AGE DIFFERENCES IN EATING TRAITS ASSOCIATED WITH RISK OF OBESITY: THE ROLE OF INTEROCEPTION.

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Declarations and Publication Statement

The candidate attests that the work he has submitted is his own. The expertise and input of coauthors is gratefully acknowledged.

Chapter 2 is based on the peer reviewed publication:

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Declarations

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

Signed..... 

Date: 19th July 2023.

This thesis is the result of my own investigations, except where otherwise stated. Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

Signed.. 

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I hereby give consent for my thesis, if accepted, to be available for photocopying and for inter-library loan, and for the title and summary to be made available to outside organisations.

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Date: 19th July 2023.

The University's ethical procedures have been followed and, where appropriate, that ethical approval has been granted.

Signed... 

Date: 19th July 2023

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Firstly, I would like to sincerely thank both of my supervisors, Professor David Benton and Associate Professor Hayley Young. Both have provided me with inexhaustible support, knowledge, and encouragement. Specifically, the guidance and mentorship you have provided have immensely aided my development in communicating my research. It has been an honour and a pleasure working under your supervision over the past few years.

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Lastly, I am grateful to Swansea University for supporting my research and to each participant for taking part in my research. Without your time and commitment, my research would not be possible. Thank you.

Timeline of research and author roles

Study 1 (now Chapter 2)

November 2018 – January 2019	fMRI study design, collaboration and methods (AB, HY, DB)
January – March 2019	AB Attended neuroimaging lectures provided by two collaborators (LM and HB) on Study 1 of the thesis (chapter 3)
March – August 2019	Participant recruitment for Study 1 (older and younger samples) (SN, CH and AB)(two people are required in scanning environment for H&S reasons) Scheduled fMRI scanning sessions dependent upon technicians' availability. *Some technical errors occurred during this time with the scanner
June – November 2019	Neuroimaging Software training (SPM8) provided by LM. September – AB converted all raw imaging files in formats compatible for pre-processing stages. October - AB conducted all pre-processing stages of the imaging data including motion correction, realignment, smoothing and normalisation
December 2019	ICA procedure, spatial map metrics and implementing a BrainMap atlas, tuition provided to AB by LM. First level analysis and first draft of interpretation was written by AB
January 2020	Feedback on initial analyses and interpretation provided by LM, HB and CH. Planning meetings held discussing developing training skills for more advanced and improved interpretive methods of neuroimaging e.g. effective connectivity, dynamic causal modelling (AB, HY, CH, LM, HB)
February 2020	Second level analysis and first draft of a results section write up (AB)
March 2020	Feedback on second level analysis and results section provided by LM and HB.
April 2020 – November 2020	Study 1 write up (AB), input and feedback from HY and DB
December 2021	Study 1 accepted for publication

Study 2 (now Chapter 4)

January – February 2022	Swansea university vice chancellor announces research may continue in person pending approval of risk assessments. AB and HY design expected satiety study. AB sets up study and prepares risk assessment

March – June 2022	Discussions held with Swansea university risk assessment team on the grounds of including older adults. It was decided that testing could proceed but without older adults. AB, CG and DK recruited, ran the study, and collected and inputted the data. Recruitment was slower than expected and only one person could be tested at a time leading to small sample size.
June 2022	AB applied for an extension of the PhD due to the disruption caused by the COVID pandemic. AB consulted with HY and DB regarding further data collection with older adults, but to avoid further disruption or delay write-up proceeded with only young adults' sample.
July 2022	AB ran analyses and provided initial interpretation with input and feedback from HY and DB
September – November 2022	Study 2 write up by AB, DB and HY.

Study 3 (now Chapter 4)

June – September 2022	Due to slow lab-based data collection it was decided that the final experimental section would be an online study. AB designed the study and collected online questionnaire data for the interoceptive sensibility measures.
1st October 2022	Write up year of PhD begins
November 2022	Structural equation modelling analysis conducted and interpreted by AB with feedback from HY
December 2022-February 2023	Study 3 write up by AB, feedback and input by HY
August 2023	Study 3 manuscript accepted for publication

Systematic Review (now Chapter 2)

NOTE – preparation of this Chapter spanned most of the candidature with initial discussions and literature familiarisation starting in 2018-2019 and periodically thereafter until final decisions about inclusion / structure were made in 2023 (to ensure an up to date literature review).

November 2018 – May 2023	Literature review development, scoping, reading, familiarisation etc. (AB)
July 2023	AB and HY explored the feasibility of turning a narrative literature review into a systematic review (now Chapter 2)
July 2023	AB formulated a clear systematic review question
August 2023	AB searched electronic databases for relevant studies (systematic review) following PRISMA guidelines.

August – September 2023	Relevant studies were screened and reviewed for inclusion in the systematic review (AB and HY).
September 2023	Write up of the systematic review AB, with input and feedback from HY.

Dedication

I would like to dedicate this thesis to Craig Coombs. I will always be appreciative of the support you have given me over the many years.

"That's all" (Miranda Priestly.)

Accompanying Conference Presentations

- Brennan, A., Marstaller, L., Burianová, H., Benton, D., Hanley, C. J., Newstead, S., & Young, H. A. (2022). Weaker connectivity in resting state networks is associated with disinhibited eating in older adults. *International Journal of Obesity*, *46*(4), 859–865. https://doi.org/10.1038/s41366-021-01056-1

    - Postgraduate Research Conference – Swansea University
        - Oral presentation
    - British Food and Drinking Group annual conference.
        - Poster presentation
    - Annual meeting of the Society for the Study of Ingestive Behaviour.
        - Poster presentation

- The Role of Interoception in Age-Related Obesity: A Structural Equation Modelling Study.

    - Swansea Nutrition, Appetite and Cognitive research group. Swansea University.
        - Spotlight oral presentation.

List of Abbreviations

AEBQ	Adult Eating Behaviour Questionnaire
AUD	Auditory Network
BMI	Body Mass Index
CS	Cross Sectional
DE	Disinhibited Eating
DMN	Default Mode Network
ECN	Executive Control Network
EE	Emotional Eating
EOF	Enjoyment of Food
EOE	Emotional Overeating
EUE	Emotional Undereating
EoF	Enjoyment of Food
FC	Functional Connectivity
fMRI	Functional Magnetic Resonance Imaging
FPN	FrontoParietal Network
FR	Food Responsivity
H	Hunger
IACC	Interoceptive Accuracy
IATT	Interoceptive Attention
IC	Independent Component
ICA	Independent Component Analysis
ICN	Intrinsic Connectivity Network
MAIA	Multidimensional Assessment of Interoceptive Awareness
OA	Older Adults
PANAS	Positive and Negative Affect Scale
RE	Restrained Eating
RS	Resting State
SEM	Structural Equation Modelling
SR	Satiety Responsiveness
TFEQ r18	Three Factor Eating Questionnaire revised 18
YA	Younger Adults

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Abstract

In younger adults, the factors driving eating behaviours associated with an increased risk of obesity have been well-researched. However, far less is known about whether the same factors apply in later life. Therefore, the over-arching aim of this thesis was to evaluate whether the same mechanisms driving eating behaviours in younger adults translate to older cohorts. The current thesis explores the extent to which mechanisms such as interoception, may be driving eating behaviours associated with obesity in young and older adults. Specifically, the studies included here identify that age-related alterations in interoceptive processing may be linked with changes in eating behaviour.

The current thesis draws from a range of scientific approaches to achieve its aims including neuroimaging, biobehavioural, and statistical approaches. Throughout the thesis, interoception is operationalised using neuroimaging methods, a novel paradigm (developed within an active inference framework), and self-report methods.

Chapter 2 presents a systematic review that considered the effects of age on interceptive processes relevant to eating behaviour. Specifically, studies that examined the effects of age on various interoceptive domains such as appetite sensations, cardioception, interoceptive sensibility, and orosensory were examined. However, across all domains, there were various limitations that need to be addressed before recommendations can be made. A roadmap was proposed for future studies, consisting of longitudinal, population-based research, paradigms that can differentiate belief from sensation-driven interoception, multidimensional research designs, and mechanistic links to eating behaviour.

Chapter 3 investigated the resting-state functional connectivity of three major brain networks previously linked with hedonic eating and interoceptive processes. Twenty-one younger (aged 19-34 years, BMI range: 18-31) and twenty older (aged 60-73 years, BMI range: 19-32) adults completed the Three Factor Eating Questionnaire and underwent a resting state fMRI scan. The analysis found that older adults reported lower levels of disinhibited eating and had weaker connectivity in the frontoparietal (FPN) and default mode (DMN) networks. Additionally, disinhibited eating was associated with weaker connectivity in the FPN and DMN – effects that were absent in the younger sample. Importantly, these effects could not be explained by differences

in habitual diet. These findings provided preliminary evidence that appetite changes in older adults may be associated with differences in the engagement of brain networks underlying executive functioning, attentional control, and interoception. The findings should be replicated in a larger sample.

Chapter 4 explored inferential cues and integrative processes involved in eating styles associated with increased risk of obesity, within a predictive coding framework. Fifty-four young adults aged 18 to 32 completed a novel paradigm which assesses the degree to which individuals rely on expectations versus sensations when determining their satiety. Participants scoring high on the restrained eating scale were more prone to depend on prior expectations and acquire an "illusionary" sense of fullness when postprandial sensations were unanticipated (after consumption of a sucralose drink [incongruent condition], but not the glucose drink [congruent condition]). In contrast, high scorers on the disinhibited eating scale showed higher levels of "rebound hunger" and were more sensitive to changes in blood sugar. A high disinhibited eating score was associated with a greater sensitivity to incongruent-unexpected interoceptive states. Regardless of the type of beverage, those scoring high in disinhibited eating were less certain about their ability to predict satiety using visual cues and had fewer specific satiety expectations. The plan was to determine whether older adults differentially relied on expectations versus sensations. It was predicted that older adults would report lower disinhibition and rely to a greater extent on prior expectations compared to younger adults. Unfortunately, due to the COVID 19 pandemic, where older adults were particularly vulnerable to serious disease, we were unable to recruit older adults into this study.

Chapter 5 examined whether general (accuracy and attention) and specific (hunger and satiety) self-reported interoception and eating traits mediated the association between age and BMI. A large sample (N= 1006, aged 18-80 years) completed the online survey. Despite being more overweight, older adults reported lower interoceptive attention, hunger drive, emotional overeating, food responsivity, and enjoyment of food. In contrast, compared to younger adults, older adults reported a higher interoceptive accuracy, and a similar responsivity to satiety. Two indirect pathways positively mediated the link between age and BMI: (1) age → interoceptive attention → satiety responsivity → emotional eating → BMI and (2) age → interoceptive attention → satiety responsivity → food responsivity → BMI. However, a stronger

antagonistic indirect pathway was also present: age → interoceptive attention → hunger drive → emotional eating → BMI. The findings indicated that reduced interoceptive attention in older adults could be harnessed to protect against weight gain by lowering hunger and the propensity towards eating behaviours associated with obesity.

Overall, the evidence presented in this thesis indicates that (1) weight gain in older and young adults may be driven by different underlying processes, (2) interoceptive attention may be an important variable to consider when studying the differences in older and younger adult eating behaviour, and (3) eating behaviour research would benefit from moving away from studying undergraduate samples to exploring factors contributing to weight gain in community samples such as older adults over 60 years old.

Chapter 1: Introduction

1.1 General introduction.

The first section of this thesis provides a broad conceptual overview of the relevant scientific background of the studies involved. This section will begin with a description of obesity, BMI, and eating styles associated with obesity i.e., disinhibited- and emotional- eating. Secondly, we explore how well age is represented in the obesity and eating behaviour literature. Next, a systematic review explores and maps the literature of the factors associated with eating behaviour and body weight in older and younger adults. Then the potential underlying mechanisms which contribute to eating hedonically, such as alterations in brain networks implicated in interoceptive processes are outlined. Lastly, the evidence connecting age and obesity with interoception is summarised.

1.2 The obesity crisis.

World Health reports, estimate that 13% of adults are living with obesity (World Health Organisation, 2021). Additionally, obesity was attributed to approximately 8% of global deaths worldwide (Ritchie & Roser, 2017). Alarmingly, the prevalence of obesity is predicted to increase by 33% over the next two decades (Finkelstein *et al.*, 2012). These projections are concerning, given that obesity-related hospital admissions have increased by 22% over the last 6 years, according to NHS reports (NHS Digital. 2020). Furthermore, the financial burden of obesity healthcare is more than £27 billion per year and is estimated to increase to £49.9 billion by 2050 (NHS, 2017). Currently, obesity is viewed as a multisystem, chronic disease, and a global healthcare challenge (Sarma, Sockalingam, & Dash, 2021). Hitherto, public health interventions have proven ineffective at reducing obesity. Therefore, further research is crucial to develop preventative and effective intervention strategies to tackle the health crisis of obesity and its associated diseases (Rodgers & Collins, 2012).

1.3 Definition and classification of obesity

Obesity is a descriptive term used as a marker of increased risk of developing comorbid diseases because of accumulated fat gain (Purnell & Jonathon, 2000). Obesity is associated with several comorbidities, including poor mental health (Gill *et al.*,

2019). From a metabolic perspective, fat mass within the body is considered an energy reserve i.e., containing triglycerides (Coin *et al*., 2007). Yet, maintaining a healthy balanced ratio of fat mass to fat-free mass is largely determined by nutritional adequacy and activity levels. Furthermore, a healthy ratio between fat and fat-free mass differs according to age, genetics, and sex (Coin *et al*., 2007).

Imaging techniques, such as underwater weighing and dual-energy x-ray absorptiometry (DEXA) scanning, accurately measure fat mass. Though these measures are impractical and costly outside of clinical settings (Lukaski, 1987). A more practical approach to estimating weight status is using Body Mass Index (BMI). BMI is calculated as a formula: weight (kilograms) / height^2 (meters squared) to determine a weight status category *(underweight, BMI < 18.5 kg/m^2; normal weight, 18.4 < BMI < 25.0 kg/m^2; overweight, 25 ≤ BMI < 30.0 kg/m^2; and obese, BMI ≥ 30.0 kg/m^2)* (World Health Organisation, 2000). Although BMI is a widely accepted measure of obesity, a BMI score tells us little about body composition e.g., adiposity (excess fatty tissue) (Sarma *et al*., 2021). Adiposity is thought to be a more accurate predictor of cardio-metabolic complications (Lotta *et al*., 2018). Furthermore, BMI is often obtained via self-reporting methods, in research. This is problematic as several studies have shown that participants often overestimate their height and underestimate their weight; and these biases have been shown to increase with age (Nyholm *et al*., 2007). Such issues are considered and discussed further in later sections of the present thesis.

1.4 The aetiology of obesity

Evidence suggests that unhealthy weight gain is associated with two factors: eating too much and not moving enough (Hill, Wyatt, & Peters, 2012). This framework views obesity as a product of energy imbalance, i.e., energy intake exceeds energy expenditure, leading to increased energy storage (Hill & Commerford, 1996). Therefore, obesity is considered a product of energy dysregulation (Basolo *et al*, 2021). However, this approach has been criticised as being 'overly simplistic', because it ignores dynamic physiological adaptations to changes in body weight and body composition that may alter metabolic rate and the energy cost of physical activity (Hall *et al*., 2011).

1.5 Eating behaviour and its association with increased risk of obesity

Eating behaviour is conceptualised as a multidimensional construct (Russell, Jansen, Burnett, Lee, & Russell, 2023), ranging from homeostatic eating (Lutter & Nestler, 2009) to eating disorders. Eating behaviours such as overeating, can differ in severity and frequency which makes it challenging to discern between eating and disordered / diagnosable clinical eating disorders (Luo, Donnellan, Burt, & Klump, 2016). Recently, research initiatives have sought to refine current models of eating behaviour, as previous models tell us little about the motivations and intentions behind eating and the associated compensatory behaviours (Rancourt, Ahlich, Levine, Lee, & Schlauch, 2019). The notion of wanting or craving food, may be a complex process involving opposing motivations i.e., food approach (e.g. "I really want to eat something sweet") and food avoidance (e.g. "I don't want to gain weight from eating something sweet") (Stritzke, Breiner, Curtin, & Lang, 2004). Cross-sectional research has shown that a higher food approach craving score was associated with a loss of control over eating (disinhibited eating), in comparison to a high food avoidance craving score, which was linked with a greater restriction of food intake (Rancourt *et al*., 2019).

More recently, models and theories have attempted to better understand the mechanisms underpinning eating behaviours that are associated with an increased risk of developing obesity. For example, eating in excess of the energy needs of the body driven by psychological distress (Tanofsky-Kraff & Yanovski, 2004). The current thesis focuses upon eating behaviours/styles that have previously been associated with an increased risk of developing obesity (i.e., disinhibited-, restraint- and emotional– eating). Of note, these eating behaviours do not meet the criteria for clinical significance).

Several theories have proposed various mechanisms which may be driving such eating behaviours. For example, (**1**) motivations to reduce psychological stress symptoms (e.g., psychosomatic theory) (Kaplan & Kaplan, 1957), (**2**) a defective ability to detect and interpret hunger and fullness sensations (e.g., internal/external hypothesis) (van Strien & Ouwens, 2003), and (**3**) feelings of deprivation and cravings, from strict dieting, prompt episodes of overeating (e.g., restraint theory) (Herman & Mack, 1975). These theories have contributed to our understanding of specific eating styles. Various studies have shown that individuals living with obesity may differ in these eating styles (e.g., increased emotionally cued eating and a poorer ability to detect

physiological hunger and fullness sensations), in contrast to their counterparts classified within the healthy weight range (Keski-Rahkonen *et al*., 2007).

The Three Factor Eating Questionnaire revised 18 (TFEQ-r18) (Karlsson, Persson, SjÖStrÖM, & Sullivan, 2000) is a widely used self-report measure of three prominent eating styles that are associated with obesity. The eating style subscales consist of "Cognitive Restraint", "Uncontrolled Eating" and "Emotional Eating". Importantly, these eating styles consider behavioural, affective, and cognitive components of eating behaviour (Ruderman, 1986). **Table 1** illustrates the relationship between eating styles and the risk factors associated with an increased risk of developing obesity. Generally, investigations using the TFEQ have found a strong positive correlation between the eating styles (emotional and uncontrolled /disinhibited eating) and BMI (Löffler *et al*, 2015). Researchers have found a similar association between body fat percentage and high scores on the uncontrolled eating subscale (Kruger, De Bray, Beck, Conlon, & Stonehouse, 2016). Whilst the TFEQ tool has been adapted and validated across many different countries (e.g., the TFEQ - French version) (De Lauzon *et al*., 2004), the pattern between BMI and eating styles is not always replicated. For example, researchers found no association between uncontrolled eating and BMI in a sample of 17- to 20-year-old females (Anglé *et al*., 2009b). Interestingly, Elfhag and Linné (2005) found similar results, where an adolescent female sample showed no association between uncontrolled eating and BMI, unlike the adult sample where a significant association was found. These findings may indicate a moderating role of age, in the association between eating styles and obesity. Emerging evidence has found that age is positively correlated with cognitive restraint over eating (Löffler *et al*., 2015), and negatively associated with uncontrolled eating, as measured by the TFEQ (Cornelis *et al*., 2014; Davison, 2013). Of note, most of the findings regarding the use of the TFEQ are based on ratings from young, female samples. Therefore, the associations between eating styles and obesity may be skewed by the paucity in research involving older adults (and male samples) (Bryant, Rehman, Pepper, & Walters, 2019).

Table 1:

Summary of the associations between eating styles and risk factors of obesity. ***Reproduced from Bryant et al. (2019).***

Eating styles			
Restraint		Disinhibition	
Flexible	**Rigid**	**Uncontrolled eating**	**Emotional Eating**
Lower BMI	Strict feeding rules	Higher food liking, wanting and addiction scores	Poor emotional regulation
Healthier diet quality	Negative self-image	Poor eating regulation	Neuroticism, anxiety, depression
Low energy intake	Neuroticism, anxiety, depression	Higher BMI	
	Sense of control	Frequent binges	
	Often followed by binges	High impulsivity	

1.6 The role of age in eating behaviour and obesity

1.6.1 An ageing population

Over the next thirty years, the global population of older adults is expected to grow by more than 1.6 billion people. Meanwhile, the population of people under the age of 35, is only expected to grow by 100 million people (Goodking & Kowal, 2015). The World Health Organisation describes a shift in population distribution towards older adults (WHO, 2021). Arguably, this is concerning from a health provision point of view, where health care inequalities already exist and complex health conditions such as diabetes, dementia, pulmonary conditions, and sensory impairment tend to be more prevalent in older populations (Prince *et al*., 2015). Furthermore, older adults are far more likely to require hospitalisation, and re-admission than younger adults (Fu *et al*., 2014). Therefore, interest in older populations' health is imperative, from a medical and financial perspective. Strategies are therefore required to mitigate service demand through the preservation of good health and independence into old age. Yet, **Table 2** highlights the sparsity of inclusion of older populations in research. For example, a recent umbrella review systematically explored the psychosocial factors associated with eating behaviour and BMI (Robinson, Roberts, Vainik, & Jones, 2020). We examined the included studies of the umbrella review to see how age was distributed across samples. **Table 2** provides clear evidence of how under-represented older

adults are in eating behaviour research. Furthermore, any inclusion of older cohorts in research tends to focus on disability, disease, or specific dwellings e.g., residential care home. Therefore, our understanding of eating behaviour in relatively healthy and community dwelling older adults is scarce.

Table 2:

Age groups represented in the Robinson *et al*. (2020) review. **Note - sample ages are categorised into young-, mid- and older adults.

Author	Psychological Factor	Factor grouping	Study design	Quality assessment	Meta-Analysis/ Systematic Review	Young Adults (18-35 y/o)	Middle-aged Adults (36-59 y/o)	Older Adults (60+ y/o)
Emery, 2017	Impulsivity*	Cognitive	C-S	Reasonable	MA	68.9%	27.6%	3.4%
Lavagnino, 2016	Inhibitory control*	Cognitive	C-S	Low	MA & SR	95%	-	5%
Amlung, 2016	Delay discounting*	Cognitive	Unclear	Reasonable	MA	100%	-	-
Rotge, 2017	Risky decision making*	Cognitive	Unclear	Low	SR & MA	29%	71%	-
Sweeney, 2017	Delay discounting) Future temporal perspective	Cognitive	Mixed	Reasonable	MA	73.9%	21.7%	4.3%
Wu, 2014	Set-shifting ability	Cognitive	Unclear	Reasonable	SR & MA	97.3%	2.7%	-
Wu, 2016	Reward-related decision making	Cognitive	Unclear	Reasonable	SR & MA	90.2%	9.7%	-
Yang, 2018	Executive function*	Cognitive	C-S	Reasonable	SR & MA	77.8%	18.1%	4.2%
Abbas, 2015	Depression	Mental health	C-S	Low	unable to find original source	-	-	-
De Wit, 2010	Depression*	Mental health	C-S	Reasonable	MA	89.3%	-	10.7%
Magallares, 2014	Overall mental health*	Mental health	C-S	Low	MA	100%	-	-
Pereira-Miranda, 2017	Depression	Mental health	C-S	Low	No full text available	-	-	-
Ul Haq, 2013	Overall mental health	Mental health	C-S	Low	Not included in MA	-	-	-
Gariepy, 2010	Anxiety*	Mental health	C-S	Reasonable	SR & MA	100%	-	-
Jae Jung, 2017	Depression*	Mental health	C-S	Reasonable	SR & MA	49%	32.8%	20.5%
Luppino, 2010	Depression	Mental health	Clinical	High	SR & MA	77.8%	-	22.2%
Xu, 2011	Depression	Mental health	C-S	Reasonable	SR & MA	80%	-	20%

Zhao, 2016	Bipolar disorder*	Mental health	C-S	Low	MA	55.6%	44.4%	-
Diener, 2016	Attachment quality*	Psychosocial	C-S	Low	MA	100%	-	-
Fernandes, 2017	Alexithymia*	Psychosocial	C-S	Low	SR & MA	100%	-	-
Vainik, 2019	The Big 5 personality traits*	Psychosocial	C-S	Low	MA	100%	-	-
Weinberger, 2016	Body dissatisfaction*	Psychosocial	Unclear	Low	SR & MA	30.9%	58.6%	10.5%

Abbreviations: C-S = Cross Sectional; MA = Meta-Analysis; SR = Systematic Review
**Note: Studies comprising of child samples were excluded from the present table

1.7 Thesis aims, and overview.

Despite the accumulating evidence in support of eating behaviours and their association with increased risk of developing obesity, the underlying mechanisms remain vastly understudied, particularly in older populations. Therefore, the over-arching goal of this thesis is to evaluate whether the same mechanisms driving the eating behaviours associated with an increased risk of developing obesity observed in younger adults, may also translate to older cohorts.

Five primary aims were identified to address this goal:

1. Systematically review the evidence that interoception changes with age and evaluate the evidence that this has consequences for eating behaviour (Chapter 2).

2. To determine whether different facets of interoception are associated with eating behaviour, body weight and obesity in younger and older adults (Chapters 2, 3, 4 and 5).

   2a. To examine the neural correlates of disinhibited eating (using resting state fMRI) in younger and older adults who were matched on their BMI (Chapter 3).

   2b. Using a novel paradigm that assesses the processes underlying satiety from the perspective of active inference (Young *et al*., 2021) to determine whether older and younger adults differ in the degree to which they use expectations versus sensation to inform their postprandial satiety.

   Note that due to the COVID 19 pandemic we were unable to recruit older adults into the laboratory. Therefore, the aim of this Chapter was changed to determine whether disinhibited eating is associated with differences in the degree to which expectations versus sensations are used to inform

postprandial satiety (Chapter 4).

2c. Use Structural Equation Modelling to investigate whether domain general (interoceptive accuracy and attention (Murphy *et al*., 2020b)) and domain specific (hunger drive and satiety responsivity (Hunot *et al*., 2016)) mediate the link between age, eating behaviour and BMI (Chapter 5).

The present research will be used to better understand the underlying mechanisms and correlates of obesity in an already vulnerable older population, with a view to propose future directions and insight for age-tailored obesity prevention.

The next section presents a systematic review conducted to identify what is known about age differences and the factors associated with eating behaviour, body weight and interoception.

Chapter 2 Systematic Review

Interoception, eating behaviour and bodyweight in community dwelling older and younger adults: a systematic review and roadmap for future research.

2.1 Introduction

The main objective of this chapter is to systematically review the literature and identify what is known, and not known about the interoceptive factors associated with body weight and eating behaviour in community dwelling older, compared to younger adults.

The obesity pandemic is a global burden affecting individuals of all ages. Across the world, evidence indicates an increased prevalence of unhealthy weight gain and obesity-associated diseases (Afshin *et al*., 2017). This trend is predicted to increase exponentially over the next century, along with life expectancy (Goodking & Kowal, 2015).

2.1.1 BMI and age

Community dwelling older adults tend to have a higher BMI, than their younger counterparts. For example, data from NHANES indicated that between 2007 and 2017 the prevalence of obesity increased by 6%, with older individuals being disproportionately affected (Hales *et al*., 2018). In addition, older adults may experience alterations in their body composition i.e., increased abdominal adiposity and diminishing muscle mass (sarcopenia) (Porter Starr, Fischer, & Johnson, 2014). Crucially, older populations may be particularly vulnerable to the health-related costs associated with obesity (Kivimäki *et al*., 2022). Despite a vast amount of research on eating behaviour and obesity, older populations are often neglected. Obtaining a more comprehensive understanding of eating behaviour and obesity in

older populations is fundamental for improving healthcare practices/interventions. Several recent reviews have considered the psychosocial factors contributing to eating behaviour and / or excess bodyweight in older individuals (Caso & Vecchio, 2022; Poggiogalle *et al*., 2021; Walker-Clarke, Walasek, & Meyer, 2022). However, research has yet to systematically review the potential mechanistic role of interoception.

