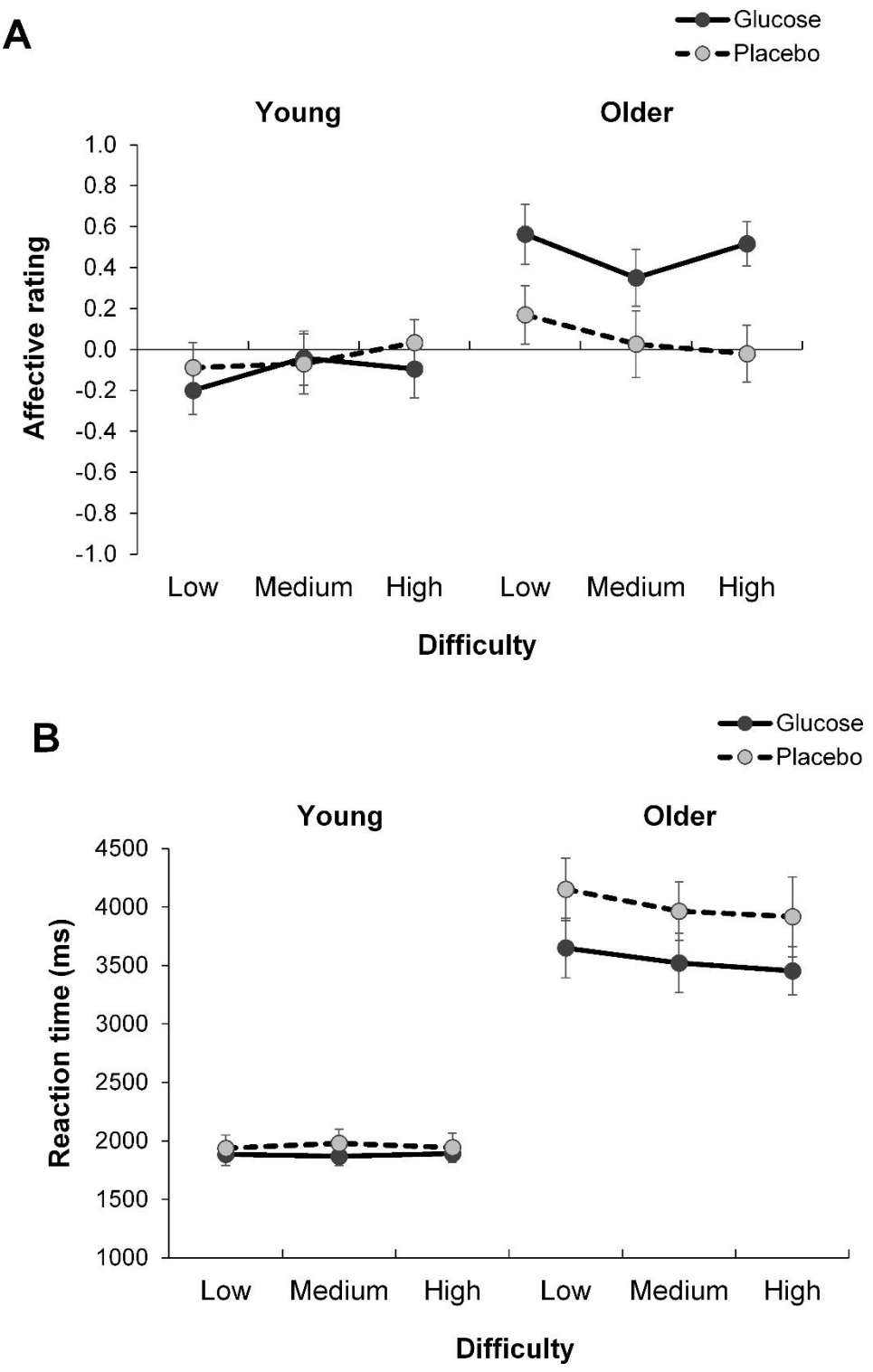

Figure 5. Performance on the affective judgment task: (A) mean affect ratings, and (B) mean RTs, as a function of age (young/older), drink (glucose/placebo) and difficulty level (low/medium/high) in Experiment 2. Error bars denote ±1 standard error of the mean.

Discussion

Experiment 2 examined the relationship between task difficulty and availability of physiological resources, and their combined effects on older adults' cognitive engagement and task performance, including subjective effort and affect. As expected, older adults performed less well in the memory task than did young adults, especially as difficulty increased, and found their performance to be more effortful. Whereas both age groups showed maximal CV reactivity at the medium difficulty level, older adults' task disengagement at the high difficulty level was more pronounced than young adults' CV withdrawal. Although glucose did not affect cognitive performance in young adults, older adults in the glucose group performed better in the cognitive task, showed greater HR change, and their affect scores were more positive, compared with their placebo counterparts. Despite older-glucose participants outperforming older-placebo, the subjective effort ratings of the two groups were similar, indicating that the older-glucose group was able to exert more effort and improve their performance without feeling more challenged. In fact, the numerical trend showed that older adults in the glucose group rated their performance to be slightly less effortful compared with placebo, in line with their more positive affect scores.

In terms of cognitive performance, we predicted that glucose administration would significantly improve participants' RTs and error rates, and this effect would be more robust for older adults (e.g., Hall et al., 1989; Macpherson et al., 2015; Manning et al., 1997). As expected, we identified a glucose-related improvement in both RTs and error rates for older but not young adults. Given that previous studies have found glucose enhancement to be more pronounced under dual-task conditions that require the

simultaneous coordination of multiple cognitive functions, and are less reliable when simply manipulating the difficulty of a single task (Sünram-Lea et al., 2002a), the absence of glucose effects on young adults' performance is not surprising. In contrast, glucose improved older adults' performance on the memory task across all difficulty levels. It is worth recalling that task difficulty was calibrated for each participant individually. Therefore, one might have expected similar low effort ratings and lack of glucose effects in the 'easy' condition for both age groups. However, there is evidence to suggest that glucose can improve older adults' cognitive performance even under relatively easy testing conditions (e.g., Manning et al., 1997, 1992, 1998; Messier et al., 2010; Riby et al., 2006). Our results suggest that in the present task, even the individually calibrated 'easy' condition was substantially more effortful for older than for young participants, in line with the observation that ageing is associated with increased subjective perceptions of difficulty (Hess & Ennis, 2012; Hess et al., 2016).

Consistent with previous findings (Ennis et al., 2013; Hess & Ennis, 2012; Hess et al., 2016; B. T. Smith & Hess, 2015), older adults showed higher task engagement than young adults during the memory-search task, reflected in higher CV responsivity and higher self-reported effort. Both young and older adults showed an increase in CV responsivity from the low to the medium difficulty condition. Similar to previous studies (Ennis et al., 2013; Hess et al., 2016), task disengagement from medium to high difficulty was more pronounced in older than in young adults (-1.37% and -0.42%, respectively, with only the former significant). This finding supports the role of CV reactivity as a measure of task engagement (Hess & Ennis, 2014; Richter et al., 2016).

The main question of interest was whether glucose would allow older adults to increase their level of task engagement, and how this would relate to cognitive performance, subjective effort ratings, and affect. As predicted, glucose administration increased effortful exertion irrespective of difficulty, with the glucose groups showing higher task engagement throughout the memory-search task compared with placebo. However, whereas older adults' increased task engagement was associated with an improvement in cognitive performance, the same was not observed in young adults. Although 'task engagement' is defined as the individual's ability to invest resources in the task, irrespective of whether this results in improved cognitive performance (Hess, 2014), the question why increased engagement was associated with improved performance in older but not young adults cannot be answered on the basis of the present data, and will have to await future studies investigating the connection between CV indices, task engagement and cognitive performance.

As expected, despite older-glucose participants outperforming their placebo counterparts in the memory-search task, the effort self-report ratings of the two groups showed no differences. Not only did glucose administration increase task engagement and improve older adults' cognitive performance, it also kept subjective perceptions of expended effort to levels comparable to those obtained from the placebo group. It has been shown that one of the main factors contributing to older adults' ability to exert effort is their subjective perception of the cognitive costs associated with performance on the task: if the cognitive cost of performing the task is seen as prohibitive, older adults are more likely to disengage and withdraw effort (Hess et al., 2016). The present

results demonstrate that glucose administration enables older adults to maintain high levels of task engagement without subjective costs.

Furthermore, in line with reports of higher positive affect in older adults (Carstensen, 1995; Scheibe & Carstensen, 2010), in the implicit affect assessment task, older adults rated the paintings as more positive than did young adults. Importantly, whereas young adults' affect ratings were not influenced by the drink condition to which they were allocated, older adults in the glucose group gave more positive ratings than their placebo counterparts despite expending more effort to perform the memory-search task. This effect might be task specific (i.e., decreasing a potential negative emotional impact of performing the memory-search task) or might be a non-specific increase in general positivity (as a by-product of ingesting glucose, unrelated to the task). However, the general conclusion remains the same: glucose can protect older adults' positive affect. Together with the findings from Experiments 1a and 1b showing that glucose can help older adults retain their positivity preference even under high cognitive load, it appears that moderate increases in glucose availability are able to protect or even enhance both positive emotionality and positivity-related cognitive strategies in old age.[4]

Closely examining the older-glucose group's behavioural performance and their physiological patterns of task engagement, it becomes obvious that glucose effects go above and beyond cognitive facilitation in ageing. Glucose increased older adults' task

[4]It should be noted that no direct links have been established between the positivity effect and mood states (for a review, see Isaacowitz & Blanchard-Fields, 2012), yet older adults' motivation to prioritise positive material appears to be closely related to affective outcomes (e.g., Isaacowitz et al., 2009).

engagement and cognitive performance without increasing subjective effort perception, instead even improving their affective state. Based on observations of heightened motivation following CHO administration (e.g., Chambers, Bridge, & Jones, 2009; Kringelbach, 2004), our findings fit with the idea that glucose facilitation could be a result of both metabolic and motivational influences (see Beedie & Lane, 2012; Molden et al., 2012). Although the present results confirm the prediction that these facilitation effects are more pronounced in older than in young adults (in line with the notion that the former are more in need of 'metabolic support' than the latter), a note of caution is in order. Whereas our older adults sample was relatively balanced in terms of gender, the young adult groups consisted primarily of female participants and, therefore, the observed age effects might in part be driven by gender differences in glucose metabolism (for reviews, see Hedrington & Davis, 2015; Varlamov, Bethea, & Roberts, 2014). To investigate this possibility, we repeated our analyses using data collected from female participants alone (n = 82). The results of the subgroup analysis largely mirrored the ones obtained from the full sample, suggesting that the glucose facilitation effect observed in our study was not influenced by gender differences. Nevertheless, future studies should aim for balanced or single-gender samples to avoid potential confounds associated with gender-related differences in glucose metabolism.

The question of how glucose leads to cognitive facilitation, however, still stands. The cascade of cognitive and affective results observed in the older group points to an intricate relationship between energy availability, cognitive performance and affect, but we do not yet possess an in-depth understanding of the directionality of these effects. It could be that glucose motivates older adults to exert effort, which improves their

cognitive performance, and this subsequently leads to more positive affect after successfully completing the task. Alternatively, if older adults use available energy resources to prioritise positivity-driven adaptive goals (see Chapter 2), it could be that the increase in energy availability enhances older adults' affect and this positivity motivates them to exert more effort and improve their cognitive performance. In light of recent evidence stressing the importance of cognitive engagement for maintaining cognitive functioning in ageing (for a review, see Hertzog et al., 2008), our results are an important first step toward understanding the physiological and behavioural mechanisms underlying cognitive engagement in old age. Finding ways to manipulate the effectiveness of these mechanisms (e.g., improving glucoregulation) could increase older adults' ability to engage in cognitive tasks and, potentially, improve their cognitive and emotional well-being.

Chapter 4: Take Heart: Older Adults' Heart Rate Variability Predicts Negativity Avoidance

Abstract

Emotion regulation depends on adjusting physiological arousal regulated by the autonomic nervous system (ANS) in a situation-appropriate manner. Heart rate variability (HRV) is an index of ANS functionality and higher levels of HRV have been associated with greater ability to regulate physiological arousal and overall emotionality. As older adults' preferential processing of positive over negative stimuli (positivity effect; PE) is thought to reflect emotion regulation attempts, we hypothesised that HRV could predict PE magnitude in older adults. We measured HRV at rest and gaze preference for positive and negative (relative to neutral) faces in 63 young and 62 older adults (mean ages of 19 and 72, respectively). Whereas young adults showed no consistent preference for positive or negative faces, older adults showed the expected PE, which predominantly manifested as anti-negativity rather than positivity bias. Crucially, older but not young adults showed a systematic association between HRV and emotional preference, with higher levels of HRV being specifically associated with higher anti-negativity (better negativity avoidance). This is the first study to uncover an age-related link between HRV and emotion regulation processes in the form of the PE. The absence of a relationship between HRV and emotional preference in young adults strengthens the assertion that the PE reflects an age-related emotion regulation mechanism and is dependent on older adults' autonomic fitness. Increasing the

efficiency of the CV system might selectively improve older adults' emotion regulation by improving their ability to disregard negative influences.

Experiment 3

Introduction

Emotionally salient information affects cognition, subjective emotionality, and physiological arousal regulated by the ANS (for reviews, see Kreibig, 2010; Levenson, 2014). When people are relaxed, the parasympathetic branch of the ANS maintains arousal at minimum levels (e.g., decreased HR) to conserve resources. During exposure to emotional information, parasympathetic control is withdrawn and is usually followed by an increase in sympathetic activity in order to adjust physiological arousal (e.g., increased HR) and help individuals meet emerging demands (Levenson, 2003). According to the polyvagal theory (Porges, 2007), fluctuations in the power of the PSNS allow the ANS to quickly mobilise resources when the situation requires it ('fight or flight'), or conserve them to induce a feeling of calmness ('rest and digest'). Successful emotion regulation is dependent on regulating both subjective emotionality and physiological arousal in a flexible and timely manner. Whereas a high functioning ANS is capable of adjusting physiological responses according to demands, ANS rigidity might lead to disproportionate autonomic reactions and, consequently, poor emotion regulation (for a review, see Appelhans & Luecken, 2006).

Successful emotion regulation is particularly salient in healthy ageing. Despite the well-documented age-related decrements in cognitive and physical domains, older adults appear to be happier than their younger counterparts (Birditt & Fingerman, 2005;

Birditt et al., 2005; Gross et al., 1997), and more capable of tailoring emotion regulation strategies to cope with emotional situations (for a review, see Blanchard-Fields, 2007). Older adults' superior emotional control appears also to influence their processing patterns (Carstensen et al., 2006; Isaacowitz, et al., 2008, 2009; Kappes et al., 2017; but see Isaacowitz & Blanchard-Fields, 2012). When presented with positive and negative stimuli, older adults tend to show a preference toward positive and away from negative information, a phenomenon known as the PE (for a review, see Mather & Carstensen, 2005).

Despite its name, the PE does not always manifest as a bias toward positive material, but can emerge as an avoidance of negativity instead (Grühn et al., 2007; Isaacowitz et al., 2008; Mather & Knight, 2005). This 'anti-negativity' conceptualization of the PE is consistent with neuroimaging findings of an age-related increase in PFC modulation of the amygdala in the presence of negative information (for a review, see Nashiro et al., 2012), suggesting that older adults actively recruit processing resources to retain their PE (Knight et al., 2007; Mather & Knight, 2005) in an attempt to minimise the affective impact of negative information. An intriguing question arises: if older adults' PE reflects emotion regulation skills and is dependent on downregulating the physiological arousal elicited by negative material, could we predict the emergence of a positivity/anti-negativity bias in older adults' cognition simply by examining their ANS functionality?

Recent advances in the field of psychophysiology have facilitated the evaluation of individual differences in autonomic functionality through the measurement of physiological mechanisms controlled by the ANS (Laborde et al., 2017). Because HR

reflects both SNS and PSNS influences (cf. Jamali, Waqar, & Gerson, 2017), information regarding the balance between the two ANS subsystems can be obtained from CV indices with relative ease. One such index is HRV, which measures the variation in the time interval between successive heartbeats and is primarily influenced by parasympathetic activity (Task Force, 1996). HRV has been consistently used as the main marker of ANS functionality (e.g., Collins, Dillon, Finucane, Lawlor, & Kenny, 2012; for a review, see Zygmunt & Stanczyk, 2010), and is considered a highly accurate marker of the ability of the ANS to adjust physiological arousal according to demands (Porges, 2007).

According to the Neurovisceral Integration Model (Thayer & Lane, 2000, 2009), measuring HRV at rest can be used as an index of the strength of the brain's emotion regulation system (i.e., PFC–amygdala connectivity) and, consequently, individuals' ability to precisely regulate physiological and emotional responses. Indeed, empirical evidence suggests that HRV is a strong index of individual differences in the efficiency of emotion regulation mechanisms (for reviews, see Appelhans & Luecken, 2006; Balzarotti et al., 2017; Thayer & Lane, 2000, 2009) and other PFC-related functions such as inhibitory control and response suppression (Colzato & Steenbergen, 2017; Gillie et al., 2014; Segerstrom & Nes, 2007). Both the polyvagal and the Neurovisceral Integration models suggest that parasympathetically mediated HRV indices reflect levels of autonomic functionality and, by extent, individuals' capacity to regulate emotional and cognitive responses appropriately. Surprisingly, whereas a relationship between resting HRV and emotion regulation has been identified in young adults (for a review, see Thayer & Lane, 2009), no research to date has examined the potential

association between HRV and older adults' PE, which is thought to reflect an age-related motivational mechanism aimed at improving emotionality (Mather & Carstensen, 2005). In light of recent findings of a relationship between resting HRV levels and the strength of the PFC-amygdala connectivity in both young and older adults (Sakaki et al., 2016), it is likely that older adults' PE is dependent on successfully adjusting physiological arousal during exposure to emotional stimuli and can therefore be indexed by HRV measures. At present, we lack an understanding of the contribution of the ANS to the strength of older adults' PE itself, and whether ANS functionality is associated with specific facets of the PE (positivity bias vs. negativity avoidance/anti-negativity).

In Experiment 3, we employed an eye tracking paradigm to assess young and older adults' preference for emotional versus neutral faces in attention, measuring both their positivity and anti-negativity biases. Participants were presented with pairs of happy-neutral and angry-neutral faces and their fixations were recorded. Positivity bias was conceptualised as larger numbers of fixations toward, and longer fixation durations on, happy relative to neutral faces, and anti-negativity bias as larger numbers of fixations toward, and longer fixation durations on, neutral relative to angry faces. As the PE is a phenomenon observed exclusively in older adults (for a meta-analysis, see Reed et al., 2014), only older adults were expected to show the PE, while young adults were expected to show either a slight negativity bias or no particular preference for emotional faces (Baumeister et al., 2001).

Participants' HRV at rest was measured to investigate whether ANS functionality can predict the magnitude of the PE. If HRV is related to emotion

regulation capabilities, it was expected that the association between HRV and emotional preference would be found in older but not in young adults who do not have chronically activated emotion regulation goals and only use such mechanisms when explicitly instructed (see Mather & Johnson, 2000). Furthermore, based on studies suggesting that the PE might manifest more as a negativity avoidance rather than a pure positivity bias (e.g., Grühn et al., 2007) and that HRV is associated with suppression and inhibitory capabilities (e.g., Gillie et al., 2014), we expected higher HRV levels to be related to higher anti-negativity (avoiding negative information) rather than to increased positivity in older adults. Implicit affect was measured to examine its association with HRV and the PE. Additionally, as previous reports have suggested that the PE disappears under high cognitive demands (Knight et al., 2007; Mather & Knight, 2005; but see Allard & Isaacowitz, 2008), we included both a single and a dual task condition to examine whether the HRV-PE relationship changes when a distracting secondary task is introduced.

Method

Participants

A total of 66 healthy young adults (age range 18-25) and 63 healthy community-dwelling older adults (age range 65-79) took part in the study. A medium effect size has been found in studies assessing the relationship between resting HRV and emotion regulation self-reports (correlation coefficient of approximately .3; Visted et al., 2017; Williams et al., 2015) as well as HRV and cognition (e.g., Colzato & Steenbergen, 2017; Gillie et al., 2014). Sample size was determined based on a meta-analysis of almost 300 effect sizes suggesting that, for a medium effect size, approximately 61 participants are

required to achieve 80% power (Quintana, 2017). Young adults received course credit as part of their course requirements and older adults were compensated £10 in exchange for their participation. The study was approved by the Psychology Department Research Ethics Committee at the University of Warwick and all participants provided written consent at the beginning of the testing session. The experimental procedures were designed and conducted in accordance with the World Medical Association Declaration of Helsinki.

Exclusion criteria included self-reported history of neurological, psychiatric or endocrine disorders, eye conditions (e.g., pupil obfuscation), and CV disease or use of medication that could affect CV functioning (e.g., β-blockers). Data from four participants (3 young, 1 older) were excluded because of use of antidepressants or other medication that could affect cognitive and CV functioning, leaving 63 young and 62 older adults in the final sample. HRV data from eight participants were unusable because of equipment malfunction (n = 3), high number of artefacts during recording (n = 4), or heart conditions not disclosed during screening (n = 1), leaving 62 young and 55 older adults for HRV analysis. Participants' eye movements were also visually inspected throughout the task to ensure the recording of high quality data and exclude trials in which the pupil was not adequately tracked or artefacts were introduced (less than 0.5% of trials across all participants). Fixation data for one single and one dual task block belonging to two different older adults had to be excluded because the pupil could not be tracked for the majority of the trials, leaving 61 older adults for eye tracking analysis in both single and dual task conditions.

Participants completed the DSST (Wechsler, 1981) and the MHVT (Raven et al., 1988) to assess age differences in processing speed and crystallised intelligence, respectively. Older adults had lower processing speed scores, $t(123) = -7.77$, $p < .001$, but higher performance on the vocabulary task, $t(123) = 12.60$, $p < .001$, and more years of full-time education, $t(123) = 10.36$, $p < .001$, compared with young adults. Characteristics of the final sample are presented in Table 4.

Table 4

Characteristics of the Sample, Cardiovascular Indices at Baseline, and Performance on the IPANAT and the Secondary Task in Experiment 3, With Results of Comparisons (T-Tests) Between Age Groups

Measure	Young	Older	*p* value
Characteristics			
N (M/F)[1]	63 (15/48)	62 (22/40)	-
Age	18.83 (1.04)	71.61 (3.66)	-
Years of education	12.89 (0.41)	16.18 (2.49)	< .001
DSST score	68.86 (9.79)	54.95 (10.20)	< .001
MHVT score	15.75 (3.67)	24.03 (3.68)	< .001
Baseline cardiovascular indices[2]			
Heart rate (bpm)	80.77 (12.46)	68.22 (9.73)	< .001
Ln RMSSD	3.54 (0.55)	2.74 (0.58)	< .001
Ln HF-HRV	6.43 (1.13)	4.28 (1.10)	< .001
IPANAT scores[3]			
Single task	0.65 (2.20)	1.20 (2.17)	.156
Dual task	0.37 (2.00)	1.18 (2.42)	.044
Secondary task			
Response time (ms)	1061.12 (128.19)	1249.18 (127.36)	< .001
Error rates (%)	1.51 (3.26)	2.27 (3.82)	.238

Note. All values except for N (M/F) are given as means (with standard deviations).

[1]Number of participants in each age group (males/females). [2]Heart rate and HRV values were available for 62 young and 55 older adults. [3]Composite scores in the IPANAT ranging from -9 for very negative to +9 for very positive.

Cognitive tasks

Emotional faces. Participants were presented with emotional and neutral faces obtained from the FACES database (Ebner, Riediger, & Lindenberger, 2010). The faces were displayed in pairs of one emotional and one neutral face presented side-by-side, one pair at a time. Based on previous findings suggesting that older adults show a stronger attentional bias toward happy and away from angry faces (e.g., Isaacowitz et al., 2006b), we opted for happy and angry facial expressions as the emotional stimuli in the current study to assess older adults' positivity and anti-negativity bias, respectively (for a face pair example, see Appendix B). We used an equal number of male and female, young and older, and happy and angry faces, and presented them in a pseudorandom order to ensure that no more than two pairs from the same gender, age group, and valence category were presented consecutively. The location of the emotional and neutral faces (left or right) was counterbalanced. Within each pair, the person depicted in both the emotional and neutral face instance was the same, with no single person appearing more than once throughout the task. Each pair remained on the screen for 5 s, followed by a 250-ms blank screen. The face pairs were preceded by a fixation cross presented for at least 750 ms on which participants had to fixate for the next trial to commence. The stimuli were presented on a 27-inch screen (grey background) with each face picture subtending a visual angle of approximately 25.8^{o} (height) × 20.9 ^{o} (width) at a 60-cm viewing distance.

Overall, participants were presented with 66 unique face pairs, 33 under single task conditions and the remaining 33 under dual task conditions. The first face pair in each list was included as a buffer and the remaining 32 face pairs were used in the analysis. For single task trials, participants were asked to look at the faces naturally, as if they were at home watching television (cf. Allard & Isaacowitz, 2008; Isaacowitz et al., 2006b). Under dual task conditions, participants had to view the faces while simultaneously performing an auditory 1-back working memory task. Single-digit numbers were played through speakers, each for 1 s and followed by an interstimulus interval of 1 s. Participants were instructed to press a key with the index finger of their dominant hand every time a number was repeated. Number onset was synchronised with the onset of the face pairs such that three numbers would be presented during each pair. Because the trial and, consequently, the first number onset would have been delayed if participants were not looking at the fixation cross within the first 750 ms, 1-back matches were programmed to occur only during the second or third number of a given trial. Numbers were presented in a pseudorandom order to ensure equal number of matches during happy-neutral and angry-neutral pairs. Participants' response times (RTs) and error rates on the 1-back task were recorded (see Table 4 for scores).

To assess the emotional bias in participants' fixations we calculated both a fixation count and a fixation duration ratio score based on previously published guidelines (Isaacowitz et al., 2006b). The ratio was calculated as (emotional - neutral)/(emotional + neutral). Hence, a ratio score of zero indicates no preference for emotional or neutral faces, a positive ratio score a preference toward emotional faces, and a negative score a preference toward neutral (away from emotional) faces.

Implicit affect. To examine whether HRV is related to emotionality, participants completed the Implicit Positive and Negative Affect Test (IPANAT; Quirin et al., 2009). At the end of each task (single and dual), participants were required to rate three nonwords (e.g., *TALEP*) based on how well they convey six different moods (happy, helpless, energetic, tense, cheerful, inhibited) by circling one option on a 4-point scale ranging from 1 ('doesn't fit at all') to 4 ('fits very well'). A different set of nonwords appeared at the end of each task. A composite affect score was created by subtracting the mean score for negative moods from the mean score for positive moods (see Table 4 for ratings). An implicit task was chosen as it has been shown to be more sensitive to changes in transient emotionality compared with explicit affect measures, and can accurately detect fluctuations in emotional states following mood manipulation (Abercrombie et al., 2005; Quirin et al., 2009). Furthermore, implicit tests require participants to use heuristic processes when giving their ratings which have been shown to better mirror affective states and are less subject to processing biases (e.g., social desirability) that can affect self-ratings in tests of explicit affect (for a review, see Quirin et al., 2009).

Eye tracking

Eye movements were recorded with an EyeLink 1000 desk-mounted eye tracker (SR Research, Mississauga, Ontario, Canada) at a 500 Hz sampling rate using the 'pupil with corneal reflection' setting. Participants were asked to place their chin on a chin rest approximately 60 cm from the screen to minimise head movements. Prior to each task, the eye tracker was calibrated using a 13-point calibration grid and subsequently validated for each participant. This procedure was repeated if the calibration/validation

was below the ‘good’ threshold. A fixation recording began each time the velocity of a saccade was below 30°/s for more than 100 ms and would stop each time this velocity threshold was surpassed (SR Research recommendation for cognitive research). Only fixations within the areas of interest were analysed.

HRV

HRV was measured at the beginning of the session. Data were recorded with a Polar H10 chest strap placed below the participants’ pectoral muscles and relayed to a Polar V800 watch (1000 Hz sampling rate; Polar Electro, Kempele, Finland). The present configuration has been shown to accurately record inter-beat (RR) intervals and produce HRV values that are highly consistent and comparable with an electrocardiogram when measures are taken at rest (D. Giles, Draper, & Neil, 2016). Conductive electrode gel (Signa gel, Parker Laboratories Fairfield, NJ, USA) was applied to the electrodes to improve contact. Participants were asked to sit with their knees bent at a 90° angle, feet flat on the floor, eyes closed, and hands on their thighs with palms facing up, for a period of 10 minutes (Laborde et al., 2017).

The raw RR recordings were loaded into Kubios Version 2.2 (Tarvainen et al., 2014) and were artefact-corrected using the ‘very low’ (450 ms) option of the program to avoid distorting natural variability. For HRV values, we calculated the root mean square of successive differences (RMSSD) and the high frequency component of HRV (HF-HRV) using the final five minutes of the 10-minute recording period (Task Force,

1996).[5] The HF-HRV component (frequency band: 0.15-0.40 Hz) was computed using a fast Fourier transformation. Across participants, less than 0.1% of RR intervals were identified as artefacts and corrected before further analysis. Prior to analysis, both RMSSD and HF-HRV values were natural log transformed to approximate a normal distribution (see Table 4 for means).

Procedure

Participants were asked to avoid consuming any food or drink (except for water) two hours before their scheduled visit to the lab as consumption of meals and caffeinated beverages is known to affect HRV indices (for a review, see Laborde et al., 2017). All participants reported to have abided by that condition. Upon their arrival, they provided written consent and demographic information. The HR strap was then attached to the participants and they were given instructions on what to do during the 10-minute resting HRV recording period. After this, participants completed a short practice.[6] This began with calibration and validation of the eye tracker, followed by one single and one dual task block (four face pairs each) to familiarise participants with the procedure and timings. The main experiment commenced after the practice and the task order (single task, dual task) was counterbalanced across participants. The eye tracker was calibrated and validated before each task. At the end of each task, participants were

[5]HRV indices for four older adults were calculated based on slightly earlier segments to avoid artefacts that were present near the end of the recording. Additionally, for one older and three young adults, the HRV recording was disrupted within the first five minutes of the 10-minute period. The recording was restarted without disrupting the participants and HRV indices were calculated using the final five minutes of the relaxation period, as per protocol.

[6]During the practice, participants also consumed an orange drink that contained either sugar or artificial sweetener. Drink had no appreciable influence on the results and was dropped from the analysis. See Appendix C for more information.

asked to give their affect ratings on the IPANAT. Finally, they completed the DSST and MHVT after which they were debriefed and compensated for their participation.

Results

Because the ratios of fixation count and fixation duration were highly correlated (all *r*s > .86, all *p*s < .001), only fixation count analyses will be reported below (see Appendix D for fixation duration graphs). Fixation count ratios were entered into a three-way mixed ANOVA with age (young, older) as the between-subjects factor, and emotion (happy, angry) and task (single, dual) as the within-subjects factors (see Figure 6 for means). This revealed a main effect of age, $F(1, 121) = 19.97$, $p < .001$, $\eta_p^2 = .142$, such that young adults looked more toward the emotional faces while older adults showed a preference toward the neutral faces. There was also a main effect of emotion, $F(1, 121) = 48.89$, $p < .001$, $\eta_p^2 = .288$, showing that participants looked more toward happy and away from angry faces, as well as a main effect of task, $F(1, 121) = 10.85$, $p = .001$, $\eta_p^2 = .082$, with participants exhibiting a preference toward emotional faces under single task conditions and a preference toward neutral during the dual task. These effects were qualified by an Age × Emotion interaction, $F(1, 121) = 5.62$, $p = .019$, $\eta_p^2 = .044$, showing that whereas no age difference was found for participants' preference for happy faces, $t(121) = 1.59$, $p = .115$), older adults showed significantly greater avoidance of angry faces compared with their younger counterparts, $t(121) = -4.05$, $p < .001$. An Emotion × Task interaction was also found, $F(1, 121) = 7.46$, $p = .007$, $\eta_p^2 = .058$: whereas participants' preference for angry faces was unaffected by task conditions, $t(122) = 0.40$, $p = .689$, their preference for happy faces was significantly

lower under dual than single task conditions, $t(122) = 4.67$, $p < .001$. There were no other interactions (both Fs < 2.22, all ps > .139).

To assess the magnitude of the PE, *t*-tests were used to evaluate whether ratio scores were different from zero (zero indicating no preference). Both young and older adults showed a preference for happy faces under single task conditions ($t(61) = 7.55$, $p < .001$ and $t(60) = 3.68$, $p < .001$, respectively), which disappeared for the dual task ($t(61) = 1.62$, $p = .111$ and $t(60) = 1.25$, $p = .216$, respectively). However, whereas young adults showed no preference for either angry or neutral faces during the angry-neutral pairs (single: $t(62) = -0.13$, $p = .895$; dual: $t(62) = -0.85$, $p = 397$), older adults exhibited a strong avoidance of angry faces under both single, $t(60) = -4.37$, $p < .001$, and dual task conditions, $t(60) = -5.27$, $p < .001$.

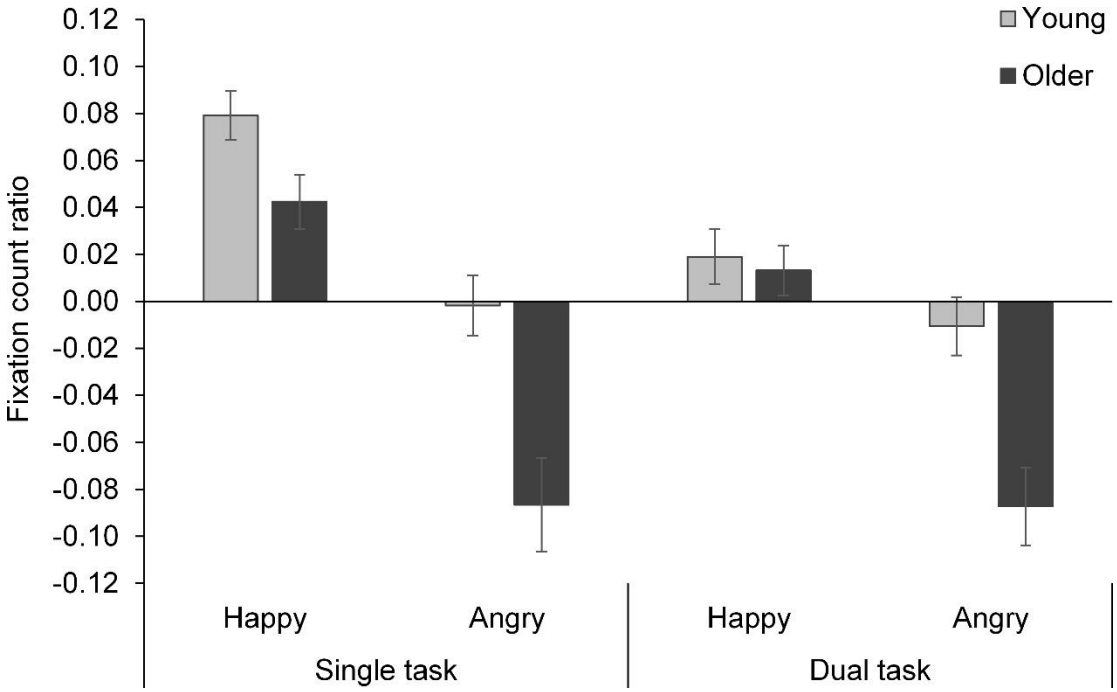

Figure 6. Fixation count ratio score (mean ± 1 standard error of the mean) during emotional-neutral face pair presentation as a function of age (young, older) emotion

(happy, angry) and task (single, dual) in Experiment 3. Zero signifies no preference, and a positive/negative ratio score shows preference toward/away from the emotional face.

Affect ratings (see IPANAT scores in Table 4) were entered into a two-way mixed ANOVA with age (young, older) and task (single, dual) as between- and within-subjects factors, respectively. This revealed a significant main effect of age, $F(1, 123) = 5.16$, $p = .025$, $\eta_p^2 = .040$, indicating that older adults gave more positive ratings than did young adults. There was no main effect of task and no interaction (both Fs < 1). There were no associations between participants' fixations and their affect ratings (all rs < .22, all ps > .093), nor were there any associations between HRV (as indexed by Ln RMSSD) and affect ratings (all rs < .1, all ps > .179).

Compared with young adults, older adults had lower baseline levels of HR, $t(115) = -6.02$, $p < .001$, and HRV (Ln RMSSD: $t(115) = -7.62$, $p < .001$, Ln HF-HRV: $t(115) = -10.41$, $p < .001$). Turning finally to the relationship between HRV and the PE, Figure 7 shows scatterplots of Ln RMSSD against the fixation count ratio for happy (left) and angry (right) face pairs under single (top) and dual (bottom) task conditions. Because Ln RMSSD and Ln HF-HRV were highly correlated, $r(117) = .94$, $p < .001$, only Ln RMSSD was used in the analysis as it is thought to be less affected by respiratory influences (Laborde et al., 2017). For young adults, there were no significant associations: $r(60) = -.229$, -.019, -.042, and -.017, for happy single, happy dual, angry single, and angry dual, respectively, with corresponding p values of .074, .881, .748, and .897. For older adults, the correlations for happy face pairs were similarly not significant: $r(52) = .090$, $p = .517$, for happy single; $r(53) = .111$, $p = .421$, for happy dual. However, for angry face pairs, the correlations were significant: $r(52) = -.429$, $p <$

.001, for angry single; $r(53) = -.373$, $p = .005$, for angry dual (these correlations survive adjustment to the critical p value to take account of multiple correlations). Moreover, the correlations for angry face pairs differed significantly between young and older adults under both single, $z = 2.18$, $p = .029$, and dual task conditions, $z = 1.97$, $p = .049$.

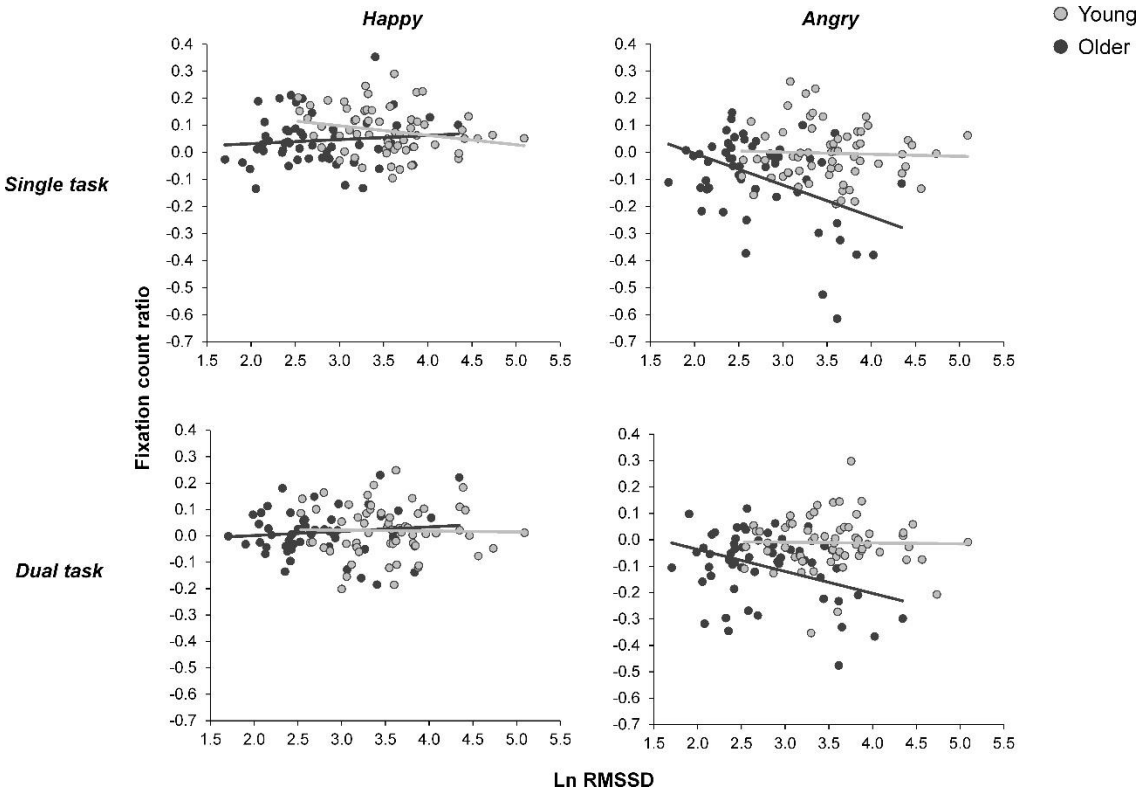

Figure 7. Association between baseline HRV (Ln RMSSD) and young and older adults' fixation count ratio during presentation of happy-neutral (left panels) and angry-neutral (right panels) face pairs under single task (top panels) and dual task (bottom panels) conditions in Experiment 3.

Discussion

Experiment 3 assessed the contribution of ANS functionality to young and older adults' preference for emotional faces and, more specifically, the relationship between individual differences in HRV and the age-related PE. As indicated by their gaze

preferences, both young and older adults were drawn toward positive faces, particularly in the single task condition. However, only for older adults did the PE also comprise an avoidance of negative faces, an anti-negativity bias that remained unchanged even under dual task conditions. In line with our predictions, higher HRV at rest was associated with a stronger PE in older adults, while no associations were found between HRV and emotional preference in young adults. Importantly, the HRV-PE relationship uncovered in older adults appeared specifically for the anti-negativity component of the PE, but not for their positivity bias. Higher HRV predicted greater anti-negativity when viewing angry-neutral face pairs under both single and dual task conditions.

Our study is the first to demonstrate that HRV can successfully predict older adults' PE. The Neurovisceral Integration Model (Thayer & Lane, 2000, 2009) suggests that HRV is an index of PFC's ability to inhibit the activity of subcortical regions (e.g., the amygdala), the arousal of the ANS and, consequently, individuals' capacity to regulate emotionality in a situation-appropriate way. In fact, high HRV levels at rest have been associated with stronger functional connectivity between brain areas responsible for emotion regulation across the adult lifespan (Sakaki et al., 2016) and improved emotion regulation capacity in young adults (e.g., Williams et al., 2015). In line with our expectations, higher HRV in our study predicted a more pronounced PE in older adults, and this association between HRV and PE was selectively found for their ability to avoid negativity rather than seek positivity. It has been suggested that the PE is related to older adults' ability to downregulate negative information, which is supported by findings of higher PFC activation and decreased amygdala activity in response to negative stimuli with increasing age (Nashiro et al., 2012; Sakaki et al., 2013). As HRV

is also related to other PFC-related functions such as response suppression/inhibitory control (Colzato & Steenbergen, 2017; Gillie et al., 2014; Segerstrom & Nes, 2007), the fact that higher HRV in our study was selectively associated with greater anti-negativity further supports the conceptualisation of HRV as an index of older adults' ability to avoid negative information and, potentially, as a proxy indicator of the connectivity between PFC and the amygdala (Sakaki et al., 2016).

It should be acknowledged that both HRV and gaze preference were unrelated to implicit affect, which complicates the interpretation of the PE as an emotion-regulation mechanism and, by extent, the relationship between HRV and emotionality. However, because of the brief nature of the cognitive task employed in our study, it is likely that the small changes in transient emotionality induced by emotional faces over a short period of time (approximately 3.5 minutes for each condition) did not have a pronounced effect on mood. Furthermore, we presented participants with a brief version of the IPANAT (three instead of six nonwords after each condition) which might have decreased the task's capacity to accurately measure emotionality. Although we found the expected age effect, with older adults giving more positive ratings than young adults, the IPANAT did not seem to be sensitive to manipulations of task difficulty. We suggest that researchers interested in the relationship between HRV, the PE and emotionality should consider employing more comprehensive measures of explicit and implicit emotion to address the connection between these constructs. Another possibility is that HRV is, in fact, primarily related to emotion regulation rather than emotionality as such. Our results indicate that there exists a relationship between HRV and the strategy that older adults employ to regulate emotions, such that those with higher HRV at rest avoid

negative stimuli more systematically than those with lower levels of HRV. High-HRV older adults might be more strongly affected by the presence of negative information and thus more likely to react to the presence of such material, whereas older adults with lower HRV might have a more blunted response to negative information and thus might be less likely avoid it. In other words, HRV might index how reactive older adults are to negative information rather than being directly related to affective outcomes. Although numerous studies have identified connections between HRV, negative affect and affective disorders (for a review, see Kemp & Quintana, 2013), further research examining how high- and low-HRV older adults respond to emotional information (e.g., electrodermal activity) could offer some interesting insights into this argument (also see Balzarotti et al., 2017, for a review of studies on HRV and emotional reactivity).

Similar to previous work (e.g., Grühn et al., 2007), older adults' PE emerged more consistently as an anti-negativity bias than as a positivity bias. The fact that the anti-negativity bias appeared unaffected by the secondary task manipulation could be attributed to the relatively undemanding nature of the distractor task used in the present study (Allard & Isaacowitz, 2008). In fact, participants' performance in the dual task was very high (approximately 1.9% error rate across the two age groups), which may explain why the anti-negativity bias remained intact. It would be interesting to further explore the relationship between HRV and the PE in a study that introduces a more cognitively demanding secondary task or cognitive paradigm.

Even more interestingly, whereas a clear relationship between HRV and anti-negativity was found in older adults, there was no association between HRV and emotional preference/avoidance in young adults. These findings provide further support

for the hypothesis that older adults use cognitive control (e.g., attention) to downregulate the potential influence of negative information on their affect (Mather & Carstensen, 2005; Mather & Knight, 2005). More importantly, to the extent that HRV is associated with emotion regulation, our study provides important evidence to suggest that older adults' PE is not simply a cognitive bias toward positive or away from negative material (see Isaacowitz & Blanchard-Fields, 2012), but represents an active attempt by older adults to regulate their emotions through selecting the information they attend to in order to minimise the affective impact of negativity. Furthermore, the absence of an HRV-emotional preference relationship in young adults suggests that young adults do not have chronically activated emotion regulation goals as do their older counterparts (Mather & Johnson, 2000), and that the ability of older adults to suppress negativity and, potentially, protect emotionality is directly dependent on the functionality of the ANS, which seems to determine the magnitude of their PE.

Overall, the finding that individual differences in HRV can predict the magnitude of the age-related PE could have important implications for older adults' health and well-being. Over the years, studies have found lifestyle factors, including exercise and dietary changes, to prominently affect HRV indices (for a review, see Kemp & Quintana, 2013). Recently, researchers have suggested that there exists a bidirectional relationship between HRV and emotion regulation, such that HRV is not simply a marker of emotion regulation capabilities but also a factor that influences the efficiency of emotional control through biological oscillations of the heart (see Mather & Thayer, 2018). This could mean that any lifestyle changes aiming to increase CV fitness could not only improve overall health, but also increase older adults' capacity to

inhibit negative emotionality and, potentially, improve their mental and psychological well-being. Building upon previous work proposing that individual differences in older adults' cognitive control capabilities might be the determining factor behind older adults' positivity preference (Mather & Knight, 2005), our results suggest that CV fitness and overall functionality of the ANS could be an equally important aspect of older adults' ability to downregulate negativity. Researchers interested in further exploring older adults' emotionality should adopt a more integrated approach that includes the evaluation of the synergistic effects of cognitive and physiological factors.

Chapter 5: Sugar Rush or Sugar Crash? A Meta-Analysis of Carbohydrate Effects on Mood

Abstract

The effect of carbohydrate (CHO) consumption on mood is at the centre of a long-standing debate, with researchers reporting both mood improvements and decrements following CHO ingestion. As global consumption of sugar-sweetened products has sharply increased in recent years, examining the validity of claims of an association between CHOs and mood is of high importance. We conducted a systematic review and meta-analysis to evaluate the relationship between acute CHO ingestion and mood. We examined the time-course of CHO-mood interactions and considered the role of methodological differences across studies (e.g., task preceding mood assessment) as moderator variables potentially affecting the CHO-mood relationship. Analysis of 174 effect sizes extracted from 29 studies (1225 participants) revealed no positive effect of CHOs on any aspect of mood at any time-point following their consumption. However, CHO administration was associated with higher levels of fatigue and less alertness compared with placebo within the first hour post-ingestion. These findings challenge the idea that CHOs can improve mood, and might be used to increase the public's awareness and inform health policies to decrease sugar consumption and promote healthier alternatives.

Meta-Analysis

Introduction

Over the last decades, consumption of sugar-sweetened soft drinks has increased dramatically. In the US alone, consumption of such drinks has increased by 135% from the 1970s to the early 2000s (Nielsen & Popkin, 2004). Similar findings have been reported in countries all over the world, including Germany, Spain and the United Kingdom (for a review, see Malik, Popkin, Bray, Despres, & Hu, 2010), with annual sales of energy drinks alone surpassing four billion EUR across Europe (490 million litres consumed; see Zucconi et al., 2013). Currently, soft drinks are the number one contributor of daily energy intake, accounting for more than 7% of energy consumption and representing the largest single source of calories in people's diets (Block, 2004). The widespread appeal of sugar-sweetened and energy drinks is associated with the marketing of these products as a way of combating fatigue, increasing energy and promoting a euphoric feeling. As the main ingredient in such drinks is sugar, research has focused on understanding how sugar-sweetened drinks, and CHOs in general, might promote cognitive facilitation and emotional well-being (for reviews, see Benton, 2002; Benton & Donohoe, 1999; Gibson & Green, 2002; M. A. Smith et al., 2011; Sünram-Lea & Owen, 2017).

Several influential studies have suggested that CHO ingestion might have mood-boosting properties. It has been observed that, compared with healthy populations, individuals suffering from affective conditions (e.g., seasonal affective disorder and depression) tend to 'self-medicate' by increasing their daily consumption of CHO-rich meals and beverages (R. J. Wurtman & Wurtman, 1989, 1995; J. Wurtman & Wurtman,

2018). On the other hand, recent studies have suggested that, on top of the metabolic health concerns associated with high levels of sugar consumption (e.g., Malik, Schulze, & Hu, 2006; Vartanian, Schwartz, & Brownell, 2007), high long-term consumption of CHOs has adverse effects on psychological well-being, even leading to higher rates of depression (Knüppel, Shipley, Llewellyn, & Brunner, 2017; Westover & Marangell, 2002). This ongoing debate has renewed the interest of researchers, media and the public in the relationship between sugar and mental well-being. As the trend for high consumption of sugary drinks shows no signs of abating, understanding the appeal of these products and the mental and physical health consequences of their consumption is of high priority.

Interestingly, despite researchers not having reached a consensus regarding the exact effects of sugar on mood, it seems that the public strongly believes in the idea that sugar improves mood ('Why is sugar so addictive?', 2013) and increases activity levels (especially in children; Furnham, 2018). Whereas it is generally accepted that children's 'sugar rush' is a myth (Wolraich, Wilson, & White, 1995), there is less agreement about the effect of sugar on mood. The purpose of the present review is to address the assertion that consumption of CHOs can affect mood. We begin by reviewing the theory behind the supposed neurobiological substrates of CHO-mood interactions, as well as the criticism that this framework has received over the years. We then present the current state of the field by discussing studies supporting and rejecting the claim that CHOs can improve mood, as well as how methodological differences among these studies could help explain these conflicting findings. Finally, we present a meta-analysis

where we investigate the relationship between acute CHO administration and mood, while also considering the effect of methodological moderator variables.

Carbohydrates and Mood: Mechanisms and Evidence

The rationale behind the assertions that CHOs improve mood has a strong physiological basis. Consumption of pure CHOs is associated with an increase in neurotransmitter synthesis and uptake in the brain. The serotoninergic system in particular is susceptible to CHO manipulations, and it has been suggested that the supposed effects on mood are related to fluctuations in serotonin availability following CHO ingestion (for a review, see Spring et al., 1987). It is well-established that serotonin and mood are intrinsically related, with the serotoninergic system being implicated in the aetiology of a number of mood disorders, including depression, mania, seasonal affective disorders, anxiety and aggression (for reviews, see Chaouloff et al., 1999; Marek, Carpenter, McDougle, & Price, 2003; Sandyk, 1992). Studies manipulating levels of tryptophan (a precursor to serotonin) using tryptophan depletion protocols have found low mood, increased irritability and aggression in human volunteers. However, restoring tryptophan levels has been shown to have antidepressant qualities and can reduce levels of aggression in human volunteers (for reviews, see Jenkins et al., 2016; Young & Leyton, 2002).

It has been observed that CHO administration is followed within one to two hours by a marked increase in tryptophan in the plasma and increased tryptophan and serotonin concentrations in the brain (Fernstrom, 1990; Fernstrom & Wurtman, 1971, 1972, Markus, 2007; Markus et al., 1998; Markus, Panhuysen, Jonkman, & Bachman,

1999; for a review, see Markus, 2008). As such, the supposed effects of CHOs on mood are posited to be related to the increase in serotoninergic activity following CHO ingestion. It should be noted that this serotonin surge is observed only when CHOs are consumed alone and not when ingested in combination with other macronutrients. Specifically, CHO meals and beverages containing as little as 5% protein do not increase tryptophan concentrations (Yokogoshi & Wurtman, 1986). Although the real-life applicability of the CHO-serotonin-mood relationship has been challenged because meals typically contain enough protein to suppress a CHO-related increase in tryptophan (for reviews, see Benton, 2002; Benton & Nabb, 2003; Spring et al., 1987), the majority of commercially available soft drinks do not contain any macronutrients other than CHOs. Considering the global increase in the consumption of CHO-rich soft drinks, investigating the extent to which sugar affects mood is an important step in understanding and managing the appeal of these products.