Notably, several interoceptive factors commonly thought to influence eating behaviour are altered during aging. For example, appetitive sensations, such as subjective hunger, decline with age (Clegg & Godfrey, 2018). Circulating concentrations of various gut hormones that promote satiety such as insulin, leptin, cholecystokinin and peptide-YY are increased in healthy older adults (Johnson *et al*., 2020). Likewise, age is negatively associated with gustatory (taste) (Kremer, Mojet, & Kroeze, 2005) and olfactory (smell) thresholds (Patel, DelGaudio, & Wise, 2015; Seo & Hummel, 2009), which may influence food enjoyment and preference. However, research to date is currently limited in considering whether these interoceptive processes similarly influence eating behaviour and obesity, in older and younger populations.

Traditionally, those interested in appetite control have predominantly studied the sensations of hunger and satiety (e.g., Brunstrom, Shakeshaft, & Scott-Samuel, 2008; Drapeau *et al*., 2013), although interoception can be considered from a number of perspectives. As defined by a recent expert group, interoception is "the process by which the nervous system senses, interprets, and integrates signals originating from within the body, providing a moment-by-moment mapping of the body's internal landscape across conscious and unconscious levels" (Khalsa *et al*., 2017). Thus, the definition of interoception now encompasses sensations related to a wide range of bodily functions beyond appetitive sensations, such as heartbeat (Herbert & Pollatos, 2014; Murphy *et al*., 2018b); a sensation that was previously linked to emotional eating (Young *et al*., 2017). Additionally, interoception is now thought to function in a hierarchical manner. This means that perceiving, interpreting, and integrating information about one's internal bodily state involves both primary (such as detecting accuracy) and secondary processes (including confidence and metacognitive awareness of one's detection accuracy) (Garfinkel *et al*, 2015; Khalsal *et al*., 2018) (see **Table 3** for a interoceptive taxonomy used in the present thesis).

These aspects of interoception have been operationalised in a variety of ways. For example, interoceptive networks in the brain (Burdette *et al*., 2020; Kleckner *et al*., 2017), heartbeat counting and detection tasks (Garfinkel *et al*., 2015), questionnaires (Mehling *et al*., 2018; Murphy *et al*., 2020b), and ratings of expected satiety confidence (Young *et al*., 2021).

Table 3

Interoceptive taxonomy used in the present review.

Afferent signal	Variation in strength / concentration of one or more neurohumoral signals such as a change in blood glucose, hormone e.g., insulin, ghrelin, CCK, GLP-1, PYY or vagal transmission (Young, Freegard, & Benton, 2022).
Interoceptive magnitude	The perception of the intensity of an internal bodily event and a measure of how strongly it is sensed. This measurement represents the amount of signal and is a continuous variable, such as indicating the degree of hunger. It is assessed through subjective reports from the individual using rating scales like visual analogue scales (VAS) and numerical rating scales. Magnitude estimation has been described as a construction of prior expectations and present sensory input underscoring its relevance to predictive coding and active inference (Young *et al*., 2021).
Interoceptive detection	The capacity to recognize whether a stimulus is present or not is a binary attribute. For example, whether a gustatory stimulus is present or not.
Interoceptive discrimination or identification	An individual's capacity to pinpoint sensations within a particular interoceptive system or differentiate one interoceptive sensation from another. For example, the ability to differentiate between two gustatory stimuli. Additionally, it may entail separating various sensations arising from the same interoceptive source, for example, identifying discrete notes in a

	fine wine. Identification tasks usually involve identifying a stimulus from a range of available options.
Interoceptive accuracy	The capacity to accurately detect and track internal sensations; it is assessed by behavioural performance measures such as the heartbeat counting and detection tasks (Desmedt, Heeren, Corneille, & Luminet, 2022a).
Interoceptive attention	The extent or the proportion of time for which interoceptive signals are the object of one's attention (attentional focus) (Murphy *et al*., 2020b). Such self-report trait-based methods include; the Interoceptive Attention Scale (Gabriele, Spooner, Brewer, & Murphy, 2022), or Body Perception Questionnaire (BPQ) (Porges, 1993).
Interoceptive sensibility	The inherent inclination to pay attention to internal bodily sensations as perceived by oneself in everyday life. Measured using self-report scales e.g. Interoceptive Accuracy Scale (Murphy *et al*., 2020b), or Interoceptive Attention Scale (Gabriele *et al*., 2022). Might also include the regulatory and accepting/non-judgmental aspects of interoceptive experience captured using the Multidimensional Assessment of Interoceptive Awareness (MAIA) (Mehling *et al*., 2018).
Interoceptive confidence.	Self-reported confidence in the accuracy of one's interoceptive percept in relation to a specific task e.g., heartbeat counting task (Garfinkel *et al*., 2015).
Interoceptive metacognitive awareness / insight.	One's meta-cognitive judgement regarding one's interoceptive accuracy, assessed as the correspondence between objective accuracy and postdictive subjective confidence ratings (Garfinkel *et al*., 2015).

Abbreviations: CCK = Cholecystokinin, GLP-1 = Glucagon-Like Protein, PYY = Peptide YY.

Note - Reproduced from Young, Freegard & Benton, (2022a) with additional terms added relevant to the current review.

There have been a number of recent narrative and systematic reviews assessing the link between eating behaviour and interoception (e.g., Badoud & Tsakiris, 2017;

Brunstrom, 2014; Hopkins, Beaulieu, Myers, Gibbons, & Blundell, 2017; Jenkinson, Taylor, & Laws, 2018; Klabunde, Collado, & Bohon, 2017; Martin *et al*., 2019; Simmons & DeVille, 2017). A general conclusion is that processing interoceptive signals may undermine healthy eating behaviour. However, most of the research reviewed in these articles have been conducted in younger samples. For example, in a review by Martin *et al* (2019) 100% of the included studies recruited samples under the age of 60 years old. Additionally, a recent meta-analysis which considered the effect of interoception on BMI, only 0.04% of the included studies recruited samples over the age of 60 (Robinson *et al*., 2021). Nonetheless, a small number of studies have examined how aging might influence interoception beyond appetitive sensations, for example, older adults were found to be poorer at detecting their heartbeat (Khalsa, Rudrauf, & Tranel, 2009). However, there has been no systematic study of how differences in interoception influence eating behaviour, bodyweight and obesity in older populations. It is not known whether deficits in interoception influence eating and body weight similarly in younger and older adults. Consequently, it is currently not possible to make recommendations about interoceptive interventions for differences in eating behaviours or weight control in older adults, as it cannot simply be assumed that research findings in young adults will translate to older cohorts.

To date, research in the area of aging and eating behaviour is dominated by clinical samples (e.g. frailty, dementia) (Saunders *et al*., 2019). Across various research disciplines, it is agreed that frailty in later life is characterised by reduced appetite, lower energy intake, as well as weight loss primarily driven by sarcopenia (Giezenaar *et al*., 2016). Yet, otherwise healthy community dwelling older adults are disproportionately affected by obesity (Hales *et al*., 2018), and have been neglected in research. Therefore, a systematic exploration of the interoceptive factors that may be driving weight gain and obesity in community dwelling older adults is needed. Although clinical groups and nursing home residence are an important factor in older adult research, these populations are beyond the scope of this review, we therefore focus upon non-clinical, community dwelling adults, aged 60 and over.

In this context, the aim of this systematic review is to identify and determine what is currently known, and not known, about eating styles, body weight, and interoception in younger and community dwelling older adults. By considering studies that have

compared an older and younger adult sample on these factors. It is hoped that this review stimulates further research interest about eating behaviours associated with an increased risk of obesity in under-researched community-dwelling older adults.

2.2 Methods

The development of this protocol conforms with the scoping review methodological framework, as specified by the Joanna Briggs Institute (Peters *et al*., 2021). All objectives, aims, inclusion/exclusion criteria and methods included in the protocol were specified and documented in advance.

2.2.1 Aims and objectives.

The aim of this review was to synthesise the evidence relating to interoceptive factors that may be driving eating behaviours and excess bodyweight in older adults compared to younger adults. Accordingly, additional objectives include:

1) identify how many of the reviewed studies analysed the link between interoception and eating behaviour in younger and older adults (or whether this is simply presumed).

2) determine whether there are plausible mechanisms by which age-related changes in interoception might affect eating behaviour in older adults.

3) determine whether older and younger adult vary in the degree to which interoception influences eating behaviour / bodyweight.

Additionally, the review sought to identify the gaps which future research should consider addressing, to further our understanding of the association between interoception, eating behaviours and aging.

The present review adopted the "Problem/Patient/Population, Intervention, Comparison/Control/Comparator, Outcome" (PICO) format. Population (Community dwelling older adults), Intervention (Interoception), Comparison (Younger adults aged

18-35 years old vs older adults ages 60 years and above), Outcome (Eating behaviour / Bodyweight). The PICO strategy informed the organisation of the research question: Do older adults living in the community, differ in interoception and its impact on eating behaviour and bodyweight compared to younger adults?

2.2.2 Search strategy

The search strategy was developed *a priori* and guided by the Preferred Reporting Items for Systematic Reviews and Meta-Analyses extension for Scoping Reviews (PRISMA-SR) (Tricco *et al*., 2018). Relevant studies were identified by searching the following electronic databases during August 2023: CINAHL Plus with Full Text; Library, Information Science & Technology Abstracts; MEDLINE; APA PsycArticles; APA PsycInfo. The terms used to search the databases adopted the following Boolean combinations: "eating" OR "BMI" OR "obesity" AND "interoception" OR "hunger" OR "satiety" OR "gustation" OR "retronasal olfaction" OR "cardioception" OR "interoceptive sensibility" AND "age" NOT "children", including MeSH Terms. The specified terms were included within the fields: *topic, article title, abstract* and *keywords*. The search limiters included human subjects, Full Text, Scholarly (Peer Reviewed) Journals, and studies published in English. These electronic searches were supplemented with a manual search of the citation lists of relevant articles.

2.2.3 Study selection and evidence screening

Articles were screened, and duplicates were removed using 'Abstrackr' (Wallace *et al*., 2012). Independently, two reviewers (H.Y. and A.B.) screened all search results for their eligibility by examining titles and abstracts. No disagreements were reported. The full text of potentially relevant papers was then screened. Consistently, all screening decisions were made in adherence with pre-specified inclusion and exclusion criteria (see below).

2.2.4 Data charting

After screening a sample of ten abstracts, the authors developed and refined a data extraction template for all included full text articles. The chart included the following

headings: Author(s) and year of publication; Design of study; Sample size and characteristics (Sex, age and BMI); Methods/tests/intervention (tests used, conditions); Primary and secondary dimensions of interest; Primary and secondary outcomes (key findings related to the reviews' question and concepts) (See **Tables 5 - 10**).

2.2.5 Eligibility criteria

We were interested in healthy populations of younger adults between the ages 18 and 35, and community-dwelling older adults aged 60 years and over. The present review explores all primary research designs including cross-sectional and longitudinal studies, and RCTs, where data therein could be used to answer the reviews questions. For example, intervention studies were included if the outcome variable was an interoceptive dimension of interest, that was compared across older and younger groups. Specifically, we searched for studies that had: (**1a**) compared older and younger adults (i.e., over 60 versus 18 - 35 year olds) on an aspect of interoception (see Table 3), or (**1b**) correlated age as a continuous variable with an aspect of interoception, so long as the age range included those specified in (**1a**), or (**2a**) considered the strength of the association between interoception and an aspect of eating behaviour / bodyweight in older and younger adults (i.e., over 60 versus 18 to 35 year olds), or (**2b**) considered whether age as a continuous variable (so long as the age range included those specified in (**2a**) moderated the association between interoception and an aspect of eating behaviour / bodyweight. Throughout the search, studies were identified that had examined the association between interoception and an aspect of eating behaviour / bodyweight in either younger or older adults. However, due to heterogeneity in outcome variables, it was not possible to compare *across* studies that focused solely on younger or older adults. As such we only considered *within*-study age comparisons, where the aim of the study was to compare older and younger adults.

2.2.6 Exclusion criteria

We did not include older adults whose health status maybe considered as "frail", residing in nursing homes, or older adults diagnosed with dementia. Exclusion also included samples undergoing tube feeding palliative care, institutionalised older adults, participants suffering with dysphagia, participants in a vegetative state and centenarians. Studies of those with clinically relevant eating disorders, including binge eating disorder, were not considered. Studies were also excluded if they primarily focused upon clinical nursing practice or adopted a qualitative design.

2.2.7 Inclusion / exclusion of interoceptive signals

Firstly, we used the definition of interoception put forward by Khalsa *et al* (2018), and the interoceptive taxonomy described in **Table 3** to determine interoceptive measures relevant to the present review. Only interoceptive domains with a plausible mechanistic link to eating behaviour / bodyweight were considered. Therefore, we searched for studies that looked at:

1. **Specific eating styles associated with interoception and an increased risk of obesity e.g., hunger drive, satiety responsiveness, disinhibited eating, emotional eating, dietary restraint.** Though several eating styles have been linked with an increased risk of obesity (e.g., Bryant *et al*., 2019), the mechanisms underlying these eating traits remain less well understood. A potential mechanistic link could be deficits in interoceptive processing, which has been observed in populations with disordered eating (e.g. Martin *et al*., 2019). Therefore, eating styles that were previously linked to interoception were included to determine the effects of age.

2. **Appetitive sensations, such as hunger, satiety, satiation, expected satiety (interoceptive magnitude).** An extensive body of literature links hunger and satiety to eating behaviour and body weight (e.g., Moriguti *et al*., 2000), therefore, this domain was included. Notably, a recent meta-analysis reported on postprandial and fasting gut hormones in older, compared to younger adults

(Johnson *et al*., 2020), therefore, these factors are not repetitively reviewed here.

4. **Cardioception (accuracy, detection, insight, confidence**). Previous research has linked cardioceptive accuracy i.e. the ability to accurately count ones heartbeat with an increased propensity towards emotional eating (Young *et al*., 2017). This suggests that this interoceptive channel may have relevance for some eating behaviours that are linked with an increased risk of developing obesity. Furthermore, it was previously noted that the interaction between cardiac and neural synchronisation may represent a source of perceptual noise from the bottom-up processing, leading to a state of uncertainty about the state and needs of the body (Tumati, 2021), which may be relevant to detecting appetite signalling. However less is known about cardioception in older populations, and so far, mixed findings are reported with its association to eating behaviour. Therefore, cardioception was included in the present review to determine the effects of age.

5. **Orosensory perception, for example gustation and olfaction (detection, identification, discrimination, and magnitude).** Retronasal olfaction occurs after the release of aromas during mastication and has been linked to eating behaviour (Ruijschop, Boelrijk *et al*. 2008). Therefore, retronasal olfaction was considered in scope to understand any effects of age. Although orthonasal olfaction involves detecting exteroceptive signals through inhalation and could be an important external cue driving consumption. However, the effects of age have been extensively reviewed previously (e.g., Doty and Kamath 2014). Therefore, as it primarily involves detecting signals outside of the body, orthonasal olfaction was considered beyond the scope of the present review (see Doty & Kamath, 2014 for a review of orthonasal olfaction and age). During our search we discovered a 2012 review of age differences in gustation (Methven, Allen, Withers, & Gosney, 2012), therefore, rather than duplicate these efforts we sought to update this review and determine whether the conclusions still stand examination.
6. **General self-beliefs (interoceptive sensibility).** Self-reported interoception is often linked to eating behaviour (e.g., Martin *et al*. 2019). However, this aspect

of interoception has not been systematically reviewed in regard to age, particularly as it relates to eating, therefore, this domain was included here.

Excluded interoceptive signals: Hydration status may have implications for eating behaviour, e.g. different types of thirst (osmotic / hypovolemic) may motivate different behaviours according to age (Larry, 2001). Additionally, dehydration is particularly prevalent in community-dwelling older populations (Elsner, 2002). However, the association between age and hydration status has very recently been reviewed with clear indications that thirst perception declines with age (Li, Xiao & Zhang, 2023). Therefore, to avoid replication, thirst perception and sensitivity were considered out of scope for the current review.

Oral tactile and thermal sensations were considered potentially relevant, however, given the challenges in accurately measuring oral tactile sensations that have hindered progress in this area (Haggard and de Boer 2014), this domain was subsequently excluded. Exteroceptive somatosensation and exteroceptive thermoception, affective touch, nociception and proprioception were all considered out of scope due to a lack of a clear aetiological relevance to eating, and a predominant focus on eating disordered populations in these domains (Irvine, McCarty *et al*. 2019). Lastly, attitudes towards the exteroceptive body i.e., body image was considered out of scope, as were body size estimation studies.

2.2.8 Study synthesis and presentation of results.

Authors devised relevant categories in which to summarise and present the included full-text articles. Studies were first organised by domain. These include interoceptive eating styles (e.g., emotional eating, hunger drive, intuitive eating, satiety responsivity), appetite (e.g., hunger and satiety), cardioception (e.g. heartbeat detection accuracy), orosensory perception (e.g., gustation, retronasal olfaction, oral tactile), and general (sensibility). Within each domain studies were further divided according to their relevant interoceptive dimension as described in **Table 3.**

2.3 Results

The initial search generated 13,321 results, 11,134 duplicates were identified and removed, leaving 2187 results exported from Abstrackr (Wallace *et al*., 2012). After excluding 217 titles and abstracts, 2187 full text articles were screened for eligibility. A further 26 studies were identified through other sources i.e., Google scholar and bibliographies. A total of 64 studies explored eating behaviour in younger and older adults relevant to the synthesised study categories mentioned above. Two researchers rated each of the included studies for potential risk of bias using the study quality assessment tool (NHLBI, 2007). Both researchers reached an acceptable level of agreement. An overview of the selection process is presented in **Figure 1**.

Narrative synthesis

Due to the heterogeneity of the included studies and a lack of available data, a meta-analysis was not plausible. Therefore, relevant findings were narratively synthesised. First, evidence that has compared specific eating styles is considered. The remaining sections are organised around domain (appetitive, cardiac, orosensory, general), dimension (magnitude, accuracy, insight, confidence, detection, identification, self-report), and type of study (those that considered the association between interoception and age, those that compared that association between interoception and eating across age) respectively.

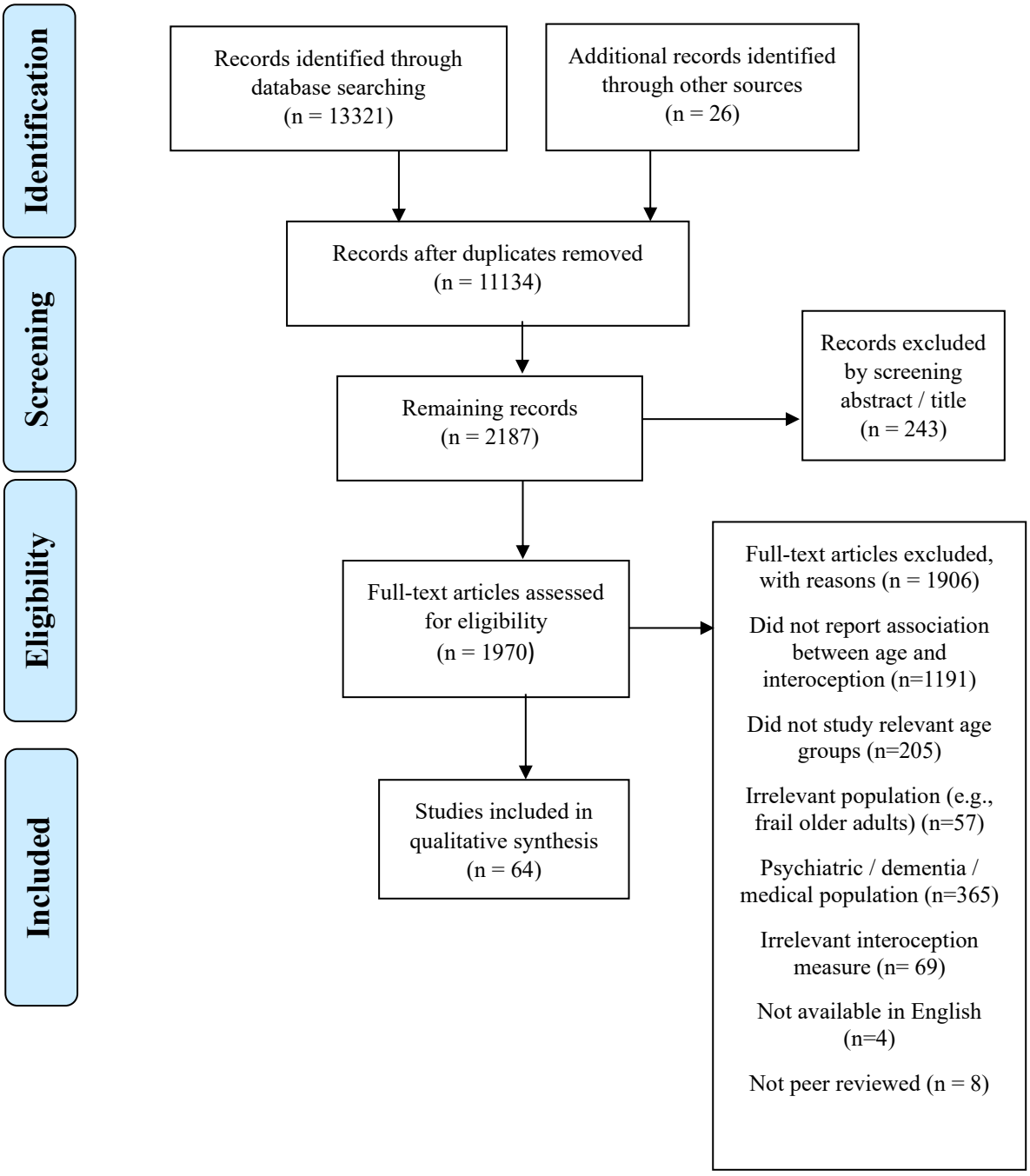


Figure 1: Preferred reporting items for systematic reviews and meta-analyses (PRISMA) flowchart. An outline of the literature search process and selection protocol of included studies.

2.3.1 Eating behaviour and age.

First, we compared the incidence of 'interoceptive' eating styles in younger and older adults. Eating styles were included if they implied a propensity to use internal sensations to guide eating behaviour to a greater or lesser degree. Eligible studies that met our search criteria are presented in **Table 5**. In total the current review found 10 studies comparing or correlating adult age groups with interoceptive eating styles. Our search strategy generated seven cross-sectional studies, two experiments, and one prospective study.

Emotional eating

Emotional eating is characterised by increased food intake in response to non-appetitive internal cues i.e., emotional arousal (Spoor, Bekker, Strien, & Heck, 2007). Previously it was suggested that emotional eating was driven by a heightened interoceptive signal but reduced meta-cognitive awareness of their interoceptive abilities (Young *et al*., 2017). The current review found seven studies with emotional eating subscales that compared this eating style in younger and older adults (Cebolla *et al*., 2014; Elran Barak *et al*., 2021; Keskitalo *et al*., 2008; Konttinen *et al*., 2019; Nagl *et al*., 2016; Pelchat & Schaefer, 2000; Samuel & Cohen, 2018). Five out of seven studies found greater self-reporting scores of emotional eating in younger, compared to older adults (Elran Barak *et al*., 2021; Konttinen *et al*., 2019; Nagl *et al*., 2016; Pelchat & Schaefer, 2000; Samuel & Cohen, 2018). Only two of these studies found no effect of age on emotional eating (Cebolla *et al*., 2014; Keskitalo *et al*., 2008). Interestingly, both studies used age as a continuous variable, where the sample age distribution may be skewed.

External eating

External eaters tend to exhibit heightened responsivity and selective attention to food cues in the environment (e.g., the smell or sight of food) (Hepworth *et al*, 2010). External eating is linked to interoception because it is thought that individuals are driven more by external cues, rather than internal appetitive sensations (Schacter, 1968).

Three studies were found that examined external eating in older compared to younger adults (Nagl *et al*, 2016; Pelchat & Schaefer, 2000; Cebolla *et al*., 2014). Across all three studies external eating was reported to decline with age. Nagl *et al* (2016) administered the Dutch Eating Behaviour Questionnaire DEBQ (German version – Grunert, 1989), and found external eating scores were highest in adults under 25 years old, compared to the other age categories. Thereafter, external eating steadily declined with age. In the study by Pelchat and Schaefer (2000), older adults tended to report lower external eating scores (DEBQ) but the effect did not reach significance. Given the small sample size (N=32), the study is likely to be under-powered. In a much larger study, albeit a female sample, Cebolla *et al*. (2014) reported a negative association between external eating and age. However, in this study the oldest participant was 65 years old, barely meeting our inclusion criteria (aged 60 years and above).

Food craving

A food craving is a physiological or psychological motivational state that promotes the ingestive behaviour of a particular food (Cepeta *et al*, 2000). One twin study using positron emission topography, found a decline in the intensity and quantity of food cravings as participant age increased (Dang *et al*., 2018). Yet, the age-related decline in food cravings was absent in heterozygous twins (allele carriers of the fat mass and obesity associated gene). This may indicate a genetic basis of an increased susceptibility of greater weight gain in later life. Pelchat (1997) conducted structured interviews in 50 younger and 48 older adults to explore age and sex differences in food cravings. Their analysis found that younger adults reported more food cravings than older adults, regardless of biological sex. Moreover, dieting marginally decreased the average number of cravings in young females (- 0.1), but not in dieting, young males (+ 0.02). In contrast, older females who declared current dieting, reported an increased number of food cravings (+ 0.3), as did older, dieting males (+ 0.1). Younger females also reported a higher number of cravings for chocolates, sweet foods, and entrées, compared to older females. On the other hand, younger and older males showed similar craving levels for all foods. Lastly, the researchers found that craving patterns throughout the day occur similarly, for younger and older adults.

Pelchat and Schaefer (2000) developed their earlier work (Pelchat,1997) exploring age changes, dietary monotony, and food cravings. Initially participants completed a 7-

day food diary and the DEBQ (van Strien, Frijters, Bergers, & Defares, 1986) (the baseline phase). Following this, participants only consumed a protein- based test drink and water for four days (monotony phase), finally participants returned to normal eating (recovery phase). The main findings revealed that during the monotony phase younger adults reported a greater number of cravings. Interestingly, those participants with a greater smell sensitivity also reported a higher number of food cravings. In contrast, food cravings remained unaltered in older adults, who reported an increased liking for the test drink, despite the monotony. Younger adults reported a drastic decline in liking for the test drink over the 4 monotony days. Additionally, older adults reported higher restraint eating scores and lower emotional eating scores, compared to younger adults (though this effect was more prevalent in young females).

Appetite traits: hunger and satiety responsiveness

Hunger and satiety responsiveness are considered appetite trait constructs. Appetite traits are characterised by specific sensations arising within the stomach, generating a behavioural outcome e.g., stomach rumbling as an interoceptive cue to initiate eating (Stevenson, Mahmut, and Rooney, 2015).

The present review found one study which reported age differences on hunger as a trait construct (Gilmour Flint *et al*., 2008). Here it was found that older adults reported lower levels of susceptibility to hunger. Additionally, our search strategy failed to generate any literature that had compared the trait satiety responsiveness in younger and older adults. Given that a considerable number of studies have looked at how state hunger / satiety may vary with age (Section 2.3.2), it was surprising not to find more studies examining trait hunger / satiety.

Intuitive eating

Tylka describes the adaptive eating style 'intuitive eating' as "having a strong connection with physiological hunger and satiety cues and eating in response to these cues" (Tylka and Mallinckrodt, 2006). Despite an expansive literature on this eating style, our search strategy did not generate any studies that have compared intuitive eating in young and older populations.

Dietary restraint

Dietary restraint is defined as a tendency to consciously restrict or control food intake, often for weight control purposes (Peñas-Lledó, Loeb, Puerto, Hildebrandt, & Llerena, 2008), i.e., deliberately eating less, irrespective of feeling hungry, in order to avoid weight gain. Extreme levels of dietary restraint were previously linked to poorer interoception (Pollatos *et al*., 2008). However, whether poorer interoception is a cause or a consequence of needing to persistently attenuate internal sensations to restrain from eating is undetermined.