Over the years, evidence has been accumulating in support of the premise that CHOs can improve mood. For instance, Benton and Owens (1993) found that an increase in blood glucose levels after the consumption of 50 g of CHOs is associated with decreased levels of tension (see also, Smit et al., 2004). CHO administration has also been related to increased ratings of activation and arousal (Backhouse, Ali, Biddle, & Williams, 2007), higher alertness following a 2-hour fast (Owen et al., 2012), higher levels of subjective positive affect (Backhouse et al., 2005; Peacock, Thompson, & Stokes, 2012), lower levels of confusion (Lieberman et al., 2002) and tension (Lieberman et al., 2002; Markus, 2007), higher levels of clear-headedness (Smit et al., 2004), and less fatigue (Markus, 2007; Reay, Kennedy, & Scholey, 2006). Furthermore,

CHO ingestion has been shown to be related to increased calmness (Spring, Maller, Wurtman, Digman, & Cozolino, 1982), particularly following a long period of fasting (i.e., overnight fast; Owen et al., 2012).

The literature on CHO effects on cognition suggests that CHOs can improve cognitive functioning, particularly under circumstances where participants are asked to perform cognitively demanding rather than easy tasks (Scholey et al., 2009; Sünram-Lea et al., 2002a). When a task is particularly difficult, CHOs have been shown to improve participants' cognitive performance and increase their ability to deal with multiple task demands simultaneously (for a review, see M. A. Smith et al., 2011). In a similar manner, studies have found the protective effects of CHOs on mood to be more robust when participants perform demanding physical and cognitive tasks. In fact, whereas participants in control groups experience higher levels of tiredness after performing a cognitively demanding task, consumption of CHOs seems to protect subjective ratings of energy against a potential drop-off after high cognitive exertion (Benton & Owens, 1993; Owens et al., 1997). Additionally, exogenous energy supply in the form of CHOs has been shown to increase vigour and reduce fatigue under conditions of increased physical stress/exercise (Ali et al., 2017; Lieberman et al., 2002; Markus, 2007; Welsh et al., 2002) and cognitive demands (Owens et al., 1997; Smit et al., 2004). Therefore, it has been hypothesised that, similar to cognition, mood improvement following CHO administration is stronger when participants have to perform demanding cognitive or physical tasks (for a review, see Benton, 2002).

Furthermore, consumption of CHO-rich foods (i.e., meals with a high CHO-to-other-macronutrients ratio) has been found to have a protective effect against increases

in subjective ratings of depression and performance-related declines in vigour, specifically in individuals prone to stress (Markus et al., 1998, 1999). Meals high in CHOs can also decrease levels of fatigue compared with meals high in protein (Lloyd, Rogers, Hedderley, & Walker, 1996) or compared with an inert placebo following a period of cognitive exertion (Sihvola et al., 2013). Additionally, whereas consumption of low-CHO diets over long periods increases depression, tension, anger and fatigue (Deijen, Heemstra, & Orlebeke, 1989), CHO-rich diets can lead to lower hypothalamic-anterior pituitary-adrenocortical axis stress response (Anderson et al., 1987; Blass, 1987; Drewnowski, Krahn, Demitrack, Nairn, & Gosnell, 1992), suggesting that CHOs might have a protective effect against stress and depression (Dallman et al., 2003; R. J. Wurtman & Wurtman, 1989, 1995). Similarly, it has been found that self-reported levels of daily CHO intake are negatively associated with depression ratings (de Castro, 1987). Researchers have hypothesised that the relationship between CHO-rich meals, serotonin and mood is so potent that CHO meals are consumed as ‘comfort foods’ by individuals suffering from mood or affective disorders in an effort to improve their mood (for a review, see Wurtman & Wurtman, 2018).

Despite the intuitive appeal of the serotoninergic hypothesis and the literature reporting CHO effects on several mood aspects, there are also studies investigating CHO-mood interactions that have reported conflicting findings. Over the last three decades, an increasing number of empirical reports have suggested that ingestion of CHOs does not lead to any pronounced increases in subjective mood and overall affect, but can even have detrimental effects on mood (Adan & Serra-Grabulosa, 2010; Brody & Wolitzky, 1983; Duckworth, Backhouse, & Stevenson, 2013; G. E. Giles, Avanzato,

Mora, Jurdak, & Kanarek, 2018; G. E. Giles et al., 2012; Green et al., 2001; Harte & Kanarek, 2004; Howard & Marczinski, 2010; Jones & Sünram-Lea, 2008; Jones et al., 2012; Miller et al., 2013; Miller, Bourrasseau, Williams, & Molet, 2014; O'Neal et al., 2013; Owen et al., 2013; Pivonka & Grunewald, 1990; Qin et al., 2017; Reid & Hammersley, 1995, 1998; Riby et al., 2004; Scholey et al., 2014, 2009; Scholey & Fowles, 2002; Scholey & Kennedy, 2004; Seo et al., 2014; Stollery & Christian, 2013; Sünram-Lea et al., 2011; Ullrich et al., 2015; van der Zwaluw et al., 2014; Zacchia, Pihl, Young, & Ervin, 1991). Researchers have acknowledged the complicated nature of the results and have challenged the reliability of CHO effects on mood (Benton, 2002; Bernard et al., 2018). Whereas CHO effects on cognition are strong and well-documented (Messier, 2004; Riby, 2004; M. A. Smith et al., 2011), the effects of CHO administration on mood are not as dependable, a finding that could be attributed to a number of factors including the diverse methodologies employed by researchers to assess CHO-mood interactions.

Methodological Considerations

Time-Course of CHO Effects

Even a quick scan of the literature reveals vast methodological differences across studies. One of the main factors influencing the reliability of the CHO-mood relationship might be related to the time-course of CHO effects. The serotoninergic mechanism that is supposed to underlie CHO-mood interactions can provide us with a plausible timeframe based on which we can infer the magnitude of the effects of CHOs at different time-points. Considering that a reliable increase in tryptophan availability

and serotonin synthesis occurs beyond the first hour post-CHO consumption (Fernstrom & Wurtman, 1971; Markus, 2007; J. Wurtman et al., 2003), it can be expected that CHO effects would be particularly pronounced around the 1- to 2-hour mark. In line with this theory, some studies have reported beneficial effects of CHO on mood 60 minutes post-ingestion (e.g., Ali et al., 2017; Lieberman et al., 2002; Markus, 2007; Reay et al., 2006; Smit et al., 2004). However, mood-boosting effects of CHOs have been observed as early as 15, 30 and 45 minutes after consumption (Benton & Owens, 1993; Owen et al., 2012; Smit et al., 2004), suggesting that there might be additional, faster-acting mechanisms mediating the CHO-mood relationship other than the influence on the serotoninergic system. In fact, CHO ingestion has been associated with a cascade of physiological effects, including alterations in neural and peripheral metabolism, and increased synthesis of neurotransmitters other than serotonin (Korol & Gold, 1998; Riby, 2004), all of which could be plausibly related to mood enhancement.

CHO Type

Additionally, studies assessing the effects of CHO on cognition and mood have administered a wide variety of CHO types and doses, and have implemented different fasting intervals prior to CHO consumption to investigate the optimal conditions under which CHO effects are most prominent. Although the majority of studies in the area routinely administer glucose (Mantantzis, Maylor, & Schlaghecken, 2018; Mantantzis, Schlaghecken, & Maylor, 2017; Scholey & Fowles, 2002; Sünram-Lea et al., 2001), a number of other reports have opted for sucrose (van der Zwaluw et al., 2014; Zacchia et al., 1991), fructose (Miller et al., 2013), galactose (Duckworth et al., 2013), and isomaltulose (Dye et al., 2010; Young & Benton, 2014). This methodological choice

could influence the magnitude of CHO-mood interactions as considerable differences exist in the way that each CHO is metabolised and converted into energy (Bantle et al., 1983; Rippe & Angelopoulos, 2013). As different CHO types are metabolised in distinct ways and within different timeframes, this should be taken into consideration when examining the potentially time-sensitive relationship between CHO and mood outcomes.

CHO Dose

In a similar way, CHO dose is an important factor whose influence has been systematically examined in previous studies (e.g., Sünram-Lea et al., 2011). Although recent work has suggested that CHO dose should be determined based on individual differences in glucoregulatory capacity and the cognitive/behavioural domain being examined (Owen et al., 2010), results from a meta-analysis suggest that 25 g of CHO is sufficient to observe facilitation effects on cognitive outcomes in both young and older adults (Riby, 2004). Studies on glucose, in particular, have shown that its effects on cognitive indices follow an inverted U-shape dose-response curve, suggesting that below and above a certain threshold glucose either has no effect on behaviour or can even lead to cognitive decrements (for a review, see Sünram-Lea & Owen, 2017). Although our knowledge of the moderating effects of CHO dose is limited to cognitive performance indices, it is possible that CHO effects on mood follow similar patterns. However, the selection of CHO doses in published reports is not always justified or adequately explained by researchers.

Fasting Interval

In addition, studies have used various fasting intervals prior to CHO administration, ranging from no fasting (e.g., Reid & Hammersley, 1998) to 2-hour (e.g., G. E. Giles et al., 2012) and overnight fasting restrictions imposed (e.g., 12 hours; Owen et al., 2013; Scholey et al., 2014). However, the moderating effect of fasting duration on CHO effects is not yet clear. In fact, one of the few studies investigating how fasting intervals affect CHO effects on mood has found calmness and alertness to be differentially affected by CHOs under different fasting restrictions (Owen et al., 2012). Specifically, whereas the CHO group's alertness ratings increased following a 2-hour fast, higher levels of calmness were found only for the CHO groups that were required to fast overnight. Although a 2-hour fast is usually the minimum requirement to observe CHO facilitation effects (for a meta-analysis, see Riby, 2004), a wide variety of fasting regimes is employed across studies measuring CHO effects on behaviour and the moderating influence of such methodological decisions is not as yet clear.

Tasks Preceding Mood Assessment

The relationship between CHO administration and mood is further complicated by the use of different testing conditions and tasks preceding the evaluation of mood. A range of experimental paradigms have been employed to assess the effects of CHO on behavioural outcomes, with effects on mood assessed after cognitively (Scholey et al., 2014, 2009) and physically demanding tasks (Ali et al., 2017; Backhouse et al., 2007; O'Neal et al., 2013), stress-inducing procedures (Markus, 2007), and periods of inactivity during which participants are not asked to perform any tasks (Reid & Hammersley, 1995, 1998). This poses a problem for the investigation of mood effects as activity prior to mood assessment is likely to affect mood ratings. Furthermore, as the

facilitation effects of CHOs are suggested to be more reliable in the cognitive domain (for a review, see Bernard et al., 2018), some studies assess mood as a variable of secondary importance, without appropriate justification as to why such measures are included and no a priori hypotheses with regards to expected mood outcomes. More importantly, the focus on cognitive outcomes means that sample sizes are selected based on the number of participants needed to observe CHO-related cognitive facilitation. It has been proposed that the effects of CHOs on mood are relatively small and observable only with large sample sizes (Benton & Owens, 1993; for a review, see Benton, 2002). As a result, studies assessing CHO effects on mood as a secondary outcome are potentially not adequately powered to identify such effects, potentially increasing the number of false negatives in published reports. A more systematic review of the literature and meta-analytic attempts are urgently needed.

The Current Study

Overall, the research area of CHO-mood interactions is surprisingly complicated, owing to methodological differences identified across empirical reports. Our goal was to investigate the relationship between CHO consumption and mood by using synthesis methods to group and analyse results from all available studies assessing CHO-mood interactions. We set out to examine whether the assertion that CHOs improve mood is robust, or whether this perception is guided by a small number of influential studies reporting a positive relationship. There have been several reviews of the CHO-mood relationship (Benton, 2002; Benton & Donohoe, 1999; Benton & Nabb, 2003; Bernard et al., 2018; Gibson & Green, 2002; van de Rest et al., 2017) but this is the first attempt at using synthesis methods to deconstruct exactly how CHOs affect mood. The purpose

of the present meta-analysis is to analyse all available data to see how different mood constructs are affected by CHOs and how methodological decisions can help us understand the discrepant nature of published findings. It should be noted that the diverse methodological choices of published studies complicate the use of synthesis methods and the grouping of effect sizes from different studies. This not only relates to the type of CHOs used, the doses, or the timeframe of mood assessment following CHO ingestion, but also to the use of different mood assessment tools to investigate similar mood constructs (Polak et al., 2015).

Therefore, we will provide an overview of the methodologies used in studies assessing CHO-mood interactions and aim to systematically disentangle the effect of moderating variables on the CHO-mood relationship. First, if the effects of CHOs are related to fluctuations in serotonin synthesis and availability, we expected that strong CHO-mood interactions would appear beyond the first hour post-CHO ingestion. As the serotoninergic system has been shown to regulate depression, anxiety and aggression, we expected the effects to be more reliable for mood constructs related to these specific aspects of emotionality. However, if CHO effects on mood are related to other mechanisms, it is possible that stronger CHO-mood interactions would be obtained at earlier time-points and for different mood constructs (e.g., fatigue and alertness). Investigating the time-sensitivity of CHO-mood interactions will provide us with a better understanding of the time-course of CHO effects: do people experience a temporary ‘sugar high’ following CHO ingestion that fades within the first hour post-CHO consumption (e.g., Benton & Owens, 1993), or are the beneficial effects of CHOs

more likely to appear hours after ingestion because of the influence of the serotoninergic system?

Second, if the suggestion that most individual studies are potentially underpowered to detect statistically significant CHO-related mood fluctuations is valid, we would not expect to see strong effects of CHO on mood in the individual reports included in this meta-analysis. However, the synthesis methods should allow us to examine how even small trends identified in individual studies can potentially be combined to provide a clear picture of how CHOs affect different aspects of mood. Finally, it was expected that the methodological differences between studies would lead to highly variable results as evidenced by high levels of heterogeneity in the meta-analyses.

Method

Search Strategy

A comprehensive literature search was conducted to identify empirical articles and original research addressing the CHO-mood relationship in the following databases: MedLine/PubMed, Scopus and Web of Science. Titles, abstracts and keywords were scanned in each database using the following search terms: *(carbohydrate* OR glucose OR dextrose OR galactose OR lactose OR sucrose OR fructose OR macronutrient* OR sugar* OR sweet*) AND (supplement* OR consume* OR admin* OR ingest* OR drink* OR eat*) AND (mood OR emotion* OR affect* OR alert* OR excite* OR elat* OR happy* OR happi* OR content* OR seren* OR relaxe* OR calm* OR fatigue* OR letharg* OR depress* OR sad* OR upset* OR stress* OR nervous* OR tense OR*

tension OR tired) AND (random*) AND (placebo*).* The final literature search was completed on August 21st, 2017.

The asterisk symbol at the end of search terms is a wildcard character that permits the inclusion of all variations of words starting with the same letters. For example, the search term *content** would additionally retrieve words such as *contented, contentedness* and *contentment*. The literature search was further limited to peer-reviewed articles published in scholarly journals and written in English, and studies conducted with human participants, when the databases offered such options. A forward and backward literature search was also performed on all eligible articles and reviews to identify relevant studies not found during the initial literature search. The search terms relating to mood constructs were chosen based on the affect circumplex model outlined in Barrett and Russell (1999). A flowchart describing the literature search process is presented in Figure 8.

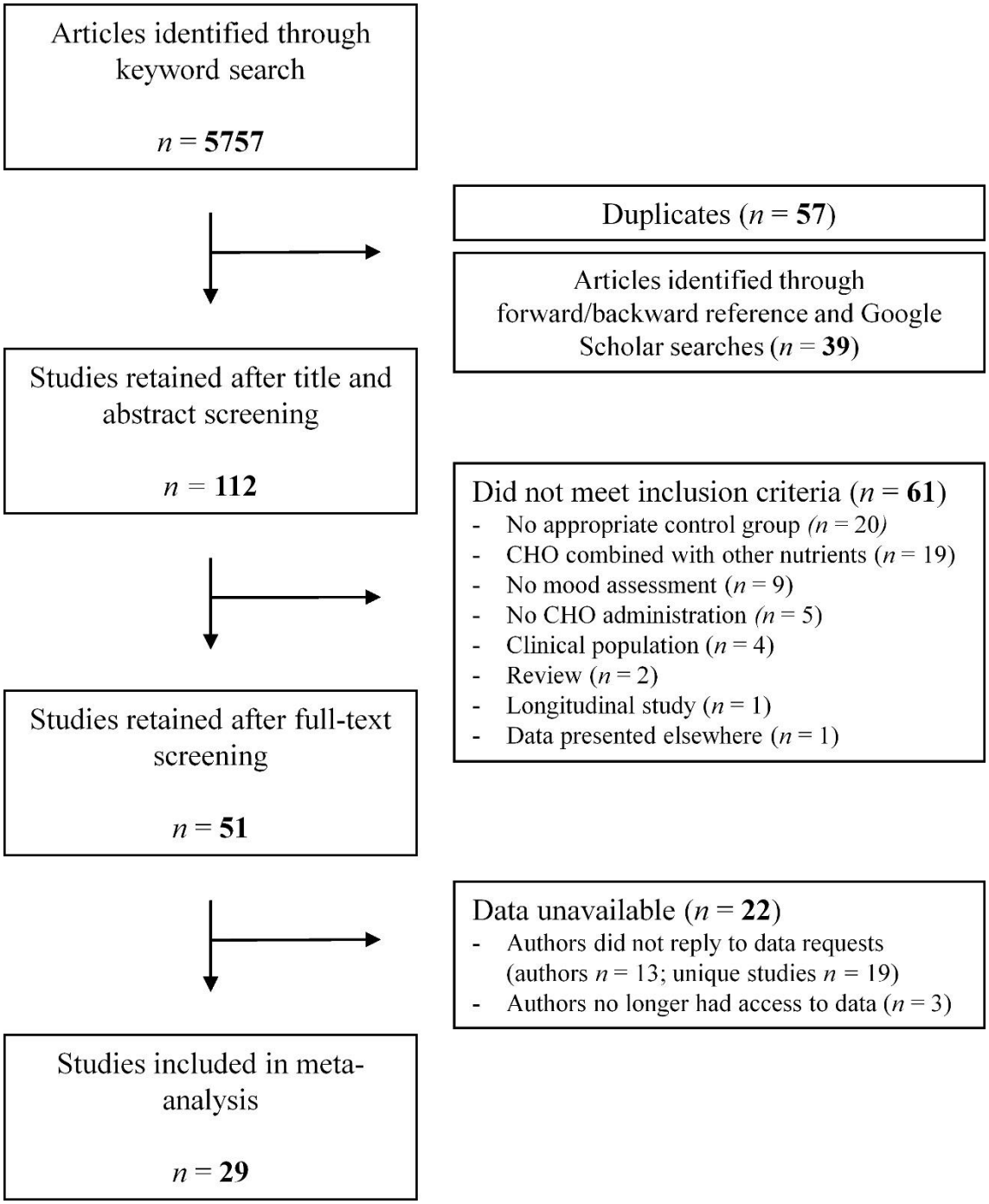

Figure 8. Meta-analysis literature search flowchart.

Inclusion and Exclusion Criteria

For a study to be included, the following criteria had to be met: 1) must be a randomised controlled trial, 2) must include a sample of healthy adults over the age of 18, 3) must investigate the acute effects of oral administration of CHO, 4) must measure mood constructs using explicit mood assessment tests, 5) CHO treatments must be compared with an appropriate placebo (not containing CHOs). As the goal of the present meta-analysis was to investigate the acute effects of CHO administration on mood, studies examining the effects of long-term (longitudinal) CHO supplementation or empirical reports investigating the relationship between participant-reported CHO consumption and mood were excluded. Although we were interested in how administration of pure CHOs affects mood, we also considered studies administering CHOs combined with other constituents in cases where a comparison was made with an appropriate placebo that would allow us to make inferences regarding the effects of CHOs. For example, we included studies that compared CHO-and-caffeine treatments with a placebo condition containing the same dose of caffeine but no CHOs (e.g., Wesnes, Brooker, Watson, Bal, & Okello, 2017). Additionally, studies not providing enough information to calculate effect sizes had to be excluded from this meta-analysis if the authors had no access to the data or did not respond to requests. Characteristics of included studies can be found in Table 5.

Table 5

Characteristics of the Studies Included in the Meta-Analysis

Study	N (F)[1]	Mean age[2]	Design	Fast	CHO type	CHO dose	CHO compared with	Mood assessment	Time-bins (minutes)	Task preceding mood assessment	Notes
Adan & Serra-Grabulosa, 2010	36 (18)	21.1	Between	Overnight	Glucose	75 g	Water	VAS	0-30, 31-60, 61+	Rest, Cognitive	*SD*s calculated from *SEM* as: *SEM* $\times \sqrt{n}$
Ali et al., 2017	9 (0)	32.7	Within	Overnight	CHO[3]	7.5% CHO, 1.5 mL/kg every 12.5% of exercise completed	AS	FAS, FS, POMS	61+	Physical	Only final mood measurement considered because of multiple doses
Brody & Wolitzky, 1983	39 (-)	18.7	Between	Overnight	Sucrose	100 g	AS	NIMH	0-30, 61+	Rest	*SD*s were imputed based on note in the article that *SD*s amounted to 1/3 of the means
G. E. Giles et al., 2012	48 (31)	20.1	Between	2 hours	Glucose	50 g	AS	POMS	31-60, 61+	Cognitive	
G. E. Giles et al., 2018	105 (74)	22.5	Between	2 hours	CHO	38 g	AS	POMS	0-30, 61+	Cognitive	Combined effect sizes from told/not told groups
Green et al., 2001	26 (-)	18-40 range	Within	Overnight	Glucose	50 g	AS	VAS	31-60	Cognitive	Combined effect sizes from told/not told groups

Howard & Marczinski, 2010	32 (18)	20.1	Between	2 hours	Glucose	29.3 g for a 78-kg ppt	No drink	MFRS	31-60	Cognitive	Glucose drink was compared to a 'no drink' condition
Jones & Sünram-Lea, 2008	28 (-)	20.0	Between	2 hours	Glucose	25 g	AS	VAS	0-30	Cognitive	Mood measurements in the morning and the afternoon. Effect sizes calculated for morning session only
Jones et al., 2012	18 (13)	19.0	Within	Overnight	Glucose	40 g	AS	VAS	0-30, 31-60, 61+	Rest, Cognitive	
Lieberman et al., 2002	143 (0)	21	Between	2 hours	Maltodextrin	CHO 6%: 2.1 g/kg (36 mL/kg) CHO 12%: 4.2 g/kg (36 mL/kg)	AS	POMS	61+	Physical	Effect sizes calculated for final treatment only (2-h after previous meal)
Markus, 2007	37 (29)	18-25 range	Within	Overnight	CHO	40 g × 2	AS	POMS	61+	Stress	
Mets et al., 2011	24 (12)	21-35 range	Within	No restrictions	CHO (glucose + sucrose)	26 g	No drink	KSS	31-60, 61+	Driving	Glucose drink compared to a 'no drink' condition
Miller et al., 2013	36 (25)	23.3	Between	3 hours	Glucose, fructose	25 g	AS	Likert	0-30	Cognitive	
O'Neal et al., 2013	36 (13)	23	Within	At least 2 and no more than 4 hours	CHO	6% CHO (mean 847 mL): three aliquots at time 0, 20 & 40 mins	AS	POMS	61+	Physical	

Owen et al., 2012	30 (-)	20	Within	2 hours, overnight	Glucose	25 g, 60 g	AS	VAS	0-30, 31-60	Rest, Cognitive	Composite scores combining different fasting and dose conditions
Owen et al., 2013	24 (-)	20	Within	Overnight	Glucose	25 g, 60 g	AS	VAS	31-60	Cognitive	
Reay et al., 2006	27 (10)	21.9	Within	Overnight	Glucose	25 g	AS	VAS	31-60, 61+	Cognitive	*SD*s calculated from *SEM* as: $SEM \times \sqrt{n}$. Composite scores combining multiple mood assessment measurements falling within the same time-bin
Reid & Hammersley, 1995	38 (-)	18-55 range	Between	Overnight	Sucrose	40 g	AS	POMS	0-30, 31-60, 61+	Rest	
Reid & Hammersley, 1998	45 (45)	33.2	Between	No restrictions	Sucrose	40 g	AS	POMS	0-30, 31-60	Rest	Effect sizes calculated only for normal weight participants (45 out of 90)
Riby et al., 2004	20 (-)	68.8	Within	Overnight	Glucose	25 g	AS	Stress and Arousal Questionnaire	0-30, 31-60	Rest, Cognitive	
Scholey et al., 2014	114 (71)	34.8	Between	Overnight	Glucose	25 g, 60 g	AS	VAS, Stress and Fatigue, STAI	0-30, 31-60	Rest, Cognitive	Mistakes were found in the *SD*s of the published article and imputed

											values were used instead
Stollery & Christian, 2013	30 (12)	20.7	Between	Overnight	Glucose	50 g	AS	STAI	0-30	Cognitive	Effect sizes calculated only for group that was told nothing regarding the constituents of drink consumed
Sünram-Lea et al., 2011	30 (24)	20	Within	Overnight	Glucose	15 g, 25 g, 50 g, 60 g	AS	VAS	31-60	Cognitive	Composite scores combining different doses
Ullrich et al., 2015 (**Experiment 1**)	17 (0)	28.5	Within	2 hours	Glucose	25 g	AS	PANAS	61+	Cognitive	
van der Zwaluw et al., 2014	43 (27)	77.7	Within	Overnight	Glucose, Sucrose	Glucose: 50 g, Sucrose: 100g	AS	s-POMS	0-30, 61+	Rest, Cognitive	Effect sizes calculated only for glucose
Welsh et al., 2002	10 (5)	24.3	Within	Overnight	CHO	6% CHO, 5mL/kg at intervals (approximately 128 g of CHO)	AS	POMS	61+	Physical	Only final mood measurement considered because of multiple doses
Wesnes et al., 2017	24 (18)	22.5	Within	Overnight (breakfast provided before testing)	CHO in energy drink	27 g	Energy drink without CHO	POMS, VAS	61+	Cognitive	CHO + caffeine energy drink compared with caffeine-only drink (no CHO)
Young & Benton, 2013	112 (-)	21.8	Between	Overnight	Glucose	39 g	AS	POMS: Fatigue	0-30	Rest	Study not included in the meta-analysis as the only available

											effect size was an outlier
Zacchia et al., 1991 (**Experiment 1**)	44 (0)	22	Between	Overnight	Sucrose	35 g, 100 g	AS	POMS, STAI, SSS	31-60, 61+	Cognitive	Effect sizes calculated only for the 'sober' condition. Composite scores for doses and multiple mood assessments within a single time-bin

Note. AS = Artificial Sweetener; FS = Feeling Scale; FAS = Felt Arousal Scale; MFRS = Mental Fatigue Rating Scale; KSS = Karolinska Sleepiness Scale; STAI = Stress and Anxiety Inventory; PANAS = Positive and Negative Affect Schedule; s-POMS = short form of the Profile of Mood States. SSS = Stanford Sleepiness Scale

[1]Only the number of participants assigned to treatment groups of interest to the meta-analysis are presented (i.e., CHO and placebo/control). The '-' sign means that either no information on gender was present in the articles or that no information regarding the gender composition of the treatment groups of interest was available. [2]For studies not reporting the mean age of the sample, we present the age range provided in the published article. [3]CHO type was unspecified or a combination of different CHOs.