The search strategy identified six studies that assessed dietary restraint in older and younger adults. Four studies reported a significant effect indicating that restraint eating was more prevalent in older, compared to younger adults (Gilmour Flint *et al*., 2008b; Keskitalo *et al*., 2008; Pelchat & Schaefer, 2000; Sturm *et al*., 2003). Gilmour Flint *et al* (2008b) examined physical activity, dietary composition and eating behaviours in weight-matched younger and older adults. The findings revealed that older adults reported higher levels of dietary cognitive restraint and lower hunger. As participants were matched across the variables of interest, the effects could not be attributed to energy intake, dietary composition, physical activity levels, nor BMI.

However, two studies found no differences in restraint eating in younger and older adults (Nagl *et al*., Cebolla *et al*., 2014; 2016). Interestingly, there was some evidence to indicate a non-linear association between age and dietary restraint. Nagl *et al*. (2016) reported that overall dietary restraint was not associated with age. However, inspection of the means shows a very small increase across age groups, up to the age of 75, after which dietary restraint begins to decline again. This could explain the non-significant effects when linear associations were considered. Another explanation concerns a possible age x sex interaction on this scale which will be important for future research to consider.

Disinhibited eating

Disinhibited eating refers to the dysregulated occurrences of overeating in the presence of negative affect or palatable foods (Stunkard & Messick, 1985). Researchers have

noted that a proportion of items in the TFEQ disinhibited eating subscale refer to hunger responsivity (Anglé *et al*., 2009).

Whilst disinhibited eating has been extensively researched in young adults (Nakamura & Koike, 2021), the present review found limited evidence indicating that disinhibited eating declines with age. One investigation of 1326 adults found that disinhibited eating was negatively associated with age (Keskitalo *et al* 2016). However, a second study, albeit with a much smaller sample size (N=80) found that disinhibited eating did not decline with age (Gilmour Flint *et al*., 2008a). The sparsity in the literature exploring age differences in disinhibited eating is surprising.

Eating style summary

Interestingly, the limited literature to date indicates that older adults report lower levels of some eating styles that may be associated with altered interoception, eating behaviour and body weight, for example, emotional eating, external eating, hunger drive, and disinhibited eating. However, findings were not always consistent, these conclusions are based on a small number of studies (**Table 5**), and there was a notable absence of evidence concerning some eating styles, for example, satiety responsivity and intuitive eating. Nonetheless, the fact that older adults may have a lower propensity for uncontrolled eating styles is interesting because it may suggest that different factors could be driving excess body weight in older, compared to younger populations. One plausible explanation for these age-related changes in eating styles is that they may reflect underlying changes in interoception. Therefore, the following sections of this review consider the evidence that interoception differs in older, compared to younger adults.

2.3.2 Appetitive sensations

Table 6 summarises age differences in appetitive sensations. 17 studies measured appetite in younger and older samples. As can be seen in **Table 6** all studies measured interoceptive magnitude i.e., the intensity of an appetitive sensation, usually hunger and fullness, using a visual analogue scale (Apolzan *et al*, 2009; De Castro, 1993; De Castro, 2002; Giezenaar *et al*., 2020; MacIntosh *et al*, 2001a; MacIntosh *et al*., 2001; Moriguti *et al*., 2000; Mulligan *et al*, 2002; Oberoi *et al* 2020a; Oberoi *et al*., 2020;

Parker *et al*., 2004; Rayner *et al*., 2000; Rolls, Dimeo & Shide, 1995; Sturm *et al*., 2004; Van Walleghen *et al*., 2001a; Van Walleghen *et al*., 2007; Vien *et al*., 2021; Zandstra *et al*., 2000). Usually, measures were taken whilst fasting and then periodically during the postprandial period, although the nature of the meal varied considerably. One study manipulated gastric compliance and distensibility through gradual inflation of an intragastric balloon (Rayner *et al*., 2000). Some studies also measured *ad libitum* energy intake or energy compensation using a preload design and others measured various appetite hormones (**Table 6**).

Although we did not seek to review energy compensation studies, energy compensation provides an indirect measure of the propensity to be 'in tune' with one's energy needs and adjust energy intake accordingly. As such, we would expect more accurate energy compensation to reflect a greater sensory sensitivity, although other factors, such as perceived volume, cannot be discounted. Therefore, these data were also extracted from the reviewed studies. Due to a recent meta-analysis on gut hormones during aging (Johnson *et al*., 2020), those studies were not reviewed. However, where a study subsequently related a change in an aspect of physiology to appetitive sensations this provides an index of sensitivity to that interoceptive signal, so these data were also extracted from the reviewed studies. Generally, studies measured both fasting and postprandial appetitive sensations. As these may represent sensitivity to different underlying processes, they are discussed separately.

Fasting hunger

In 12 out of the 17 investigations, older adults reported levels of fasting hunger. Of these 12 studies, eight reported that older adults had lower levels of fasting hunger compared to their younger counterparts (de Castro, 2002; MacIntosh *et al*., 2001a; MacIntosh *et al*., 2001; Mulligan *et al*., 2002; Rolls, Dimeo & Shide, 1995; Sturm *et al*., 2004; Van Walleghen *et al*., 2007a; Van Walleghen *et al*., 2007). Fasting duration varied considerably, ranging from two hours (Zandstra *et al*., 2000) to 36 hours (Mulligan *et al*., 2002). There were also two studies that ecologically sampled hunger prior to each meal, in a food diary (de Castro1993; 2002). There was no obvious pattern explaining the four non-significant studies (de Castro1993; Giezenaar *et al*., 2020; Oberoi *et al*., 2020a; Oberoi *et al*., 2020). However, given the small sample sizes that characterise all studies in **Table 6,** it is not surprising to see some non-significant

results. A further two studies either monitored hunger every hour for one day (Apolzan *et al*., 2009), or asked participants to recall their hunger levels after a 6-week underfeeding episode (Moriguti *et al*, 2000). Both studies found that older adults reported less hunger overall. However, it is not clear from these studies whether participants were reporting fasting or postprandial hunger levels.

Notably in one study, a 12-hour fast resulted in lower hunger levels for older compared to younger participants (Mulligan *et al*., 2002). Interestingly, blood glucose levels at the beginning and end of the fast correlated with hunger ratings in younger participants, whereas there was no association in older participants (Mulligan *et al*., 2002). This may suggest reduced sensitivity to blood glucose levels in older adults. However, in contrast, MacIntosh *et al*., (2001) reported that intraduodenal glucose infusion suppressed *ad libitum* energy intake more in older, compared to younger adults. Together, these findings suggest that older adults might lack sensitivity to low blood glucose that occurs during a prolonged fast but may not lack sensitivity to a rise in blood glucose levels. This also speaks to the inconsistent findings regarding satiety and satiation (see below). A second observation, in the two 7-day diary studies (De Castro *et al*. 1993; 2002) was that there was an association between fasting (pre-meal) hunger and meal size, but only in younger adults. Similarly, MacIntosh *et al*., (2001) reported that the relationship between baseline hunger scores and the amount of food eaten at the buffet meal was only significant in the younger sample. Together these findings may suggest that older adults are less likely to take their hunger into account when selecting portion size during eating.

Satiety and satiation

Fifteen out of 17 studies reported postprandial sensations, most commonly feelings of fullness, but also less commonly postprandial hunger (Apolzan *et al*., 2009; de Castro, 1993; 2002; Giezenaar *et al*., 2020; MacIntosh *et al*., 2001a; MacIntosh *et al*., 2001; Moriguti *et al*., 2000; Oberoi *et al*., 2020a; Oberoi *et al*., 2020; Rayner *et al*., 2000; Sturm *et al*., 2004; Van Walleghen *et al*., 2007a; Van Walleghen *et al*., 2007; Vien *et al*., 2021; Zandstra *et al*., 2000). As hunger may not simply be the inverse of fullness, it is unclear whether during the postprandial period participants are able to differentiate these feelings. Therefore, where possible, we specify which measure was used.

Additionally, due to the way many studies were reported e.g., fullness - area under the curve (AUC), it was not always possible to identify rating times, post consumption.

Rayner *et al*. (2000) were the only group to use isovolumetric and isobaric distensions to assess hunger and fullness in response to gastric distention in a controlled way. During both isobaric and isovolumetric distensions, the pressure-volume relationship did not differ significantly between older and young subjects. However, during gastric distension, perceptions of fullness, abdominal discomfort, and bloating were less in older than young subjects, whereas the perception of hunger after distension was less in the young, than the older subjects (Rayner *et al.*, 2000). Speculatively, this may indicate that hunger and fullness perception in older and younger adults, could be driven by different underlying processes e.g., gastric distention versus humoral or chemosensory aspects.

Two studies tracked food intake and pre-and post-meal hunger for seven days in older and younger adults (de Castro, 1993; 2002). In one study, post-meal hunger was lower in older adults (de Castro, 2002), and in both studies post-meal hunger correlated less strongly with meal size in older, compared to younger adults (de Castro, 1993; 2002). This may indicate that older adults were using postprandial hunger to inform the amount of food consumed to a smaller degree than younger adults were. One further study asked participants to recall their satiety at the end of a 6-week underfeeding period (Moriguti, 2000). No differences in satiety were reported between older and younger adults. Similarly, when fullness ratings were sampled every hour for one day, older adults did not differ from younger adults in their overall fullness (Apolzan *et al*., 2009). Taken together, it seems that on average (over time), satiety / fullness may not differ that much by age group; but older adults may have a lower propensity to use satiety signals to inform their eating behaviour.

Given that orosensory stimulation can induce expectations that affect postprandial responses (Yeomans, 2015), one study sought to bypass this mechanism using isovolumetric, intraduodenal (ID) infusions of saline (control), lipid, and glucose for 120 mins, on separate days (MacIntosh *et al*., 2001). Irrespective of condition neither post-infusion hunger or fullness differed between older and younger adults (MacIntosh *et al*., 2001). In a second study, MacIntosh *et al*, (2001a) gave younger and older participants a standard meal followed by an intravenous (IV) infusion of either a high-

or low- dose cholecystokinin (CCK-8) or saline. Participants rated their postprandial hunger, fullness and consumed an *ad libitum* meal. There was a larger decrease in postprandial hunger in older adults. In addition, *ad libitum* food (energy) intake was suppressed by IV CCK-8 infusion more in older, than young subjects. However, older participants also had higher CCK plasma levels after infusion, which may suggest a poorer ability to suppress endogenous CCK levels. The higher plasma CCK levels may have driven the lower hunger levels seen in older adults. This accords with a recent meta-analysis showing higher postprandial CCK levels in older adults (Johnson *et al*., 2020).

The remaining studies used a preload design whereby participants were given a portion of a food or drink (the preload) and asked to rate their subsequent hunger / fullness. The pre-load is then followed with a measurement of energy intake in a test meal (food served in excess of likely intake, at a fixed interval after the preload). Studies compared a variety of different preloads, making synthesis challenging. Van Walleghen *et al* (2007) used the simplest manipulation of pre-meal water consumption, compared to nothing, to assess older and younger adults' appetitive sensations and subsequent energy intake (30 minutes later). Older subjects reported more fullness than younger subjects during the water pre-load condition and more postprandial fullness overall. In addition, meal energy intake after the water preload was significantly reduced relative to the no preload condition in the older, but not younger subjects.

Four other studies used a yogurt-based vehicle as the preload although the overall composition varied considerably (e.g., various macronutrient and energy compositions). Sturm *et al* (2004) reported that after a high or low energy yogurt-based preload, irrespective of the drink, older adults reported feeling fuller and less hungry, but did not differ in their overall *ad libitum* energy intake 70 minutes later. In a similar study, Zandstra *et al*. (2000) manipulated the energy, carbohydrate, and fat content of yogurt-based preloads. Again, older adults reported lower post-drink hunger irrespective of the pre-load. There was no difference in *ad libitum* energy intake between groups. Again, van Walleghen *et al* (2007a) compared a high energy yogurt preload to no preload. Post-preload hunger did not differ between older and younger adults, but older adults reported feeling fuller after the yogurt pre-load, compared to the younger adults (but not lower hunger). In addition, older adults were

less accurate in compensated for the preload at an *ad libitum* meal 30 minutes later. Finally, Rolls *et al* (1995) also examined the effects of a yogurt preload on energy intake 30 minutes later. Older men consumed less energy than their younger counterparts in the baseline (no yogurt) condition, indicating reduced appetite in general. In addition, compensation for energy in the preloads was less precise in older men, who consistently overate at the self-selected lunch. Together these four studies suggest that older adults may feel fuller after a preload. An important methodological observation is that participants may not be using ratings of hunger and fullness synonymously, so more research is needed to identify how specific populations interpret these measurements. In addition, regarding energy compensation, findings seem to vary based on whether absolute energy intake is reported or whether the accuracy of energy compensation is used, i.e., (energy compensation as a percentage of kcal consumed at meal after water control − kcal consumed at meal after preload)/ (kcal in the preload − kcal in control) × 100. Those that reported energy compensation found that older adults are less accurate in their ability to compensate for a yogurt-based preload (Rolls, Dimeo & Shide., 1995; van Walleghen *et al*., 2007), although overall energy intake was not different (Zandstra *et al*., 2000).

In contrast, Vien *et al*. (2021) examined the effects of various types of dairy products (skimmed milk 180kcal, whole milk 320kcal, plain Greek yoghurt 260kcal, cheddar cheese 240kcal, or water). It was reported that overall appetite suppression (a composite score of hunger and fullness reversed) was less in older, than in younger adults, irrespective of the type of dairy. This contradictory finding might be because hunger and fullness were compiled into a composite score. Vien *et al*. (2021) also reported that in all treatment conditions, younger adults were more accurate in their caloric compensation during an *ad libitum* meal, 120 mins later.

Other studies have focused specifically on the effects of protein. Giezenaar *et al*. (2020) gave older and younger participants high protein or mixed macronutrient preload drinks and examined the effects on postprandial hunger and fullness repeatedly, up to 180 minutes post drink. *Ad libitum* energy intake (buffet 180-210 mins post drink) was also determined. Across the entire postprandial period, older adults showed less stimulation of overall fullness by drink ingestion, irrespective of drink indicating that they may be less sensitive to fullness. In older adults, AUC

hunger was suppressed more by the protein only preload, during the first half of the postprandial period. Similarly, energy intake during the buffet meal (energy compensation) was reduced in older adults after protein. In a similar study, Oberoi *et al* (2020) also examined the effects of protein by comparing flavoured water to a high or low whey protein drink at breakfast. Older adults were less full after the protein drink; and suppression of energy intake (sum of breakfast, lunch, and dinner) by protein was less in older, compared to younger participants. In a second study, Oberoi *et al* (2020a) compared whey protein to a no-calorie control drink. This time postprandial fullness did not vary between older and younger groups. There was a trend towards older adults consuming less energy (20% less) at a subsequent *ad libitum* buffet 180-minutes after the preload, but the effect did not reach significance. Given that this latter study only included 10 older and 10 younger participants it was probably underpowered. Overall, the findings on protein consumption are conflicting, such that no firm conclusions can be drawn.

In summary, the findings concerning age differences in satiety and satiation vary, and study designs are heterogeneous. Although the preload design was common, the nature of the preload varied considerably, as did the time post preload that the *ad libitum* meal was provided. The literature also suffered from a range of methodological limitations including, but not limited to: (1) a tendency to confound energy manipulations with macronutrient manipulates, (2) small sample sizes, (3) the use of hunger and fullness ratings as though they are synonymous, (4) a tendency not to differentiate between the early postprandial period and the late postprandial period (where time gap before that *ad libitum* meal would have allowed this), (5) a tendency not to report or control pre-prandial influences on satiety such as texture, taste, flavor, perceived volume, and palatability, (6) in most studies older adults had a slightly higher BMI but this was rarely controlled for and neither were particular eating styles that may vary with age (**Table 5**). Consequently, conclusions cannot yet be made discerning whether or not age groups differ in satiety or satiation.

Overall, there is evidence that compared to younger adults, older adults are less hungry while fasting. In addition, there is evidence that older adults may be less likely to use hunger sensations to inform their decisions about meal size. There was some preliminary evidence suggesting that older adults may be less accurate in

compensating for an energy preload which might imply a reduced sensitivity to internal sensations signaling energy balance, but this could also be driven by pre-prandial factors like portion size or individual differences like restraint. Due to methodological limitations and heterogeneity in study design no conclusions can be drawn regarding satiety or satiation. No studies were identified that examined expected satiety (i.e., how full a person expects to feel after consuming a certain food) in older, compared to younger adults. A final consideration is the reliance on VAS appetite ratings. Increasing evidence now points to 'interoceptive magnitude,' measures of this kind consist of 'top-down' expectations and 'bottom-up 'sensations, such that it is currently unclear which aspects are driving fasting or postprandial ratings (Young *et al*., 2021). For example, it is possible that reduced hunger in older adults might reflect lower expectations of hunger after a fast, or alternatively reduced sensitivity to low blood glucose, ghrelin etc. that are released during a fast. Identifying the cause of reduced fasting hunger in older adults will be important for the development of interventions.

Associations with eating behavior / bodyweight

As can be seen in **Table 6** it was common for studies assessing appetite sensations in older and younger adults to also consider acute caloric intake and / or energy compensation. However, it was rare that ratings of hunger or fullness were correlated with intake in younger and older samples. Therefore, it is unclear whether lower fasting hunger or differences in postprandial fullness were driving any differences in energy intake. Notably, studies observed that hunger ratings were not associated with meal size in older adults, although they were associated in the young samples (De Castro *et al*. 1993; 2002). Similarly, the relationship between baseline hunger scores and the amount of buffet food consumed was only significant in the young (MacIntosh *et al*., 2001). This suggests an alternative perspective to the view that lower hunger drives reduced consumption in older adults. Rather, older adults may come to rely on alternative exteroceptive eating cues, in the absence of reliable internal sensations. Further research is needed to determine the factors driving consumption in older adults. Although BMI was measured in most studies presented in **Table 6**, no study correlated BMI and appetitive sensations. Thus, it is unclear whether changes in interoceptive magnitude have consequences for the long-term control of bodyweight in older adults.

2.3.3 Cardioception

Interoceptive accuracy

Five studies were identified that examined the effects of age on cardioceptive accuracy (**Table 7**). Two studies operationalised this as the association between changes in physiology (heart rate) and subjective arousal during an emotional task (viewing emotional pictures) (Mikkelsen *et al*., 2019; Ulus & Aisenberg-Shafran, 2022). Two studies used the Heartbeat Counting Task (Murphy *et al*.,2018a; Teraoka, Kuroda & Teramoto, 2023), and one used the Heartbeat Detection Task (Khalsa *et al*., 2009). Three of the five studies reported that older adults had lower cardioceptive accuracy, than younger adults (Khalsa *et al*., 2009; Murphy *et al*., 2018a; Ulus & Aisenberg-Shafran, 2022). Each of these three studies used different tasks (**Table 7**), so the effect does not seem to depend on the nature of the task.

Besides the small number of studies, this literature had a range of other limitations. In general, the small sample sizes meant that the present conclusions are based on N=386. In addition, the study by Khalsa *et al* (2009) only included participants up to age 65 years old, barely meeting our inclusion criteria. Finally, three out of five studies failed to consider the potential influence of BMI, which generally increases with age (Mikkelsen *et al*., 2019; Teraoka, Kuroda & Teramoto, 2023; Ulus & Aisenberg-Shafran, 2022). However, Khalsa *et al* (2009) found that cardioceptive accuracy and age remained inversely associated after accounting for BMI. Interestingly, Murphy *et al*. (2018a) reported that BMI mediated the link between age and cardioceptive accuracy, although alternative models i.e., that cardioceptive accuracy mediated the link between age and BMI, were not examined in this cross-sectional dataset. The associations between these three variables (age, cardioceptive accuracy and BMI) might indicate that reduced cardioception during aging has implications for eating behaviour and body weight, although more research is needed to confirm this. Finally, in the study by Ulus and Aisenberg-Shafran (2022), the correspondence between changes in physiology and subjective arousal were determined *across* participants in each group. A more meaningful measure of interoceptive accuracy would be to determine the *within* person correspondence over several observations.

Interoceptive confidence and insight

No studies were identified that assessed the link between age and interoceptive confidence or insight in this domain.

Associations with eating behaviour / body weight

Of the studies reported in **Table 7**, no study reported an association between cardioception and eating behaviour in older and younger groups, to determine if similar links exist, irrespective of age. Therefore, it is unclear whether a decline in cardioception may influence eating behaviour in older adults. Given that older adults report lower levels of emotional eating (see emotional eating in section 2.3.1 and **Table 5**), and that higher cardioception was associated with more emotional eating (Young *et al*., 2017), it is plausible that the two factors are related, but more research is needed to confirm this. Only Murphy *et al*. (2018a) examined the associations with BMI, and reported that a higher age was associated with a higher BMI and lower heartbeat counting accuracy. However, given the cross-sectional nature of that dataset, it is unclear whether older adults have lower cardioception, which may affect the control of body weight, or whether a higher bodyweight in older adults contributes to lower interoceptive accuracy.

No studies were identified that assessed the link between age, eating behaviour / bodyweight and interoceptive confidence or insight in this domain.

2.3.4 Interoceptive sensibility

For the purpose of this section, questionnaires were identified as part of a systematic review which sought to identify self-report measures, that had been used according to the definitions of interoceptive sensibility, put forth by Garfinkel *et al*. (2015) and Khalsa *et al*. (2017) (Desmedt, Heeren, Corneille, & Luminet, 2022c). Twelve studies were identified which assessed Interoceptive sensibility in older and younger adults (Bowling *et al*., 2019; Brown, Proulx, & Stanton Fraser, 2020; Elliott & Pfeifer, 2022; Fiskum *et al*., 2023; Mahlo & Windsor, 2021; Murphy *et al*., 2018a; Palser *et al*., 2018; Raimo *et al*., 2021; Teraoka, Kuroda & Teramoto., 2023; Todd *et al*., 2019). Questionnaire measures included the Multidimensional Assessment of Interoceptive

Awareness (MAIA) (Mehling *et al*, 2018)(six studies), the Body Perception Questionnaire (BPQ) (Cabrera *et al*., 2018) (three studies), one study used the Self Awareness Questionnaire (SAQ) (Longarzo *et al*., 2015), and one study used the Body Consciousness Scale (BCS) (Brockner & Swap, 1983). One further study sought to determine the nature of emotional concepts in older versus younger adults, specifically the degree to which older adults incorporate interoceptive experiences into their emotional representations (MacCormack *et al*., 2021) (**Table 8**).

Overall, the three studies that used the BPQ reported small- to- medium negative associations between age and interoceptive sensibility (Elliott & Pfeifer, 2022; Murphy *et al*., 2018a; Palser *et al*., 2018). However, four studies reported no association with either the MAIA subscales or a global MAIA score (Teraoka, Kuroda & Teramoto, Bowling *et al*., 2019; Elliott, Jones, & Schmidt, 2020; 2023; Todd *et al*., 2019), one study reported a positive association with the self-regulation scale of the MAIA (Fiskum *et al*., 2023), and one reported a negative association between age and the global MAIA score (Mahlo & Windsor, 2021). It should be noted that the MAIA was developed to assess different components of interoception, and therefore assessing a total score may not be appropriate (Mehling, 2016). Finally, age was not associated with BCS global score (Brown *et al*., 2020) or the SAQ (Raimo *et al*., 2021). Again, it should be noted that the BCS scale contains subscales that measure private aspects of body awareness (those not observable by others, such as heartbeats) and public aspects (those that are observable by others, such as posture), such that a global score may not be appropriate.

The pattern of results supported the view that different interoceptive sensibility measures do not assess the same construct (Desmedt, Heeren, Corneille, & Luminet, 2022b), and that only some aspects decline with age. For example, the BPQ measures awareness of autonomic nervous system reactivity, whereas the MAIA was designed to focus on a wider range of sensations, and to distinguish between mindful- and angst-driven interoceptive attention styles. The present results suggest that older adults may specifically lack an awareness of autonomic reactivity. This might explain findings from studies that have assessed the qualitative nature of older adults' emotional concepts. Specifically, that older adults' mental representations and self-reported

experiences of emotion, are less associated with interoceptive sensations than are those of younger adults (MacCormack *et al* .,2021).

An important observation is that many of these studies did not set out to examine the effects of age on interoceptive sensibility. Rather, they just happened to recruit a wide age range (usually through an online recruitment platform e.g., MTurk / Prolific) and report the correlation with age (e.g., Bowling *et al*., 2019; Brown *et al*., 2020; Fiskum *et al*., 2023; Palser *et al*., 2018; Teraoka, Kuroda & Teramoto, 2023; Todd *et al*., 2019). In addition, it was often not possible to determine the distribution of ages. As such, whilst the age range encompassed those that met the present inclusion criteria i.e., 18-35 and >60 years (or a continuous variable spanning these ages), it is plausible that the true number of adults over the age of 60 was small in some studies. Furthermore, it was often the case that the maximum age in a study only just made the inclusion criteria. For example, Palser *et al*. (2018) only recruited adults up to 65 years of age. Lastly, important covariates like BMI, gender, mood, and physical health status (e.g., blood pressure) were often missing.

Associations with eating behaviour / body weight

Of the studies reported in **Table 8** no studies examined whether interoception was associated with eating behaviour and body weight in younger and older adults alike. Therefore, it is unclear whether associations between interoceptive sensibility and eating behaviour / body weight observed in younger populations (see Martin *et al*, 2019 for a review) translate to older populations. One study considered associations between interoceptive sensibility and body image which is known to drive dietary restraint (Todd *et al*., 2019). Older adults had less weight preoccupation, but age was not associated with interoceptive sensibility (assessed using the MAIA). So, it seems unlikely that age associated declines in interoception has an aetiological significance here. Importantly, age was used as a covariate (not a moderator) in the model, so it is not clear how associations between interoceptive sensibility and body image vary across age groups (Todd *et al*., 2019). Interestingly, some evidence implied that older adults did not incorporate physiological sensations into their emotional concepts (MacCormack *et al*., 2021). It would be interesting to determine whether this observation may also apply with appetitive concepts in mind.

2.3.5 Chemical senses

With some senses, the boundary between interoception and exteroception becomes blurred (Chen *et al*., 2021), and the debate about whether the chemical senses can be considered 'interoceptive' is ongoing (Khalsa *et al*., 2022). A full discussion of the arguments around whether the chemical senses are 'interoceptive' is beyond the scope of the present review. However, recent evidence indicates that the chemical senses share common neural pathways with other interoceptive modalities (Avery *et al*., 2015; Roelofs *et al*., 2021). In addition, the chemosensory features of food are assumed to be a primary driver of consumption (Olszewski & Levine, 2007). Therefore, understanding how the chemical senses change during aging and the effects on eating behaviour and body weight is critical.

Olfaction

It is estimated that as much as 75–95% of what we think we taste, we actually smell (Spence, 2015a). Importantly, there is a distinction between orthonasal olfaction (such as when we sniff food) and the retronasal olfaction (when volatile aromas are released from food and are sensed at the back of the nose) (Ni *et al*., 2015).

Orthonasal olfaction can be robustly assessed by several psychophysical tests, e.g., odour detection, identification, discrimination, with the University of Pennsylvania Smell Identification Test (UPSIT) and the Sniffin' Stick test, being most widely employed (Doty & Kamath, 2014). Using these tests, considerable evidence supports a decline in orthonasal olfaction after the age of 65 (see Attems, Walker, & Jellinger, 2015 for a review). Given the already robust evidence, and a general agreement, that this sense declines with age, it is not reviewed again here. Instead, we focus on retronasal olfaction for which evidence has lagged behind orthonasal olfaction, despite its major role in flavour perception (Spence & Youssef, 2021).