Mood Constructs

Reviewing all eligible articles, we found that most studies investigating CHO-mood interactions employed either the Bond-Lader Visual Analogue Scales (VAS; Bond & Lader, 1974) or the Profile of Mood States (POMS; McNair, Lorr, & Droppelman, 1971). Both mood assessment scales are widely used in nutritional research and have been found to be particularly sensitive to nutritional manipulations (for a review, see Polak et al., 2015).

Bond-Lader VAS. The VAS consists of 16 adjective antonym pairs (e.g., 'alert' – 'drowsy'). Each of the two mood states (forming an antonym pair) is placed at the end of a 100-mm horizontal line. Participants are asked to indicate where their current subjective experience falls along the continuum. Ratings are calculated as distance from the negative antonym in millimetres. Ratings on the individual item scales are combined to calculate composite mood scores to assess levels of 'alertness', 'contentedness', and 'calmness'.

POMS. The Profile of Mood States consists of 65 single items. Participants give their ratings on 5-point unipolar scales ranging from 0 (not at all) to 4 (extremely) to indicate their current subjective levels of affective experience for each item. Single-item ratings are grouped to create composite scores to evaluate both negative (i.e., 'tension/anxiety', 'depression/dejection', 'anger/hostility', 'fatigue/inertia', 'confusion/bewilderment') and positive (i.e., 'vigour/activity') aspects of mood.

As most eligible studies employed one of these two mood assessment tools, we used the composite mood constructs derived from the Bond-Lader VAS and the POMS

as the outcome measures in the present meta-analysis. With many studies reporting discrepant findings regarding the effects of CHOs on different mood items, it is possible that different facets of positive and negative mood would be differentially affected by CHOs and the supposed serotonin surge that accompanies their consumption. The inclusion of mood constructs from both scales allowed for a more comprehensive investigation of CHO-mood interactions across a number of positive and negative mood aspects. Data from empirical reports using other mood assessment tools to investigate CHO-mood interactions were grouped with the mood scales from VAS and POMS if an overlap between constructs was identified. For example, in the meta-analysis of the POMS 'tension/anxiety' construct, studies measuring anxiety and stress using tools other than the POMS were additionally included (e.g., Stress and Arousal Questionnaire, and Positive and Negative Affect Schedule, Riby et al., 2004, and Ullrich et al., 2015, respectively). If a study provided multiple measures of similar mood constructs, only the mood measure closest to the mood construct of interest was included in the meta-analysis. The grouping of constructs from different scales was based on research reporting associations between constructs and discussions among myself and my supervisors. See Table 6 for a summary of the outcomes and mood constructs that were combined.

Table 6

Mood Constructs Assessed in the Meta-Analysis and Combinations of Mood Outcomes Derived from Different Mood Assessment Tests

Mood constructs assessed	Combined with
Bond-Lader VAS	
Alertness	Activation, arousal, drowsiness, sleepiness
Calmness	Composed
Contentedness	Elation, happy, pleasure
Profile of Mood States	
Anger/Hostility	-
Confusion/Bewilderment	Clearheaded
Depression/Dejection	-
Fatigue/Inertia	Energetic, tired
Tension/Anxiety	Stress
Vigour/Activity	-

Effect Size Calculation

Effect sizes were calculated as standardised mean differences (SMDs) between CHO and inactive placebo. The mean difference between the two groups was divided by their pooled *SD* and further corrected for sample size-related biases using the Hedges and Olkin (1985) correction. To account for pre-treatment baseline differences in mood, effect sizes were calculated after adjusting for baseline mood levels or by using the change from baseline scores, if either was available in the included articles. If neither format was available, the authors were contacted and asked to provide this information. When the correlation between pre- and post-treatment mood ratings was not available, a default correlation coefficient of .5 was used to address the dependency of

measurements arising from the within-subjects nature of the pre- and post-treatment scores (see Borenstein, Hedges, Higgins, & Rothstein, 2009; Duke, Bègue, Bell, & Eisenlohr-Moul, 2013; Wampold et al., 1997). To assess the appropriateness of this default coefficient, we calculated the correlation between pre- and post-treatment mood ratings in one of the databases available (Jones et al., 2012), which produced an average coefficient of approximately .58 across all mood constructs.

Although calculating effect sizes using change from baseline scores provides a more powerful analysis as it removes individual variability in subjective mood ratings, in some cases only final values were available and, therefore, effect sizes were calculated based on that information alone. In the meta-analyses, effect sizes calculated using change from baseline scores and final values are presented together as there is no statistical reason to present them separately (Deeks, Higgins, & Altman, 2008). An effort was made to calculate effect sizes using statistics appropriate for each study design (i.e., *t*-tests for within-subjects designs, *M*s and *SD*s for between-subjects designs) but this was not always possible because of insufficient information in the published articles. Authors were contacted to provide the appropriate statistics but in cases of no replies or data being unavailable effect sizes were calculated based on the information reported in the published article.

If multiple mood assessment ratings were taken over the course of a single study visit (multiple assessment time-points), composite scores were created to address the dependency of measures (i.e., same participants providing measures on multiple outcomes). We used previously published recommendations on calculating the mean effect size and variance of the composite scores (Borenstein et al., 2009). The mean

effect size of the composite score ($\bar{Y}$) was calculated as the average of the effect sizes of the outcomes and the variance of the composite score as:

$$V_{\bar{Y}} = \left(\frac{1}{m}\right)^2 \left(\sum_{j=1}^{m} V_i + \sum_{j \neq k} (r_{jk} \sqrt{V_j} \sqrt{V_k})\right)$$

where *m* = number of outcomes combined, *V* = variance and *r* = correlation coefficient for each combination of outcomes. When the correlation between outcomes was unknown, a default conservative coefficient of .5 was assumed. The actual correlation coefficient was used for studies whose authors provided us with data. For studies giving participants multiple CHO treatments at intervals throughout a single experimental session (e.g., 10 g every 10 minutes), we calculated effect sizes only for the final mood measurement, after all individual doses had been consumed. If a study provided participants with different types of CHO, only one CHO type was included in the meta-analysis. This was done for within-participants studies to address the dependency of measures, but not for between-participants designs where different participants were assigned to different treatments.

Analytic Strategy

Analyses were performed in R using the 'metafor' package (Viechtbauer, 2010). Meta-analyses were conducted using random-effects models with Hedges *g*-corrected SMDs as the measure of effect size and 95% CIs. Mixed-effects models were used to evaluate the effect of moderators only when heterogeneity (Cochran's *Q* and I^2 statistics) was significantly high. Both random- and mixed-effects models were estimated using restricted maximum likelihood estimation. The Knapp and Hartung

(2003) adjustment was employed to account for the uncertainty in the estimation of residual heterogeneity. As the presence of outliers can significantly affect the strength and validity of meta-analyses (Viechtbauer & Cheung, 2010), studies were excluded from the pooled effect size estimate if their standardised residual *z* value was above the ± 2.5 threshold (Camfield, Stough, Farrimond, & Scholey, 2014). We only present random- and fixed-effects models for meta-analyses of mood items where at least three studies were available. As one of the main goals of this meta-analysis was to examine the time-course of CHO effects on mood, we assessed how the CHO-mood relationship changes over time by running separate meta-analyses for three time-bins covering immediate (0-30 minutes), short-term (31-60 minutes) and long-term (61+ minutes) effects of CHO consumption. If a study involved taking multiple mood measurements within the same time-bin (e.g., mood measured at 10 and 20 minutes post-CHO consumption), composite scores were created using the method described earlier. Moderator variables included CHO dose (higher or lower than 25 g), CHO type (e.g., glucose, sucrose, fructose etc.), fasting interval (e.g., no restriction, equal/less than 2 hours, and more than 2 hours before CHO administration), and the nature of the activity preceding mood assessment (e.g., physical task, cognitive task, rest). Two raters coded the moderator variables independently (all Cohen's $\kappa s > .889$). Coding differences were discussed among the raters and the supervisors until an agreement was reached.

To assess the impact of publication bias in our analysis ('file drawer' problem; Rosenthal, 1979), we created funnel graphs by plotting effect sizes against the standard error of the estimates and visually inspected them for signs of asymmetry that could be interpreted as an indication of publication bias. It should be noted that funnel plot

asymmetry is not always a sign of publication bias and it can also be associated with other factors, including chance (for a review, see Egger, Davey Smith, Schneider, & Minder, 1997). Begg's adjusted rank correlation (Begg & Mazumdar, 1994) and Egger's test (Egger et al., 1997) were employed to provide a quantitative index of publication bias. Similar to the visual examination of funnel plots, these statistical tests are not infallible as they are low-powered and are more appropriate when (a) heterogeneity is low (I^2 < 50%), (b) there are at least 10 studies included in each meta-analysis, with at least one study reporting statistically significant findings, and (c) the ratio of extreme variance across studies is greater than four (see Ioannidis & Trikalinos, 2007).

Results

Of the 5757 studies identified in the literature search stage, 51 met the inclusion criteria and were considered relevant to the present meta-analysis. However, 22 studies had to be excluded at the final stage because of data not being available or authors not replying to data requests (for a list of these studies, see Appendix E), leaving 29 studies (N = 1225) available for the meta-analysis (see Figure 8). Separate meta-analyses are presented for each of the three time windows, as specified in the method section.

Separate forest plots are presented for each mood construct. In the plots, we present the effect sizes and 95% CIs for all available studies assessing mood at each of the three time-bins, as well as the pooled effect size estimate, calculated separately for each time window. Results in the forest plots are presented such that 'favours CHO' or 'favours Pla' means that participants in the CHO or placebo group experienced more positive outcomes compared to the other group with regards to a particular mood construct. For example, if for the 'fatigue' construct the pooled effect size estimate

favours placebo, it should be interpreted as participants in the placebo group experiencing less fatigue (i.e., more positive outcomes) compared with the CHO group. Heterogeneity and publication bias statistics are presented in Table 7 and Table 8, respectively. It should also be noted that most of the random-effects models presented do not meet the criteria to ensure the robustness of the asymmetry tests (Ioannidis & Trikalinos, 2007) and, therefore, results on publication bias should be interpreted with caution.

Table 7

Number of Studies Available and Heterogeneity Statistics for Each Random-Effects Model in the Meta-Analysis, Assessed Separately for Different Mood Constructs and Time Windows

	Time window											
	0-30 minutes				31-60 minutes				61+ minutes			
Mood constructs	*k*	*Q*	I^2	*p*	*k*	*Q*	I^2	*p*	*k*	*Q*	I^2	*p*
Bond-Lader VAS												
Alertness	8	4.73	0.00%	.693	11	8.09	0.01%	.620	7	4.31	0.00%	.738
Calmness	7	4.83	0.00%	.566	9	2.39	0.00%	.966	4	5.50	43.94%	.139
Contentedness	7	2.62	0.00%	.855	8	5.22	0.00%	.634	5	1.93	0.00%	.748
Profile of Mood States												
Anger/Hostility	3	1.58	0.00%	.454	2	-	-	-	8	3.66	0.00%	.820
Confusion/Bewilderment	3	0.20	0.00%	.903	4	1.83	0.00%	.609	7	7.39	29.76%	.286
Depression/Dejection	3	1.35	0.00%	.508	3	0.06	0.00%	.971	9	10.32	24.89%	.243
Fatigue/Inertia	9	2.08	0.00%	.979	9	4.60	0.00%	.799	13	31.25	61.87%	**.002**
Tension/Anxiety	7	1.29	0.00%	.972	6	3.70	0.00%	.593	9	6.40	0.00%	.603
Vigour/Activity	2	-	-	-	2	-	-	-	9	14.38	43.54%	0.72

Note. Random-effects models were not conducted for mood constructs that had fewer than three studies available. *P* values are presented in bold if heterogeneity is significant.

k = number of studies included in the model; *Q* = Cochran's test of heterogeneity; I^2 = measure of heterogeneity; *p* = significance of Cochran's *Q* statistic.

Table 8

Publication Bias Tests (P-Values) for Random-Effects Models in the Meta-Analysis, Presented Separately for Each Mood Construct and Time Window

	Time window					
	0-30 minutes		31-60 minutes		61+ minutes	
Mood constructs	*Begg*	*Egger*	*Begg*	*Egger*	*Begg*	*Egger*
Bond-Lader VAS						
Alertness	.720	.345	.761	.570	.562	.181
Calmness	.239	.087	.761	.967	.333	.149
Contentedness	.381	.122	.548	.671	.083	**.003**
Profile of Mood States						
Anger/Hostility	1.00	.413	-	-	.905	.997
Confusion/Bewilderment	.333	.585	.333	.654	.773	.684
Depression/Dejection	1.00	.541	1.00	.867	.477	.809
Fatigue/Inertia	.761	.951	.477	.688	1.00	.887
Tension/Anxiety	.239	.277	.469	.791	.359	.767
Vigour/Activity	-	-	-	-	.920	.957

Note. P values in bold indicate significant publication bias.

Bond-Lader VAS

Alertness. Effect sizes and 95% CIs for the three time windows are presented in Figure 9. In all three time-bins (0-30, 31-60 and 61+ minutes), alertness was lower for CHO than for placebo. This difference was significant for the second time-bin (11 studies; $p = .028$), though not for the first (eight studies; $p = .194$) or the third (seven studies; $p = .343$). Heterogeneity for all time-bins was low and, therefore, no moderator analyses were conducted. No evidence of publication bias was found across the three alertness time-bins.

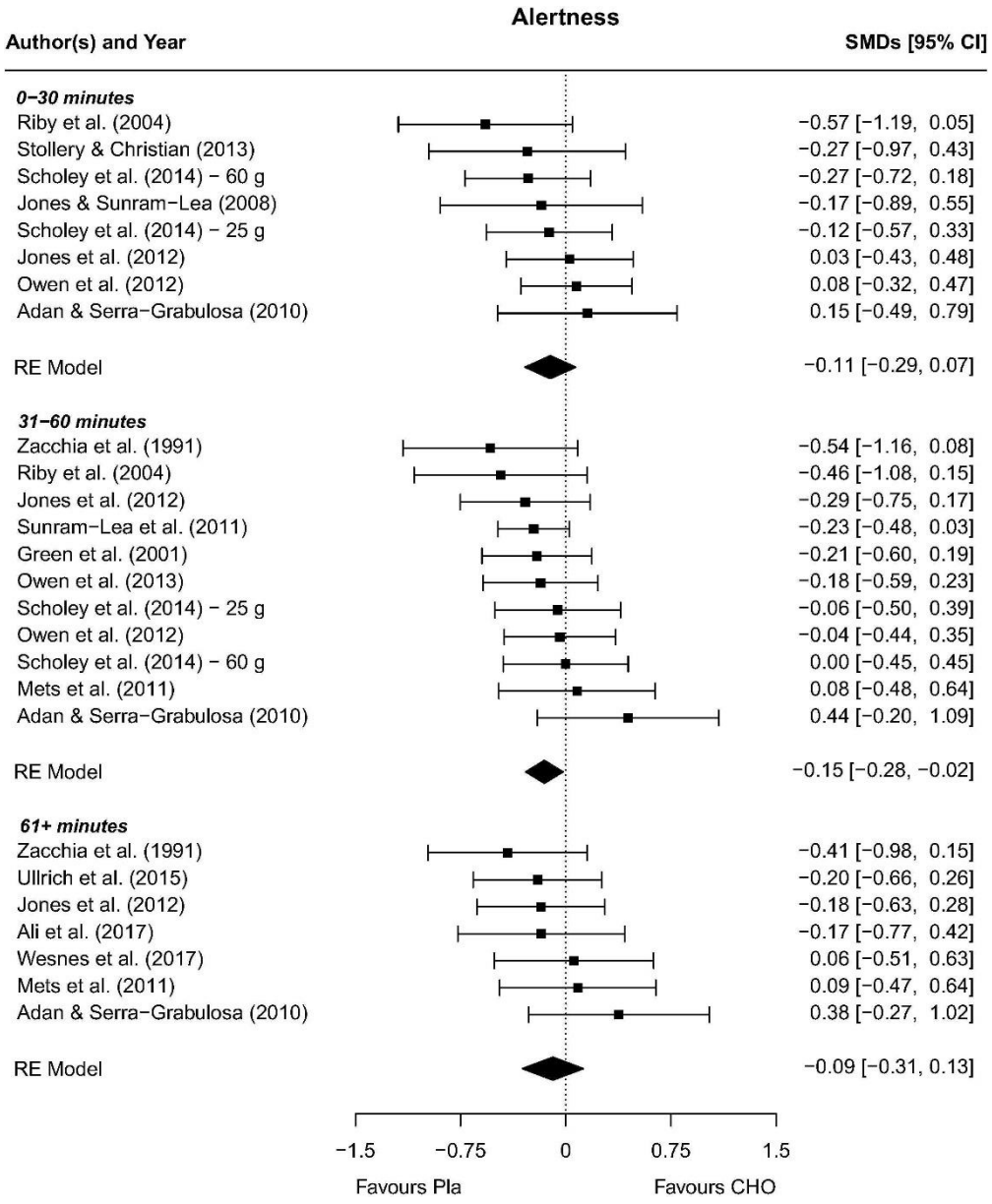

Figure 9. Forest plot of alertness effect sizes with 95% confidence intervals.

Calmness (Figure 10). Seven studies were included in the meta-analysis of the 0-30 minutes' time-bin. No evidence of increased calmness following CHO consumption was found (p = .391). For the 31-60 minutes' meta-analysis, nine studies were included. CHOs were shown to increase calmness compared with placebo but the effect was not significant (p = .201). For the 61+ minutes' time-bin, four studies were

included. The meta-analysis showed no evidence of increased calmness with either CHOs or placebo (p = .813). Heterogeneity was not significantly high and no evidence of publication bias was found.

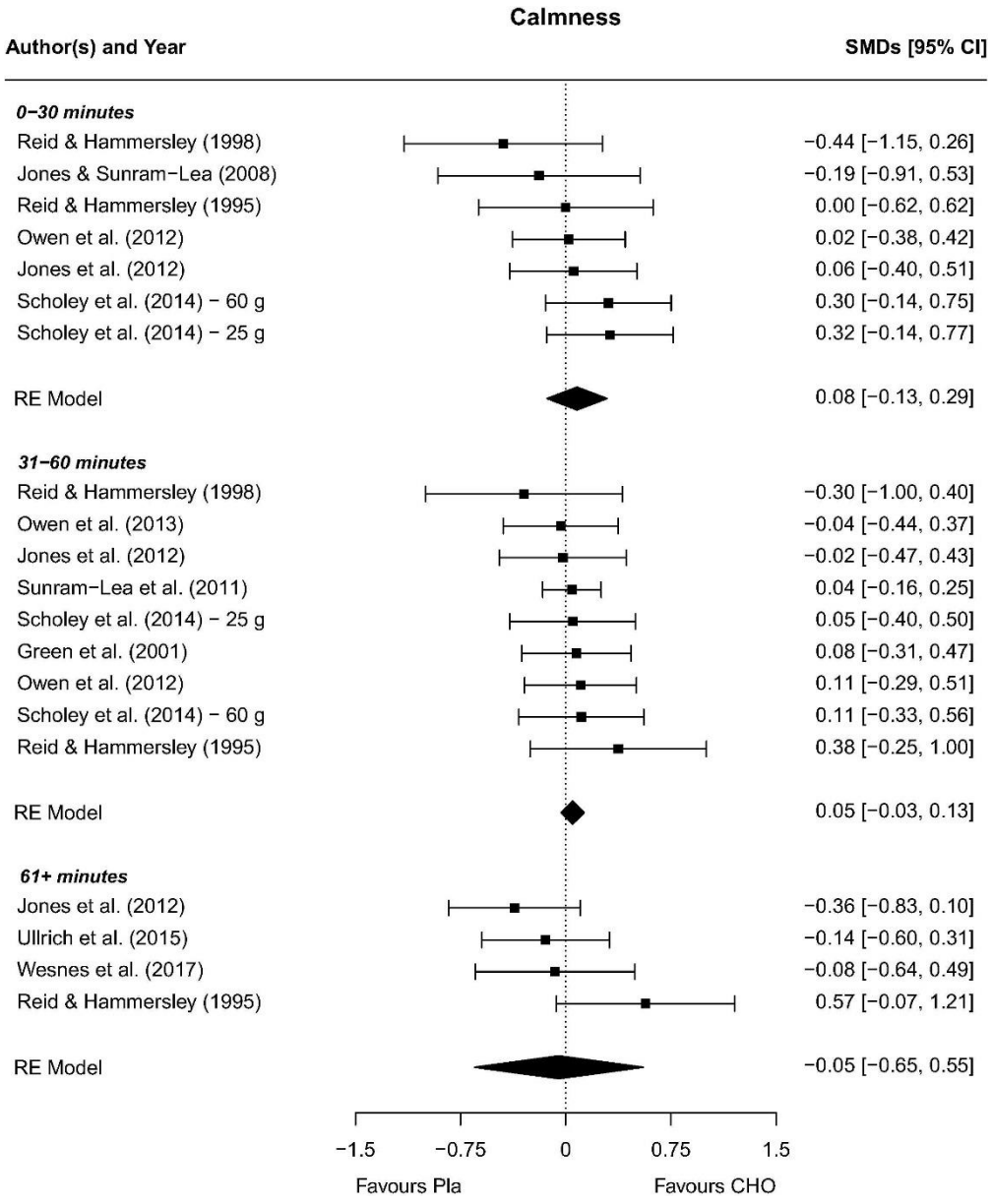

Figure 10. Forest plot of calmness effect sizes with 95% confidence intervals.

Contentedness (Figure 11). In all three time-bins, contentedness was higher for CHO than placebo. However, the difference was not significant in any of the time

windows (0-30 minutes: seven studies, p = .313; 31-60 minutes: eight studies, p = .600; 61+ minutes: five studies, p = .199). Although Begg's test did not show evidence of publication bias for any time-bins, Egger's test suggested significant publication bias for the 61+ time-bin. It should be noted that only five studies were included in the meta-analysis of the 61+ bin and so the results of Egger's test could be influenced by the low number of studies.

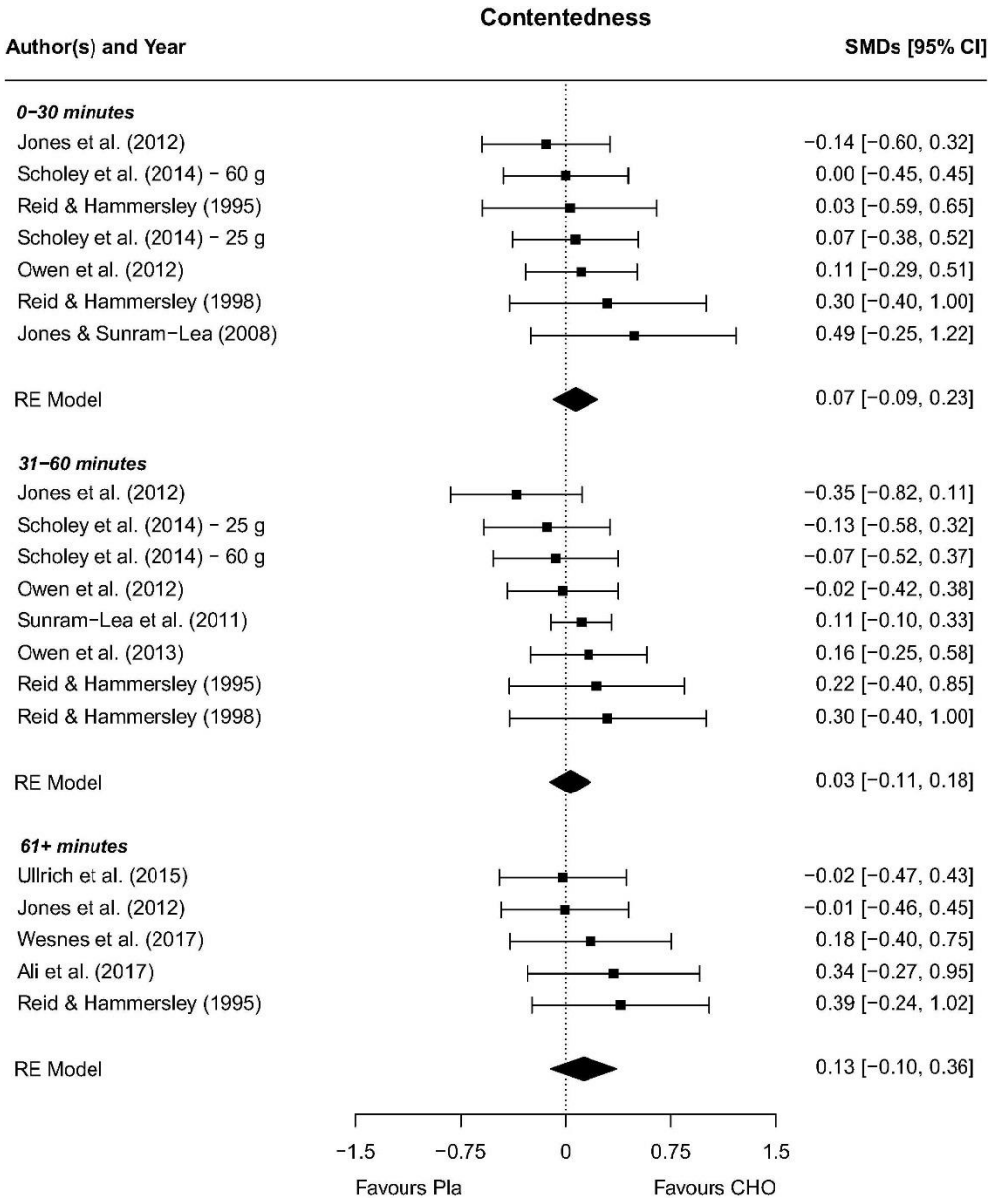

Figure 11. Forest plot of contentedness effect sizes with 95% confidence intervals.