Seven studies were identified that assessed the effects of age on retronasal perception (Croy *et al*., 2014; Flaherty & Lim, 2017; Heilmann *et al*., 2002; Hernandez *et al*., 2023; Li *et al*., 2022; Renner *et al*., 2009; Ruijschop *et al*., 2008) (**Table 9**). The most commonly measured interoceptive dimension was interoceptive identification (Croy *et al*., 2014; Heilmann *et al*., 2002; Hernandez *et al*., 2023; Z. Li *et al*., 2022; Renner *et al*., 2009), followed by intensity (magnitude) (Li *et al*, Flaherty & Lim, 2017; 2022).

Only one study assessed retronasal detection thresholds (Li *et al*, 2022). Interestingly, one study assessed the influence of retronasal aroma release pattern (short versus long) on feelings of satiety (Ruijschop *et al*., 2008), and one study examined the synergistic effects between retronasal olfaction and gustation (Flaherty & Lim, 2017).

Four out of five studies found that retronasal identification declined with age (Heilmann *et al*., 2002; Hernandez *et al*., 2023; Li *et al*., 2022; Renner *et al*., 2009). Across these studies, three different tests were used that varied in their degree of ability to isolate retronasal abilities. Two studies used the retronasal olfaction test technique (grocery condiments and powders) (Heilmann *et al*., 2002; Li *et al*., 2022). Whilst high in ecological validity, this task is confounded by differences in gustatory abilities which may also decline with age (See below in 'gustatory' section and **Table 10**). Notably, one study using this method did not observe any age related differences (Croy *et al*., 2014), so controlling for this confound could be important.

Renner *et al*. (2009) developed the candy smell test to measure retronasal identification and found a steady decline with age. The aromas for this test were chosen according to the odorants used in the validated orsonasal olfaction ''Sniffin' Sticks'' test, although only the sweet smells were utilised due to the sweet taste of the candy. Thus, this test benefits from holding the effects of gustatory stimuli constant in the form of a sweet taste. However, when gustatory and olfactory stimuli are congruent (e.g., both sweet), they often act synergistically leading to a greater ability to detect a subthreshold stimuli, than when either are presented alone (Dalton, Doolittle, Nagata, & Breslin, 2000). Thus, presenting a congruent sweet taste with a sweet retronasal aroma, may disguise the true magnitude of any age-related differences - especially given that the ability to detect gustatory sweetness may be the least likely tastant to decline with age (Methven *et al*., 2012). Unfortunately, there is a striking absence of evidence concerning multisensory flavour perception in older adults. We were unable to identify any studies that had considered the interaction between retronasal olfaction and gustation on identification or detection thresholds, in older and younger adults. The final study to report an effect of age on retronasal identification, used Q-powders which are tasteless, thereby, eliminating gustatory effects (Hernandez *et al*., 2023). However, they would still stimulate oral tactile receptors, and it is currently unclear whether this would have a confounding effect.

Regarding eating behaviour, it is plausible that perceived intensity at suprathreshold levels might be a more meaningful indicator of future food consumption. For example, it was suggested that those with a reduced intensity perception, tend to prefer higher concentrations of specific tastants (e.g., salt or sugar) (Spence & Youssef, 2021). We only identified one study that assessed intensity in older and younger adults using a 'labelled magnitude scale' (Flaherty & Lim, 2017). This study used a device to deliver aroma to the back of the nose, thereby bypassing both taste and tactile stimulation. Notably, older adults rated NaCl (salt), strawberry and chicken aromas similarly to younger adults, whereas they found sucrose, vanilla, and soy sauce to be less intense than their younger counterparts. Interestingly, this was the only study to assess the interaction between retronasal olfaction and gustation. Crucially, presenting an odour with a congruent taste reduced the variation in intensity responsivity in older, more than younger adults. Given that flavour perception is a multisensory experience involving all our senses (Spence, 2015b), this finding highlights the importance of determining how the different senses interact in older versus younger individuals.

Finally, the one study that assessed retronasal thresholds reported a decline in older adults (Li *et al*., 2022). However, while both orthonasal and retronasal olfaction decreased with age, retronasal odour identification tended to decline to a lesser degree (Li *et al*., 2022).

Associations with eating behaviour / body weight

Interestingly, it was suggested that one mechanism through which retronasal olfaction influences eating behaviour is through enhancing satiety, hastening the end of a meal. For example, one study compared two aroma release profiles: (i) a short, less pronounced and (ii) a longer, more pronounced aroma – both delivered to the back of the nose whilst participants consumed a sweet drink. Participants reported feeling more satiated after the longer, more pronounced profile. However, older adults felt on average less satiated after retronasal stimulation and had less of a decrease in the desire to eat sweet products (Ruijschop *et al*., 2008). Whilst this was a post hoc analysis, it suggests that older adults may benefit less from retronasal olfaction when it comes to satiety, potentially leading to longer eating episodes and greater food intake. This suggestion accords with earlier observations that older adults had lower sensory-specific satiety (i.e., decrease in the pleasantness of a specific food that has just been

eaten to satiation (Rolls & McDermott, 1991), and provides one plausible mechanism through which, deficits in retronasal interoception may compromise eating behaviour regulation in older adults. Conversely, given that retronasal olfaction plays a major role in our experience of flavour, reduced sensitivity or perceived intensity may render food bland and unappetising (Spence, 2015a). As flavour perception is a multisensory experience involving all our senses, it is plausible that other senses might be able to compensate for a loss in olfactory functioning (Spence, 2015b). However, understanding multisensory flavour integration in older individuals will be a key future research avenue to determine whether this is the case.

Gustation

During our search we discovered a 2012 meta-analysis that considered the effect of aging on taste perception (detection thresholds, identification thresholds and supra-threshold intensity perception) (Methven *et al*., 2012). Search criteria were that the papers had to investigate both younger and older adults (over 60 years), who were healthy, and that were published up to April 2012. The meta-analysis included 29 studies and concluded that across all modalities, taste detection thresholds increased with age. Identification thresholds were also reported to be higher for older adults, while taste intensity at supra-threshold levels were significantly lower for older adult, with the possible exception of sucrose (Methven *et al*., 2012). Therefore, this section reviews studies published since April 2012 to determine whether those conclusions still stand examination or can be expended to include other interoceptive dimensions.

Thirteen studies were identified (**Table 10**) and overall, the pattern remained consistent with that reported by Methven *et al*. (2012). Five considered the effect of age on taste identification. One used fruit flavoured drinks (Appleton & Smith, 2016), while the other three focused on the basic tastes (sweet, sour, bitter, salty, umami) using either taste strips or taste sprays (Hernandez *et al*., 2023; Hoogeveen *et al*., 2015; Iannilli *et al*., 2017; Li *et al*., 2022). It should be noted that while fruit drinks are more ecologically valid, they also allow participants to use retronasal olfaction, thereby reducing the ability to isolate gustatory functioning. In all five studies, participants were asked to select the choice from a range of responses. Three out of the five studies confirmed that older adults were poorer at identifying tastes, than younger samples (Li *et al*., Appleton & Smith, 2016; Iannilli *et al*., 2017; 2022). One study did not find a

significant effect of age, which could be attributed to only using one presentation of each taste (Hernandez *et al*., 2023); although the same method was used by Li *et al*. (2022), who did report significant results. The use of only one trial per taste may have reduced the reliability of the tests and have contributed to these mixed findings. A second study used four concentrations of basic tastes (sweet, sour, bitter, salty) to determine threshold identification, but found no effect of age. However, this was a brain imaging investigation, which inevitably had a small sample size (Hoogeveen *et al*., 2015), and may not have been sufficiently powered to detect behavioural effects. Interestingly, one study reported that congruent versus incongruent colour, facilitated older adults taste identification (Appleton & Smith, 2016), indicating that visual cues may help compensate for sensory impairment in older adults.

Two studies used the alternative forced choice method (2-AFC) to determine age differences in taste identification thresholds (Mingioni *et al*., 2017; Wiriyawattana, Suwonsichon, & Suwonsichon, 2018). One assessed high and low concentrations of sugar and sour (acid) apple puree (Mingioni *et al*., 2017). It was reported that older adults were as effective as the young group at differentiating apple purée samples. The samples were based on sugar or sour differences of at least 10 g/kg or 0.25 g/kg, respectively. This suggests that findings based on basic tastes may not extend to a real food matrix. The second study found that older adults had higher identification threshold for sucralose (sweet), NaCl (salty), KCl (salty), citric acid (sour), acetic acids (sour), caffeine (bitter), MSG (umami), and ISG (umami), but not sucrose (sweet), aspartame (sweet), or acesulfame-K (sweet). Though previous findings have been mixed, the above observations offer some support to the literature on sweetness (Methven *et al*., 2012).

Three studies measured detection thresholds using a 3-AFC paradigm (Guido *et al*., 2016). Both Wiriyawattana *et al*. (2018) and Yoshinaka *et al* (2016) reported that older adults had higher detection threshold than younger adults in all tastes except for sweetness. Conversely, Guido *et al*. (2016) reported that whereas sweetness and saltiness detection thresholds were higher in older adults, sour and bitterness were not. Again these findings are consistent with previous research which suggests that there might be greater individual variability in older adults' sweet detection thresholds than for other tastes (Methven *et al*., 2012)

Finally, four studies considered taste intensity (Barragán *et al*., 2018; Flaherty & Lim, 2017; Heft & Robinson, 2014; Rolls, Kellerhals & Nichols, 2015). When basic tastes were used the general pattern supported that older adults tend to perceive less intensity (**Table 10**). However, when Rolls, Kellerhals & Nichols (2015) tested flavoured drinks (orange and vegetable juice) no age differences in intensity ratings were observed. This might indicate that effects using basic tastes do not translate to more complex flavours, and that older adults may be able to utilise retronasal olfaction additively, to enhance their intensity perception. Yet, brain imaging studies such as these tend to be characterised by small sample sizes and therefore underpowered for any behavioural effects. Future research using simple and complex tastes will be important to understand the effects further.

Gustatory confidence and insight

Interestingly, we identified one study which assessed interoceptive confidence in the chemical senses domain and compared this across older and younger adults (Christensen, 1985). This study used different strength cheese and grape jelly, in a 2-AFC paradigm to measure intensity discrimination. In separate tasks, flavour and aroma were tested. The study also assessed the effect of colour by manipulating the depth of colour of the food items and present pairs that were either similar or different in colour. After each trial, participants rated their confidence in their intensity rating. Notably, older and younger adults did not differ in their ability to discriminate aroma or flavour, even when the samples were differently coloured. This is in contrast to Appleton and Smith (2016) reported above, although an important difference might be whether taste identification or intensity is being assessed. These non-significant results could be due to the small sample size (N=46). Interestingly, there was a high correlation between the level of certainty and the number of food pairs correctly discriminated (-0.81). In addition, older adults were more certain in their responses, irrespective of their accuracy (Christensen, 1985). Potentially this may reflect a interoceptive bias; theoretically, this may have implications for perceptual learning in this domain. Future work will be crucial to confirm this hypothesis.

Associations with eating behaviour / body weight

Taste and flavour are probably the most understood of all interoceptive domains when it comes to eating and weight regulation. One way that gustation is thought to influence

eating behaviour is through pleasantness, liking, and reward. However, the way gustatory stimuli are identified, and their intensity perceived, is distinct from the neural encoding of the rewarding and pleasurable aspects of sensory stimuli related to food (Rolls, 2015). For example, taste and olfactory stimuli are computed first, and are represented in the taste insula and pyriform cortex. The perception of pleasantness and reward value is then processed in specific brain regions, such as the orbitofrontal cortex and pregenual cingulate cortex (Rolls, 2015). This is an important distinction because hedonic responses to sensory stimuli may be the predominant driver of dietary behaviour, and consequently health outcomes (Rolls, Kellerhals & Nichols., 2015). Therefore, important questions are (**i**) whether taste preferences change with age, and (**ii**) whether age-related taste thresholds or intensity ratings contribute to food liking and reward. Of the studies reported in **Table 10**, five assessed either taste liking or pleasantness. In general, there was evidence that older compared to younger adults preferred vegetable juice (Rolls, Kellerhals & Nichols, Guido *et al*., 2016; 2015), although preference for sweetness was mixed (Barragán *et al*., 2018; Hoogeveen *et al*.,2015). Whether perceived healthiness influences older adults' preferences for certain foods needs to be considered. One study reported that an age-related decline in perceptions of pleasantness was associated with poorer identification and lower perceptions of sweetness (Appleton & Smith, 2016). On the other hand, Barragán *et al*. (2018) reported that a higher taste intensity rating, was not associated with a higher preference for the same taste across the whole sample, however, effects were not analysed in older and younger samples separately. It is plausible that individuals may vary in the degree to which they use sensory information from modalities to inform palatability judgements. For example, given that sweet liking was associated with a higher trait hunger drive (Iatridi *et al*., 2020), it is plausible that reduced hunger sensations in older adults (**Table 6**) could explain a lower liking for sweet foods in some individuals, but will need to be confirmed in future work.

2.4 General discussion and roadmap for future research

To the best of our knowledge this is the first paper to systematically review how those interoceptive abilities, with relevance to eating behaviour, may vary with age. Specifically, appetitive, cardioceptive, self-reported sensibility, and the chemical senses (gustation and retronasal olfaction) were considered. There was evidence that

interoceptive deficits exist across all included domains in older adults, with plausible consequences for the regulation of food intake and body weight. However, across all domains there were various limitations that warrant further discussion. For example, the preponderance of young adult populations in studies, that have assessed the role of interoception in eating / obesity was concerning. Currently, little is known about the aetiological mechanisms involved with interoceptive senescence. The tendency for paradigms to confound one sensory channel with another, and an inability to differentiate between 'bottom-up' and 'top-down' interoceptive processes limits interpretation. In all domains, many interoceptive dimensions that were presented in **Table 3** remain unexamined in relation to age. Addressing these limitations will be crucial to advancing our understanding of the role of interoception in age-related eating and bodyweight dysregulation. Based on the limitations, we present a roadmap for future research (**Table 4**).

Whilst we observed a generalised decline in interoceptive abilities with age, the mechanisms behind these declines requires deeper exploration. These mechanisms are also likely to vary by domain. For example, hypertension was previously linked to cardioception (Yoris *et al*., 2018), and is known to be more prevalent amongst older adults (Oliveros *et al*., 2020). The quantity and quality of saliva changes with age (Xu, Laguna, & Sarkar, 2019), which can reduce retronasal olfaction sensitivity (López-Dávalos, Requena, Pozo-Bayón, & Muñoz-González, 2023). A change in the production or sensitivity to gut hormones, may be related to appetitive changes during aging (Johnson *et al*., 2020). Understanding the aetiological processes involved in age-related interoceptive deficits will be key to the development of remedial interventions. In addition, neural changes are also likely to be involved. For example, one way interoception has been studied, is by examining the brain networks associated with interoceptive functions (Kleckner *et al*., 2017). Indeed, neuroimaging studies have identified that key networks in the brain, such as the frontoparietal and default mode networks play key roles in interoception, including the filtering and prediction of incoming afferent sensations (Barrett, 2015; Barrett, 2017; Kleckner *et al*., 2017). Interestingly, these networks were previously associated with disordered eating and obesity (see Donofry, Stillman, & Erickson, 2020 for a review), and intrinsic network connectivity is altered during aging; with the default mode network being particularly vulnerable (Sala-Llonch, Bartrés-Faz, & Junqué, 2015). As studies are yet to consider

how brain network connectivity links to eating behaviour / body weight in younger, compared to older adults, this will be an important future direction. Finally, given the nearly exclusive reliance on cross-sectional designs, reverse causality cannot be ruled out. For example, it is possible that interoceptive abnormalities may reflect exposure to an environment characterised by poor diet / eating habits, which cumulates with age (Young, Freegard, & Benton, 2022b).

A major limitation of the present evidence base is the tendency to consider a unitary and primarily 'bottom-up' concept. This has hindered understanding of the processes involved in altered interoception in older populations, and currently prevents the development of remedial interventions. Due to recent applications of the active inference framework (an extension of predictive processing) (Barrett, 2015; Barrett, Quigley & Hamilton, 2016; Garfinkel *et al*., 2015; Young *et al*., 2021), our understanding of interoception has evolved in recent years. In short, rather than viewing interoception as a 'stimulus–response' system, driven by afferent inputs, our perception of the internal state of the body is suggested to primarily reflect predictions about the likely state of the body, given past experiences. These predictions are then updated in an iterative fashion by incoming afferents. In other words, predictions are tested against actual sensory input with any mismatch resulting in prediction errors (surprise) (i.e., that part of incoming interoceptive sensation not accounted for by prior expectations). As there is a need to minimise prediction error, this can be achieved by (1) revising top-down predictions, (2) by modifying the sensory signals so that they comply with the predictions (active inference), or (3) change how the brain attends to or samples incoming sensory input (Barrett, 2015; Young *et al*., 2021). Importantly, the method of prediction error minimisation is determined by the relative precision (inverse variance) of predictions and sensations (Young *et al*., 2019). Understanding interoception in this way, has profound implications for the way interoception and aging is studied.

For example, although it is not explicitly stated, interoceptive magnitude (**Table 3**) (operationalised using VAS) is the interoceptive dimension assessed most often in relation to appetite, i.e., fasting hunger or postprandial satiety. Similarly, gustatory and retronasal intensity ratings (operationalised using a labelled magnitude scale) are an example of interoceptive magnitude. From a predictive coding perspective, magnitude estimation can be explained as a combination of prior beliefs and ongoing sensory

input (Khalsa *et al*., 2018; Petzschner, Glasauer, & Stephan, 2015). Therefore, methods are needed that can differentiate between sensory insensitivity and inaccurate / ridged beliefs about internal states (Smith *et al*, 2020). It was recently reported, that when rating their postprandial satiety, individuals vary in the degree to which they rely on prior satiety expectations and postprandial sensations (Young *et al*., 2021). This also highlights the need to experimentally control factors, that might induce expectations in participants (e.g., a sweet taste signalling energy) - given that participants will use those expectations to inform their interoceptive perceptions to various degrees (i.e., depending on their sensory sensitivity to information delivered through that additional sensory channel). This is particularly problematic in studies that have provided different meals, without considering their sensory properties (**Table 6**). It is also troubling that most retronasal olfaction paradigms confound gustatory (**Table 10**) and retronasal olfactory sensitivity (**Table 9**). Similar issues have been raised regarding the heartbeat counting task, in the cardioception domain. It is thought that performance on this task partially reflects knowledge about heartrate, rather than sensory sensitivity *per se* (see Brener & Ring, 2016 for a review).

This shift away from viewing interoception as a stimulus-response system has inspired the development of a range of additional 'higher-order' interceptive indices. For example, in the cardiac domain 'interoceptive confidence' and 'interoceptive insight' have been defined (Garfinkel *et al*., 2015; Khalsa *et al*., 2018) (**Table 3**). These measures were previously linked to eating behaviour (Young *et al*., 2017). However, we were unable to identify any studies that have assessed age-related differences in these interoceptive indices. Similarly, 'expected satiety' and 'expected satiety confidence' (Brunstrom *et al*., 2008; Young *et al*., 2021) remain unexplored in regards to age. We only identified one study that assessed confidence in the chemical senses domain (Christensen, 1985). Furthermore, the predominant paradigms, used in each domain, vary in the interoceptive constructs assessed. For example, cardioception studies have focused mostly on interoceptive accuracy (**Table 7**), appetitive studies have assessed interoceptive magnitude (**Table 6**), and those focused on chemical senses have tended to focus on identification, thresholds or suprathreshold intensity (**Tables 9 and 10**). Whilst this partially reflects the challenges of operationalising some interoceptive dimensions in some domains (e.g., the difficulty manipulating the strength of cardiac signals in a controlled way), it limits evidence synthesis, and the

ability to compare findings across domains. There is scope to further develop and align methods that tap currently unexplored dimensions, for example confidence in one's ability to differentiate tastes / aromas, or olfactory meta-cognition (Jönsson & Olsson, 2003).

Finally, in each section of the review we have alluded to plausible processes through which interoceptive senescence may have consequences for eating and bodyweight regulation. However, in the studies reviewed here, it was rare that associations between interoception and eating were considered across different age groups. Thus, it is unclear whether interoceptive changes that occur with aging are of any functional consequence. This is particularly important in the context of predictive processing, as described above, as it may simply be the case that in the face of diminished interoception, older adults are able to substitute alternative cues to guide their eating behaviour. For example, an early study that tracked appetitive sensations and food intake, reported a smaller correlation between pre-meal hunger and subsequent meal size in older adults, however the influence of other food cues like social facilitation and time of day were unaffected (de Castro, 2002). Understanding how older adults compensate for blunted interoceptive signalling and whether those compensatory actions are adaptive or not, will be an important area for future research.

Table 4

Roadmap for future research.

Domain	Future research directions
Appetitive sensations	- Determine whether lower hunger in older adults reflects reduced sensory sensitivity to afferent sensations or lower expectations of hunger after a fast. - Examine whether reduced feelings of hunger in older adults have consequences for diet and / or BMI. - Understand the degree to which older adults compared to younger adults use hunger sensations to inform portion size decisions. - Reduce the heterogeneity of methods used to examine satiety, satiation, and energy compensation in older adults to facilitate evidence synthesis. - Understand whether older adults' satiety expectations differ from younger adults', and the factors that influence them.
Cardioception	- Determine the association between cardioception and eating styles like emotional/disinhibited eating. - Examine a wider range of cardioceptive dimensions such as cardioceptive confidence and / or insight.
Interoceptive sensibility	- Determine whether self-reported interoception is a useful indicator of wider interoceptive abilities in older adults. - Understand how different aspects of interoceptive sensibility are differentially altered in older adults. - Determine whether interoceptive sensibility is related to eating behaviour and BMI in older and younger adults alike. - Examine whether and how physiological feelings are incorporated into older adults' appetitive concepts.

Chemical senses	- Understand whether deficits in retronasal olfaction reduces satiety and / increases food intake in older adults. - Study multisensory flavour perception in older adults to understand cue integration mechanisms may differ from younger adults.
Other	- Given the lack of remediation devices available for the interoceptive senses: o Understand the physiological, neural, computational, and psychological mechanisms underpinning interoceptive senescence. o Examine the efficacy of interoceptive interventions e.g., interoceptive attention for improving interoception in older adults.

2.5 Summary tables of eating behaviours and the various interoceptive domains relevant to eating in younger and older adults.

Table 5

A summary of the included studies examining eating behaviours associated with risk of obesity in adulthood.

Author / Date	Variable of Interest	Design	Sample Characteristics	Emotional eating	Restraint eating	Disinhibited eating	External eating	Appetite traits: Hunger / satiety responsiveness	Food craving	Intuitive eating
(Samuel & Cohen., 2018)	DEBQ (16 item)	CS	N = 210 YA: 20 – 40y/o n = 90 MA: 41 - 59 n = 68 OA: 60–87y/o n = 51 M: F	OA < YA	Not reported	-	Not reported	-	-	-
(Gilmour *et al*, 2008)	TFEQ-R18	CS	N=60 YA: n=30 (18-35 y/o) BMI: 24.6 ± 0.4 OA: n=30 (60-80 y/o) BMI: 24.7 ± 0.4 M: F *Body fat % (OA > YA)	Not reported	OA > YA	OA > YA	-	Hunger OA < YA	-	-
(Nagl, *et al.*, 2016)	DEBQ (30 item German version)	CS	N = 2513 < 25 y/o (n = 277) 25 – 34 y/o (n = 377) 35 – 44 y/o (n = 374) 45 – 54 y/o (n = 471) 55– 64 y/o (n = 461) 65– 74 y/o (n = 347) >75 y/o (n = 206) Mean BMI: 25.78(4.98) M: F	OA > YA	No effect of age	-	YA > OA	-	-	-

(Elran-Barak, *et al*., 2021)	'desire to eat when emotionally upset or stressed' Single item	CS	N = 5863 (21 – 39 y/o) : n = 786 (40 – 49 y/o) n = 1605 (50 – 59 y/o) n = 1796 (60+ y/o) n = 1676 Age reported as a continuous variable. BMI details not reported. M: F	OA < YA	-	-	-	-	-	-
(Konttinen *et al*., 2019)	TFEQ-R18	Prospective	N = 3735 25-74 y/o Age reported as a continuous variable. BMI details not reported. M: F	YA: EE > BMI and WC OA: EE < BMI and WC	Not reported	Not reported	-	-	-	-
(Pelchat., 1997)	Food craving (interviews)	CS	N = 98 YA: n = 50 (18-35 y/o) BMI: 21·4±0·4 – 24·0±0·9 OA: n = 48 (65+ y/o) BMI: 25·1±0·7 – 25·4±0·9 M: F	-	-	-	-	-	OA < YA	-
(Pelchat & Schaefer., 2000)	Food craving DEBQ (33 item)	E	N = 32 YA: n = 18 (Mage: 24.2±1.3 - 23.4 ± 1.4) OA: n = 14 Mage: 73.9±1.1 - 71.8 ± 3.0 BMI not reported. M: F	OA < YA	OA > YA	-	OA < YA	-	OA < YA	-

(Keskitalo *et al*., 2016)	TFEQ-R18	CS	N = 1326 17– 82 y/o Age reported as a continuous variable. Mage: 55.6±12.7 y/o BMI: 25.3±4.5 (range: 15.8–48.6) M: F	No effect of age	OA > YA	OA < YA	-	-	-	-
(Cebolla *et al*., 2014)	DEBQ (33 item) Restrained scale revised	CS	N = 593 18 – 65 y/o (Mage) 25.55 (8.27) Age is reported as a continuous variable. BMI: 18.5-40 *M* = 22.12, *SD* = 2.96 F	No effect of age	No effect of age	-	OA < YA	-	-	-
(Sturm *et al*., 2003)	TFEQ R18	E	N = 24 Undernourished OA: n =8 (Mage): 80.4 ± 2.6 y/o BMI: 16.9 ± 0.57 Well-nourished OA n = 8 77.0 ± 0.9 y/o BMI: 23.7 ± 0.8 Well-nourished YA: n = 8 22.0 ± 1.3 y/o BMI: 20.5 ± 0.4 F	Not reported	OA > YA	-	-	Not reported	-	-

(Dang *et al*., 2018)	Food cravings questionnaire	CS PET scan	N = 78 22-83 y/o M*age*: 49.9±18.0 BMI: 27.0±5.1 M: F Age = continuous	-	-	-	-	-	OA < YA	-

Abbreviations: BMI = Body Mass Index; CS=Cross Sectional; DEBQ=Dutch Eating Behaviour Questionnaire; F = Female; L=Longitudinal; M = Male; MA=Middle-age Adults; Mage = Mean age; OA = Older Adults; TFEQ=Three Factor Eating Questionnaire; YA = Younger Adults;

Table 6

Studies comparing appetite sensations (hunger and fullness) in younger and older adults.

Author / Date	Design	Sample Characteristics	Intervention	Primary Interoceptive Outcome of Interest	Secondary outcomes of interest	Results Primary Outcome	Results Secondary outcome	Comments
(Rayner *et al*., 2000).	Experimental WS Age (dichotomous)	N = 10 YA: n = 5 20 - 27 y/o OA: n = 5 68 - 73 y/o M	Day 1: Isovolumetric & isobaric distensions Day2: Nasogastric intubation Day 3 control *Ad libitum* meal	Hunger in response to distension. Fullness in response to distention	Abdominal discomfort Bloating Energy intake	Hunger OA > YA Fullness OA < YA	Abdominal discomfort OA < YA Bloating OA < YA Energy intake OA = YA.	
(Moriguti *et al*., 2000)	Longitudinal WS Age (dichotomous)	N=41 YA_1: n = 11 19–30 y/o, BMI: 23.18 ± 1.58 YA_2 : n = 12 19–30 y/o, BMI: 27.88± 2.10 OA: n = 18 64–78 y/o, BMI: 27.48± 3.36 M: F	6-week underfeeding (BMR – 896 kcals) 6-mouth follow-up to establish weight regain	Hunger and satiety questionnaire at the end of underfeeding (only in a subgroup of n= 19)	Weight regained at the end of follow-up. Thirst recall at end of underfeeding.	Hunger OA < YA No differences in satiety	OA did not regain the weight they lost after 6- months. No differences in thirst	Reduced hunger during low energy intake in OA may have consequences for body weight
(Apolzan *et al*., 2009)	Cross-sectional WS Age (dichotomous)	N = 56 YA inactive: n = 13 25±1 y/o BMI: 26.6±1.0 YA active: n = 11 25±1y/o BMI: 23.5±0.6 OA inactive: n = 16 69±1 y/o	Ecological sampling of appetite throughout one day	Hunger Fullness	Desire to eat. Food intake	Hunger OA < YA Hunger intensity. OA < YA (Peak and nadir values)	Desire to eat. OA inactive < YA and OA active OA consumed less protein and carb but no difference in total energy	

	*Additionally grouped by active status	BMI: 27.7±1.0 OA active: n = 16 72±1 y/o BMI: 24.2±0.7 M: F					
(De Castro., 1993)	Cross-sectional WS Age (dichotomous)	N= 307 n = 92 20-34 y/o BMI: 25.1 ± 0.5(M); 22.9 ± 0.5 (F) n = 127 35 – 49 y/o BMI: 26.3 ± 0.5(M); 22.6 ± 0.3 (F) n = 44 50 - 64 y/o BMI: 26.8 ± 0.8(M); 24.6 ± 0.8 (F) n = 44 65-80 y/o BMI: 25.3± 0.8 (M); 25.4± 1.0 (F)	7-day diary study Eating episodes, subjective hunger, anxiety, depression, and activity recorded	Pre-meal hunger Post meal hunger	Energy intake	Pre-meal hunger did not vary by age group. Post meal hunger OA < YA	Older adults consumed less energy. Older group had smaller correlation between premeal hunger and meal size, and between after meal hunger and meal size
(De Castro., 2002)	Cross-sectional WS Age (dichotomous)	N = 762 20 – 34 y/o (YA) n = 325 BMI: 25.3 ± 0.3 M; 23.2 ± 0.3 F 35 – 49 y/o n = 292 BMI: 26.5 ± 0.3 M; 23.7 ± 0.3 F 50 - 64 y/o n = 99 BMI: 27.0 ± 0.5 M; 25.9 ± 0.7 F 65+ y/o n = 46 BMI: 25.4 ± 0.7 M 25.3 ± 0.9 F	7-day diary study Eating episodes, subjective hunger, anxiety, depression, and activity recorded	Pre-meal Hunger Post meal hunger (satiety / fullness)	Pre-and post-meal thirst, depression, anxiety, and the attractiveness of the food	Pre-meal Hunger OA < YA OA more satiety after an eating episode	Correlation between pre-meal hunger and subsequent meal size was smaller in OA. OA lower correlation between post meal satiety and meal size OA ate small meal sizes

(Mulligan *et al*., 2002)	Experimental WS Age (dichotomous)	N= 13 OA: n=7 (65-80 y/o); YA: n=6 (18-35 y/o) Sex and BMI not reported.	Fasting (36 hour)	Fasting hunger taken at 12 hours	Blood Glucose Smell intensity	Fasting Hunger (after 12 hours i.e., first third of the fast) OA < YA (Stimulated by sour smell)	Blood glucose correlated with hunger in YA, but not in OA. Blood glucose OA > YA (fasting & PP)	
(MacIntosh *et al*., 2001)	Experimental WS Age (dichotomous)	N = 26 YA: n = 13 18 -32 y/o 23.9 (0.6) OA: n = 13 65-84 y/o 23.5 (1.0) M	12-h overnight fast Isovolumetric, intraduodenal (ID) infusions of saline (control), lipid, and glucose for 120 min, on separate days.	Hunger (fasting and postprandial) Fullness (fasting and postprandial	Diet diary energy intake (pre-study) (g) of food consumed at the buffet meal (*ad libitum* intake)	Fasting hunger OA<YA Fasting fullness (ns) Post infusion hunger and fullness did not differ between OA and YA irrespective of condition.	Habitual diet intake 10% lower in OA Glucose infusion supressed *ad libitum* energy intake more in OA, whereas lipids supressed energy intake similarly in both ages.	The relationship between baseline hunger scores and the amount of food eaten at the buffet meal was significant in the young
(MacIntosh *et al*., 2001)	Experimental WS Age (dichotomous)	N=24 YA: 18–33 y/o, BMI: 23.5± 0.8 OA: 67–83 y/o, BMI: 24.1± 0.7 M: F	12-h overnight fast At t = 90 min a preload consisting of 125 g banana blended with 150 ml low-fat (0.1%) milk and 150 ml water (744 kJ; 21% protein, 2% fat, 75% carbohydrate) was consumed within 3 min. IV: CCK-8 low VS high dose (1 or 3 ng/kg p/min) VS 50 ml saline (control) Buffet meal (*ad libitum* intake)	Hunger (fasting and postprandial) Fullness (fasting and postprandial	Energy intake d libitum) Leptin Insulin Blood glucose CCK8 CCK >12	Fasting hunger OA < YA Postprandial hunger – larger decrease in OA Fasting fullness (ns) Postprandial fullness (ns)	Older adults ate 41% less than YA *ad libitum* over the three days combined. CCK satiating effect OA > YA (Fasting, preload & dosage) CCK8 & >12 OA > YA Glucose OA > YA Insulin OA < YA (fast & PP)	CCK suppression of energy intake in OA was related to their relatively higher CCK levels after infusion i.e., reduced endogenous CKK suppression.

(Sturm *et al*., 2004)	Experimental WS Age (dichotomous)	N=24 OA: n = 12 67-83 y/o BMI: 24.1± 0.5 YA: n = 12 18-33 y/o BMI 23.2 ± 0.6 M: F	12-hour overnight fast 400 mL of a drink containing either 0 kcal (water), 250 kcal, or 750 kcal (yogurt-based drinks) 70 min before a buffet-style meal.	Fasting hunger Postprandial hunger Postprandial fullness	CCK Blood glucose Insulin *Ad libitum* energy intake Antral area of stomach	Fasting hunger: OA < YA Fasting fullness (ns) PP hunger OA<YA irrespective of preload PP fullness OA>YA irrespective of preload	CCK OA > YA Antral area OA > YA (PP only) *Ad libitum* energy intake: OA = YA Blood glucose and insulin (ns) but higher blood glucose more sustained in OA
(Giezenaar *et al*., 2020) .	Experimental WS Age (dichotomous)	N = 26 YA: n = 13 23 ± 1 y/o BMI: 24 ± 1 OA: n = 13 75 ± 2 y/o BMI: 26 ± 1 M	Overnight fast Protein / mixed macronutrient drink: (i) a control drink (~2 kcal) or drinks (450 mL) containing protein/fat/carbohydrate: (ii) 70 g/0 g/0 g (280 kcal/'P280'), (iii) 14 g/12.4 g/28 g (280 kcal/'M280'), (iv) 70 g/12.4 g/28 g (504 kcal/'M504'), on four separate days. *Ad libitum* meal (energy intake)	Fasting hunger Fasting fullness Postprandial hunger Postprandial fullness	Blood glucose and insulin (HOMA) Gut hormones (CKK, GLP) Nausea Bloating Energy compensation	Fasting hunger and fullness OA = YA ΔAUC hunger was suppressed less by control, M280, and M504 during the first phase of gastric emptying in OA.	ΔAUC GLP-1 was stimulated more by P280, M280, and M504 in OA vs YA. Fasting CCK OA < YA Energy intake at buffet meal (energy compensation) was reduced in OA after protein.

(Zandstra *et al*., 2000)	Experimental WS Age (dichotomous)	N = 87 YA: n=33 18 - 26 y/o BMI: 23.3 ± 2.3 OA: n =24 61 - 86 y/o BMI: 26.6 ± 3.5 *child sample excluded (n = 30)	2-hour fast in between breakfast and preload Preload yoghurt meal 1) Low (fat, carb, energy (control); 2) Low fat-medium energy 3) high-carb-medium energy 4) high (fat, carb, & energy) 5) No preload conditions *Ad libitum* meal @ 90 minutes	Post meal Hunger	Sensory pleasantness-intensity *Ad libitum* energy intake	Hunger across all conditions OA < YA (fasting not reported by itself)	No age differences in perception of sensory properties across conditions No difference in *ad libitum* energy intake between groups.
(Oberoi *et al*.,2020a)	Experimental WS Age (dichotomous)	N = 20 YA: n = 10 27 ± 2 y/o BMI: 36 ± 2 (obese) OA: n = 10 72 ± 1 y/o BMI: 33 ± 1 (obese) M	12 hours fast overnight a whey protein drink (30 g/120 kcal) and a control drink (~0 g whey protein/~2 kcal) *Ad libitum* energy intake (buffet @ 180mins)	Fasting hunger Postprandial Fullness	Gastric emptying *Ad libitum* Energy intake	Fasting hunger OA=YA PP fullness OA=YA	OA consumed ~20% less energy after the drinks than younger subjects, although this difference was not statistically significant ($p = 0.16$) due to small sample. Did not vary by condition. The whey protein drink slowed gastric emptying, to a comparable degree in both age groups.
(Oberoi *et al*., 2020b)	Experimental WS Age (dichotomous)	N = 30 YA: n = 15 27 ± 1 y/o BMI: 25.8 ± 0.7 (healthy weight) OA: n = 15 75 ± 2 y/o BMI: 26.6 ± 0.8 (healthy weight) M	12-h overnight fast Flavoured water or High vs low whey protein drink *Ad libitum* (breakfast, lunch, and dinner – test days were separated by 3-10 days).	Fasting Hunger Postprandial Fullness	Desire to eat. Prospective consumption Energy intake Antral area Gastric retention	Fasting hunger OA=YA Fullness throughout the day - OA < YA especially after test drink	Effect of Test drink on Desire to eat OA < YA. Test drink suppression of subsequent intake OA < YA Antral area Gastric retention OA > YA

(Van Walleghen *et al*., 2007a)	Experimental WS Age (dichotomous)	N=54 Active (A) vs Sedentary (S) YA: n = 29 21 – 35 y/o BMI: 24.8 ± 0.7 (M) 21.9 ± 0.5 (F) OA: n =21 60 – 80 y/o BMI: 24.6 ± 0.7 24.7 ± 0.9 M: F	3 h fast (from breakfast) 375 mL (women) or 500 mL (men) of water followed 30 minutes later by an *ad libitum* meal.	Fasting hunger Fasting fullness Fasting thirst Pre-meal hunger Pre-meal fullness Pre-meal thirst Postprandial hunger Postprandial fullness Postprandial thirst	Energy intake	Fasting hunger and thirst OA<YA Fasting fullness OA=YA After water fullness OA >YA No significant age difference in thirst was noted during the test meals	Energy intake after the water preload OA<YA
(Van Walleghen *et al*., 2007b)	Experimental WS Age (dichotomous)	N=54 Active (A) vs Sedentary (S) YA: n = 29 21 – 35 y/o BMI: (A) 23.1 ± 0.7 (S) 23.5 ± 0.8 OA: n =25 60 – 80 y/o BMI: (A) 24.5 ± 0.8 (S) 24.8 ± 0.7 M: F	3-hour fast High-energy yogurt preload beverage (YP: 500 ml, 1988 kJ, men; 375 ml, 1507 kJ, women), or no preload (NP), 30 min before an *ad libitum* test meal.	Fasting hunger Fasting fullness Postprandial hunger Postprandial fullness	Glucose Energy compensation	Fasting hunger: OA < YA across both conditions Fasting fullness OA=YA Postprandial hunger OA=YA age groups Postprandial fullness OA > YA after yogurt preload	Glucose OA > YA Energy compensation OA < YA

(Vien *et al*., 2021)	Experimental WS Age (dichotomous)	N= 58 YA: n = 28 20-30 y/o BMI: 18.5 – 24.9 OA: n = 3 60-70 y/o BMI: 18.5 – 29.9 M: F	12-hour overnight fast 5 dairy treatments: (Skimmed milk 180kcal, whole milk 320kcal, plain Greek yoghurt 260kcal, cheddar cheese 240kcal OR water) *Ad libitum* meal @ 120mins (carbohydrate - pizza)	Appetite score: average of individual VAS using the equation: (Hunger + (100 – Fullness) + Desire to Eat + Prospective Food Consumption) / 4.	Blood glucose *Ad libitum* energy intake and energy compensation	Hunger OA < YA Appetite suppression (post dairy) OA > YA	Blood glucose OA > YA Energy intake (kcal): contrast between age groups not provided. Energy compensation: For all treatments YA >OA
(Rolls *et al*., 1995)	Experimental WS Age (dichotomous)	N = 32 YA: n = 16 18 - 35 y/o OA: n =16 60 - 84 y/o M	Overnight fast Yogurt preload: varied in energy and macronutrient content. *Ad libitum* meal (30 mins after preload)	Fasting hunger Fasting fullness	Energy compensation precision	Hunger (pre-meal) OA < YA Fullness (pre-meal) OA > YA	Energy compensation Precision OA < YA

Abbreviations: BMI = Body Mass Index; BS = Between Subjects; CCK = Cholecystokinin; F = Female; g = grams; GLP-1 = Glucagon like Peptide; HOMA = Homeostatic Model Assessment for Insulin Resistance; IV; Intravenous; KJ = KiloJoules; L = Longitudinal; M = Male; NP = No Preload; n.s. = not significant; OA = Older Adults; PP= Postprandial; VAS = Visual Analogue Scale; WS = Within Subjects; YA = Younger Adults; y/o = years old; YP = Yoghurt Preload..

Table 7

Studies that have explored the influence of age on cardioception.

Author / Date	Design	Sample Characteristics	Intervention	Primary Interoceptive Outcome of Interest	Secondary Outcomes of interest	Results Primary Outcome	Results Secondary outcome	Comments
(Ulus & Aisenberg-Shafran., 2022 Study 1)	CS BS	N = 37 n = 17 younger 25.72(3.21) y/o 13F, 66.22 (14.5) kg n = 20 older - 79.65(5.72) y/o 10F, 72.45 (17.41)kg M: F	Emotional pictures	Correlation between HR/BP and subjective physiological arousal while viewing emotional pictures	HR change BP change	Subjective ratings correlated with HR (.51), diastolic (.61), systolic (.53) in YA but not OA (-.20, -.14, -.18 respectively.	No difference in change in HR, DB, SB between YA and OA	Also used the body perception questionnaire short form (Porges body perception) Analysis was done *across* individuals in each group not *within* each personal across multiple observations.
(Khalsa *et al*., 2009)	CS correlations	N = 59, 22 to 63 y/o Mage = 48 (11). BMI: 24.7 (5.6) BMI range: 16.6 – 44.2 M: F	HBD task on two occasions	HBD task accuracy	BMI SEX	OA lower accuracy than YA on both visits (r = -.49, r = -.45)	Not significant when in the model with age	Remained significant after controlling for BMI and sex

(Murphy *et al*., 2018a Study 2)	CS Correlations	N = 136 (after removing 4 cases for MMSE scores < 23) 20–90 y/o Mage = 55.10 (19.50); M: F	HCT	HBC task accuracy	BMI Beliefs about HR HRV timing accuracy	Negative association between age and accuracy (-.21)	Negative association between age and timing accuracy (-.21), and HRV (-.16). Age positively associated with BMI (.25). Age not associated with HR, BP, beliefs,	HBC accuracy negatively associated with BMI (–.19). BMI mediated effect of age on HBC accuracy but alternative models not tested.
(Mikkelsen *et al*., 2019)	CS BS	N = 97 YA: n =65 19–46 y/o Mage = 23.91 (4.62); 52.3% F OA: n = 32 50–77 y/o Mage = 61.78(8.76) 46.9% F	Emotional pictures HCT	HBC task accuracy	Emotional reactivity, negative affect, positive affect during emotion task	No effect of age on HBC accuracy	No main effects of age on emotional reactivity, negative affect, positive affect during emotion task	HBC accuracy predicted emotional reactivity during task in YA (-.38) but not OA (.11)
(Teraoka *et al*., 2023)	CS BS	N = 57 OA: n = 25 Mage: 74.5 ±3.81 YA: n =32 Mage: 20.9 ±1.80 y/o	-	HBC task accuracy	Hand localization task (proprioceptive drift)	No effect of age on HBC accuracy	Proprioceptive drift higher in OA	No association between HBC accuracy and proprioceptive shift across all participants

Abbreviations: BMI = Body Mass Index; BP = Blood Pressure; BS = Between Subjects; CS = Cross Sectional; DB = Diastolic Blood Pressure; F = Female; HBC = Heartbeat Counting Task; HBD = Heartbeat Detection Task; HR = Heart Rate; HRV = Heart Rate Variability; M = Males; Mage = Mean age; MMSE = Mini Mental State Examination; OA = Older Adults; SB = Systolic Blood Pressure; WS = Within Subjects; YA = Younger Adults; y/o = years old.

Table 8

Studies that have explored the influence of age on interoceptive sensibility.

Author / Date	Design	Sample Characteristics	Intervention	Primary Interoceptive Outcome of Interest	Secondary Outcomes of interest	Results Primary Outcome	Results Secondary outcome	Comments
(Murphy *et al*., 2018a Study 1)	CS Correlations	N = 345 18–89 y/o Mage = 38.66 (17.59), M: F		Body Perception Questionnaire (BPQ; Porges, 1993)		Negative association between age and interoception (-.337)		Secondary analysis Age was part of the studies aim
(Raimo *et al*., 2021)	CS BS	N= 137 18-40y/o (n=50, 25F), 41-60y/o (n=50, 30F), 60+ y/o (n = 37, 26F)		Self-Awareness Questionnaire (SAQ; Longarzo *et al*., 2015).	Body schema (hand mental rotation task) Body structural representation (“Frontal Body Evocation task”) Assessment of body semantics (Object-Body Part Association Task)	SAQ did not vary with age	Those aged 60+ had lower performances on the tasks probing the body schema and body structural representation than both lower groups	Higher SAQ = poorer body schema and body structural representation task in older participants Age was part of the studies aim

(MacCormack *et al*., 2021 Study 1)	E WS	Study 1: N = 150, aged 18-75 y/o, 57% F M: F	Bespoke interoception – emotion matching task		Older adults incorporate les interoception into their emotion representations		Is this different to self – beliefs? Age was part of the studies aim
(MacCormack *et al*., 2021 Study 2)	E WS	Study 2: N= 198 Mage = 34.27(12.15), 18–67 y/o; 65.2% F M: F	Modified day Reconstruction Method (DRM; Kahneman *et al*., 2004) to collect participants' self-reported emotional experiences		Age significantly predicted less intense high arousal emotions (b = −.09, S.E.=.42, p=.036, 95% CIs [−.17, −.01]), and more intense low arousal emotions (b = .15, S.E.=.04, p<.001, 95% CIs [.07, .24]),		Is this different to self – beliefs? age significantly predicted more intense positive emotions (b =.23, S.E.=.05, p<.001, 95% CIs [.14, .32]), and less intense negative emotions (b = −.12, S.E.=.04, p=.003, 95% CIs [−.19, −.04]), Age was part of the studies aim
(Elliott & Pfeifer., 2022)	CS Correlations	N = 232. Age 18-24 y/o 42 (18.1) Age 25-34 y/o 108 (46.6) Age 35-54 y/o 51 (22.0) Age 55-76 y/o 31 (13.4) 165F M: F	BPQ-SF and Multidimensional Assessment of Interoceptive Awareness (MAIA; Mehling *et al*., 2012).)	Trait anxiety	Age negatively associated with BPQ (-.11) BUT ns after Bonferroni. Age not associated with any of the MAIA scales	Trait anxiety lower in OA (-.34)	Age was part of the studies aim

(Mahlo & Windsor, 2021)	CS	N = 623 18 – 84 y/o Mage = 48.78(16.74) M: F	Noticing and Emotional Awareness subscales of the Multidimensional Assessment of Interoceptive Awareness (MAIA; Mehling *et al*., 2012). Summed to produce single score	FFMQ (present moment attention, nonjudgement). Decentering subscale of the Experiences Questionnaire. Brief Experiential Avoidance Questionnaire Nonattachment Scale Scale of Positive and Negative Experience	Age was negatively associated with interoception. (-.18)	Present-moment attention, nonjudgment, acceptance, non-attachment and decentring were all positively associated with age.	Age was part of the studies aim
(Fiskum *et al*., 2023)	CS Correlations	N = 306 (81%F) 16–20 (1.4%), 21–25(8.2%), 26–30(14.1%), 31–35(12.7%), 36–40(11.1%), 41–45(17.6%), 46–50(15.7%), 51–55(10.5%), 56–60(2.9%), 61–65(4.6%) > 66 y/o (1.3%)	MAIA-v2 translated to Norwegian		Age positively associated with self-regulation (.21) and negatively associated with not distracting (-.11) sub-scale of MAIA		
(Todd *et al*., 2019)	CS Correlations	N= 646 18 - 76 y/o (Mage =38.92(11.71) 446F M: F	Multidimensional Assessment of Interoceptive Awareness (MAIA; Mehling *et al*., 2012),	Body Appreciation Scale-2 (BAS-2; Tylka & Wood-Barcalow, 2015b). Functionality Appreciation Scale (FAS; Alleva, Tylka, & Kroon Van Diest, 2017). Authentic Pride subscale of the Body and Appearance Self-Conscious Emotions Scale (BASES; Castonguay, Sabiston, Crocker, & Mack, 2014).	Age not associated with any of the MAIA scales	Age negatively associated with body pride (-.10), appearance orientation (-.19), overweight preoccupation (-.17)	

				Two subscales from the Multidimensional Body-Self Relations Questionnaire-Appearance Scales (MBSRQ-AS; Cash, 2000) were used to assess appearance orientation and overweight preoccupation, respectively.				
(Teraoka *et al*., 2023)	CS BS	N = 77 OA: n=25 Mage: 74.5 ±3.81 y/o YA: n =32 Mage: 20.9 ± 1.80 y/o		MAIA	Hand localization task (proprioceptive drift)	No effect of age on MAIA (total score). Individual scales not reported	Proprioceptive drift higher in older adults	positive association between MAIA (total) accuracy and proprioceptive shift across all participants (only in synch condition)
(Bowling *et al*., 2019)	CS correlations	N=608, 469, aged 18-66 y/o		MAIA	Toronto Alexithymia Scale State-Trait Anxiety Inventory	Age not associated with any of the MAIA scales (all p>0.08) (individual coefficients not given)	Age not associated with TAS or anxiety scales (individual coefficients not given)	

(Brown *et al*., 2020)	CS correlations	N = 154 18 to 70 y/o 69.2%F M: F		Body Consciousness Questionnaire (BCS) (Miller *et al*., 1981). Global score was used.	State and Trait Anxiety Scale (Spielberger and Gorsuch, 1983).	Interoception not associated with age (–0.004)	Lower state (−0.318**) and trait (−0.294**) anxiety in OA.
(Palser *et al*., 2018)	CS correlations	N=384. 18 - 65 y/o 255 F M: F		Porges Body Perception Questionnaire (BPQ)	State Trait Anxiety Inventory Toronto Alexithymia Scale (TAS-20)	OA had lower interoception interoceptive sensibility [r = -0.26, p<0.001]	OA had lower trait anxiety [r = -0.30, p<0.001] and alexithymia [r = -0.24, p<0.001]

Abbreviations: BMI = Body Mass Index; BPQ Body Perception Questionnaire; BS = Between Subjects; CI = Confidence Interval; CK = Cholecystokinin; F = Female; L = Longitudinal; M = Male; MAIA = Multidimensional Assessment of Interoceptive Awareness; n.s. = not significant; OA = Older Adults; PP= Postprandial; SAQ = Self Awareness Questionnaire; SE = Standard Error; SF = Short Form TAS = Toronto Alexithymia Scale; WS = Within Subjects; YA = Younger Adults; y/o = years old.

Table 9

Studies that examined retronasal function in relation to age.

Author / Date	Design	Sample Characteristics	Intervention	Primary Interoceptive Outcome of Interest	Secondary outcomes of interest	Results Primary Outcome	Results Secondary outcome
(Croy *et al*., 2014)	Cross-sectional Age (dichotomous)	N= 518 Healthy: n = 292 17 - 81 y/o (Mage) 40.0± 6.1 BMI not reported.	Retronasal olfaction test technique (grocery condiments and powders) 1-minute testing intervals Forced choice ¼ 1 Target and 3 distractor verbal items 20 odours	Retronasal Identification		No correlation between retronasal identification and age	
(Heilmann *et al*., 2002)	Cross-sectional Age (continuous)	N=230 100M Age range 14 – 89 BMI not reported	Retronasal olfaction test technique (grocery condiments and powders) 30 odours	Retronasal Identification Forced choice	Orthonasal (sniffing sticks)	Retronasal decrease with age	Orthonasal results for age not reported but orthonasal and retronasal identification of odours was found to correlate
(Ruikschop *et al* 2008)	Cross-sectional Age (continuous)	N = 27 14M 13F 18 - 65 y/o (Mage: 44±15) BMI of 19–37 kg/m^2 TFEQ, restraint scores ≤9, disinhibition emotional eating scores ≤ 8), and	Olfactometer delivering aroma to back of nose. Compared two aroma release profiles. A: short, less pronounced Profile B: longer, more pronounced Main difference between profiles was length of aroma release not intensity of aroma.	*Ad libitum* drink: sweetened strawberry flavour milk VAS ratings of hunger, fullness, satiety, desire to eat, and thirst.	Sensory specific satiety assessed: sweetened strawberry flavour milk. VS chocolate milk drink (both sweet)	Older people (age ≧45 years) felt on average less satiated and had less decrease in desire to eat sweet products (post hoc analysis). Effects of age on drink intake not reported. Overweight participants consumed more *ad libitum*	Subjects perceived no decrease in pleasantness of flavour or desire to drink the sweetened strawberry-flavoured milk drink compared to the chocolate milk drink (sensory specific satiety less likely to be the cause)

		physiological hunger scores ≤ 8				, but this did not vary aroma profile.	
(Hernandez *et al* 2023)	Cross-sectional Age (continuous – displayed as groups)	N = 400 18 – 82 y/o (Mage): 46 18-29 y/o: n = 395 30–39 y/o: n = 347 40-49 y/o: n = 250 50-59 y/o: n = 164 60-69 y/o: n = 91 70-82 y/o: n = 19 M: F No chemosensory complaints BMI or S.D. not reported	Q powders (3 item retronasal olfaction test: cinnamon, banana, garlic) – identify the odour by selecting 1/6 descriptor flash cards.	Retronasal Identification	Q-sticks (3-item orthonasal odour identification test) (cloves, coffee, and rose) Four-choice taste identification (Taste spray - sweet, sour, salty, and bitter)	Those aged 60 and older had lower q-powders scores.	Those aged 70 and older also had lower q-sticks scores No age differences observed for identification of basic tastes (whole mouth spray test)
(Flaherty & Lim, 2017)	Experimental Age (dichotomous)	N=102 68F 34M Age range 18-70 54 YA, 35F, 18-35 Years 48 OA, 33F, 53-70 Years	Aroma delivery to back of nose avoiding taste / tactile stimulation. Four odour qualities (i.e., strawberry, vanilla, chicken, or soy sauce) Taste: pipette filled with 2 mL of stimulus (0.32 M sucrose or 0.18 M NaCl) on the top of the tongue.	Labelled magnitude scale (intensity)	Interaction between taste and odour	Odor intensity NaCL, strawberry, chicken did not vary by age Sucrose, vanilla, soy sauce OA<YA.	Presenting an odour with a congruent taste reduced the variation in intensity responsivity in OA more than YA

			A total of 10 trials (2 taste alone, 4 odours alone, and 4 taste-odour pairs)				
(Renner *et al*., 2009)	Cross-sectional Age (dichotomous)	N = 353 G1 n = 55 (preschool children: 4–6 years), mean age/SD 5.3/0.6 y/o G2 n = 102 (primary school age: 7–9 years), mean age/SD 8.0/0.9 y/o G3 n = 73 (puberty and adolescence: 10–15 years), mean age/SD 11.3/1.3 y/o A1 n = 61 (16–35 years), mean age/SD 24.7/5.4 y/o A2 n = 31 (36–55 years), mean age/SD 47.0/5.6 y/o A3 n = 31 (>55 years) mean age/SD 64.7/6.6 y/o M: F. BMI not reported	Age related olfactory performance using the orthonasal "Sniffin' Sticks" 16 test (TDI [threshold, discrimination, and identification] score and the retronasal Candy Smell Test (23 items)	Retronasal identification Orthonasal (Intensity, discrimination, and identification) Forced choice	Orthonasal (Intensity, discrimination, and identification)	Retronasal identification scores steadily increase peaking in 20-29 y/o for females and 30-39 y/o males, then steadily declining with a drastic decline in the over 70 y/o	Orthonasal scores steadily increases, peaking at 30-39y/o in females and 20 – 29y/o males before steadily declining and a drastic decline in over 70y/o Note: TDI scores in 50-59 y / o > 40-49y/o (males only)
(Li *et al* 2022)	Cross-sectional Age (dichotomous)	N = 171 n = 98 18 – 35y/o (Mage) 25.8 ± 5.3 y/o n = 73 >55y/o	Taste powders 20 bottles assessed retronasal identification. Retronasal odour threshold test (Yoshino *et al*., 2021a) Taste sprays – suprathreshold assessment of taste identification	Retronasal identification and threshold	Orthonasal intensity and identification Taste identification	Retronasal identification, and detection OA < YA	Orthonasal identification and detection OA < YA

		(Mage) 68.3 ± 10.6 BMI not reported. M: F	(sour, sweet, salty, and bitter) Orthonasal odour threshold test (Sniffin sticks) assessed threshold detection. Sniffing stick assessed orthonasal identification. .		