POMS

Anger (Figure 12). For the 0-30 time-bin, three studies were included in the analysis. No evidence of fluctuations in anger was identified within the first 30 minutes post-CHO ingestion (p = .580). As there were only two studies available for the 31-60 time-bin, a meta-analysis was not conducted and the results will not be discussed. For the 61+ time-bin, eight studies were included in the model. Anger levels did not change as a result of ingestion of CHOs or placebo during this time window (p = .837). No evidence of high heterogeneity or publication bias was found.

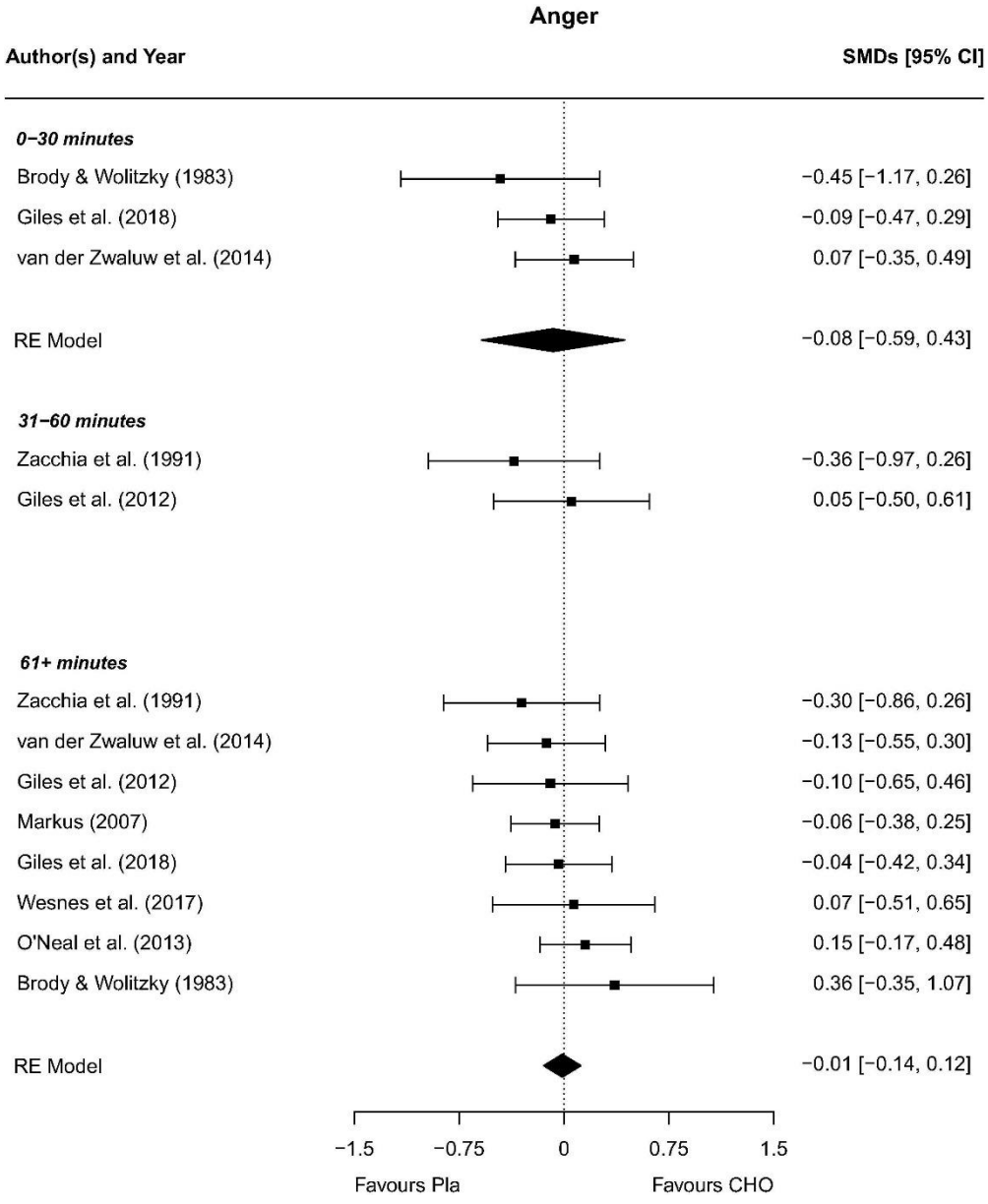

Figure 12. Forest plot of anger effect sizes with 95% confidence intervals.

Confusion (Figure 13). No effects of CHOs were found in any of the three time-bins. Confusion was lower in placebo compared with CHOs during the first two time windows, but the difference was not significant (0-30 minutes: three studies, $p = .096$; 31-60 minutes: four studies, $p = .435$). For the 61+ time-bin, seven studies were found to be relevant. Similar to the previous time-bins, confusion did not seem to be affected by

CHO administration compared with placebo (p = .927). Heterogeneity was low and no evidence of bias was obtained.

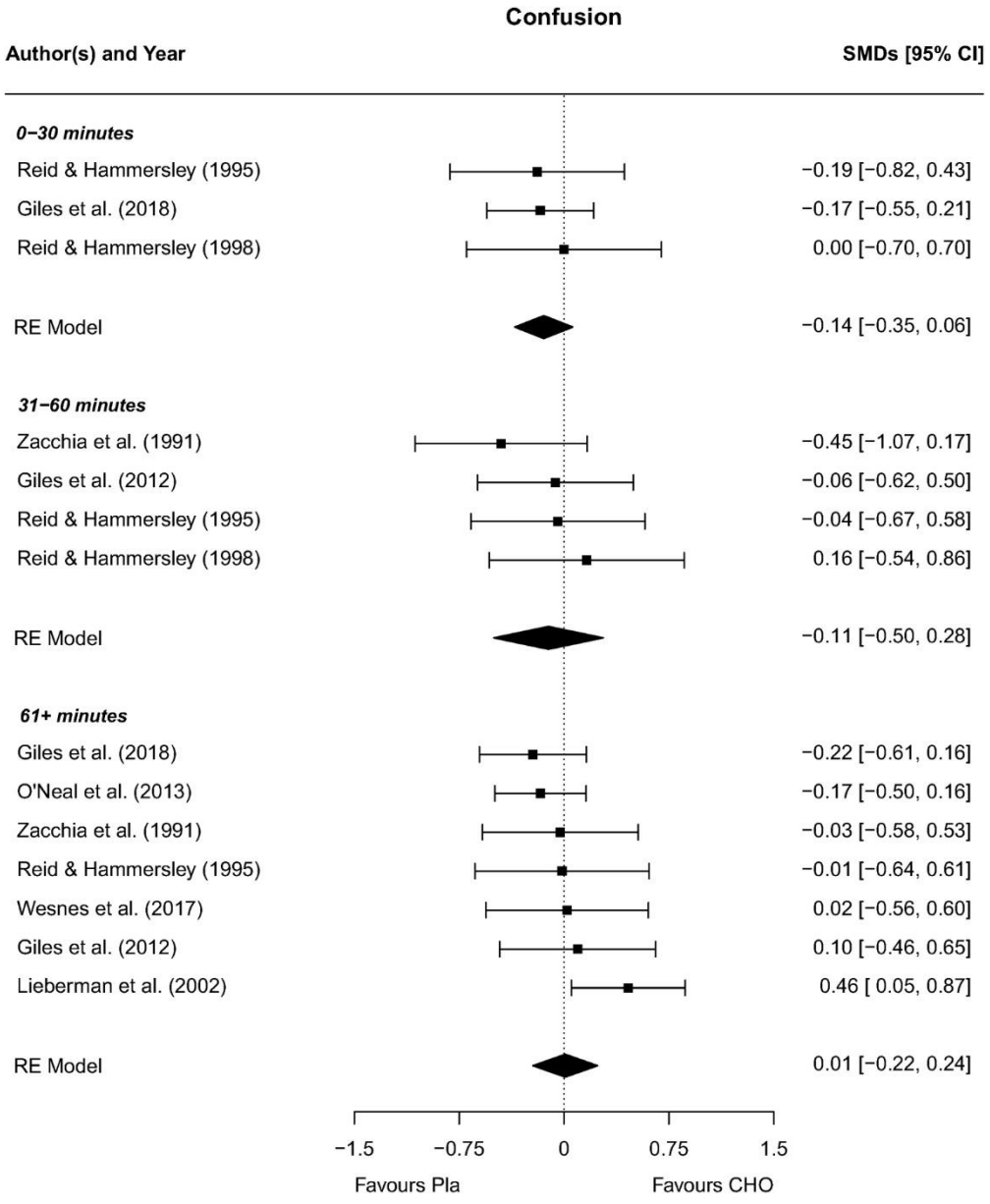

Figure 13. Forest plot of confusion effect sizes with 95% confidence intervals.

Depression (Figure 14). Depression levels did not appear to be affected by CHO or placebo consumption at any time-point. Depression was slightly lower with

CHOs during the first and third time-bin, but the difference was not significant (0-30 minutes: three studies, p = .694; 61+ minutes: nine studies, p = .742). A pattern of lower levels of depression for placebo compared with CHO was obtained during the 31-60 time window, but the observed difference failed to reach significance (three studies, p = .158). Heterogeneity was not statistically significant and no evidence of bias was identified.

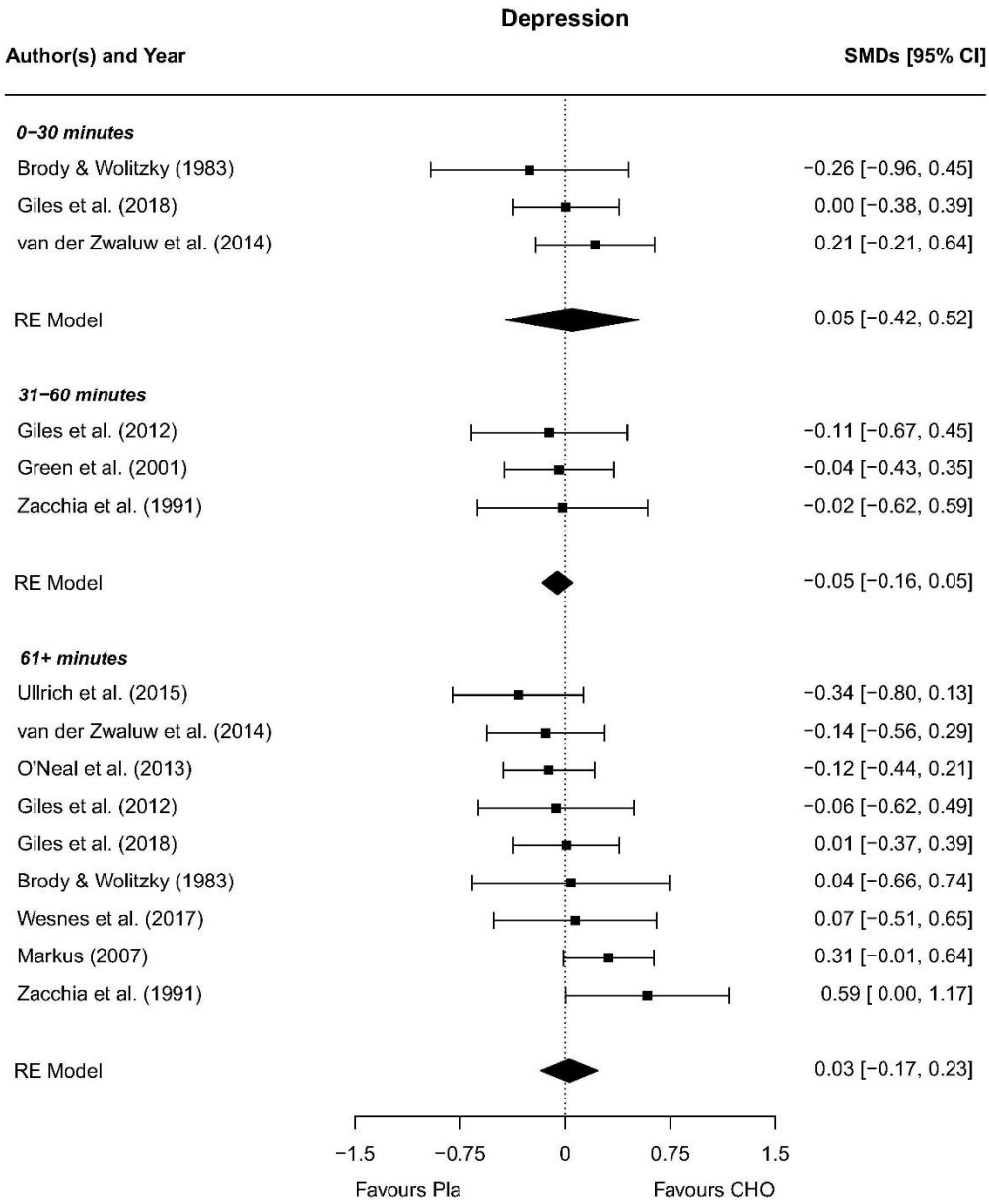

Figure 14. Forest plot of depression effect sizes with 95% confidence intervals.

Fatigue (Figure 15). For the 0-30 time window, 10 studies were initially available. However, the Young and Benton (2013) study had to be excluded as it was found to be an outlier (*z* value = 5.07, favouring CHOs), leaving nine studies in the analysis. The meta-analysis showed that participants receiving CHO reported significantly higher levels of fatigue compared with placebo across these studies (p = .011). For the 31-60 time-bin, nine studies were identified. Although a similar pattern to the 0-30 time window was observed (i.e., higher fatigue in the CHO group), the difference between CHO and placebo was not significant (p = .201). For the 61+ time-bin, 13 studies were available. In contrast to the previous time windows, a pattern of slightly lower fatigue with CHO treatments was found an hour after CHO ingestion, but this was not significant (p = .404). Whereas no heterogeneity was found for the first two time-bins, studies included in the 61+ time window showed significantly high levels of heterogeneity and moderator analyses were conducted to assess the influence of methodological discrepancies among these studies. Separate analyses were run for each moderator variable described in the method section. CHO dose, CHO type and fasting interval did not influence fatigue self-reports (all Fs < 1.67, all ps > .236). However, a trend was found for the type of task preceding mood assessment ($F(3, 9) = 3.14$, p = .080). Although this trend was not significant, further analysis revealed that CHO groups reported significantly less fatigue compared with placebo only after performing physically demanding tasks (b = 0.474, 95% CIs [0.04, 0.91], p = .037), and not after a cognitive task (p = .578) or a period of inactivity/rest (p = .517). A trend was also found for CHO groups to show lower levels of fatigue following a stress-inducing task (p =

.078), but only one study using a stressful task was included in the meta-analysis of fatigue at 61+ minutes.

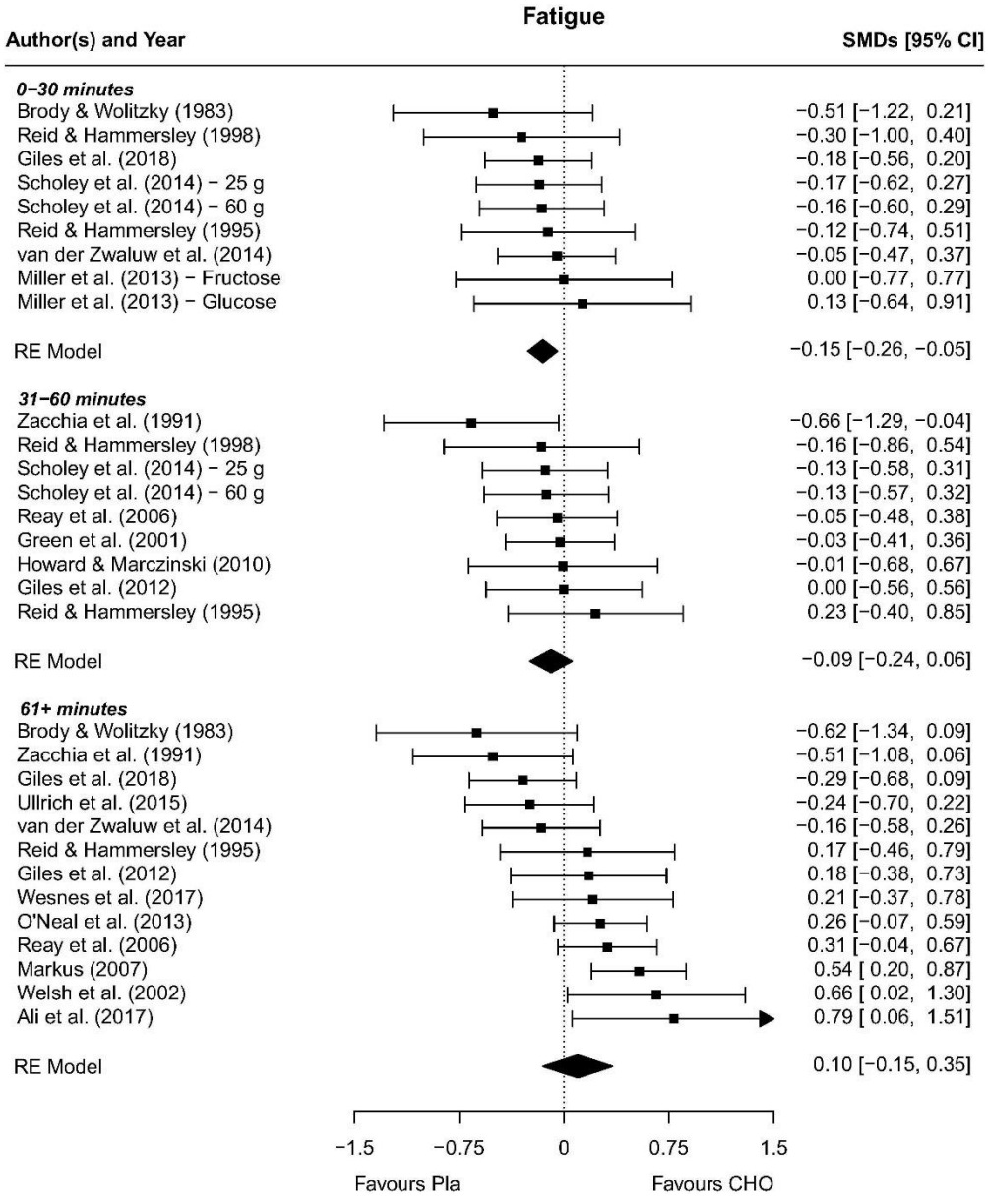

Figure 15. Forest plot of fatigue effect sizes with 95% confidence intervals.

Tension (Figure 16). For the 0-30 time-bin, seven studies were identified. Results showed that CHO treatments led to lower tension compared with placebo, but

the effect was not significant (p = .089). For the 31-60 time window, six studies were included in the analysis. Tension levels did not seem to be sensitive to CHO or placebo treatments during this time window (p = .794). For the final time-bin (61+ minutes), nine studies were identified as relevant. Similar to the previous time window, tension levels did not seem to fluctuate as a result of CHO or placebo administration (p = .605). No evidence of high heterogeneity or publication bias was found.

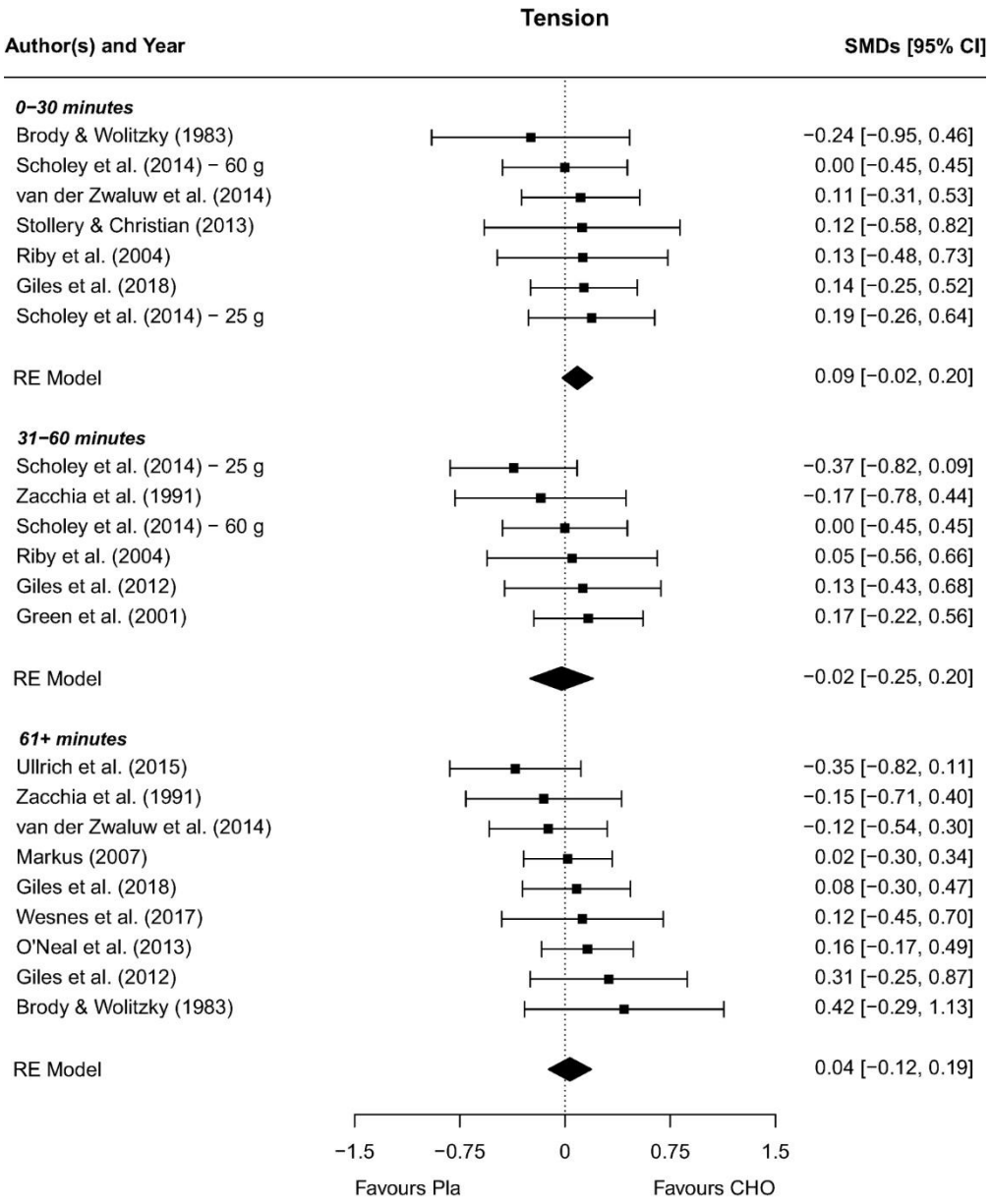

Figure 16. Forest plot of tension effect sizes with 95% confidence intervals.

Vigour (Figure 17). Both for the 0-30 and 31-60 time windows, there were only two studies available for each meta-analysis and, therefore, the results of the random-effects models are not presented. For the 61+ time-bin, nine studies were found and included in the meta-analysis. Consumption of CHOs did not have an appreciable effect on levels of vigour (p = .260). Heterogeneity was not significantly high and no evidence of publication bias was found.

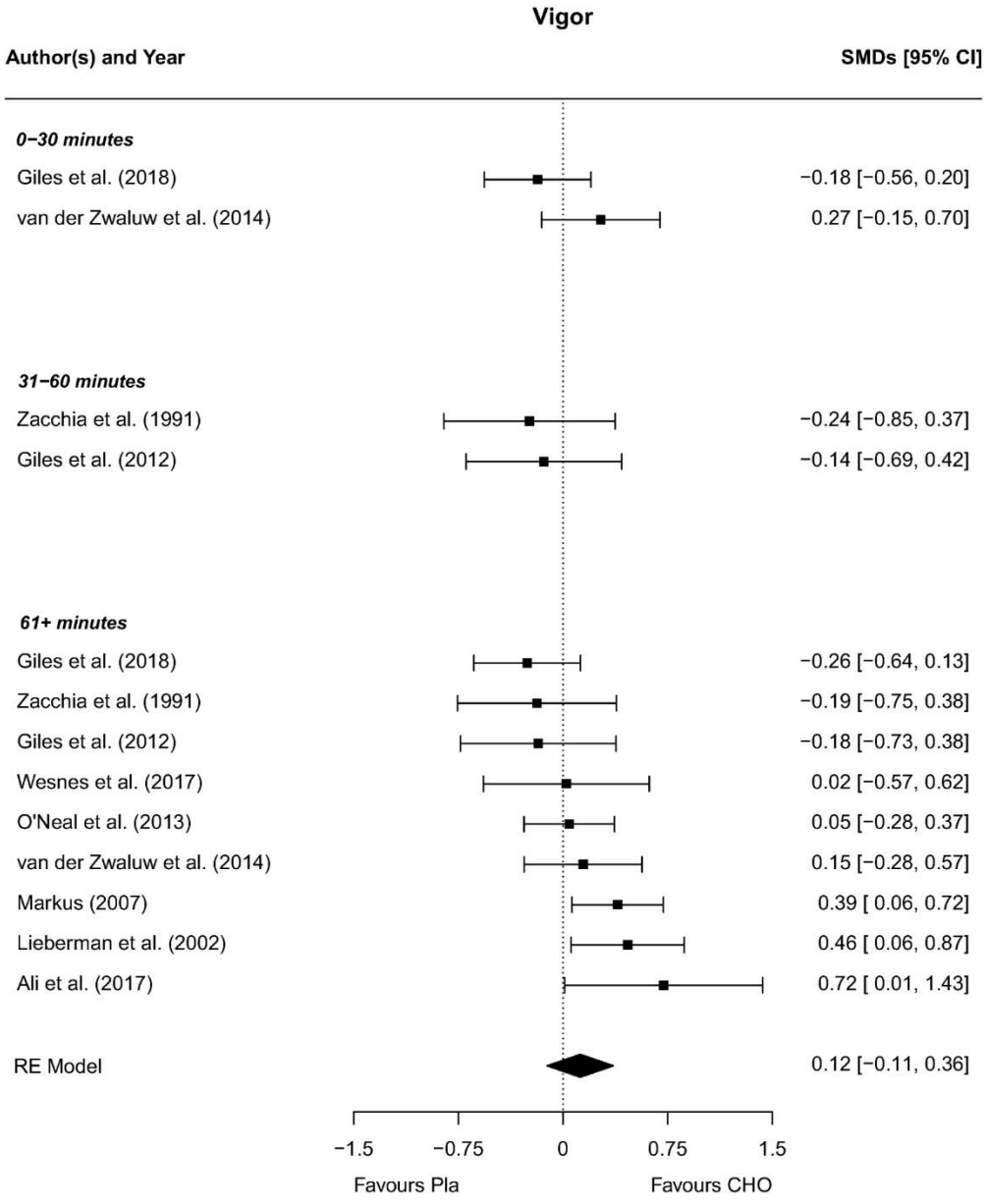

Figure 17. Forest plot of vigour effect sizes with 95% confidence intervals.