Abbreviations: BMI = Body Mass Index; F = Female; M = Male; MA = Middle-Aged Adults; Mage = Mean Age; ml = Millilitres; NaCl = Sodium Chloride; OA = Older Adults; ROT= Retronasal Olfaction test; SD = Standard Deviation; TDI = Threshold (intensity), Discrimination, Identification; TFEQ = Three Factor Eating Questionnaire; WS = Within Subjects; YA = Younger Adults; y/o = Years Old.

Table 10

Studies that considered gustation in relation to age.

Author / Date	Design	Sample Characteristics	Intervention	Primary Interoceptive Outcome of Interest	Secondary outcomes of interest	Results Primary Outcome	Results Secondary outcome
(Li *et al* 2022)	Cross-sectional Age (dichotomous)	N = 171 n = 98 18 – 35y/o (Mage) 25.8 ± 5.3 y/o n = 73 >55y/o (Mage) 68.3 ± 10.6 BMI not reported. M: F	Taste sprays – suprathreshold assessment of taste identification (sour, sweet, salty, and bitter) Taste powders 20 bottles assessed retronasal identification. Retronasal odour threshold test (Yoshino *et al*., 2021a) Orthonasal odour threshold test (Sniffin sticks) assessed threshold detection. Sniffing stick assessed orthonasal identification. .	Taste identification	Orthonasal intensity and identification Retronasal identification and threshold	Taste identification OA < YA	Orthonasal identification and detection OA < YA Retronasal identification, and detection OA < YA
(Hernandez *et al* 2023)	Cross-sectional Age (continuous – displayed as groups)	N = 400 18 – 82 y/o (Mage): 46 18-29 y/o: n = 395 30–39 y/o: n = 347 40-49 y/o: n = 250 50-59 y/o: n = 164 60-69 y/o: n = 91	Four-choice taste identification (Taste spray - sweet, sour, salty, and bitter) Q powders (3 item retronasal olfaction test: cinnamon, banana, garlic) – identify the odour by selecting 1/6 descriptor flash cards.	Taste identification	Retronasal Identification Q-sticks (3-item orthonasal odour identification test) (cloves, coffee, and rose)	No age differences observed for identification of basic tastes (whole mouth spray test)	Those aged 60 and older had lower q-powders scores. Those aged 70 and older also had lower q-sticks scores.

		70-82 y/o: n = 19 M: F No chemosensory complaints BMI or S.D. not reported					
(Appleton & Smith., 2015)	Cross-sectional Age continuous	N = 264 16 to 85 y/o BMI not reported	6 fruit flavoured drinks (strawberry / orange and peach) uncoloured, coloured correctly, or coloured incorrectly	Taste identification	Sweetness and strength of drink perception rating Thirst	Identification accuracy declined with age. But colour congruency increased identification with age	Perception of drink pleasantness declined with age. $\beta = -0.22$
(Iannilli *et al*., 2017)	Cross-sectional Age dichotomous	N = 96 n = 30 18 – 30 y/o (Mage): 23.1(2.1) y/o n = 24 31 - 44 y/o (Mage): 35.7(4.4) y/o n = 22 45 -60 y/o (Mage): 51.1(4.3) y/o n = 20 61 -70 y/o (Mage): 65.2(3.3) y/o BMI not reported M: F	taste strips (Sweet, salt, sour, umami, and bitter) multichannel scalp electroencephalography (EEG) gustatory Event Related Potential recordings. Sniffing sticks assessed olfactory function	Taste identification	Orthonasal identification	Taste identification OA < YA	Orthonasal identification OA <YA

(Hoogeveen *et al*, 2015)	Cross-sectional Age dichotomous	N = 77 n = 41 18 – 30 y/o (Mage): 23(3) y/o n = 36 60 - 72 y/o (Mage): 65(4) y/o BMI: Not reported M	Taste strips 4 X increasing concentrations of sweet, sour, salty, and bitter tastes. fMRI scanning Taste pleasantness scale	Threshold Identification	Taste pleasantness	Age groups did not differ in detection and identification scores. Multisensory integration OA < YA	Sweet and salty liking OA > YA Sour liking OA < YA No age-related liking differences in bitter
(Mingioni, *et al*, 2017)	Cross-sectional Age dichotomous	N = 235 N = 105 18-40y/o 28 ± 6 years N = 130 71 ± 5 years 65 – 83 y/o BMI not reported F	Apple puree Acid low vs high Sugar low vs high 2-AFC method	Taste discrimination	Sweetness Sourness	Discrimination performance was matched between age groups	Older adults were more accurate on discriminating lower Concentrations of sweet and sour stimuli
(Guido *et al*., 2016)	Cross-sectional Age continuous	N = 203 20 – 95y/o Mean age 58.2 (19.8) BMI: 26.7(5.63) Olfactory sensitivity assessed.	Threshold test: 4 concentrations Sucrose NaCl solution Citric acid Caffeine Food preferences questionnaire	Taste detection 3AFC	Detection of salt and sweet concentrations OA < YA Citric acid and caffeine OA=YA	Food preference	Fruit and vegetable preference OA > YA Spicy food preference OA < YA

(Wiriyawattana *et al*., 2018)	Cross-sectional Age dichotomous	N = 90 YA N = 30 20–39 y/o mean age 23.0 ± 4.70 MA N= 30 40–59 y/o mean age 47.8 ± 5.34 OA N = 30 60–85 y/o mean age 69.4 ± 8.14 M: F BMI not reported Asian sample	SWEET (sucrose, aspartame, acesulfame-K, sucralose), SALTY (sodium chloride, potassium chloride), SOUR (citric acid, acetic acids), BITTER (caffeine), UMAMI (monosodium glutamate, inosine 5′-monophosphate)	Taste detection thresholds Taste identification thresholds 3AFC		Taste detection thresholds SWEET Sucrose: (n.s) Aspartame: (n.s) acesulfame-K: (n.s) Sucralose (OA > MA) SALTY NaCl: OA > MA > YA KCl: OA > MA > YA SOUR citric acid OA > MA acetic acids OA > MA BITTER caffeine: OA > MA > YA UMAMI MSG: OA > MA > YA ISG: OA > MA > YA	Taste identification thresholds SWEET Sucrose: (n.s) Aspartame: (n.s) acesulfame-K: (n.s) Sucralose (OA > MA) SALTY NaCl: OA > MA > YA KCl: OA > MA > YA SOUR citric acid OA > MA acetic acids OA > MA BITTER caffeine: OA > MA > YA UMAMI MSG: MA > OA > YA ISG: OA > MA > YA
(Yoshinaka *et al*., 2016)	Cross-sectional Age grouped	N = 2015 n = 70 24 – 32y/o 26.6 ± 3.1 y/o n = 996 69 – 71y/o n = 949 79 – 81 y/o BMI not reported M: F	Taste strip tests: sweet (saccharose), salty (sodium chloride), sour (tartaric acid) bitter (quinine hydrochloride)	Taste detection	Sweet Sour Salty Bitter	All taste detection thresholds except sweet 79-81y/o > 69-71y/o > 24-32y/o 69-71y/o displayed similar detection thresholds to YA for sweetness concentrations		

(Heft & Robinson, 2014)	Cross-sectional Age dichotomous	N = 178 20-89y/o n = 92 20-44 y/o n = 86 65–89 y/o M: F	Cross-modality matching (CMM) procedure using Peltier contact thermode (lip/chin) thermal, tactile, and taste stimuli Control task: word rating to assess age differences in scale use	Supra-threshold intensity ratings Salty (sodium chloride) Sour (citric acid)	Sensory intensity Tactile Warm Cool Pain	Sour and salty taste intensity ratings OA < YA	Touch, warm, cool intensity ratings OA < YA No differences in pain intensity ratings
(Rolls *et al*., 2015)	Cross-sectional Age grouped	N = 57 n = 18 18-26y/o 22.2 ± 3.1y/o n = 20 34-46y/o 39.8 ± 4.1y/o n = 19 53-67y/o 59.7 ± 3.9 BMI <30 M: F	Fanta Fanta zero Fanta without label Orange juice Vegetable juice fMRI scanning Intensity and pleasantness ratings	Flavour intensity	Flavour pleasantness	No difference in intensity ratings	Fanta and fruit juice similar pleasantness Vegetable juice pleasantness OA > YA
(Barragán *et al*., 2018)	Cross-sectional Age continuous	N = 1020 18 – 80 y/o (Mage): 43.2 ± 14.3 y/o BMI: 27.1 ± 5.3 M: F	Taste perception tests , scored on a scale from 0 to 5 5 concentrations: PROP (bitter), sucrose (sweet), NaCl (salty), citric acid (sour), L-glutamic acid monopotassium salt monohydrate (MPG) (umami)	Taste intensity	Taste preference (liking)	Perception of taste intensities: Bitter OA < YA Sweet OA < YA Salty OA < YA Sour OA < YA Umami OA < YA	Liking ratings for bitter and sweet OA < YA Higher intensity rating for a taste was not associated with a higher preference for same taste

(Flaherty & Lim, 2017)	Experimental Age (dichotomous)	N=102 68F 34M Age range 18-70 54 YA, 35F, 18-35 Years 48 OA, 33F, 53-70 Years	Aroma delivery to back of nose avoiding taste / tactile stimulation. Four odour qualities (i.e., strawberry, vanilla, chicken, or soy sauce) Taste: pipette filled with 2 mL of stimulus (0.32 M sucrose or 0.18 M NaCl) on the top of the tongue. A total of 10 trials (2 taste alone, 4 odours alone, and 4 taste-odour pairs)	Labelled magnitude scale (intensity)	Interaction between taste and odour	Sucrose OA<YA. Saltiness OA=YA	Odor intensity NaCL, strawberry, chicken did not vary by age Presenting an odour with a congruent taste reduced the variation in intensity responsivity in OA more than YA

Abbreviations AFC = Alternative Forced Choice; BMI = Body Mass Index; BS = Between Subjects; EEG = Electroencephalography; F = Female; L = Longitudinal; M = Male; MA = Middle aged Adults; NaCl = Sodium Chloride; n.s. = not significant; OA = Older Adults; VAS = Visual Analogue Scale; WS = Within Subjects; YA = Younger Adults; y/o = Years old.

Overview of the evidence regarding differences in eating behaviour, body weight and interoception in younger and older adults.

Chapter 2 provides an in-depth systematic review of what is known (and not known) about interoception and age-related differences in eating behaviours that may be associated with an increased risk of developing obesity.

Key findings and patterns from the literature are summarised below:

- Obesity has a higher incidence amongst older adults.
- Older adults self-report poorer appetite, compared to younger adults.
- Appetite hormones and chemosensory factors may contribute to changes in eating behaviour.
- Older adults are underrepresented in this research area.
- Underlying attributable mechanisms in general are not fully understood in older cohorts.
- Several interoceptive indices have not been examined in older adults.
- Eating behaviour linked with increased risk of obesity is less prevalent in older adults.
- Interoceptive ability declines with age.

Chapter 3 Study 1

Weaker connectivity in resting state networks is associated with disinhibited eating in older adults.

3.1 Introduction.

In the previous chapter, several gaps in research were identified. Specifically, inconsistencies remain regarding the association between age and disinhibited eating. Furthermore, conclusions from the previous chapter calls for a better mechanistic understanding of interoception in older and younger adults. Therefore, the main objective of this study is to examine the link between disinhibited eating and resting state functional connectivity of intrinsic brain networks associated with eating, in younger and older adults.

As outlined throughout Chapter 1, the problem of obesity affects all age groups but is greatest amongst those aged 60 and over (Ogden, Carroll, Kit, & Flegal, 2014). Increased accumulation of body fat mass, coupled with age-related declines in health, impose a huge burden on health and social care provisions (Kent *et al*., 2017). Therefore, understanding the mechanisms associated with obesity in already vulnerable populations is critical. Neuroimaging offers an insight into the neural underpinnings of obesity. Several neural networks, such as the frontoparietal (FPN) and default mode (DMN) networks, have been associated with obesity and eating behaviour (Park, Seo, & Park, 2016). However, studies in older populations are scarce and researchers are yet to compare older and younger populations.

Although older adults are the most at risk of developing obesity and its complications (Keaver, Xu, Jaccard, & Webber, 2020), the desire to lose weight and attempts at dieting are similar across age groups (Hetherington & Burnett, 1994). Interestingly, eating styles that are associated with an increased risk of obesity, such as disinhibited

eating (i.e. the propensity to lose control over food consumption), are less prevalent in older adults, as are hunger sensations (e.g. Abdella *et al*., 2019; Giezenaar *et al*., 2016). However, the neural mechanisms underlying eating behaviour in older adults remain unknown. Recently, functional magnetic resonance imaging (fMRI) based functional connectivity analysis has contributed to our understanding of obesity (Donofry, Stillman, & Erickson, 2019). Although most research has considered the connectivity between brain regions in response to specific tasks (Tregellas *et al*., 2011) as opposed to at rest (i.e. resting -state). For example, whilst viewing high calorie / palatable foods, participants with a higher BMI showed stronger connectivity between the amygdala, insula, and prefrontal cortex (Nummenmaa *et al*., 2012). However, it is also possible to observe functional connectivity during the 'resting-state' (Biswal, 2012), a task free, intrinsic exploration of interactions between brain regions (Biswal *et al*., 1995). This approach bypasses issues concerning food presentation e.g., subjective preference (Smitha *et al*., 2017). Interestingly, there are reports that during the resting state, those living with obesity differ in the connectivity of networks involved with emotional regulation, interoception, self-referential thinking, and inhibitory control (Donofry *et al*., 2020).

Although most functional connectivity research has been conducted in younger adults, it is notable that activity in the same frontal and parietal networks linked to excess body weight have been found to decline in older individuals (Varangis, Habeck, Razlighi, & Stern, 2019). In this context, it is plausible that changes in functional connectivity in older adults might be linked to their differing eating behaviour. For example, it was recently observed that in older adults with obesity, confidence to resist eating was associated with connectivity between attentional control regions of the brain, and the limbic circuitry involved in interoceptive, emotional, and hedonic responses (Burdette *et al*., 2020). Although similar effects are reported in young samples (Boehm *et al*., 2014; Pan *et al*., 2018), researchers have used various scanning/analysis techniques, making comparisons between ages difficult. In addition, to date no research has directly contrasted older and younger individuals in the same study, and under the same experimental conditions. Therefore, we examined the link between resting state functional connectivity and disinhibited eating in younger and older adults who were matched on their BMI, whilst statistically controlling for habitual diet. Specifically, in line with previous research we hypothesised that

disinhibited eating would be associated with altered connectivity in the FPN and DMN networks.

3.2 Methods

3.2.1 Participants

Participants were recruited from the local community using email or poster advertisements. Older adults were recruited from the Dementia Research Group's volunteer database (Department of Psychology, Swansea University). Participants were excluded if they had implanted magnetic objects/devices or recent tattoos which prohibited entry into the scanning environment, were showing early signs of cognitive decline according to the Montreal Cognitive Assessment (Nasreddine *et al*., 2005), were suffering from a clinically relevant metabolic or eating disorder, or were currently dieting or adhering to a specific diet for ethical or other reasons e.g., veganism/vegetarianism. Estimated sample size was based on previous neuroimaging research that had investigated the neural correlates of obesity and eating behaviours (Prehn *et al*., 2017). Twenty-four younger and 23 older right-handed adults took part after giving written consent. However, during the preprocessing phase, data from six participants (three younger and three older) needed to be removed; one due to anatomical abnormalities and the remainder for technical reasons that made processing impossible, e.g., movement artefacts. Of the remaining sample 21 were younger (aged 19-34, 11F, 10M, BMI range 18.4 to 30.5 kg/m^2), and 20 were older (aged 60-73, 10F, 10M, BMI range 19.4 to 31.8 kg/m^2) (**Table 12**). All participants were naïve to the aims of the study and were required to fast for a period of two hours prior to the study.

3.2.2 Procedure

During the morning testing sessions, participants provided their written informed consent, and height and weight were measured using an electronic weighing scale and a portable stadiometer, prior to scanning. They then completed the Profile of Mood States Questionnaire. The POMS (72Q) visual analogue scale was performed prior to- and post- scanning where data was analysed for differences in mood. Participants then entered the scanner for a five-minute resting state scan (to improve the reliability of

BOLD signal detection and facilitate network delineation, participants' sustained visual focus on a central cross, placed against a plain background (Allen *et al*., 2011)). After the scanning procedure was finished, participants completed the Three Factor Eating Questionnaire and Food Frequency Questionnaire. Ethical approval was gained from the Swansea Psychology Department Ethics Committee and the study was carried out in accordance with the Declaration of Helsinki - Ethical Principles for Medical Research Involving Human Subjects.

3.2.3 Three factor eating questionnaire (TFEQ)

Eating style was assessed using the Three Factor Eating Questionnaire (TFEQ)-R18 (Karlsson *et al*., 2000; Stunkard & Messick, 1985). The TFEQ measures Cognitive Restraint (6 items e.g., 'I deliberately take small helpings as a means of controlling my weight.'), Disinhibited Eating (9 items e.g., 'Sometimes when I start eating, I just can't seem to stop'), and Emotional Eating (3 items e.g., 'When I feel lonely, I console myself by eating.'). Participants were asked to rate their response on a 4-item scale ranging from 1 'Definitely False' to 4 'Definitely True'. Here, we focused on disinhibited eating, as this dimension most reliably differs according to age and BMI (Young and Watkins, 2016a). Importantly, the factor structure of the TFEQ has been replicated across older and younger samples (Karlsson *et al*., 2000). The internal consistency was moderate for the Cognitive Restraint subscale (Cronbach α= 0.67), high for the Disinhibited Eating subscale (Cronbach α= 0.89), and high for the Emotional Eating subscale (Cronbach α= 0.84).

3.2.4 EPIC Norfolk food frequency questionnaire (FFQ)

Participants also completed the EPIC Norfolk Food Frequency Questionnaire (FFQ) version 6 - a measure of dietary intake (Thornton & Villamor, 2016). Participants were asked to rate, on a scale of 0-9 ('never' to '6+ per day'), the frequency of consumption of foods. A score was calculated for each of the following food groups: fruit, vegetables, ratio of white (e.g., seafood and poultry) to red meat, ratio of polyunsaturated fatty acids to saturated fatty acids, fibre, nuts, and seeds. The sum of

these food group scores was then used as a modified version of the Alternate Healthy Eating Index (AHEI) score; a higher score is indicative of a healthier diet (Young and Watkins, 2016a). This approach is consistent with similar research with a focus upon influencing effects of dietary patterns (Young *et al*., 2017; Young and Watkins, 2016a).

3.2.5 Profile of mood states (POMS)

As mood is known to correlate with resting-state functional connectivity (Takamura & Hanakawa, 2017) and is associated with disinhibited eating (Young *et al*., 2017), there was a need to statistically control for this variable. The Profile of Mood States - Bipolar form (Lorr & McNair, 1988), is a 72-item Likert-type, self-report measure of mood across 6 dimensions. Six positive and six negative adjectives are listed for each of the six mood dimensions: (1) Composed-Anxious; (2) Energetic-Tired; (3) Elated-Depressed; (4) Clearheaded-Confused; (5) Agreeable-Hostile; (6) Confident-Unsure. Participants were asked to rate each adjective on a four-point scale (1 'Much unlike this' to 4 'Much like this') in order to capture the participants' mood over the past week. Participants' overall mood score was calculated by the sum of all six dimensions of mood (following a coding procedure on reversed scoring items). The internal consistency for the POMS-72Q was excellent (Cronbach $\alpha = 0.83$).

3.2.6 Resting state functional connectivity

Neuroimaging studies have consistently identified ten resting state networks (see **Figure 2** and **Table 11** below) (Beckmann, Deluca, Devlin, & Smith, 2005; Salvador *et al*., 2005; van den Heuvel, Mandl and Hulshoff, 2008). Resting-state (or *intrinsic*) functional magnetic resonance imaging (RS-fMRI) is used to explore the "intrinsically functionally segregation or specialization of brain regions/networks" (Nikos, 2008). fMRI provides the ability to observe brain functioning during specifically designed, attention-demanding tasks or whilst the brain is in a state of rest (Shah, Anderson, Lee, & Wiggins, 2010). However, significant neural metabolic differences exist between task-based and resting-state fMRI methods with implications for interpretation. The brain in its resting state (in the absence of elicit tasks) consumes

55 - 75% more energy than during a task-based activity (Smitha *et al*., 2017). Additionally, the synchrony of signal fluctuations is likely to differ for "resting" and "task" conditions.

RS-fMRI is advantageous due to the absence of explicit tasks/stimuli and minimal participant input, which may elicit higher group-level inter-individual variability. RS-fMRI focuses on mapping functional communication channels between brain regions, by measuring the level of correlated dynamics of fMRI time series (van den Heuvel and Hulshoff, 2010). Further advantages of using RS-fMRI include **1.)** The signal-to-noise ratio is improved in RS-fMRI, as overall spontaneous low-frequency fluctuations are considered (Smitha *et al*., 2017) **2.)** The approach bypasses issues relating to; task complexity, and subjective preferences, (for example, subjective desirability of food cues). **3.)** RS-fMRI allows researchers to study multiple resting state networks simultaneously (Figley, Asem, Levenbaum, & Courtney, 2016; García-García *et al*., 2013) **4.)** Disrupted communication in brain regions can be cross-correlated with cognitive, behavioural- and physiological- measures (García-García *et al*., 2013).

Table 11

Summary of spatial maps and corresponding functional network organisation from 20 decomposed Independent Components. ***Reproduced from (Stephen et al., 2009).***

Spatial Map	Matched pairing of networks from the 20-component analysis	Brain Areas of correspondence
Maps 1_{20}, 2_{20} and 3_{20}	visual network	to medial, occipital pole, and lateral visual areas.
Map 4_{20}	default mode network	medial parietal (precuneus and posterior cingulate), bilateral inferior–lateral–parietal and ventromedial frontal cortex.
Map 5_{20}	cerebellum network	cerebellum
Map 6_{20}	sensorimotor network	supplementary motor area, sensorimotor cortex, and secondary somatosensory cortex.
Map 7_{20}	auditory network	superior temporal gyrus, Heschl's gyrus, and posterior insular
Map 8_{20}	executive control network	several medial–frontal areas, including anterior cingulate and paracingulate.
Maps 9_{20} and 10_{20}	frontoparietal network	several frontoparietal areas, insular areas, Broca's and Wernicke's areas

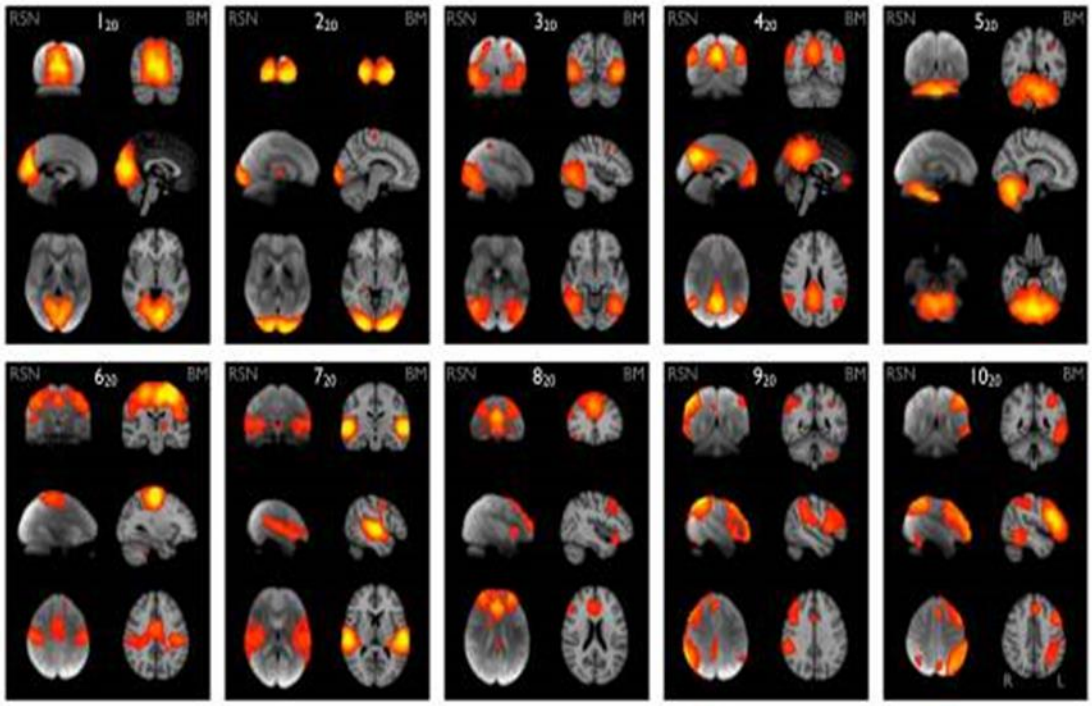


Figure 2: fMRI spatial maps of ten resting state networks

Note: *This figure shows the 3 most informative orthogonal slices for each pair. (Left column of each pair) Resting fMRI data, shown superimposed on the mean fMRI image from all subjects. (Right column of each pair)*

Corresponding network from BrainMap, shown superimposed on the MNI152 standard space template image. Modified from (Stephen et al., 2009) with permission.

Though resting-state networks contain anatomically separated brain regions and sub-networks, they are functionally linked. Functional connectivity allows neuroimaging researchers to make inferences about the functional interaction between two or more brain regions by examining the cerebral signal over time (Gaudet, Hüsser, Vannasing, & Gallagher, 2020) Ongoing functional connectivity within the brain is dynamic, and continuously active (Sadaghiani, Jean-Baptiste, Andreas, & Mark, 2015). Common functions are shared amongst overlapping structures within networks (van Den Heuvel & Hulshoff, 2010). Therefore, exploring the brains organisation at a systems (network) level may be profitable, compared to a brain region focus.

3.2.7 fMRI data acquisition, preprocessing & analysis.

3.2.7.1 fMRI data acquisition.

Anatomical and functional images were acquired with a Siemens Magnetom Skyra 3T scanner and a 32-channel head coil at the Institute of Life Science at Swansea University. For each participant, a T1-weighted volumetric anatomical MRI was acquired with the following parameters: 176 slices sagittal acquisition MP2-RAGE; 1 mm isotropic voxel size; TR = 4000 msec; TE = 2.89 msec; flip angle = 6°; FOV = 256 mm. Functional images were acquired over 10 minutes of eyes-open rest using a T2*-weighted echo-planar image sequence with the following parameters: 45 slices; 2.5 mm isotropic voxel size; TR = 3000 msec; TE = 30 msec; FOV = 190 mm; flip angle = 90°.

2.2.7.2 fMRI pre-processing & analysis

Functional images were preprocessed with Statistical Parametric Mapping software (SPM8; http://www.fil.ion.ucl.ac.uk/spm). Images were realigned to the mean image for head-motion correction and then spatially normalised into standard stereotaxic space with a voxel size of 2 mm^3 (Montreal Neurological Institute template) using segmented T1 tissue maps. Head movement and rotation in the three dimensions did

not exceed 2 mm or 2º and no dataset had to be excluded from analysis. Finally, the functional images were spatially smoothed with a 6-mm full width half maximum Gaussian kernel.

Following preprocessing, functional networks were identified for the entire dataset (younger and older adults combined) with group independent component analysis (ICA) using the Group ICA of fMRI Toolbox (GIFT; https://trendscenter.org/software/gift/). ICA is a method of blind source separation, which identifies source signals (independent components) in the fMRI data by maximising the signal's statistical independence. The resulting Independent Components (ICs) are defined as functional networks in which neural activity operates in concert to generate a statistically independent signal. Each Independent Component (IC) consists of a time-course and a 3D map. The 3D map indicates the spatial extent of the network while the time-course indicates, across time, the strength of the network signal (i.e., functional connectivity) in the data.

Individual images were first normalised by removing the mean value of each image at each time point, and then concatenated across time. After data reduction with principal component analysis, 20 ICs were identified using the infomax algorithm (Bell, 1995). To estimate the stability of ICs, this analysis was repeated 5 times using ICASSO (Himberg & Hyvarinen, 2003; Himberg, Hyvärinen, & Esposito, 2004). Only those ICs with a stability index larger than 0.95 were selected for further analysis. Finally, back reconstruction was applied to estimate the spatial maps and time courses of each IC for each participant using GICA3 (Calhoun, Adali, Pearlson, & Pekar, 2001).

3.2.8 Overlap of independent components with target networks

Resting-state networks associated with eating behaviour were selected as variables of interest given the advantages outlined in section 3.2.6, along with the *a priori* design of the present study. Specifically, the Default Mode (DMN), and Frontoparietal (FPN) networks were chosen as targets because of their established associations with eating behaviour (Boehm *et al*., 2014; Donofry *et al*., 2019; Fox & Raichle, 2007; Menon, 2011). The auditory network was selected as an additional target network to serve as a control, given the absence of associated behavioural domain correlations. This allowed us to determine that any associations with the networks of interest were not

simply due to more global reductions in functional connectivity, in older versus younger populations (Stephen *et al*., 2009).

On the group level, the overlap between the 20 ICs with each of the three targets networks was assessed using ICN_atlas (https://icnatlas.com/) (Kozák, van Graan, Chaudhary, Szabó, & Lemieux, 2017). ICN atlas enables the calculation of 15 metrics of overlap, between an IC and resting-state network templates, defined by a number of atlases (Kozák *et al*., 2017). Here, templates from the SMITH10 atlas were chosen because they have been derived from a 20-dimensional ICA and have been matched to behavioural domains using BrainMap (Laird *et al*., 2011). Demonstrated with strong test re-test repeatability, this atlas provides a fast, objective, and flexible comparative quantification of connectivity patterns within a resting-state fMRI dataset. As a measure of overlap, the spatial involvement was chosen because of its interpretable capabilities. We identified the highest value, within the output metric, to determine a representative independent component. This value indicates the level of engagement from each of the pre-specified brain networks. Spatial involvement is defined as the proportion of an intrinsic connectivity network [ICN] that is activated in the input map. In spatial terms, it is the ratio of ICN voxels to ICN volume to capture the degree of engagement of the network in a given activation map (Kozák *et al*., 2017). Analysing the spatial properties is often the preferred choice (over temporal properties), given the small number of time points in a given resting-state fMRI dataset (Zuo *et al*., 2010). From the set of 20 ICs, the three ICs with the highest spatial involvement measures for the target networks were selected for further analysis. Then, for each participant, the three back-reconstructed ICs identified on the group level were assessed for their overlap with the three target networks using the same procedure. The resulting three overlap measures (spatial involvement) for each participant were used for further analysis.

2.2.9 Statistical analysis

A multivariate ANOVA was used to detect group differences. A chi-squared test was performed on the categorical variable sex (**Table 12**). To examine whether the association between resting-state functional connectivity and disinhibited eating varied according to age, a moderated regression analysis was performed using the

PROCESS macro (Model 1) for SPSS (v. 25.0, IBM Corp.) version 3.5.2 (Hayes, 2014). A bootstrap sample specified at 5000, and a 95% CI was applied. Resting-state functional connectivity of selected networks (DMN, FPN, and AUD networks) were outcome variables (Y). Disinhibited eating was the predictor variables (X), and age was considered a potential moderator (W) of the (X) and (Y) association. To overcome problems of multicollinearity, variables were mean centred. We conducted separate analyses for each network, where BMI, mood and diet were included as covariates. A False Discovery Rate (FDR) procedure was used to correct the *p*-values of the univariate tests. Statistical significance was set at an $\alpha = 0.05$ with FDR correction (Yoav & Yosef, 1995). Potential outliers were determined using the Cooks distance diagnostics. To avoid removal of natural variability, we specified a conservative Cook's distance threshold of 0.2 (Bollen & Jackman, 1985).

3.3 Results

3.3.1 Demographic / group comparisons.

Younger adults (YA) reported significantly higher levels of disinhibited eating ($F (1, 39) = 8.61$, $p = .006$, $\eta = .987$); consumed a poor-quality diet ($F (1, 39) = 4.82$, $p = .034$, $\eta = .110$), and reported a less positive mood state ($F (1, 39) = 9.28$, $p = .004$, $\eta = .192$) (**Table 12**). The two samples did not significantly differ on the restraint or emotional eating scale. The groups were well matched on BMI ($F (1, 39) = 2.62$, $p = .113$, $\eta = .063$) and sex ($\chi^2 (1, N = 41) = 0.02$, $p = .879$, $\varphi = .02$). After the False Discovery Rate correction, mood and disinhibited eating score remained significant.

Table 12

Demographic data of younger and older adult groups (mean and standard deviations [SD])

Participant Characteristics	Younger Adult Group	Older Adult Group	χ^2	F ratio	*p*-value
Sex	10M, 11F	10M, 10F	.02	-	.880
Age (years)	23.59 (4.22)	67.01 (3.68)		-	-
Age Range	19 – 34	60 – 73		-	-
BMI (kg/ m^2)	25.01 (5.12)	26.62 (4.13)		2.63	.063
DE	19.56 (5.92)	15.0 (4.33)		7.52	.009*
RE	15.42 (3.84)	17.0 (3.64)		1.60	.213
EE	6.45 (2.67)	5.95 (2.39)		0.39	.536
Diet	-3.03 (28.08)	21.13 (30.34)		6.83	.013*
POMS	32.99 (4.69)	37.02 (3.49)		9.51	.004*

Note. $N = 41$ (n=21 for younger adult sample and n = 20 for older adult sample).

* $p < 0.05$

Abbreviations: BMI - body mass index; DE – disinhibited eating; EE – emotional eating; F-female; M - male; POMS – Profile of Mood States; RE – restrained eating

3.3.2 Disinhibited eating and network connectivity

3.3.2.1 Frontoparietal network (FPN)

One outlier with a Cook's distance of 0.29 was removed from the older adult (OA) sample. Overall, the model was significant, accounting for 53% of the variance in FPN connectivity ($R^2 = 0.539$, F (6, 32) = 6.252, $p < 0.002$) (**Figure 3**). As expected, OA had weaker connectivity in the FPN (β = - 0.829, $p < 0.0001$, LLCI -1.154, ULCI -0.504). There was also a significant negative association between DE and FPN connectivity (β = - 0.431, $p = 0.003$, LLCI -0.713, ULCI -0.148). However, both effects were superseded by a significant interaction between DE and age (β = - 0.402, $p < 0.013$, LLCI -0.714, ULCI -0.091). Probing this interaction revealed that there was a significant negative association between DE and FPN connectivity in OA (β = -0.838, $p < 0.001$, LLCI -1.326, ULCI -0.351), but not in YA (β = - 0.043, $p = 0.795$, LLCI -0.381, ULCI 0.294). Although, those with a higher BMI tended to have stronger connectivity in the FPN, the effect was not significant (β = - 0.272, $p = 0.056$, LLCI -

0.008, ULCI 0.551). Additionally, neither mood (β = - 0.059, *p* = 0.662, LLCI -0.332, ULCI 0.214), nor diet quality (β = 0.032, *p* = 0.808, LLCI -0.235, ULCI 0.299) were associated with FPN connectivity.

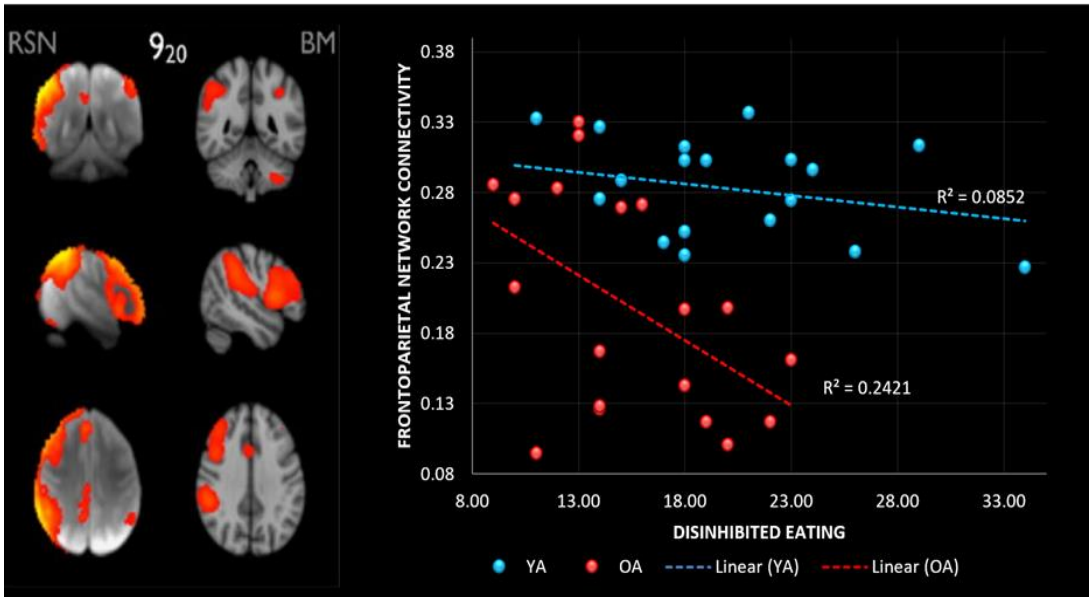


Figure 3: The association between frontoparietal network connectivity and disinhibited eating in older and younger adults.

Note: Data does not include the participants removed as identified outliers.

3.3.2.2 Default mode network (DMN)

The same participant within the OA sample was removed from this analysis, as the data indicated a Cook's distance score of 0.24. The model was again significant, accounting for 39% of the variance in DMN connectivity ($R^2 = 0.392$, F (6,32) = 3.433, p = 0.010). Similar to the analysis of the FPN, OA had weaker connectivity in the DMN (β = -0.708, *p* < 0.001, LLCI −1.082, ULCI -0.334) (**Figure 4**). However, neither DE (β = -0.211, *p* = 0.195, LLCI -0.536, ULCI 0.11S), BMI (β = -0.009, *p* =0.956, LLCI -0.330, UL 0.313), Mood (β = 0.112, *p* = 0.472, LLCI -0.202, UL 0.426) nor Diet (β = 0.131, *p* = 0.389, LLCI −0.202, UL 0.438) correlated with DMN connectivity. The interaction between DE and Age (β = -0.353, *p* = 0.053, LLCI -0.712, ULCI 0.05) approached significance. Similar to the findings reported above for FPN, this effect reflected a significant negative association between DE and DMN connectivity in OA (β = - 0.569, *p* = 0.047, LLCI -1.130, ULCI -0.008), but not in YA (β = 0.129, *p* = 0.504, LLCI -0.260, ULCI 0.518).

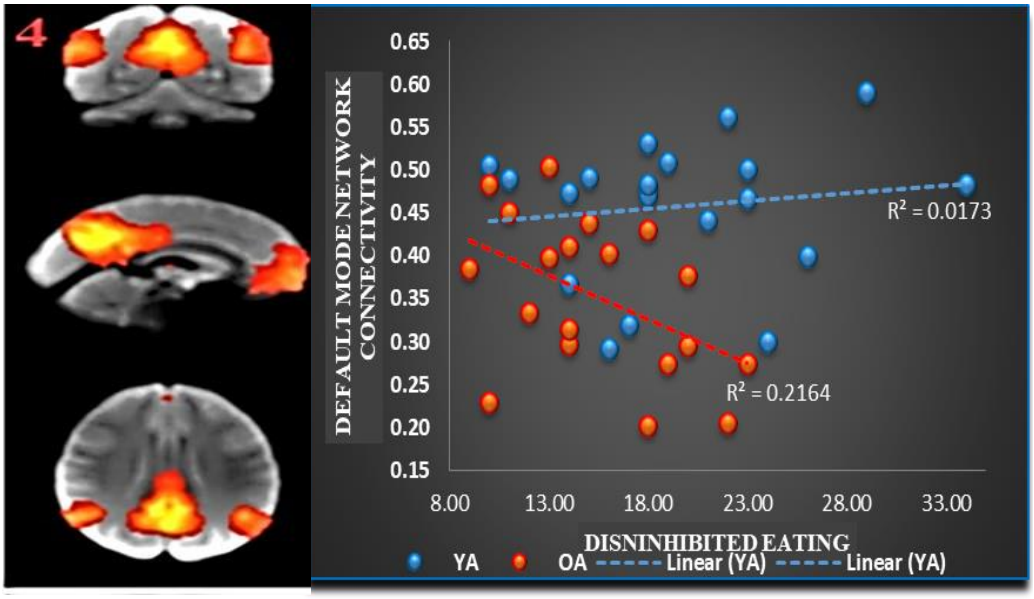


Figure 4: The association between default mode network connectivity and disinhibited eating in older and younger adults.

3.3.4 Auditory network (AUD).

Sensitivity analysis (control network)

No outliers were identified in the AUD network analysis. Expectedly, the model was not significant (R^2 = 0.170, F (6,33) = 1.124, p = 0.370). Likewise, none of the predicted variables were associated with AUD connectivity; Age (β = -0.310, p = 0.148, LLCI −0.736, UL 0.116), DE (β = 0.214, p = 0.253, LLCI -0.160, ULCI 0.588), the interaction between DE and age (β = -0.012, p = 0.950, LLCI -0.408, ULCI 0.384), EE (β = 0.062, p = 0.752, LLCI -0.334 ULCI 0.457), BMI (β = -0.028, p = 0.877, LLCI -0.392, ULCI 0.336), Mood (β = 0.152, p = 0.404, LLCI -0.214, UL 0.517) and diet (β = 0.294, p = 0.100, LLCI −0.059, UL 0.647).[1]

[1] See Appendix B8 for a summary of findings in the association between emotional eating, network connectivity, and age.

3.4 Discussion

As older adults remain a relatively neglected population in the obesity and eating behaviour research, the objective of this study was to determine whether associations between resting state functional connectivity and differences in eating styles that have been observed in young adults are also evident in older adults. The key findings were that: (**1**) in comparison to young individuals, older adults reported lower levels of disinhibited eating, and had weaker connectivity in the FPN and DMN, (**2**) in older adults, but not younger adults, disinhibited eating was negatively associated with connectivity in both the FPN and DMN (**Figures 3** and **4** respectively), (**3**) these effects were not explained by differences in BMI, mood or habitual diet quality, and (**4**) the specificity of these effects was demonstrated as no associations were observed in the sensitivity analysis of the auditory network.

Despite decades of research into eating behaviour associated with an increased risk of obesity, older samples remain scarcely investigated. Interestingly, obesity rates increase across adulthood (Keaver *et al*., 2020), however, there is evidence that self-reported disinhibited eating declines each decade between the ages of 40 and 90 years (Löffler *et al.*, 2015). Additionally, a recent meta-analysis reported that healthy older adults (aged 70–74) have 25–39% lower subjective hunger than younger adults (aged 26–27) (Giezenaar *et al*., 2016). The present data support these observations – older individuals reported lower levels of disinhibited eating than those who were younger (**Table 12**). Notably, over 50% of the items on the TFEQ-18 disinhibited eating scale specifically ask about eating in response to internal cues e.g., "I am always hungry enough to eat at any time". In studies that have explored the factor analytic structure of eating behaviour, it is not uncommon for 'hunger' items to load together with items asking about the ability to control food intake such as "Sometimes when I start eating, I just can't seem to stop" (Anglé *et al*., 2009a). Thus, responsivity to internal sensations may play a significant role in disinhibited eating, and it is plausible that one reason why older adults may report lower levels of disinhibited eating may be linked with a diminished sense of hunger. Future research identifying the processes involved in reduced hunger and disinhibited eating in older populations might be beneficial.

In this context, we observed weaker FPN connectivity in older individuals (**Figure 3**). The FPN is an integrated network of domain-general brain regions including frontal, parietal, and anterior insular brain regions that are activated in response to a wide range of task conditions requiring self-regulation and meta-cognition (Marek & Dosenbach, 2018). In addition, the FPN is highly interconnected with other brain networks such as the DMN, and is thought to be involved in their task-related modulation (Marek & Dosenbach, 2018). In particular, there is evidence that a key function of the FPN is to instantiate and flexibly switch self-control in response to feedback (Rossi, Bichot, Desimone, & Ungerleider, 2007). Therefore, the present finding of weaker FPN connectivity in older adults may support previous research where is has been found that older individuals are generally poorer at information updating, and adapting to changing task demands (Wilson, Nusbaum, Whitney, & Hinson, 2018). Importantly, a body of research has documented a negative link between obesity and performance on tasks involving working memory, self-control, and cognitive flexibility (Favieri, Forte, & Casagrande, 2019), although fewer studies have considered specific eating styles (Calvo, Galioto, Gunstad, & Spitznagel, 2014). Therefore, it is plausible that weaker connectivity among nodes of the FPN, involved in flexible self-control, may be associated with increased risk of disinhibited eating behaviour. Indeed, the present findings suggest that reduced FPN connectivity may be associated with disinhibited eating in older adults (**Figure 3**). Future research could explore task-related functional connectivity in relation to cognitive flexibility and eating behaviour in older adults.

Additionally, the FPN has significant anterior insular and dorsal ACC connections (**Figure 2**). These areas of the brain are often associated with the prediction, detection, and filtering of salient afferent signals, especially those originating from inside the body (interoceptive signals) (Barrett, 2017; Kleckner *et al*., 2017). This suggests that the FPN may also have a role in regulating the internal state by guiding relevant behaviours that generate the expected interoceptive inputs (Barrett, 2017). In this way reduced connectivity of the FPN in older adults, may interfere with eating behaviour and by extension, the regulation of the energy needs of the body. This will be an important question for future research to address.

Consistent with prior research (Ward *et al*., 2015), we also observed that older adults had weaker connectivity within the DMN (**Figure 4**), which comprises the medial

parietal (precuneus and posterior cingulate), hippocampus, and prefrontal cortices. Additionally, in older adults weaker DMN connectivity correlated negatively with disinhibited eating, meaning that weaker DMN connectivity is demonstrated particularly in those older adults with higher disinhibited eating scores. Research indicates that the DMN may be a key network involved in the representation of the brains internal model of the world (Barrett, 2017; Kleckner *et al*., 2017) . This internal model is used to inform predictions about sensory inputs, including predictions about ongoing changes to the body's internal milieu (Barrett, 2017; Kleckner *et al*., 2017). Previous research has shown that weaker DMN connectivity might reflect a diminished capacity of this network to categorise and integrate afferent information with internally generated concepts (Barrett, 2017; Donofry *et al*., 2020). Though further exploration is required to enhance our understanding of the link between the functional connectivity of this network, eating styles and age. Although speculative, this interpretation is consistent with evidence suggesting that older adults' mental representations of emotion are less associated with interoceptive sensations, than are those of younger adults (MacCormack *et al*., 2021), and that poorly differentiated emotional and interoceptive experiences might exacerbate differences in eating behaviour (Westwood, Kerr-Gaffney, Stahl, & Tchanturia, 2017). This suggests that future studies assessing the role of emotion differentiation might be profitable. For instance, we controlled for mood in our analysis, however, as older adults reported a better mood (**Table 12**), and that a poorer mood was previously linked to disinhibited eating (Young *et al*., 2017), future research might profit from considering the role of mood and / or emotion in the link between age and disinhibited eating, and whether any such effects are related to network connectivity.

Interestingly, the present observation that FPN connectivity was not associated with disinhibited eating in younger adults (**Figure 3**), this is in contrast to previous findings (Park *et al*., 2016). Park *et al* examined functional connectivity in samples within the healthy weight BMI range (aged 29.83 (9.95)) or a BMI over 25 (aged 33.24 (10.09)) individuals, and observed positive associations between the FPN, BMI, and disinhibited eating. One explanation for our inability to replicate this effect is our small sample size, although our sample size was sufficient to observe a significant negative association in the older group (**Figure 3**). It is worth noting that when applying Fisher's r to z transformation there was no significant difference between associations

for the different age groups (disinhibited eating and functional network connectivity), (see Appendix B9 for full reporting of Fishers transformation). Therefore, replication of the current study using a larger sample and with a more even distribution of scores is required. A second explanation is that here we controlled for a number of important confounds which have not been considered in prior research (Park *et al*., 2016). For example, our samples were matched on BMI, and we also controlled for differences in mood and habitual diet quality. Each of these factors has previously been shown to influence brain functioning (Donofry *et al*., 2020; Takamura & Hanakawa, 2017), and in the present study varied according to age (**Table 12**). Regardless of the explanation, the present data are important as they suggest that findings obtained from young undergraduate populations cannot be assumed to translate to older populations. In the future, better characterisation of research samples will be needed to understand phenotypic differences, and their association to the activation patterns of neural networks and to personalise interventions.

Interestingly, emotional eating was not associated with the functional connectivity of any of the included resting state networks. Previous research using region of interest (ROI) fMRI methods have shown a positive association between emotional eating scores and activation of the insula and dorsolateral prefrontal cortex (Wood *et al*., 2016). Both areas are implicated within the frontoparietal network (Stephen *et al*., 2009). Inconsistencies in findings between the current study and Wood *et al* (2016) may be attributable to heterogeneity in methods i.e., task-based ROI vs resting-state ICA, and measures i.e., TFEQ vs Weight-related eating questionnaire (Schembre, Greene, & Melanson, 2009).

A strength of the current study is that we were able to demonstrate the specificity of our findings to the FPN and DMN. The sensitivity analysis showed no associations between disinhibited eating, age, and connectivity in the auditory network. The auditory network includes the primary and association auditory cortices, superior temporal gyrus, Heschl's gyrus, and notably the posterior insular cortex. It was proposed that in the insular cortex there is a posterior-to-anterior gradient (Craig, 2003), with the posterior insula processing the physical features of interoception, while the anterior insula being responsible for the integration of interoception with cognitive and motivational information, and the subjective awareness of feelings (Seth, 2013). Interestingly, previous observations noted that age-related declines in connectivity were more apparent in the dorsal insula (associated with executive functioning), while

connectivity in the ventral insula (associated with affect) is relatively spared (Touroutoglou, Zhang, Andreano, Dickerson, & Barrett, 2018). Therefore, future research scrutinising functional connectivity in insular sub-regions using similar ages of the current study might be profitable.

3.4.1 Limitations

Due to the cross-sectional design of this research reverse causality cannot be ruled out. For instance, an alternative explanation for the present results is that a lifetime of disinhibited eating combined with the aging process (which is known to affect cerebral vascularisation) results in weaker FPN and DMN connectivity. However, if this were the case, we would expect habitual diet quality and / or BMI to have influenced the results and they did not. Nonetheless, longitudinal data will be required to fully exclude this possibility. A second limitation relates to our small sample size: it is possible that we lacked the power to detect significant effects in our younger sample. However, altered resting state network connectivity has been observed in smaller samples. For example, a higher BMI was associated with reduced connectivity of the posterior DMN. This study comprised of a sample of 43 (Dietrich, Hollmann, Mathar, Villringer, & Horstmann, 2016). In fact, an evaluation of the neuroimaging research, published in high impact journals over the past 30 years revealed that 96% of studies comprised of a single group, with a median sample size of 12 (Szucs & Ioannidis, 2020). Importantly, interpreting the results is further limited by the older adults' narrow range of disinhibition scores, again a common issue in fMRI research where sample sizes tend to be small. Nevertheless, attempts to rectify such limitations should be addressed in future work. Additionally, the comparison of small, cross-sectional groups (e.g., younger vs. older adults) can increase the likelihood of the groups being confounded by unmeasured individual differences. Although we controlled for known differences (i.e., mood, habitual diet, BMI), it is possible that unknown individual differences remain. Therefore, future replication of these findings within larger sample sizes is crucial.

Although our choice of target networks was theoretically driven, the observed effects may extend beyond those networks. For example, a wider network of brain regions

(bilateral frontal and parietal regions, amygdala, temporal pole, hippocampus, fusiform gyrus, and inferior insula) was previously associated with confidence to resist eating in the absence of hunger (Burdette *et al*., 2020). Future research comparing older and younger adults might profit from assessing global brain connectivity and / or applying graph theoretic metrics that are able to provide a more comprehensive understanding of the network topology and their interactions. Finally, we used the Profile of Mood States bipolar scale which prevents us from examining the individual effects of positive and negative affect. Future research might explore the potential differential contributions of positive and negative affect.

3.4.2 Conclusion

The aim of the current chapter was to examine age-related differences in the link between disinhibited eating and functional connectivity of resting state networks associated with eating behaviour. We observed age-related associations between disinhibited eating and resting state connectivity in the frontoparietal and default mode networks. These observations may direct future work to confirm whether the present associations indicate changes in appetite related interoceptive signalling, and whether they contribute to behavioural changes in energy intake during senescence.

Chapter 4: Study 2

Individual differences in sensory and expectation driven interoceptive processes: a novel paradigm with implications for eating behaviour and risk of obesity.

4.1 Introduction

The neuroimaging research in Chapter 3 found a negative association between disinhibited eating and frontoparietal (FPN) and default mode network (DMN) connectivity, specifically in older adults. As outlined in Chapter 3 (Study 1) both networks are thought to play a key role in interoceptive processes. Additionally, an overlap of the factor loadings of disinhibited eating and hunger (from the self-report TFEQ measure in Chapter 3) was noted. Therefore, further exploration of how individuals with these dietary styles differ in their experiences of interoceptive signals relevant to eating may be beneficial. In addition, Chapter 2 highlighted that while there is evidence that older adults experienced reduced fasting hunger (albeit the evidence base is more limited for postprandial sensations), there was a need to identify whether these age-related differences were driven by expectations or sensations.