Discussion

Although several reviews have been published to investigate the complex relationship between CHO and mood, no research has attempted to systematically deconstruct CHO-mood interactions and assess the influence of moderator variables. In

light of studies presenting conflicting findings regarding the effects of CHOs on different aspects of mood at different time-points, the aim of this study was to assess the immediate (0-30 minutes), short-term (31-60 minutes), and long-term (61+ minutes) effects of acute CHO consumption on a number of positive and negative mood constructs. The methodological differences among eligible studies were also reviewed and used in the analysis as moderator variables when heterogeneity was high. Overall, our meta-analysis provides no evidence of mood facilitation following CHO ingestion at any time-point following consumption. In fact, CHO consumption was related to decreased alertness and higher levels of fatigue within the first hour post-ingestion. Despite the methodological differences between studies, the effect sizes were relatively homogeneous across all mood constructs and time-bins. High heterogeneity was found for fatigue at 61+ minutes, which was partially explained by the nature of the task preceding mood assessment.

From the serotoninergic hypothesis of CHO effects on mood, we expected a positive effect of CHO ingestion on mood ratings beyond the first hour post-CHO consumption. Interestingly, no beneficial effects of CHO were found compared with placebo during the time window where a CHO-related serotoninergic surge is posited to occur (i.e., 61+ minutes). This was the case for all mood constructs, including depression, tension and anger, on which one would expect the supposed CHO-related increase in serotoninergic activity to have the strongest effect (Benton & Owens, 1993; Chaouloff et al., 1999; Markus, 2008; Wurtman & Wurtman, 2018). Considering that no beneficial effects of CHOs on mood were identified, our meta-analysis calls into question the existence of a mood-boosting mechanism (serotonin-based or otherwise)

related to CHO consumption. In fact, the validity of the CHO-serotonin mechanism and, by extension, the CHO-mood relationship has received criticism and has been difficult to replicate in experimental settings (for a review, see Benton, 2002). Interestingly, even in studies that have found CHO to influence serotoninergic activity, it is suggested that this effect is observable only under specific conditions (e.g., stress; Markus, 2007), and for clinical populations rather than healthy individuals (for a review, see Wurtman & Wurtman, 2018).

The present meta-analysis also examined the effect of CHOs on mood at earlier time windows (0-30 and 31-60 minutes post-CHO consumption). With a number of studies uncovering mood effects as early as 15 minutes post-ingestion (e.g., Benton & Owens, 1993), we wanted to assess whether the effects of mood are stronger during earlier time-points. This would allow us to investigate the time-course of CHO effects and the influence of other mechanisms through which CHOs could potentially affect mood (e.g., mood improvement because of a rapid increase in energy availability). However, similar to the results obtained from the 61+ time-bin, CHOs did not seem to lead to improvements in any mood constructs during the earlier time windows. In fact, the only significant effects identified in our meta-analysis speak against CHO-related facilitation and suggest that, compared with placebo, CHO leads to mood decrements. Specifically, CHO consumption was related to greater fatigue and less alertness, 0-30 minutes and 31-60 minutes post-ingestion, respectively. It should be noted that the decreased alertness observed in the meta-analysis could be related to the sedative effect of tryptophan/serotonin, but the timeframe in which this effect was observed (i.e., 31-60 minutes) does not corroborate this theory. Although small trends of decreased tension as

well as increased calmness and contentedness were observed within the first hour following CHO administration, they failed to reach significance. Overall, CHOs do not seem to improve any aspect of mood at any time point after their consumption, challenging the notion that CHOs could offer a temporary 'high'.

Previous studies have shown that, similar to CHO-cognition interaction, the effects of CHO ingestion on mood are stronger when participants have to perform difficult cognitive or physical tasks (e.g., Backhouse et al., 2007; Lieberman et al., 2002; Markus, 2007; Owens et al., 1997; Reay et al., 2006). Additionally, methodological choices such as dose, type of CHO and fasting intervals have been shown to affect the magnitude of the CHO facilitation effect and could, theoretically, affect the CHO-mood relationship as well (Riby, 2004; M. A. Smith et al., 2011; Sünram-Lea & Owen, 2017). Therefore, one of the predictions of this meta-analysis was that methodological differences across studies would lead to significant heterogeneity in the results. Although our goal was to evaluate the influence of such moderators on CHO-mood interactions, our results turned out to be not heterogeneous enough to justify conducting moderator analyses for most mood constructs and time windows. Significant heterogeneity was found for fatigue at 61+ minutes, but our pre-specified moderators failed to account for the heterogeneity obtained. The only moderator variable that approached significance was the nature of the task preceding mood evaluation. Specifically, we found that CHOs can alleviate fatigue only under physically demanding conditions (e.g., strenuous physical exercise), but not under high cognitive load or periods of inactivity. These findings are in line with studies that have found positive effects of CHOs on mood after exercise (e.g., Ali et al., 2017; Backhouse et al., 2005),

but do not support previous work showing that CHOs can improve mood under high cognitive demands (David Benton & Owens, 1993; Owens et al., 1997; Smit et al., 2004). Overall, the homogeneity of the results points to little variance across studies with regards to the effects of CHO on mood, suggesting that the influence of methodological variables is not as pronounced as previously thought (for a review, see Benton, 2002).

Limitations and Recommendations

Although our results are consistent with the interpretation that CHOs do not affect mood, limitations of the present meta-analysis should be considered when attempting to generalise our findings to broader contexts. First, we examined the effects of CHOs on mood in samples of healthy adults. The literature on CHO-mood interactions has also investigated the effect of CHOs in clinical populations (e.g., depression and obesity; Wurtman & Wurtman, 2018; Wurtman & Wurtman, 1989, 1995), participants with high sensitivity to stress (Markus et al., 1998), and women during the luteal phase of the menstrual cycle (for a review, see Benton, 2002). Interestingly, researchers have also coined the term ‘carbohydrate-craving’ depression to describe a clinical population showing excessive CHO intake as a means of ‘self-medicating’ to improve mood (Wurtman & Wurtman, 1995). It is possible that mood in clinical or subclinical populations exhibiting emotional disturbances could be more sensitive to CHO manipulations. Further meta-analytic attempts focusing on examining the effects of CHO on mood in these populations could shed light on this topic, and, potentially, the neurobiological or behavioural mechanisms behind CHO-mood interactions.

Second, our meta-analysis included studies that provided participants with CHO in isolation to other macronutrients or nutraceutical constituents. In recent years, because of the sharp increase in the consumption of energy drinks, research has also focused on the synergistic effects of CHO with other psychoactive constituents such as caffeine. These studies have found the effects of CHO-caffeine combinations to go beyond the facilitation observed when either of these constituents is administered alone (e.g., D. O. Kennedy & Scholey, 2004; Scholey et al., 2014, 2009; Scholey & Kennedy, 2004; Sünram-Lea, Owen-Lynch, Robinson, Jones, & Hu, 2012). However, the effects of energy drink consumption on mood are not clear and more investigations and meta-analytic attempts are warranted. Furthermore, other studies have examined the effects of CHO combined with macronutrients such as protein and fibre (e.g., Benton, Slater, & Donohoe, 2001; Lloyd et al., 1996; Sihvola et al., 2013) or by creating experimental diets controlling for the content of CHO compared with other constituents (Markus et al., 1998; for a review, see Dye, Lluch, & Blundell, 2000) to examine CHO-mood interactions. Although the purpose of our meta-analysis was to investigate how pure CHO administration can affect mood, it would be interesting to discover whether CHO interactions with other nutrients could more prominently affect mood and emotionality.

Based on the evidence presented in this meta-analysis, recommendations can be made to improve both the quality of future work in the field and assist in further meta-analytic attempts. First, we recommend that open and reproducible science practices should be followed by all researchers in the field. This would lead to less selective reporting and greater transparency of the research process. In the present meta-analysis, 22 out of the 51 eligible studies had to be excluded at the final stage because of no

responses from authors or data being unavailable. Data being freely available for other researchers to use would greatly facilitate research synthesis by increasing the number of studies included in such meta-analyses, which would provide more accurate estimation of the true nature of a studied effect.

With regards to the research area itself, several methodological issues should be considered when assessing CHO-mood interactions to facilitate the comparison of studies and the interpretation of their results when grouped. Methodological decisions regarding sample size should be justified and accompanied by appropriate power analysis to ensure that studies are adequately powered to detect mood fluctuations following nutraceutical interventions. What is evident from the present meta-analysis is that studies investigating CHO-mood interactions test varied numbers of participants (see Table 5), not always accompanied by power analyses. Similarly, justifications should be provided when deciding on dosage, types of CHO, fasting intervals and even mood assessment tools to allow researchers to critique and assess the appropriateness of such decisions and measures. A common issue with the CHO-mood research area is related to the fact that mood is primarily assessed as an outcome of secondary importance over cognitive outcomes, which are thought to be more strongly affected by CHO manipulations (for a meta-analysis, see Riby, 2004). This also means that no a priori hypotheses are made regarding CHO effects on mood, and statistical results are rarely presented if CHOs do not have a statistically significant effect on mood. Providing more detailed descriptions and presenting all available results would facilitate future meta-analytic efforts and increase confidence in the field and its reporting standards. In fact, researchers investigating CHO- and nutrition-related changes in

behaviour have called for greater detail in the description of nutraceutical intervention protocols and the methodological justifications presented by researchers, to allow for more accurate comparisons across different studies (Gilsenan, de Bruin, & Dye, 2009).

Conclusions

As the public consumes sugar-sweetened energy drinks to cope with fatigue and negative mood, our goal was to understand whether this pervasive perception holds under scrutiny. Overall, our meta-analysis does not provide support for the supposed CHO-mood relationship and casts doubt on how the neurobiological mechanisms implicated translate into observable mood outcomes. Interestingly, the only evidence uncovered in the present work points to a detrimental effect of CHO on mood constructs such as alertness and fatigue, suggesting that the idea of a positive CHO-mood relationship is unsubstantiated. In the last couple of decades, consumption of sugar-sweetened soft drinks has seen a sharp increase, leading to a renewed interest by researchers and the public in understanding how CHOs affect physical and mental health. Our results can be used to increase the public's awareness of the effects of sugar consumption and inform public health policies aimed at decreasing sugar consumption and promoting healthy alternatives.

Chapter 6: General Discussion

The general aim of this thesis was to increase our understanding of the mechanisms underlying emotion-cognition interactions in ageing. Specifically, the thesis investigated the relationship between physiology, cognition, and affect in older adults, focussing on the physiological underpinnings of the age-related positivity phenomenon, the contribution of glycaemic resources to cognitive engagement and affect, and the relationship between CHO consumption and overall emotionality. The purpose of this final chapter is to summarise the findings of the four studies comprising the thesis. An overview of the results will be discussed along with their theoretical and practical implications for the study of emotion-cognition interactions in ageing. Potential limitations associated with each study will be presented as well as recommendations for researchers in the area. Finally, proposals for future research will be discussed.

Overview of Findings

Chapter 2

Chapter 2 assessed the relationship between glycaemic resource availability and the PE under low- and high-load conditions. The aim of this study was to evaluate the premise that older adults' PE is dependent on cognitive control resources. It was hypothesised that if the PE is tied to cognitive control, reinstating or increasing cognitive resources via an increase in glucose levels would allow older adults to retain their PE even when a task is particularly difficult to perform. In Experiment 1a, young adults showed a slight preference for negative information across low- and high-load conditions. For this age group, glucose administration led to improved memory under high-load conditions (cf. Sünram-Lea et al., 2002a), not moderated by the valence of the

to-be-remembered material (see Brandt et al., 2010). In contrast, older adults showed the expected preference for positive information under single-task conditions. In line with the postulates of the cognitive control hypothesis, this positivity turned into a preference for negative information under high-load conditions (see Knight et al., 2007; Mather & Knight, 2005), specifically for the placebo group. More importantly, the PE remained intact in the glucose group, despite having to perform a highly demanding dual task during encoding. The purpose of Experiment 1b was to replicate the crucial interaction found in older adults and introduce methodological improvements (i.e., double-blind procedure and palatability ratings) to control for the possibility that extraneous factors could have influenced the results. The results were identical to Experiment 1a, which substantially increases confidence in the glucose-PE relationship uncovered.

These findings are of importance to the study of ageing for numerous reasons. First, they provide novel support for the cognitive control hypothesis and the dependence of the age-related PE on cognitive resources. The positivity reversal (i.e., negativity preference) found in the older-placebo group under high-load conditions successfully replicated previous studies reporting that the PE is highly sensitive to cognitive load (e.g., Mather & Knight, 2005). Furthermore, as discussed in the introduction of this thesis, glucose is well-known to improve cognitive capacity in both young and older adults (for a meta-analysis, see Riby, 2004). Therefore, it is highly plausible that the glucose-related sparing of the PE under high-load conditions is a result of a glucose increase in cognitive control capabilities, which allowed older adults to retain their positivity preference. It would also be interesting to consider the possibility that the PE might be a reflection of older adults' positive emotionality rather than a

mechanism aimed at promoting positive mood. It is possible that, whereas the placebo group's mood could have deteriorated while performing the dual task, affecting their ability to focus on positive material, glucose protected older adults' affect from a potential drop-off and allowed them to memorise and recall material that was consistent with their positive mood. Considering the results reported in Experiment 2 showing that glucose administration has the capacity to improve older adults' affect, this possibility should be further explored in glucose intervention studies where both the PE and mood indices are assessed.

Second, our findings are the first to point out the presence of age-related differences in glycaemic resource allocation. Whereas young adults use the additional glucose resources to prioritise overall task performance when difficulty is high, older adults' allocation of resources is motivated by positivity-driven goals. That is, older adults use glucose to favour the encoding and/or recall of positive material rather than improving their overall performance. Therefore, older adults' PE motivation seems to profoundly affect how available metabolic resources are used. Third, our results can be used to develop guidelines to protect older adults' PE under conditions that burden cognitive control capacity, which, in turn, could have important implications for emotionality and mood in older age. Our findings indicate that higher availability of glucose resources allows older adults to keep their positivity irrespective of task conditions. This could mean that providing older adults with individually-tailored dietary guidelines aimed at achieving optimal energy availability could improve cognitive processing patterns and maximise positivity in ageing. However, older adults' mood was not assessed in Experiments 1a and 1b, and no direct inferences can be made

regarding older adults' affective states following glucose based on these data alone (see Isaacowitz & Blanchard-Fields, 2012). Further studies examining the effect of glucose on both the PE and mood indices would allow us to draw more concrete conclusions regarding the relationship between these components.

One potential limitation with regards to this study is the absence of blood glucose measurements during the experiments. Knowing participants' baseline blood glucose levels can be used to ensure that they have abided by the 2-hour fasting rule prior to the administration of the drinks. More importantly, assessing blood glucose change during the experiment could have provided an index of levels of mental effort exerted during the task. Researchers have consistently found blood glucose levels to be sensitive to task load manipulations, with performance on cognitively demanding tasks (e.g., high-load conditions) lowering blood glucose concentrations in the periphery (Fairclough & Houston, 2004; Scholey et al., 2001; Scholey et al., 2006). Critics of the cognitive control hypothesis have suggested that the positivity preference is not always accompanied by substantial changes in physiological markers of effort (e.g., pupil dilation), disputing the effortful nature of the PE (Allard et al., 2010). Therefore, it would be interesting to assess whether the PE is sensitive to alterations in blood glucose levels and how individual differences in glucose concentrations following a glucose drink could predict the magnitude of the PE in older adults' memory. It should be noted that assessing capillary blood glucose levels is a relatively painless procedure but it could be unpleasant for some participants. It is possible that simply expecting a blood glucose measurement at the end of each task could have an effect on participants' mood, which, in turn, could lead to unforeseen consequences for the emergence of the PE (for

an example of how mood affects the PE, see Isaacowitz et al., 2008). A carefully designed study would be necessary to investigate whether the PE depletes older adults' energy resources, and how individual differences in glycaemic responses to a glucose drink can predict the emergence of the PE.

Chapter 3

Chapter 3 examined the role of glucose resources on older adults' levels of objective and subjective effort exertion, memory performance and affect. Research has found older adults to reduce their levels of engagement when a task is of high difficulty (Ennis et al., 2013; Hess et al., 2016). With theories suggesting that this might be related to resources being limited in ageing (Hess, 2014), we investigated the possibility that cognitive engagement could be constrained by the levels of a functional, albeit finite, physiological resource such as glucose. It was hypothesised that increasing glucose availability before a task could have a positive effect on older adults' engagement, which could also be accompanied by improved memory performance and affect primarily in older adults, as a result of their higher sensitivity to the glucose facilitation effect (e.g., Macpherson et al., 2015).

Results from Experiment 2 provided support for the mediating role of glycaemic resources in cognitive engagement. Specifically, it was found that a small dose of glucose can significantly increase both young and older adults' ability to exert effort in a task, measured through changes in HR responsivity during the cognitive task. Of note, this increase in engagement was found across all levels of difficulty and not just for the highest difficulty level. Although one would expect the glucose facilitation to be stronger under high cognitive load (e.g., Gagnon et al., 2010; Scholey et al., 2009),

glucose was unable to prevent a significant drop-off in engagement from medium to high difficulty in the older group.

The overall increase in engagement was accompanied by improved memory performance and higher positive affect in the older group, effects that were not found in young adults. Similar to the cognitive engagement results, older adults' memory and affect scores showed improvement across all difficulty levels compared with placebo. In line with studies suggesting that older adults might be more sensitive to glucose manipulation than their young counterparts (Hall et al., 1989; Manning et al., 1997), it is possible that older adults require additional resources even when performing objectively easy tasks. Notably, in Experiments 1a and 1b, older adults in the glucose group showed a (non-significant) numerical advantage when recalling words under low-load conditions compared with placebo, an observation which is consistent with the idea that older adults could be susceptible to glucose manipulations even when difficulty is relatively low. Of interest, both older-glucose and older-placebo groups reported similar levels of subjective effort in the task, with the glucose group even showing patterns of lower subjective effort at medium and high difficulty. Considering how the glucose group exhibited significantly higher levels of objective effort (HR change) compared with the placebo group, findings of equal (or even slightly decreased) subjective effort in the glucose group are of particular interest to the study of cognitive engagement. With researchers suggesting that subjective perception of effort could be one of the motivating factors behind older adults' engagement patterns (Hess et al., 2016), it is highly likely that glucose decreased the older-glucose group's subjective effort

perception, which could have contributed to findings of increased engagement, improved memory performance and higher affect in that group.

Experiment 2 is the first to uncover a potential physiological resource underlying cognitive engagement in both young and older adults. Manipulating the availability of glucose resources can have significant effects on both age groups' ability to perform demanding cognitive tasks. However, the cascade of positive behavioural effects (i.e., improved affect and cognitive performance) observed alongside the older-glucose group's increased cognitive engagement begs the question of how glucose leads to these results in older adults. As mentioned in the discussion of Chapter 3, it could be assumed that glucose decreases levels of subjective effort and improves mood, and this enables older adults to put more effort into a task and perform at their highest capacity. Equally plausible is the possibility that glucose works by increasing cognitive engagement and improving memory performance, which leads to higher positive affect in older adults as a result of a higher sense of self-efficacy. Although glucose increased older adults' positive affect in Experiment 2, the meta-analysis reported in Chapter 5 suggests that CHOs do not to have the capacity to improve mood or decrease self-reported levels of fatigue. Here, it should be noted that the meta-analysis was conducted with studies using explicit self-report mood scales (e.g., POMS), whereas Experiment 2 used an implicit affect task (affective judgment task; Bartoszek & Cervone, 2017). It is possible that the effects of CHO ingestion on mood are subtle and more likely to manifest in tasks that are sensitive to even small changes in transient emotionality, such as implicit tests (e.g., Quirin et al., 2009). However, based on the experiment presented in Chapter 3 alone, we cannot make any inferences regarding the mechanisms of the glucose facilitation effect.

An adequately powered replication would be necessary to justify the use of statistical tests that would allow us to deconstruct the relationship between cognitive engagement patterns, cognitive performance, subjective effort and affect in each age and drink group (e.g., multiple regressions).

Irrespective of what the exact glucose facilitation mechanism might be, the findings of Experiment 2 are striking, with glucose improving behavioural and cognitive aspects of older adults' performance. This is particularly important in ageing as reviews have noted that engagement in cognitive tasks could be one of the factors that determines cognitive maintenance in older age (Hertzog et al., 2008). Based on our findings, as well as studies suggesting that older adults experience difficulties in mobilising counterregulatory responses to low or high levels of circulating blood glucose in everyday life (Marker et al., 1992; Melanson et al., 1998; Meneilly et al., 1994), it is possible that findings of reduced engagement in older adults could be related to glucoregulatory decrements. If that is the case, creating interventions to improve older adults' glucoregulatory capacity and insulin sensitivity could significantly improve/optimise effort exertion in this age group. As this is only a speculation, more research is needed to address the idea of a connection between glucoregulatory capacity and effort mobilisation (glucoregulatory capacity is further explored later in this chapter).

Some inconsistencies in the obtained data should also be addressed. First, young adults in the placebo group showed HR deceleration at all difficulty levels of the cognitive task when compared with their HR levels at baseline. This is particularly interesting as no previous studies investigating age-related changes in effort exertion

have found young adults' CV responses to be smaller during cognitive exertion than baseline (e.g., Ennis et al., 2013). It should be noted that the baseline measurement was taken at the beginning of the experiment. As most young adults do not have experience with ECG procedures and the electrode setup, it is possible that their first exposure to this type of measurement increased their levels of stress and, consequently, their HR reactivity. By the time they were asked to perform the cognitive task, they had probably become more comfortable with the equipment, which reduced their anxiety and calmed their CV system. As most older adults routinely undergo assessments of CV functionality as part of regular health check-ups, the familiarity with the equipment and electrode setup could have protected them against an anxiety-related increase in HR during baseline. A way of circumventing this problem would be to increase the length of baseline period. In Experiment 2, the baseline lasted seven minutes, with the final five being used as an index of baseline HR levels. Although other studies have used similar baseline periods (e.g., eight minutes; Zafeiriou & Gendolla, 2017), guidelines suggest employing a 10-minute inactive period to allow for more accurate baseline CV measurements (Laborde et al., 2017). This limitation was addressed in Experiment 3. Additionally, introducing participants to the equipment on a separate day, before the intervention and cognitive tasks are scheduled to take place, could decrease the novelty of the ECG procedure and make them more comfortable with the equipment. More research into the young-placebo group's HR deceleration is needed.

Second, one could argue that the reason behind the higher HR observed across both glucose age groups and all difficulty levels is simply because glucose ingestion leads to higher sympathetic activity. As such, higher HR change following glucose

might not necessarily reflect an actual increase in engagement, but it could be a by-product of a glucose-related general increase in physiological arousal. It is important to note that researchers have found 25 g of glucose (the dose employed in all the experiments in this thesis) to increase HR only when participants have to perform a cognitive task, and not during inactive/baseline periods during which participants are asked to sit quietly (D. O. Kennedy & Scholey, 2000; Scholey & Kennedy, 2004). If the glucose-related increase in HR does not occur during inactive periods, the assumption that glucose ingestion leads to higher overall arousal does not appear to be valid. In fact, it has been suggested that the HR increase found in glucose groups during cognitive performance is part of a mechanism that increases the delivery of glycaemic resources to the brain processing centres during cognitive exertion in an effort to support participants' performance (D. O. Kennedy & Scholey, 2000). As the brain does not require the additional resources during rest, glucose would not increase HR in that case. Of note, other researchers have found large doses of CHOs (e.g., 60 g of fructose) to significantly increase HR during rest in young adults (see C. M. Brown, Dulloo, Yepuri, & Montani, 2008). A systematic examination of how different CHO doses affect CV reactivity in young and older adults before and during cognitive performance could help disentangle the exact role of CHO administration in cognitive engagement and general sympathetic activation.

Finally, an interesting finding uncovered in Experiment 2 is that older adults experienced glucose-related cognitive facilitation even when difficulty was objectively low. Although similar findings have been reported in previous studies (e.g., Riby et al., 2004), construed as older adults requiring the additional energy resources even when a

task is easy, these results are somewhat inconsistent with findings reported in Chapter 2. Although glucose in Experiments 1a and 1b increased older adults' cognitive capacity and allowed them to retain their PE under high-load conditions, only a small numerical advantage was observed for the glucose group's performance under low-load conditions, which failed to reach significance. This discrepancy in the emergence of the glucose facilitation effect could be related to the nature of the tasks employed. Specifically, the memory task used in Experiments 1a and 1b lasted approximately two minutes, whereas the memory search task employed in Experiment 2 lasted five minutes.

Interestingly, research has not systematically examined the effects of temporal demands and task duration on the emergence of the facilitation effect in older adults. A study conducted with young adults has found circulating blood glucose levels to linearly decrease with more time spent on task (Fairclough & Houston, 2004). As decreases in glucose levels appear to be proportionate to the duration of the task, tasks of long duration can be particularly demanding and performance on them should be more heavily constrained by energy availability. Based on our results, it is possible that the glucose facilitation in older adults might be dependent both on task difficulty and task duration, with performance on lengthy tasks being more susceptible to manipulations of glycaemic availability. It could be that even a relatively small 3-minute increase in task duration can significantly deplete glucose resources and lead to performance decrements in ageing (for a review, see Gold, 2005), an effect that could be reversed by glucose administration. Measuring blood glucose levels after each task would be imperative to gauge the exact energetic demands of performing a 2-minute and 5-minute task. With studies reporting conflicting findings regarding the circumstances under which older

adults experience glucose facilitation, further investigations in this area are necessary to understand how task demands and task duration differentially predict glucose-related cognitive enhancement in young and older adults.

Chapter 4

The purpose of Chapter 4 was to assess the relationship between ANS functionality and the age-related PE. With studies suggesting that ANS capacity is related to emotion regulation success (Levenson, 2014; Levenson, 2003) and that the PE reflects an emotion regulation mechanism (for reviews, see Isaacowitz, 2012; Mather & Carstensen, 2005), we investigated the possibility that indices of ANS functionality (e.g., HRV) could predict older adults' PE magnitude. Indeed, it was found that HRV levels at rest can selectively predict older, but not young, adults' negativity avoidance under both single- and dual-task conditions. Interestingly, although we hypothesised that both HRV and the PE might be related to affective outcomes, participants' ratings on the implicit affect task did not corroborate the idea of an association between these components.

Experiment 3, reported in Chapter 4, is the first to assess the relationship between ANS capacity and the PE. In line with Experiments 1a and 1b showing that the PE, particularly under high-load conditions, is dependent on physiological factors such as energy availability, Experiment 3 took this idea a step further and found that the PE is also related to overall ANS functionality. This finding is important for a number of reasons. First, although evidence exists to support the idea that the PE reflects emotion regulation mechanism (e.g., Isaacowitz et al., 2008; Noh et al., 2011), the association between the PE and affective outcomes has been contested (Isaacowitz & Blanchard-

Fields, 2012). With an overwhelming number of studies reporting that HRV is an index of emotion regulation capacity (for reviews, see Appelhans & Luecken, 2006; Thayer & Lane, 2009), it is possible that the association between HRV and the PE could be an indication that the PE is related to emotion regulation capabilities. Although this is an exciting possibility, more research is needed to establish the relationship between emotion regulation capacity, the PE and HRV indices.

Second, these findings promote a greater understanding of the mechanisms underlying the emergence of the PE itself. Studies investigating the behavioural underpinnings of the PE have focused on cognitive capacity as the underlying factor behind PE magnitude, and have consistently reported a positive association between baseline levels of executive control capacity and the PE (Isaacowitz et al., 2009; Mather & Knight, 2005; Sasse et al., 2014). Evidence from Experiment 3 suggests that physiological factors, such as ANS functionality, can be equally strong predictors of older adults' positivity preference and, particularly, their ability to downregulate negative influences. Additionally, the fact that older adults' HRV was specifically associated with negativity avoidance and not positivity preference provides further evidence for the role of HRV as a marker of the PFC's capacity to downregulate the amygdala's activity during the processing of negative information, and participants' overall inhibitory capacity (see Colzato & Steenbergen, 2017; Gillie et al., 2014). The novel nature of these findings poses important questions for the role of physiological functionality in older adults' processing patterns, and creates many avenues for future research in the area (see later). Researchers examining older adults' emotion regulation capacity and the PE should carefully consider how underlying individual differences in

ANS capacity could affect their results. Evaluating the influence of physiological indices alongside cognitive and behavioural outcomes could offer a more in-depth understanding of the age-related PE phenomenon and its impact on older adults' emotionality.

Finally, findings of an association between HRV and the PE can have important implications for developing interventions aimed at improving emotion regulation and positivity in older adults. Recent work has suggested that HRV is not solely an index of emotion regulation capacity, but it is itself a contributing factor to the efficiency of brain networks supporting emotionality (Mather & Thayer, 2018). The suggestion of a bidirectional relationship between these two components has resulted in a number of studies investigating ways of increasing HRV to improve emotion regulation capacity. Researchers have developed biofeedback protocols based on resonance breathing methods that have been shown to successfully increase HRV levels (Lehrer et al., 2013). Practicing such methods over a short time period has been associated with significant improvements in a number of conditions ranging from asthma to depression and anxiety (Lehrer & Gevirtz, 2014), suggesting that this intervention can have important implications for emotional well-being. Additionally, research has found HRV indices to be sensitive to lifestyle factors such as diet, nutrition and levels of exercise (for a review, see Kemp & Quintana, 2013). Given the relationship between HRV and negativity avoidance uncovered in Experiment 3, it is possible that prescribing simple breathing exercises or lifestyle changes to older adults could improve their ability to downregulate negativity, increase the magnitude of their PE and their emotion regulation efficiency via an increase in ANS functionality.

However, some limitations should also be addressed. Although the relationship between HRV and emotionality is well-established (Thayer & Lane, 2009), no associations were found between resting HRV levels and ratings on the implicit affect task in either young or older adults. As discussed in Chapter 4, the lack of an association between HRV and implicit affect could have been because of methodological decisions made in this study. Specifically, participants were presented with only three of the six IPANAT pseudo-words at the end of each task (i.e., three for the single and three for the dual task). The decision to only present participants with half the targets could have plausibly affected IPANAT's ability to effectively uncover task-related changes in emotionality. Using all six targets comprising the IPANAT could have provided a more accurate index of participants' emotional state. A replication of the study using more comprehensive implicit and explicit mood assessment tools would offer important insights into the relationship between HRV and emotionality.

In a similar manner, although we expected to find an association between older adults' PE and their affect ratings, we failed to uncover such a relationship. Once again, this could be attributed to the methodological choice of not using the full version of the IPANAT to assess affect. However, it could also be argued that the eye-tracking task employed was not demanding or lengthy enough to cause affective decrements in either young or older adults — that is, decrements strong enough to be indexed by the IPANAT. In fact, researchers have observed older adults' PE to be associated with mood outcomes only when participants are asked to perform lengthy eye-tracking tasks. Researchers have argued that, because of their long duration, such tasks can decrease positive affect, thereby triggering older adults' PE as a counterregulatory response to

mood decrements (Isaacowitz et al., 2009). Using more demanding eye-tracking tasks could allow researchers to investigate the relationship between the PE and affect more closely.

Further supporting the idea that the eye-tracking task used in Experiment 3 was relatively undemanding, older adults' negativity avoidance remained intact during the dual task, despite having to perform a secondary task at the same time as viewing the face pairs. It is important to recall that the secondary task used in this study was the same as the one employed in Experiments 1a and 1b. In contrast to Experiment 3, increasing task demands via the 1-back task in Experiment 1 made the PE disappear, suggesting that the task was demanding enough to decrease the level of cognitive control resources allocated to producing the PE. A crucial difference between Experiments 1 and 3 lies in the difficulty of the primary task: arguably, the eye-tracking task in Experiment 3 was not as difficult to perform as the memory task used in Experiment 1. Whereas task difficulty in Experiment 1 originated from both tasks (i.e., memorising words while performing a 1-back task), viewing face pairs in Experiment 3 did not seem to require the same level of resources as the memory task and, therefore, difficulty during the dual task was increased solely via the 1-back manipulation. Apparently, this was not enough to make the PE disappear. These findings are consistent with literature showing that introducing a dual task component during a passive eye-tracking PE task does not necessarily diminish older adults' positivity preference (Allard & Isaacowitz, 2008). At the same time, studies that have used a more demanding PE task (e.g., memory recall) alongside a secondary task have found significant PE reductions in older adults' processing patterns (e.g., Mather & Knight, 2005). Further

research into the sensitivity of the PE to different levels of task demands is clearly needed to understand the exact circumstances under which the PE is more likely to disappear. With regards to the HRV-PE relationship, it would also be important to see how the association found in this study (i.e., higher HRV – higher negativity avoidance) would be altered during a more demanding secondary task (e.g., 2- or 3-back task).

Chapter 5

In this chapter, the effects of CHOs on mood were investigated. With researchers reporting conflicting accounts of the relationship between acute CHO ingestion and mood outcomes, we gathered data from all available studies that have assessed CHO-mood interactions to investigate the accuracy of reports of positive mood outcomes following CHO administration. Meta-analysis methodologies were employed to group effect sizes from available studies. Moderator analyses were used to disentangle the role of methodological differences across studies in explaining conflicting findings. With researchers suggesting that CHOs can increase serotonin levels in the brain (Fernstrom & Wurtman, 1971), it was hypothesised that CHOs could have a positive effect on serotonin-sensitive mood constructs (e.g., depression), at specific time-points following their consumption (e.g., beyond 60 minutes following consumption). As most studies are not considered adequately powered to uncover CHO effects on mood (for a review, see Benton, 2002), it was expected that the effect sizes extracted from relevant studies would be of small magnitude.

Results of the meta-analysis did not offer support for the premise that CHOs can improve any aspect of mood at any time-point following CHO ingestion. This was true for all mood constructs assessed, including those that are considered to be sensitive to

manipulation of serotoninergic activity (e.g., depression and stress; for reviews, see Chaouloff et al., 1999; R. J. Wurtman & Wurtman, 1995; Young & Leyton, 2002). On the contrary, CHO administration was found to lead to higher levels of fatigue and lower alertness within an hour post-CHO ingestion, suggesting the CHOs can even have detrimental effects on mood. Of note, despite the largely different methodologies used across the experiments comprising the meta-analysis, heterogeneity was low, indicating that the overall null effects of CHOs on mood are not moderated by methodological decisions. The only exception was fatigue measured beyond 60 minutes following CHO consumption: CHOs appear to decrease fatigue during that time-point, but only when mood assessment is preceded by a demanding physical task (e.g., maximal effort exercise) rather than a cognitive task or a resting/inert period.

The findings of this meta-analysis are of particularly high importance for both the CHO-mood research area and the public. Our meta-analysis is the first to systematically examine the CHO-mood relationship and deconstruct the role of methodological differences across studies. Although several reviews have been published to date (Benton, 2002; Benton & Donohoe, 1999; Benton & Nabb, 2003; Bernard et al., 2018; Gibson & Green, 2002; van de Rest et al., 2017), none of them has attempted to use synthesis methodologies to provide a statistically robust index of the true effect of CHOs on mood. Additionally, the majority of these reviews have not run exhaustive and replicable literature searches to identify all suitable studies within the area, undermining the validity of their observations. Of importance to the research area, the systematic review and meta-analysis presented in Chapter 5 can be used as a reference point and guide for researchers interested in further investigating CHO-mood

interactions. Through the systematic examination of the methodological differences of included studies, our review provides a ‘checklist’ of factors and key points that all researchers should address before running similar experiments (e.g., sample size calculations).

Across Chapter 5, it was repeatedly argued that all methodological decisions should be carefully considered and appropriate justifications must be provided at each stage of the study design to ensure replicability, and that readers have enough information to assess the appropriateness of the methods employed (Gilsenan et al., 2009). Furthermore, as evident in Figure 8, a high number of studies had to be excluded from the meta-analysis because of data not being available or authors not responding to requests (see Appendix E). Open science guidelines should be followed by all researchers to facilitate future synthesis attempts. It is hoped that this meta-analysis will become a starting point for discussions that will improve the reporting standards of researchers in the area and actively shape the way CHO-mood interactions are examined in the future.

Additionally, findings of no association between CHOs and mood should be a great interest to the public. As described in the introduction of Chapter 5, soft drinks are posited to be the largest source of energy provision in people’s diets (Block, 2004), with millions of litres being consumed globally each year (Zucconi et al., 2013). Although the public seems to believe in the premise that sugar can combat negative mood, our findings indicate that the idea of sugar-sweetened products being able to reduce fatigue and improve mood, alertness and overall well-being is largely unsubstantiated. In recent years, consumption of such drinks has also been associated with a host of negative

physical outcomes, including obesity and higher prevalence of diabetes (Malik et al., 2006; Vartanian et al., 2007). In addition to these concerns, findings of no positive mood outcomes related to CHO ingestion further support the argument in favour of public policies aimed at decreasing consumption of soft drinks (e.g., sugar tax) and the promotion of healthier alternatives.

Although the results of the meta-analysis are striking, some limitations should also be considered. As mentioned in the discussion of Chapter 5, the current meta-analysis focused on healthy populations, CHOs given in isolation to other constituents (e.g., caffeine), acute CHO administration, and studies assessing mood using explicit mood measures. Understandably, these decisions limit the scope of the meta-analysis and the ability to generalise findings to broader contexts. In fact, studies have suggested that CHO consumption is particularly pronounced in populations suffering from affective conditions, with these populations consuming larger quantities of CHOs in an effort to alleviate the severity of their affective symptoms (R. J. Wurtman & Wurtman, 1989, 1995). It is possible that, in clinical populations, administration of CHOs could result in more robust mood improvements.

Furthermore, studies administering experimental diets controlling for the content of different macronutrients have found positive effects of CHO-rich diets on mood (e.g., Markus et al., 1998; Markus, Panhuysen, Jonkman, & Bachman, 1999). Although it is known that even 5% of protein can dampen the CHO-related increase in tryptophan and serotonin concentrations (for a review, see Spring et al., 1987), research has not systematically examined how CHO interactions with other macronutrients or constituents can affect mood. For example, in the last decade, research into the

behavioural effects of caffeine consumption has increased, with studies reporting consistently positive effects of caffeine supplementation on mood (for a recent meta-analysis, see Camfield, Stough, Farrimond, & Scholey, 2014). As caffeine is very often consumed with CHOs in the form of energy drinks, further studies into their combined effects on mood would be of particular importance to the public. Additionally, the present meta-analysis did not include studies assessing long-term effects of CHO supplementation on mood. With studies reporting that consumption of CHO-rich diets can decrease tension, depression, fatigue and depression (Deijen et al., 1989), especially compared with diets high in protein (Anderson et al., 1987), examination of long-term behavioural and neurobiological effects of high CHO consumption could increase our understanding of the mechanisms behind CHO-related mood facilitation.

In line with the results of the CHO-mood meta-analysis, Experiment 2 reported no beneficial effects of glucose on young adults' affect ratings. However, glucose was found to selectively increase older adults' positive affect in an implicit affective judgment task, a finding that seems to be inconsistent with both the present meta-analysis and individual studies assessing glucose effects on older adults' mood (Riby et al., 2004; van der Zwaluw et al., 2014). Interestingly, the vast majority of studies included in the meta-analysis were conducted with young adults. If CHO effects are stronger in older than young adults, the paucity of ageing studies included in the current meta-analysis could have influenced the results. It should also be noted that whereas an implicit affective judgment task was used in Experiment 2, the meta-analysis was limited to studies assessing mood using explicit mood assessment tools (e.g., POMS). Although speculative, it is possible that CHO effects on mood are subtle and more

reliably identified using implicit tasks (see Quirin et al., 2009). Experiments should be conducted to address the possibility that older adults are more sensitive to the affect-boosting effect of CHOs, and that implicit affect could be more sensitive to glycaemic manipulations.

One could also assume that findings of glucose protecting older adults' PE (Experiments 1a and 1b) further corroborate the premise that CHOs can selectively increase positive affect in older adults. However, the PE is thought to reflect a cognitive mechanism and suggesting that it is indicative of emotional states would not be accurate (Carstensen & Deliema, 2018), especially considering that participants' mood was not assessed alongside the PE in Experiments 1a and 1b. It is imperative that more ageing studies examining CHO-mood interactions should be conducted, employing both explicit and implicit mood assessment tools. This would provide a deeper understanding of age-related differences in the CHO facilitation effect and the exact circumstances that determine the magnitude of CHO enhancement in each age group.

Directions for Future Research

This section discusses proposals for future projects, motivated by the findings uncovered in the thesis. Although suggestions for addressing the limitations of each experiment have already been provided in the overview of findings, this section focuses on overarching projects that have the potential to impact how the study of cognitive and emotional ageing is approached.

Ageing and Glucoregulatory Capacity

One of the main limitations across the studies comprising this thesis is the absence of glucose measurements for experiments in which glycaemic resources were

manipulated. In the preceding section, the importance of measuring circulating blood glucose levels was discussed with regards to two main issues. First, measuring blood glucose levels at baseline would be the most reliable way of ensuring that participants have abided by the 2-hour fasting rule. Second, with studies suggesting that there is an association between mental effort exertion and blood glucose levels (see Fairclough & Houston, 2004; Scholey et al., 2001; Scholey et al., 2006), it would be interesting to assess potential age-related differences in glucose depletion/usage during cognitive performance to assess the energetic demands of older adults' positivity and their patterns of task engagement.

More importantly, assessing blood glucose levels can provide an accurate index of participants' ability to regulate, metabolise and use energy efficiently. Glucoregulatory capacity can be measured through a simple oral glucose tolerance test (OGTT), in which participants are given 75 g of glucose and their blood glucose levels are assessed at baseline and at every 30 minutes following glucose consumption, for a total duration of two (Messier et al., 2010; Stumvoll et al., 2000) or three hours (Owen et al., 2013). Whereas many studies have examined the effect of glucose administration on cognitive performance, there is a surprising paucity of research on glucoregulatory capabilities.

Faster return of blood glucose to baseline values after reaching nadir levels, has been shown to predict improved memory performance in young adults (Donohoe & Benton, 2000). Interestingly, in a study where participants were split into 'good' and 'bad' glucoregulators based on an OGTT, it was found that whereas glucose provision prior to cognitive testing led to significant memory improvement in the 'bad'

glucoregulators, the same dose caused decrements in memory recall and accuracy in 'good' glucoregulators (Owen et al., 2013). In the same study, 'good' glucoregulators experienced higher levels of calmness after glucose ingestion but 'bad' glucoregulators reported being less calm following consumption of a relatively high dose of glucose (60 g). Although the results of this study seem to suggest that those with lower glucoregulatory capacity seem to benefit more from glucose ingestion in terms of cognitive performance, they also, unexpectedly, experience more negative mood outcomes. The conflicting nature of these findings warrants further investigations. Nevertheless, it is clear that individual differences in glucoregulation should be carefully examined when assessing the glucose facilitation effect on cognition and mood. This may be particularly important in ageing studies, considering the highly variable nature of cognitive trajectories in older adults.

Researchers have also attempted to examine the relationship between glucoregulation and behavioural performance in ageing. Similar to the findings uncovered in young populations, studies have found poor glucose tolerance and recovery to be correlated with worse performance in a range of cognitive tasks (Hall et al., 1989; Messier et al., 1997; Messier et al., 2010). However, whereas young adults with good glucoregulatory capacity appear to experience cognitive decrements following glucose consumption (Owen et al., 2013), older adults with good glucose regulation benefit more from glucose provision compared to poor glucoregulators whose memory performance is subject to decrements under high glucose load (Messier et al., 1997). It should be noted that, in the ageing studies discussed, researchers did not use a typical OGTT task to assess glucoregulatory capacity (i.e., lower glucose doses and

different procedure; but see Messier et al., 2010), and these findings should be treated with caution.

Based on these studies, it becomes apparent that glucoregulatory capacity could be the factor that determines the ability of both young and older adults to manage their glycaemic resources and allocate them in an appropriate manner to adequately perform a cognitive task. When it comes to age-related differences in emotion-cognition interactions and cognitive engagement, no studies have evaluated the influence of glucoregulatory capacity. The experiments presented in this thesis suggest that energy availability contributes to the protection of the PE under dual task conditions, increases positive affect and improves task engagement in ageing individuals. However, our knowledge of how glucoregulatory capacity determines which older adults are more likely to experience the glucose facilitation effect in the domains discussed is practically non-existent. Although the findings presented in the thesis have important implications for future research on age-related changes in cognitive and emotional well-being, studies on the role of glucoregulatory capacity would provide us with a deeper understanding of how age-related changes in metabolic capabilities translate into the cognitive and emotional profile we observe in older age. This knowledge would allow researchers and clinicians to develop individually-tailored guidelines aimed at improving glucoregulatory capacity and concomitant behavioural outcomes in older adults.

An important first step would be to investigate how individual differences in glucose regulation capabilities can predict older adults' PE magnitude and their ability to invest effort in cognitively demanding tasks. A simple OGTT followed by the cognitive and affective tasks employed in this thesis would allow researchers to study

potential associations between these constructs. As glucose metabolism is a system regulated by the ANS, it could be assumed that indices of overall ANS functionality would also be indicative of glucoregulatory capacity. It would be interesting to assess whether ANS markers such as HRV are highly correlated with glucoregulation indices. In that case, based on the results of Experiment 3 showing that the PE is more pronounced in older adults with higher resting HRV levels, it is plausible that older adults with better glucose regulation capacity would also show a stronger PE. The second step would be to examine how additional glucose resources are used by 'good' and 'poor' glucoregulators. Is it only older adults with good glucoregulatory capacity who are able to use the boost of additional energy resources (e.g., Messier et al., 1997), or are 'poor' glucoregulators more likely to show a strong PE and higher task engagement following glucose provision (e.g., Owen et al., 2013)? As mentioned in an earlier section, blood glucose measurements can be a source of discomfort for participants, and this can have effects on mood and emotionality. Therefore, studies assessing the relationship between glucoregulation and the PE would benefit from the development of non-invasive glucose monitoring systems (e.g., Geng, Tang, Ding, Li, & Wang, 2017).

As mentioned in Chapter 1, researchers have argued that the cognitive decrements observed in typical ageing could be related to (or stem from) decrements in glucoregulatory capacity that are typically found in normal ageing (Gold, 2005). Establishing an association between glucoregulation and emotion-cognition interactions would allow researchers to develop interventions that could have important practical implications for older adults' cognitive and emotional well-being. Research has recently

focused on examining the neurobiological and behavioural substrates of highly successful ageing. These so-called ‘superagers’ appear to be impervious to age-related cognitive decline, showing levels of cognitive performance usually found in healthy middle-aged and young adults (Gefen et al., 2014). In fact, neuroimaging and post-mortem studies have found brain areas critical to cognitive functioning to be thicker in superagers compared with healthy middle-aged adults (e.g., cingulate cortex; see Gefen et al., 2015; Harrison, Weintraub, Mesulam, & Rogalski, 2012), and structurally indistinguishable to that of their young counterparts (e.g., hippocampus; see Sun et al., 2016). It would be particularly interesting to examine the glucoregulatory capacity of superagers to determine whether regulation of metabolic resources also contributes to their preserved cognitive skills.

Vagal Tone and Emotion Regulation

A novel and interesting finding of this thesis is the relationship between vagal tone, as measured by resting HRV levels, and negativity avoidance in older adults. As discussed in previous sections, this association can have practical and theoretical implications for older adults’ well-being that are yet to be examined. Considering that this is the first study to uncover a direct relationship between ANS functionality and older adults’ ability to suppress negative information, an important question arises: how can we use this knowledge to explore and further improve older adults’ cognitive engagement, affect and overall well-being? In this section, possibilities for future projects within the general area are discussed.

Susceptibility to stereotype threat

In modern societies, older adults are often portrayed as helpless and less competent than young adults, a stereotype that is internalised in young age, persisting throughout adulthood and transforming into a self-stereotype in older age (Levy, 2003). As a result, research into how age-related stereotypes affect older adults' cognitive performance has started to receive a lot of attention in recent years. It has been repeatedly shown that priming participants with stereotypes on how they are expected to perform on a task can impair their performance on that specific cognitive domain (for a review, see Barber, 2017). For example, when female students are primed with the stereotype that women are not good at maths, they tend to perform less well compared with their actual academic capacity (Spencer, Steele, & Quinn, 1999). In a similar manner, presenting older adults with stereotypes regarding age-related cognitive decline has been shown to significantly affect their performance on cognitive tasks (Hess, Auman, Colcombe, & Rahhal, 2003; for a review, see Barber & Mather, 2014). A recent meta-analysis has provided strong evidence confirming that older adults are particularly susceptible to stereotype threat manipulations, especially when it comes to cognitive performance (Lamont, Swift, & Abrams, 2015).

The negative effect of stereotype threat has been attributed to a number of factors. Schmader, Johns, and Forbes (2008) suggested that performance decrements are a result of a stereotype threat-related stress response requiring participants to use cognitive resources in order to suppress/downregulate the negative affect elicited. As such, having to use available resources to regulate the stereotype-related negative affect significantly decreases the magnitude of resources that can be allocated to the task,

leading to inevitable decrements in cognitive performance. The role of emotion regulation capabilities in protecting participants from the negative consequences of stereotype threat has also been examined. Across four experiments conducted with young adults, researchers have confirmed that the anxiety caused by stereotype threat can deplete cognitive control resources and lead to decreases in cognitive performance (Johns, Inzlicht, & Schmader, 2008). However, instructing participants to employ emotion regulation mechanisms (e.g., cognitive reappraisal) can successfully protect them from the stereotype threat-related consequences on cognition (Johns et al., 2008).

It is important to note that no studies have examined the role of emotion regulation capacity in older adults' susceptibility to stereotype threat. As reported in Experiment 3, vagal tone at rest can successfully predict older adults' ability to inhibit negative information and show a stronger negativity avoidance in their gaze preferences (i.e., the PE). It is possible that older adults with high vagal tone at rest are also better able to shield their cognitive performance from the effects of stereotype threat, simply by being more efficient in using emotion regulation strategies to avoid the negativity associated with exposure to the stereotype. First, it would be important for future studies to measure resting HRV levels to try and uncover potential associations with participants' cognitive performance following a stereotype-threat manipulation. Second, projects could examine how different emotion regulation strategies (i.e., cognitive reappraisal vs. suppression) can mitigate cognitive decrements, and whether vagal tone at rest can predict which older adults are more likely to successfully employ such regulatory mechanisms. With an abundance of studies reporting associations between HRV, self-regulation (Segerstrom & Nes, 2007), and emotion regulation capacity

(Appelhans & Luecken, 2006; Thayer & Lane, 2009), it is plausible that these ideas would yield interesting results that would shed light on the relationship between physiological functionality, emotionality and cognitive engagement.

Recently, researchers have also found the PE to be susceptible to stereotype threat manipulations. It has been found that exposing older adults to stereotypes regarding age-related cognitive decline can diminish the PE, which is not reinstated even if a positive stereotype intervention is introduced (Barber, Seliger, Yeh, & Tan, in press). As mentioned earlier, researchers have argued that exposure to stereotype threat requires participants to use additional processing resources to downregulate the negativity associated with the stereotype, which decreases the levels of available resources allocated to the cognitive task and diminishes performance (Schmader et al., 2008). Therefore, it is possible that stereotypes prior to a PE task increase task demands by introducing a dual task-like component (i.e., regulating emotions while performing a task) that decreases older adults' ability to allocate all available resources towards achieving positivity. In Experiment 3, it was reported that vagal tone can predict older adults' negativity avoidance even under dual-task conditions. It would be interesting to see whether high-HRV older adults are more likely to retain their PE even when a stereotype threat manipulation is introduced before the cognitive task. Additionally, based on findings that glucose can alleviate the effect of high cognitive demands on the PE (see Experiments 1a and 1b), it would also be important to investigate whether a small dose of glucose can mitigate the effects of stereotype threat on the PE. If stereotype threat diminishes the PE because of an increase in task demands, glucose

could provide older adults with the necessary resources to successfully manage the emotional impact of the stereotype while retaining their PE.

Implications for cognitive engagement

In Experiment 2, it was found that energy availability is a potential resource underlying older adults' cognitive engagement capacity, improved cognitive performance and increased positive affect. This suggests that ANS processes such as glucose metabolism can significantly affect cognition and emotion in older adults. However, little is known about how overall ANS functionality contributes to older adults' cognitive engagement patterns. As mentioned in an earlier chapter, understanding which factors contribute to cognitive engagement can have important real-life implications for cognitive maintenance and emotional well-being in older age (Hertzog et al., 2008).

Researchers in the area have argued that older adults' engagement patterns are related to the effortful nature of cognitive control. Reduced engagement is a result of an age-related adaptive/selective mechanism designed to protect valuable resources from being spent on tasks that might offer little benefit (for a review, see Hess, 2014). This pattern of selectivity in older adults' engagement of resources is also seen in the selectivity that gives rise to the age-related PE: older adults recruit cognitive control resources to selectively prioritise positive over negative information. Interestingly, the PE-related selectivity is posited to be motivated by older adults' emotion regulation goals, aimed at retaining a positive mood (Mather & Carstensen, 2005). It is possible that selective engagement of resources is similarly affected by an emotion regulation motivation. That is, effortful cognitive exertion might deplete resources and,

additionally, increase negative or decrease positive affect. Therefore, older adults reduce their levels of engagement to not only conserve energy resources but also to protect themselves from a drop-off in mood.

Although this is simply a speculation, some evidence exists that offers support for the negativity-inducing nature of effortful cognitive exertion. Despite effort mobilisation being associated with positive life outcomes (e.g., exercising to lose weight), some researchers have suggested that exerting effort is inherently aversive (Kurzban, 2016). The negative emotions that accompany cognitive exertion and self-control are posited to motivate participants to disengage from such negativity-inducing activities and focus on more intrinsically rewarding tasks (e.g., less resource-intensive activities/rest; Inzlicht, Schmeichel, & Macrae, 2014). If this is correct, it is possible that resource depletion and the negativity that follows high levels of cognitive exertion make participants reduce effort mobilisation as a way of regulating their mood/emotionality. To investigate this possibility, it would be interesting to see how individual differences in emotion regulation capacity can predict older adults' ability to invest effort in cognitive tasks. Examining vagal tone at baseline and subsequent levels of cognitive exertion could help identify a potential association between the two. Are older adults with higher HRV levels at baseline more likely to show higher levels of engagement? Using comprehensive measures of mood (both explicit and implicit) before and after cognitive exertion could also provide an index of how emotionality fluctuates as a consequence of different levels of cognitive engagement.

Interestingly, G. E. Giles et al. (2018) found that asking participants to mobilise emotion regulation strategies to moderate psychological responses to high endurance

exercise can improve engagement in physical tasks by decreasing participants' perceptions of subjective effort levels. As older adults' ability to engage in cognitive tasks is influenced by their subjective perception of effort (see Hess et al., 2016), emotion regulation strategies (e.g., reappraisal) could improve engagement by reducing the perception of effort associated with performance in a cognitive task. Similar to what was suggested in the stereotype threat section, it would also be interesting to assess whether high-HRV older adults are more successful at employing emotion regulation strategies to increase engagement compared with their low-HRV counterparts. The notion of an association between ANS functionality, emotionality and levels of engagement is intuitively interesting and would allow researchers to further explore the mechanisms underlying successful cognitive engagement.

Emotional memory vividness

Whereas many studies have been conducted to assess the PE in older adults (for a meta-analysis, see Reed et al., 2014), researchers have only recently started to investigate how age-related positivity influences the quality and vividness of valenced memories. Findings from this line of research could be of particular importance to research areas interested in the quality of retrieved memories and the factors that influence memory vividness (e.g., false memory; Karpel, Hoyer, & Toglia, 2001). J. H. Ford, Morris, and Kensinger (2014) presented young and older participants with positive, negative and neutral pictures with accompanying titles. Following a 30-minute delay, participants were presented with only the titles and performed a recognition task. After each response, participants were given a 5-second elaboration period during which they had to think about the image attached to the title and the emotion they experienced

during encoding of that particular item. In the elaboration phase, participants showed higher activation of PFC sub-areas (e.g., dorsomedial PFC) for negative over positive material. In a follow-up study using the same cognitive task, the researchers uncovered an age-related difference in PFC-hippocampus connectivity, with increasing age being associated with stronger connectivity specifically during the retrieval of negative material. This age-related retrieval pattern was interpreted as older adults' attempt to downregulate the affective impact of negative memories (J. H. Ford & Kensinger, 2017; J. H. Ford, Morris, & Kensinger, 2014b).

Even more interesting, whereas a positive relationship between PFC recruitment and vividness ratings for negative material has been found in young adults, older adults tend to show the exact opposite pattern, with higher PFC recruitment leading to lower memory vividness when retrieving negative memories. Additionally, while no PFC-vividness relationship for positive material was identified in young adults, older adults' PFC recruitment predicted higher vividness for positive information during retrieval (J. H. Ford & Kensinger, 2017b). These results show that older adults' vividness for emotional material is modulated by valence, in line with their positivity motivation. As an association has already been identified between older adults' vagal tone and their ability to suppress negativity in an attention task (see Experiment 3), it would be interesting to explore whether older adults' vagal tone is also related to negativity suppression during retrieval of negative material. If that is the case, can ANS functionality help us predict the vividness of older adults' memory for emotional material?

Physiological Profile of Successful Ageing

Although the studies comprising the thesis provide an important first step in addressing how energy availability and overall ANS functionality contribute to emotion-cognition interactions in ageing, our understanding of how individual differences in physiological functionality determine cognitive and emotional functionality is still very limited. As mentioned in the introduction, the ANS is a complicated system that regulates all major biological functions in the human body. Therefore, it would be important to examine how other biological processes nested within the ANS can help create a unified autonomic profile of successful ageing. In turn, this will help researchers and clinicians to develop individually-tailored strategies targeting specific physiological functions to improve behavioural outcomes. As the importance of measuring glucoregulatory and metabolic capacity was discussed earlier, the focus of this section will shift to other biological functions that can have an impact on the study of ageing.

Gut microbiota

An important system that has not received much attention in ageing is the gastrointestinal tract and, more specifically, the role of the gut microbiota in cognitive and emotional well-being. In addition to the two main divisions of the ANS, namely the SNS and the PSNS, it also has a third division known as the Enteric Nervous System that is responsible for regulating gut functions. In recent years, researchers have suggested that the Central Nervous System is in direct communication with the gut via the SNS and PSNS (among other routes), which dictate the rate of digestion and other gut-related functions. This connection between the gut and the Central Nervous System,

known as the gut-brain axis, has received extensive attention in the last decade, with numerous studies suggesting that gut microbiota (gut flora) health directly influences cognition, mood and overall behaviour (for detailed reviews, see Cryan & Dinan, 2012; J. A. Foster & McVey Neufeld, 2013). Indeed, research conducted with mice has found that, whereas perturbed gut microbiota can significantly increase stress and depressive symptomatology (J. A. Foster & McVey Neufeld, 2013; Neufeld, Kang, Bienenstock, & Foster, 2011), healthy gut flora contributes to reduced anxiety and normal brain development (Heijtz et al., 2011). In human subjects, studies administering psychobiotics that are known for their ability to improve gut health (i.e., probiotics and prebiotics; see Sarkar et al., 2016) have reported beneficial effects on affective indices such as cognitive reactivity to sadness (e.g., rumination and aggression; see Steenbergen, Sellaro, van Hemert, Bosch, & Colzato, 2015), which can have important implications for the management of depressive symptomatology (Logan & Katzman, 2005).

Although not much research has been done with human participants, the importance of a healthy microbiome for behaviour has recently started to become evident. Interestingly, a study that tested the composition of older adults' microbiota has found a strong relationship between microbiome structure and frailty, nutrition/diet, as well as CV and inflammation indices, suggesting that successful ageing is potentially related to the health of the microbiome (Claesson et al., 2012). As no studies have directly assessed how older adults' gut microbiota relates to indices of cognitive functionality and mood, it would be important to examine the association between these components. Considering the intimate connection between the gut and the brain, it is

also possible that psychobiotic supplementation can significantly improve older adults' cognitive functioning and emotionality.

It should be noted that one of the few studies to assess longitudinal (3-week) probiotic supplementation in middle-aged and older adults has found improved affect in participants with poor mood at baseline but also, unexpectedly, slight cognitive decrements on measures of memory in the probiotic group (Benton, Williams, & Brown, 2007). With studies suggesting that the gut microbiota might be altered as a result of increasing age (for a review, see Leung & Thuret, 2015), it is possible that psychobiotic supplementation could exert a stronger influence on older adults' behaviour. Investigating the possibility of an association between the microbiome and age-related emotion-cognition interactions could bring us a step closer to building the physiological profile of successful ageing.

Immunosenescence

Typical ageing is associated with alterations in the composition and responsivity of cells responsible for producing antibodies and fighting infections (for a review, see Ginaldi et al., 1999). Animal models have shown that ageing is associated with increased innate immune system activity, leading to higher levels of pro- and lower levels of anti-inflammatory cytokines in the brain (Ye & Johnson, 1999, 2001). This is a particularly important finding as studies have found the symptoms of inflammatory cytokines-related sickness to be strikingly similar to those of mood/affective conditions such as depression. Therefore, a perturbed immune system could potentially contribute to impaired mood and affective decline, particularly in old age (for a review, see Dantzer, O'Connor, Freund, Johnson, & Kelley, 2008). Indeed, a large study that

included 267 older adults free from psychiatric conditions found markers of inflammation to predict an increase in future depressive symptomatology (but not cognitive decline; van den Biggelaar et al., 2007).

These findings pose important questions regarding the role of immunosenescence in older adults' cognitive and emotional well-being. There has only been one study investigating the association between the immune system and emotion-cognition interactions in ageing. Researchers examined older adults' positivity preference using a memory recall PE paradigm along with the assessment of biomarkers of immune system functionality. Participants were tested three times, with each time point separated by one year (two years in total). The researchers reported that higher positivity in older adults' memory predicted stronger immune system functionality across the experiment, a finding that could have important implications for understanding the role of the PE in emotional functioning (Kalokerinos, Von Hippel, Henry, & Trivers, 2014). It would be interesting to further investigate how age-related changes in immune system functionality affect older adults' emotionality, cognitive performance and their ability to actively engage in cognitive tasks.

Of note, although the gut-brain axis was discussed separately to the immune system, these two systems are intricately connected. The gut microbiota has both direct and indirect connections with the immune system. Consumption of psychobiotics has been shown to have beneficial effects on a host of medical conditions (e.g., autoimmune disorders), regulate inflammation and improve overall health, both within and outside the gastrointestinal tract (for reviews, see Duerkop, Vaishnava, & Hooper, 2009; Forsythe & Bienenstock, 2010). Furthermore, it has been found that probiotic

supplementation affects levels of pro- and anti-inflammatory cytokines, which can significantly influence brain functions relating to mood and cognition (Cryan & Dinan, 2012). Therefore, it would be interesting to investigate how gut health and the immune system work together to exert an influence on older adults' cognitive and emotional well-being. Developing interventions aimed at improving the health of the microbiome could also improve immune system functionality, which could have important implications for older adults' cognitive and physical health.

Concluding Remarks

The purpose of the thesis was to examine the physiological mechanisms underlying emotion-cognition interactions in ageing, with a specific focus on energy availability and overall ANS functionality. The results can be summarised as follows:

- Glucose administration helps older adults retain their PE even under dual-task conditions (Chapter 2, Experiments 1a and 1b)
- Glucose increases cognitive engagement, improves cognitive performance, and enhances affect in older adults (Chapter 3, Experiment 2)
- Older adults' PE is dependent on ANS functionality: higher ANS capacity, as measured by resting HRV levels, predicts higher negativity avoidance in older adults (Chapter 4, Experiment 3)
- Acute CHO administration does not lead to mood facilitation — instead, CHO ingestion is associated with higher fatigue and lower levels of alertness within the first hour post consumption (Chapter 5, meta-analysis)

This thesis has found an important connection between peripheral physiology and older adults' preference for positive material, cognitive engagement and affect. It has also provided answers to a topic of high societal importance, namely, the relationship between CHO consumption and mood. These results suggest that physiological mechanisms play an integral role in older adults' cognitive and emotional well-being, and should be carefully considered when investigating age-related changes in these domains. The paucity of studies assessing physiological outcomes along with behavioural indices is surprising and should be addressed in forthcoming years. With the studies comprising this thesis suggesting the presence of a strong synergy between peripheral physiology and emotion-cognition interactions, it would be useful for researchers in the area adopt a more integrated approach to the study of ageing, combining the evaluation of both behavioural and physiological factors. Such approaches will not only enrich our understanding of successful ageing but will also allow us to develop strategies and interventions to combat age-related decline and decrements in cognitive and emotional well-being.

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Appendix A

Word Lists Used in Experiments 1a and 1b

List 1			List 2			List 3			List 4		
Word	*Valence*	*Arousal*	*Word*	*Valence*	*Arousal*	*Word*	*Valence*	*Arousal*	*Word*	*Valence*	*Arousal*
iron	Neut	L	knee	Neut	L	engine	Neut	L	cap	Neut	L
cow	Neut	L	basket	Neut	L	seat	Neut	L	cellar	Neut	L
vision	Pos	L	gang	Neg	H	dream	Pos	L	resort	Pos	L
strike	Neg	H	angel	Pos	L	despair	Neg	L	struggle	Neg	H
barrel	Neut	L	harsh	Neg	H	gold	Pos	H	dawn	Pos	L
movie	Pos	L	safe	Pos	L	compare	Neut	L	clue	Neut	L
cry	Neg	H	clock	Neut	L	slaughter	Neg	H	decline	Neg	L
plain	Neut	L	weary	Neg	L	grateful	Pos	L	glory	Pos	H
gossip	Neg	L	pride	Pos	H	mad	Neg	H	fist	Neg	L
magic	Pos	H	bullet	Neg	H	tool	Neut	L	mate	Pos	H
lie	Neg	L	detail	Neut	L	star	Pos	H	bomb	Neg	H
kiss	Pos	H	honey	Pos	L	habit	Neut	L	phase	Neut	L
vice	Neg	L	pit	Neg	L	harm	Neg	H	alive	Pos	H
laugh	Pos	H	horror	Neg	H	meadow	Pos	L	suffer	Neg	L
network	Neut	L	spray	Neut	L	waste	Neg	L	score	Pos	H
pure	Pos	L	fancy	Pos	H	genius	Pos	H	shy	Neut	L
combat	Neg	H	sleep	Pos	L	hazard	Neg	H	fail	Neg	H
romance	Pos	H	sin	Neg	H	wise	Pos	L	virtue	Pos	L
awkward	Neg	L	repeat	Neut	L	boot	Neut	L	contract	Neut	L

chin	Neut	L	fat	Neg	L	sad	Neg	L	scream	Neg	H
nice	Pos	L	surprise	Pos	H	anger	Neg	H	soft	Pos	L
arrest	Neg	H	item	Neut	L	saint	Pos	L	fury	Neg	H
rich	Pos	H	stubborn	Neg	L	swim	Pos	H	secure	Pos	L
grip	Neut	L	win	Pos	H	sewer	Neg	L	budget	Neut	L
sick	Neg	L	fatigue	Neg	L	embrace	Pos	H	tomb	Neg	L
rabbit	Pos	L	bath	Pos	L	mould	Neg	L	fortune	Pos	H
argue	Neg	H	weekend	Pos	H	code	Neut	L	caution	Neg	L
bench	Neut	L	taxi	Neut	L	tower	Neut	L	bowl	Neut	L
wagon	Neut	L	lamp	Neut	L	bus	Neut	L	input	Neut	L

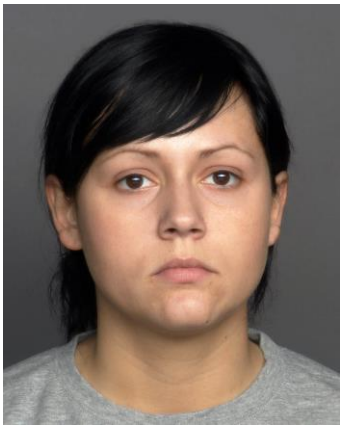
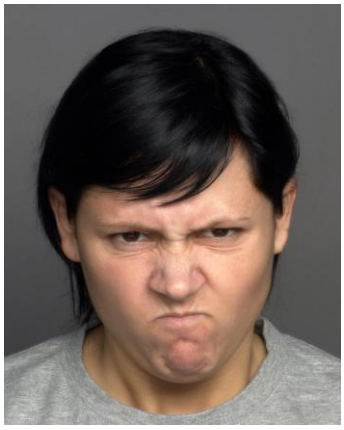
Note. Neut = Neutral, Pos = Positive, Neg = Negative, L = Low Arousal, H = High Arousal

Appendix B

Examples of Face Pairs Used in Experiment 3

Happy-Neutral Male


Neutral-Angry Female

(Ebner et al., 2010)

Appendix C

Glucose Manipulation in Experiment 3

A randomised, placebo-controlled, double-blind design was employed. Participants were randomly assigned to consume either a glucose or a placebo drink (25 g of glucose or five aspartame tablets, respectively, dissolved in 300 ml of water). To improve palatability, 25 ml of sugar-free orange-flavored cordial was added to both drinks. The drinks were labelled by an assistant not involved in the design of the study or data collection. The glucose dose was chosen based on previous work indicating that 25 g is an appropriate dose for observing glucose facilitation effects on cognition (Riby, 2004; Sünram-Lea et al., 2011) and on older adults' PE (see Chapter 2). Furthermore, the drink composition used in Experiment 3 has been shown to lead to comparable palatability ratings across glucose and placebo groups (see Chapter 2).

Two separate two-way between-subjects ANOVAs were conducted on mean correct RTs and error rates in the secondary 1-back task, with age (young, older) and drink (glucose, placebo) as factors. In terms of RTs, older adults were slower than young adults, $F(1, 121) = 69.14$, $p < .001$, $\eta_p^2 = .364$, but the main effects of drink and the Age × Drink interaction failed to reach significance (both *p*s > .09). Although the interaction was not significant, it should be noted that whereas the older-glucose group was significantly faster than the older-placebo group, $t(60) = 2.21$, $p = .031$, the young glucose and placebo groups did not differ, $t < 1$. In terms of error rates, the main effects of age and drink were not significant (both *p*s > .202). However, the Age × Drink interaction was significant, $F(1, 121) = 5.80$, $p = .018$, $\eta_p^2 = .046$: whereas young adults' error rates were not affected by drink, $t < 1$, older adults in the glucose group made

fewer errors compared with placebo, $t(60) = -2.46$, $p = .017$. These results are similar to the glucose facilitation effect uncovered in Experiment 2: recall that glucose improved older adults' performance in the memory search task, but young adults did not benefit from the extra glucose resources.

Fixation count ratios were entered into a four-way mixed ANOVA with age (young, older) and drink (glucose, placebo) as the between-subjects factors, and emotion (happy, angry) and task (single, dual) as the within-subjects factors. With the exception of a marginal Drink × Emotion interaction, $F(1, 119) = 3.57$, $p = .061$, $\eta_p^2 = .029$ (slightly higher negativity avoidance for placebo compared with glucose, $t(121) = -1.82$, $p = .072$; no differences in positivity preference, $t < 1$), no main effect of drink and no interactions between drink and other variables were uncovered (all ps > .271). Additionally, participants' affect ratings were entered into a three-way mixed ANOVA with age (young, older) and drink (glucose, placebo) as the between-subjects factors, and task (single, dual) as the within-subjects factor. No main effect of drink and no interactions between drink and other variables were identified (all ps > .102).

Appendix D

Analysis of Fixation Durations in Experiment 3

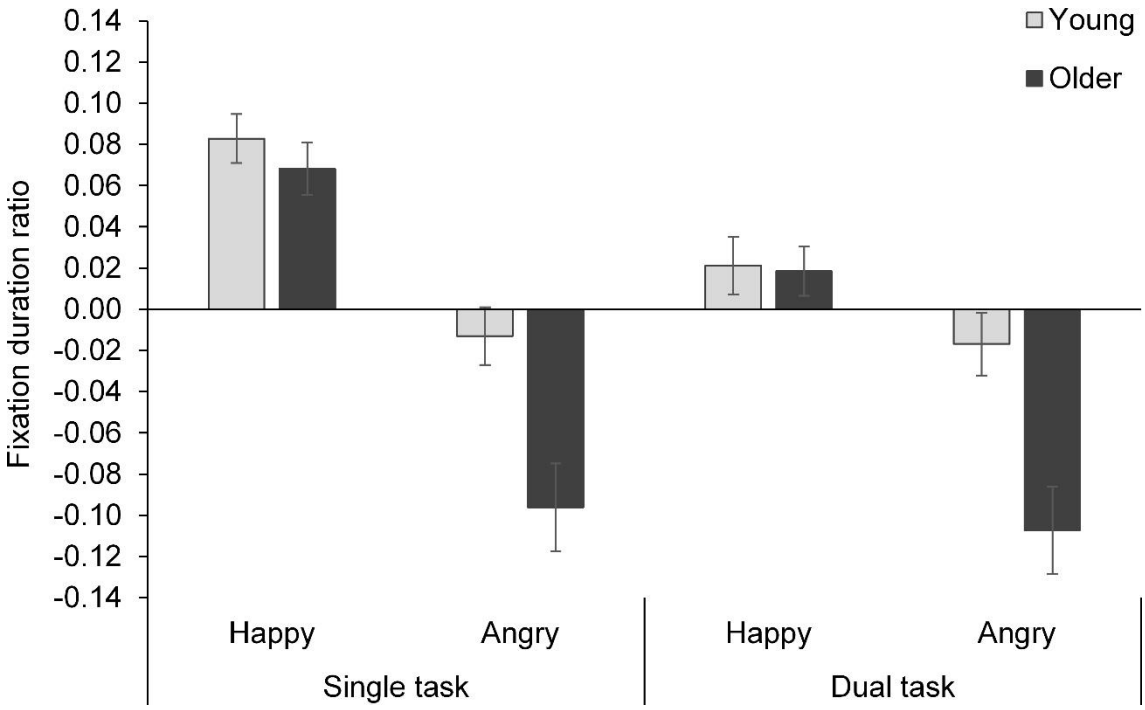


Figure C1. Fixation duration ratio score (mean ± 1 standard error of the mean) during emotional-neutral face pair presentation as a function of age (young, older) emotion (happy, angry) and task (single, dual) in Experiment 3. Zero signifies no preference, and a positive/negative ratio score shows preference toward/away from the emotional face.

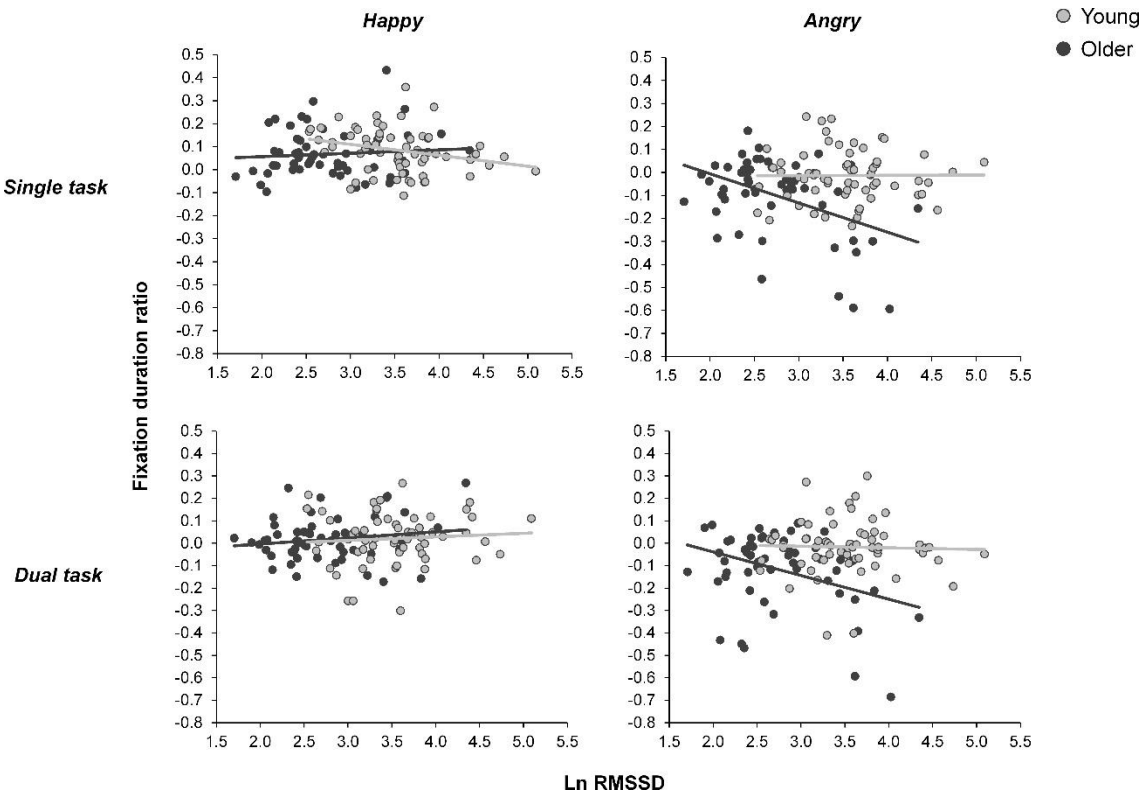


Figure C2. Association between baseline HRV (Ln RMSSD) and young and older adults' fixation duration ratio during presentation of happy-neutral (left panels) and angry-neutral (right panels) face pairs under single task (top panels) and dual task (bottom panels) conditions in Experiment 3

Appendix E

List of Studies Excluded at the Final Stage of the Meta-Analysis Because of Relevant Data Not Being Available

Authors	Year	Journal
Backhouse, Bishop, Biddle, & Williams	2005	*Medicine and Science in Sports and Exercise*
Backhouse, Ali, Biddle, & Williams	2007	*Scandinavian Journal of Medicine and Science in Sports*
Benton & Owens – **Experiment 1**	1993	*Journal of Psychosomatic Research*
Benton & Owens – **Experiment 2**	1993	*Journal of Psychosomatic Research*
Benton & Owens – **Experiment 3**	1993	*Journal of Psychosomatic Research*
Duckworth, Backhouse, & Stevenson	2013	*Appetite*
Harte & Kanarek	2004	*Nutritional Neuroscience*
Meikle, Riby, & Stollery	2004	*Human Psychopharmacology: Clinical and Experimental*
Miller, Bourrasseau, Williams, & Molet	2014	*Physiology & Behavior*
Owens, Parker, & Benton – **Experiment 1**	1997	*Physiology & Behavior*
Owens, Parker, & Benton – **Experiment 2**	1997	*Physiology & Behavior*
Owens, Parker, & Benton – **Experiment 3**	1997	*Physiology & Behavior*

Peacock, Thompson, & Stokes	2012	*Appetite*
Pivonka & Grunewald	1990	*Journal of the American Dietetic Association*
Qin et al.	2017	*Physiology & Behavior*
Scholey & Fowles	2002	*Neurobiology of Learning and Memory*
Scholey & Kennedy	2004	*Psychopharmacology*
Scholey, Sünram-Lea, Greer, Elliott, & Kennedy	2009	*Psychopharmacology*
Seo et al.	2014	*Journal of the International Society of Sports Nutrition*
Sihvola et al.	2013	*The British Journal of Nutrition*
Smit, Cotton, Hughes, & Rogers – **Experiment 2**	2004	*Nutritional Neuroscience*
Smit, Cotton, Hughes, & Rogers – **Experiment 3**	2004	*Nutritional Neuroscience*

End