Recently researchers in our laboratory developed an ecologically valid paradigm for assessing satiety from the perspective of active inference (Young *et al*., 2021). Active inference is an extension of the predictive coding framework (Friston, FitzGerald, Rigoli, Schwartenbeck, & Pezzulo, 2017), which suggest that individuals weight the relative reliability of different incoming signals, including afferent internal signals. It follows that individuals will likely vary, in the degree to which, they rely on different sensory channels when judging their satiety. Indeed, using their paradigm, Young *et al* (2021) were able to identify those individuals who primarily relied on prior expectations (based on visual and gustatory cues), rather than incoming sensations (changes in blood glucose) to inform their postprandial satiety (Young *et al*., 2021). Specifically, it was reported that those with a higher BMI were less confident in their satiety expectations and relied on this information to a lesser degree when inferring

their fullness (Young *et al*., 2021). In addition, those with less reliable expectations were more likely to experience "rebound hunger", that is, an increase in hunger in response to a "surprising" interoceptive state (Young *et al*, 2021).

In Chapter 3 we reported that older adults with lower disinhibited eating scores had higher connectivity in the FPN and DMN. As these networks play a central role in interoception, including representing, predicting, filtering and modulating afferent signals, we would expect older adults who are low in disinhibited eating to be able to utilise prior expectations to inform their feelings of satiety to a greater extent. It is possible to test this hypothesis using the paradigm developed by Young *et al*. (2021).

Note *that due to the COVID 19 pandemic it became impossible to recruit older adults into a laboratory study - given their vulnerability to severe disease. Therefore, in the event, only effects with younger adults are reported. Chapter 4 proceeds on the basis that variability in eating style (e.g., the TFEQ eating styles) may be related to the degree to which individuals are driven by 'top-down' expectations versus 'bottom-up' sensations.*

Importantly, some of eating traits have already been linked to alterations in the way internal sensations are experienced, albeit in the cardiac domain (Young *et al*., 2017; Young & Watkins., 2016b). However, a clear understanding of the processes underpinning differences in eating styles had remained elusive, limiting the ability to develop effective interventions. Therefore, the present study sought to determine whether trait differences in eating style were related to differences in the degree to which postprandial satiety is driven by prior expectations rather than incoming sensations. Specifically, disinhibited eating (DE), emotional eating (EE) and restrained eating (RE) were investigated.

4.2 Methods

4.2.1 Procedure

This procedure was approved by Swansea University Department of Psychology ethics committee and was conducted in accordance with the principles laid down by the declaration of Helsinki 2013. Participants abstained from food for eight hours before attending the laboratory and refrained from drinking alcohol and taking part in any

physical activity within twenty-four hours of the study. All participants completed the study between 9.00am and 1.00pm. Upon arrival at the laboratory, participants provided their written informed consent, then had their height, weight and fasting blood glucose measured. Subsequently participants completed the questionnaires detailed below, then rated their fasting hunger before being randomly allocated to receive either a flavour-nutrient congruent (glucose) or a flavour-nutrient incongruent (sucralose) drink. The random sequence was computer generated; solutions were produced in sequentially numbered tumblers. Participants were then allocated using a double-blind technique.

Once allocated to their condition, participants were asked to rate the drinks expected satiety, and their confidence in this rating based solely on its appearance. They then took one sip of the drink and completed the ratings a second time so that these second rating were based on both the drinks appearance and its taste. Participants then had five minutes to consume the entire beverage. Ten minutes after consuming the drink (15 min after they started drinking), participants evaluated how full they felt at that moment, how much they liked the drink, and provided another glucose measurement. After 30 and 60 mins, blood glucose and hunger were assessed for a third and fourth time.

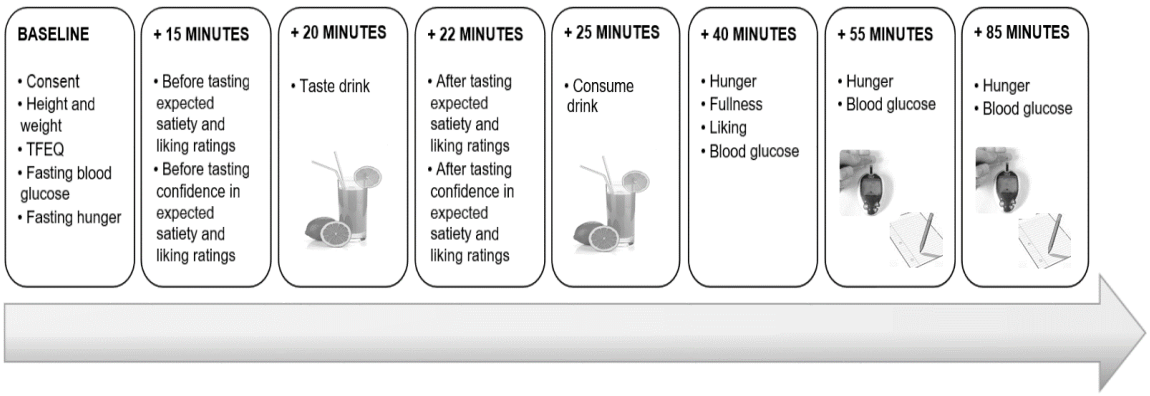


Figure 5: The experimental procedure

Note: TFEQ – Three Factor Eating Questionnaire

4.2.2 Test Drinks

Drinks were 500 ml and provided in a clear plastic tumbler. The glucose drink contained 75 g of glucose dissolved in water. The sugar free beverage was sweetened with sucralose to produce a similar sweetness to the glucose drink, which was confirmed in previous research (Young *et al*, 2019; Young & Watkins, 2016). Note that the two drinks were designed to be identical in terms of their visual, orosensory, and volumetric properties, differing only in their energy content. Given the complexities of the postprandial milieu, the paradigm is based on a simple dietary manipulation involving only one macronutrient (Booth, Campbell, & Chase, 1970), with which most individuals are familiar i.e., a sweet tasting drink (Irvine *et al*., 2013).

4.2.3 Expected satiety.

Upon being presented with their drink participants were asked to answer the following questions, using 100mm visual analogue scales (VAS) anchored by 'Extremely' and 'Not at all'. '*To what extent do you think the drink would fill you up?', 'Are you confident about the extent to which the drink would fill you up?'.*

4.2.4 Actual fullness

Participants were asked to describe the way they felt 'at that moment' by answering the following question, using 100mm visual analogue scales (VAS) anchored by 'Extremely' and 'Not at all'. '*How full do you feel right now?'*

4.2.5 Body Mass Index (BMI)

An objective measure of body weight was taken using an accurate electronic scale (Kern KMS-TM, Kern and Sohn GmbH, Germany) that took 50 assessments over a 5 second period and produced an average value. A stadiometer was used to measure height. The formula weight (kg) /height (m^2) was used to calculate BMI.

4.2.6 Blood glucose

Blood glucose was monitored from finger pricks using an ExacTech sensor (Medisense Britain Limited) that using an enzymic method, coupled with microelectronic measurement, which has been shown to be accurate (Matthews *et al*., 1987).

4.2.7 Participants

The sample comprised of 54 females between 18 and 32 years of age that were recruited from the local area through posters on university notice boards and online adverts on popular social media websites (e.g., Facebook). The sample size was based on our previous research using this paradigm which found medium to large effect sizes (Young *et al*., 2021). Exclusion criteria included any gastrointestinal problems, metabolic or cardiovascular disorder, pregnancy, a current diagnosis of a mood or eating disorder, and/or if they were taking medications or herbal supplements to manage body weight or control appetite. BMI ranged from 18.5 – 35.0 (average 23.1) $kg/m^{2.}$ Participants were well matched across experimental conditions (see **Table 13**).

Table 13

Descriptive statistics of the glucose vs sucralose beverage conditions

	Glucose	Sucralose	F	*p*
Age	22.8(3.3)	21.7(3.5)	1.213	0.276
BMI (kg/m^2)	23.4(3.3)	23.0(3.7)	0.167	0.684
DE	22.1(4.1)	21.5(5.6)	0.190	0.665
EE	6.6(2.3)	2.3(1.9)	0.413	0.524
RE	17.5(5.4)	16.2(4.4)	0.856	0.359

Note. N = 54. BMI - body mass index; DE – disinhibited eating; RE – restrained eating; EE – emotional eating.

4.2.8 Three factor eating questionnaire (TFEQ)

Eating style was assessed using the Three Factor Eating Questionnaire (TFEQ)-R18 (Karlsson *et al*., 2000; Stunkard & Messick, 1985). The TFEQ measures Cognitive Restraint (6 items e.g., 'I deliberately take small helpings as a means of controlling my weight.'), Disinhibited Eating (9 items e.g., 'Sometimes when I start eating, I just can't seem to stop'), and Emotional Eating (3 items e.g., 'When I feel lonely, I console myself by eating.'). Participants were asked to rate their response on a 4-item scale ranging from 1 'Definitely False' to 4 'Definitely True'. Cronbach α's was 0.75, 0.93, and 0.84 for the Restraint, Disinhibited, and Emotional Eating subscales respectively.

4.2.9 Interoceptive indices

The interoceptive indices used in the present paradigm have been detailed previously (Young *et al*., 2021). Briefly, post-prandial hunger and fullness were considered posterior expectations (i.e., those assimilated by combining prior expectations and afferent sensations).

An index of *satiety divergence* (SD) was calculated using the following transformation:

1- ((absolute (expected satiety – actual satiety))

Two scores were calculated: one using expected satiety before tasting (i.e., based solely on visual information only) and one using expected satiety after tasting (i.e., based on both visual and gustatory information). A higher score indicating a lower divergence between the participants expected and actual satiety (more precise satiety expectations).

Expected satiety confidence (ESC) i.e., participants' confidence ratings before and after tasting, provided a further indication of expectation precision. Again, this measure was considered before and after tasting the drink. The difference between the two confidence measurements indicated the degree to which expectation precision was updated based on receiving new gustatory evidence. Similarly, the difference between raw expected satiety ratings before and after the drink indicated the degree to which the participant updated their belief based on receiving new gustatory information.

Afferent sensations with high precision are more likely to be experienced subjectively (e.g., hunger) (Gonder-Frederick & Cox, 1991; Seth & Friston, 2016; Young *et al*., 2019). Therefore, we calculated an *interoceptive coherence* index - the within person correlation coefficient between blood glucose values (0, 15, 30, and 60 minutes) and hunger (0, 15, 30, and 60 minutes) - to indicate sensory sensitivity to glucose. This variable was reversed so that a higher score indicated that blood glucose tracked hunger more coherently. Individuals with a higher score would be more likely to retrospectively integrate changes in blood glucose when judging their post-prandial hunger.

Rebound hunger after the sensory incongruent drink (sucralose) provided an indication of prediction error responsivity. This measure reflects observations that when a "sensory incongruent" food is consumed, the flavour-nutrient 'mismatch' results in varying degrees of rebound hunger (Yeomans, 2015). Therefore, experimentally manipulating flavour/nutrient congruity allowed us to examine individual differences in the sensitivity to unpredictable interoceptive states (note that this measure is subtly different to our *interoceptive coherence* index in that interoceptive coherence measures sensitivity to *predictable* sensations, whereas *rebound hunger* indicates the response to 'newsworthy' information that is not predicted). Note that within the active inference framework it is possible to have precise beliefs about action outcomes (the interoceptive consequences of consuming

the drink), yet still be 'surprised' (rebound hunger). This is because prior precision is based on 'expected prediction error', whereas surprise is based on 'actual prediction error'.

4.2.10 Statistical analyses used to test the paradigm.

To determine whether those with different eating styles differed in terms of their satiety divergence (SD) / Expected satiety confidence (ESC) 2×2 repeated measures ANCOVAs were used: Taste (SD/ESC before tasting / SD/ESC after tasting) was the repeated measures factor, Drink (Glucose/Sucralose) was the between subjects' factor, and RE / EE / DE was the covariate in their respective analysis. Where significant interactions resulted, bivariate correlation analysis (Pearson's r) assessed associations between SD / ESC and eating style. These analyses determined (**1**) whether those with different eating styles differed in the precision of their prior expectations, and (**2**) whether they differed in their ability to adjust prior precision given new contextual sensory information. Univariate ANOVAs determined whether eating style was associated with interoceptive coherence (IC) / rebound hunger (90 min minus baseline) depending on the nature of the drink: Drink (Glucose/Sucralose) was the between subjects' factor, and RE / EE / DE was the covariate in their respective analysis. Bivariate correlation analysis probed significant interactions.

4.2.11 Assumptions, control of outliers and the proportion of type 1 errors

All variables met the assumption of normality except SD which was transformed using an arcsine transformation prior to analysis. When tests involved between group comparisons Levene's test was used to assess the equality of variances and Box's M was used to determine whether the covariance matrices are similar. Cooks distance, with a threshold of 4/N, was used to detect possible outliers (Cook, 1977). Unless removal of such cases altered the results, the cases were retained. The potential of detecting false positives was controlled using Benjamini and Hochberg's false discovery rate (FDR) (Yoav & Yosef, 1995). The FDR was controlled at $\delta = 0.05$. Where significant interactions did not reach this threshold, it is indicated in the text.

4.3 Results

4.3.1 Restrained eating (RE)

Data were missing for two participants who failed to complete three or more questions on the restraint scale. Therefore, the analysis proceeded with n = 26 for glucose and n = 26 for sucralose.

Expected satiety confidence.

The Drink X Taste X RE interaction was not significant (F (1,48) = 1.113, p = 0.297, η^2 = 0.023), and neither was the Drink X RE interaction (F (1,48) = 1.159, p = 0.287, η^2 = 0.024). The main effect of RE was also not significant (F (1,48) = 0.680, p = 0.414, η^2 = 0.014).

Satiety divergence.

The Drink X Taste X RE interaction approached significance (F (1,48) = 3.865, p = 0.055, η^2 = 0.075). However, the Drink X Taste interaction was significant (F(1,48) = 5.452, p = .024, η^2 = .102). Follow up tests indicate that after (r = 0.505, p < 0.008), but not before (r = 0.142, p = 0.488), tasting the sucralose drink restrained eaters had more precise expectations. Both effects were not significant in the glucose condition: before (r = -.159, p = 0.438), after (r = -0.253, p = 0.212). See **Figure 6.**

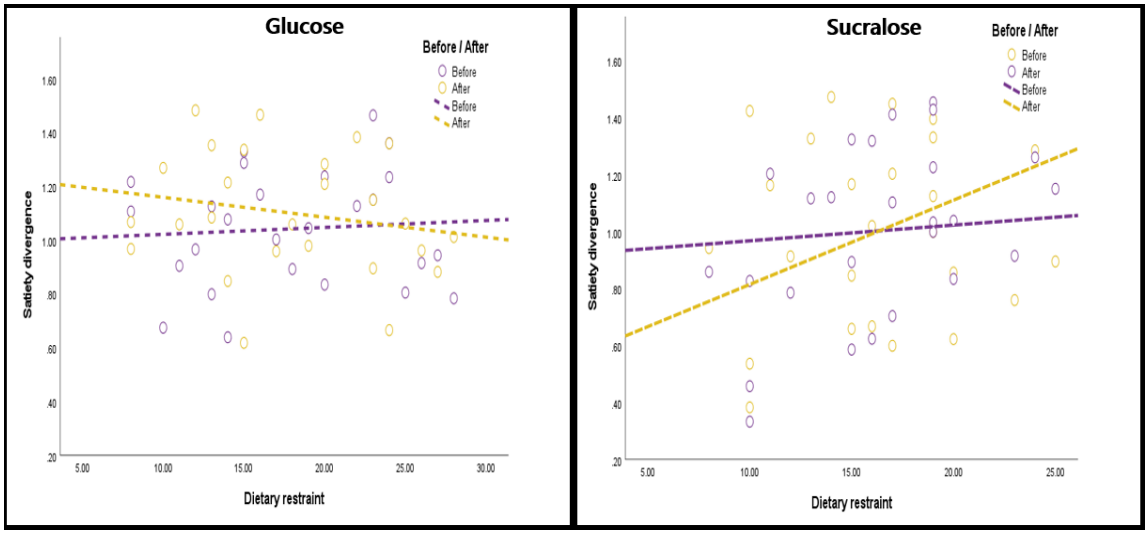


Figure 6: Association between satiety divergence before and after tasting glucose and sucralose.

Note. After ($r = 0.505$, $p < 0.008$), but not before ($r = 0.142$, $p = 0.488$), tasting the sucralose drink restrained eaters had more precise satiety expectations. There were no effects in the glucose condition: before ($r = -.159$, $p = 0.438$), after ($r = -0.253$, $p = 0.212$).

Interoceptive coherence

The Drink X RE interaction was not significant ($F(1,48) = 0.032$, $p = 0.860$, $\eta^2 = 0.001$), and neither was the main effect of RE ($F(1,48) = 0.320$, $p = 0.574$, $\eta^2 = 0.007$).

Rebound hunger.

The Drink X RE interaction was not significant ($F(1,48) = 0.063$, $p = 0.080$, $\eta^2 = 0.001$), however there was a main effect of RE ($F(1,48) = 9.808$, $p = 0.003$, $\eta^2 = 0.170$). Regardless of the nature of the drink consumed, RE experienced a decline in hunger ($r = -0.420$, $p = 0.002$).

4.3.2 Emotional eating (EE)

Again, data were missing for two participants who failed to complete two/three questions on the EE scale. Therefore, the analysis proceeded with n = 26 for glucose and n = 26 for sucralose.

Expected satiety confidence.

The Drink X Taste X EE interaction was not significant ($F(1,48) = 0.215$, $p = 0.645$, $\eta^2 = 0.004$). In addition, neither the Drink X EE interaction ($F(1,48) = 1.062$, $p = 0.308$, $\eta^2 = 0.022$), nor the main effect of EE ($F(1,48) = 1.137$, $p = 0.292$, $\eta^2 = 0.023$) were significant.

Satiety divergence.

Again, the Drink X Taste X EE interaction was not significant ($F(1,48) = 0.471$, $p = 0.496$, $\eta^2 = 0.010$). Neither did the Taste X EE interaction reach significance ($F(1,48) = 0.950$, $p = 0.335$, $\eta^2 = 0.019$).

Interoceptive coherence

There was no effect of either EE (F (1,48) = 0.742, p = 0.393, η^2 = 0.015), nor a Drink X EE interaction (F (1,48) = 0.001, p = 0.976, η^2 = 0.000).

Rebound hunger.

Again, on no occasion did EE relate to interoceptive coherence: main effect (F (1,48) = 0.097, p = 0.757, η^2 = 0.002), and EE X Drink interaction (F (1,48) = 0.243, p = 0.624, η^2 = 0.005).

4.3.3 Disinhibited eating (DE)

Data were missing for one participant who failed to complete three or more questions on the disinhibition scale. Therefore, the analysis proceeded with n = 27 for glucose and n = 26 for sucralose.

Expected satiety confidence.

Although the Drink X Taste X DE interaction was not significant (F (1,49) = 0.655, p = 0.422, η^2 = 0.013), there was a significant Taste X DE interaction (F (1,49) = 13.112, p = 0.001, η^2 = 0.211). Disinhibited eaters were less confident; both before (r = -0.665, p = 0.001), and after (r = -0.381, p = 0.005) tasting (Figure 7). However, disinhibited eaters also had a significant increase in confidence as a result of tasting the drink (r = 0.475, p = 0.001).

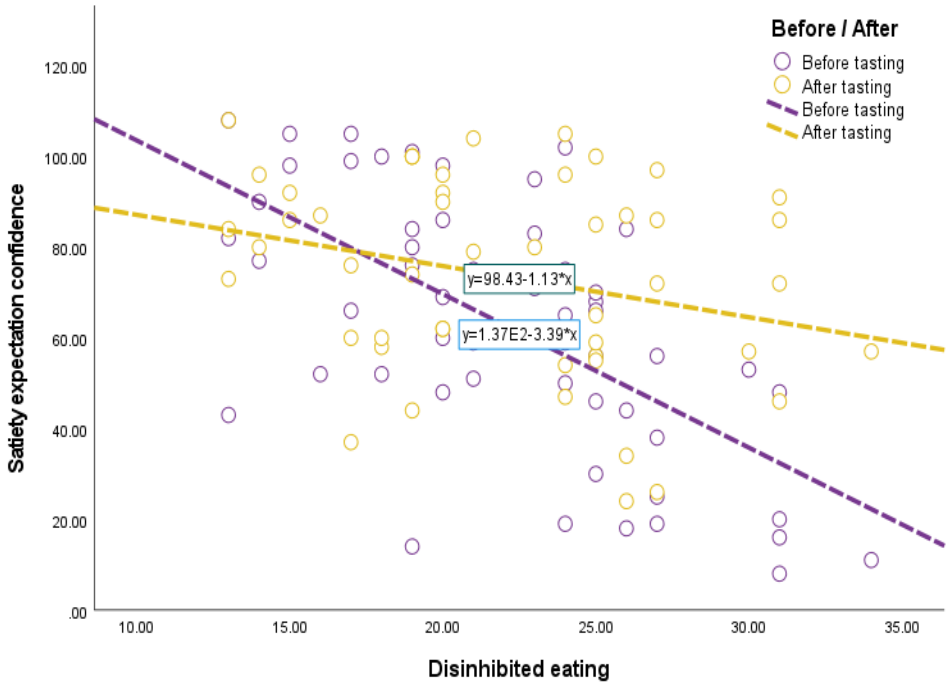


Figure 7: Association between disinhibited eating and expected satiety confidence before and after tasting a drink.

Note. Irrespective of the drink consumed disinhibited eaters were less confident both before (r = -0.665, p = 0.001), and after (r = -0.381, p = 0.005) tasting.

Satiety divergence

Drink X Taste X DE interaction was not significant (F (1,49) = 0.211, p = 0.648, η^2 = 0.004), neither was the Taste X DE interaction (F (1,49) = 1.043, p = 0.312, η^2 = 0.021).

Interoceptive coherence

The drink X DE interaction was significant (F (1,49) = 6.523, p = 0.014, η^2 = 0.117). Disinhibited eating was positively associated with interoceptive coherence in the sucralose (r = 0.464, p = 0.017), but not the glucose r = -0.232, p =0.245) condition.

Rebound hunger.

Again, the drink X DE interaction was significant (F (1,49) = 4.251, p = 0.045, η^2 = 0.080). Disinhibited eaters had an increase in hunger in the sucralose (r = 0.560, p = 0.003), but not the glucose (r = 0.033, p =0.872) condition.

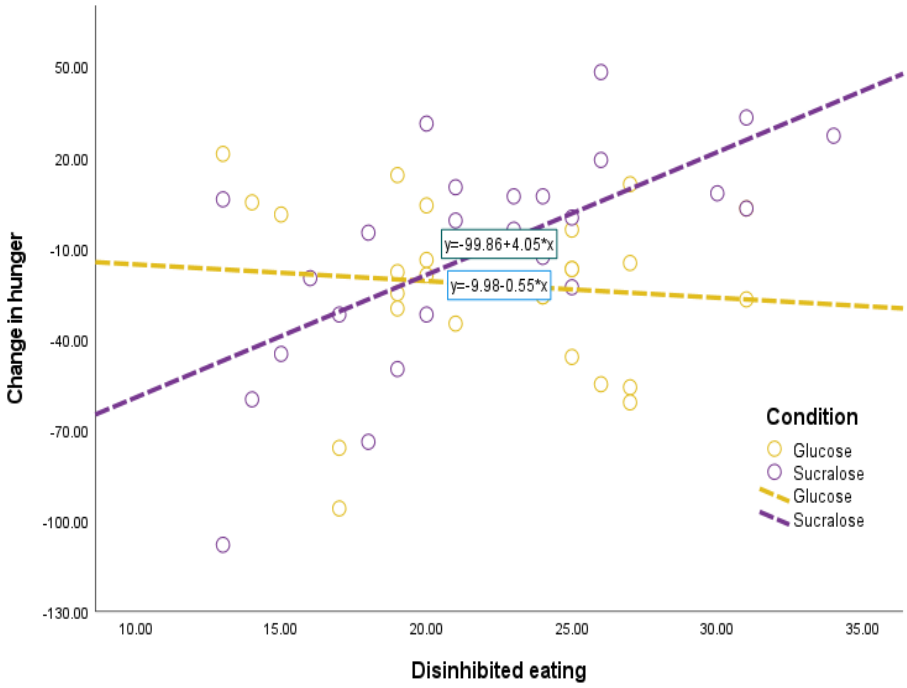


Figure 3: Association between disinhibited eating and rebound hunger in the glucose and sucralose condition.

Note. Disinhibited eaters had an increase in hunger in the sucralose ($r = 0.560$, $p = 0.003$), but not the glucose ($r = 0.033$, $p = 0.872$) condition.

4.3.4 Exploratory analysis

From the perspective of active inference there are different kinds of uncertainty. Expected uncertainty refers to one's belief about the predictability of action outcomes. In other words, if the sensory outcome of one's action are believed to be predictable then expected uncertainty is low. Conversely, if the sensory outcome of one's action is believed to be unpredictable the expected uncertainty is high. We liken expected certainty to expected satiety confidence in that participants are confident that they can predict the satiety consequences of drinking the drink. Unexpected uncertainty or 'surprise' occurs when an outcome falls outside the range of expected outcomes. It follows that to accurately estimate unexpected uncertainty, the participant should consider what is already known about the variability in

outcomes or expected uncertainty (**Figure 9**). In this sense expected satiety confidence would modulate the 'gain' or precision of incoming postprandial sensations. That is, those with the lowest confidence would be least sensitive to 'surprising' interoceptive states. As such it is interesting that disinhibited eaters were characterised by both lower confidence and a high sensitivity to interoceptive prediction error. Therefore, in this exploratory analysis we considered whether there may be more than one mechanism driving disinhibited eating. That is, whether confidence moderated the association between sensory sensitivity and disinhibited eating when sensations are unpredictable (sucralose) or predictable (glucose).

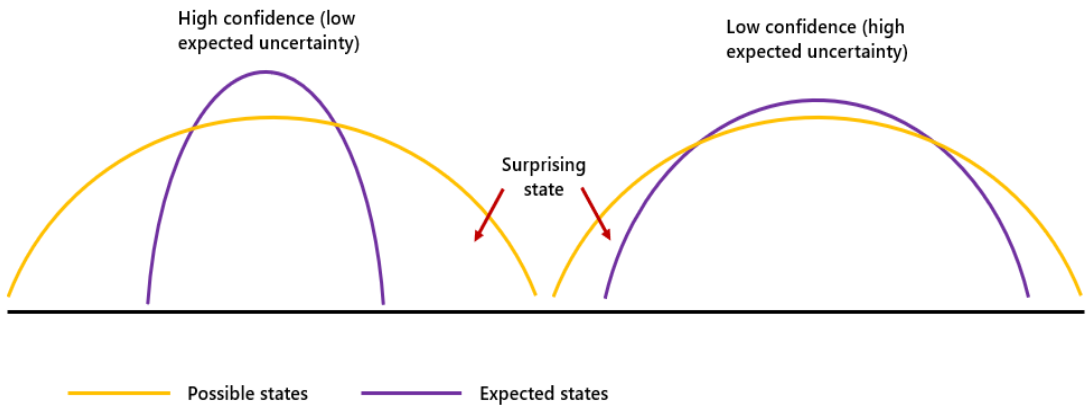


Figure 9: Schematic illustration of the interaction between expected uncertainty and unexpected uncertainty.

Note. In active inference it is possible to have very precise expectations about the sensory outcome of action and still be surprised. This is because the precision of beliefs about action outcomes is governed by one's anticipated prediction error in the future, whereas 'surprise' is determined by 'state' prediction error i.e., when model beliefs (about one's current state) are updated with an unexpected new observation. Illustrate is a scenario where individuals with a high expected uncertainty (low confidence) are less likely to be 'surprised' by unexpected sensations. Conversely, those with low expected uncertainty (high confidence) are more likely to be 'surprised'.

To determine whether expected satiety confidence moderated the association between interoceptive coherence and disinhibited eating a moderated regression analysis was carried out using Hayes PROCESS model 1 (Hayes, 2013). Interoceptive coherence was entered as the independent variable (X), disinhibited eating was the dependent variable (Y), and expected satiety confidence (after tasting as this is the most proximal belief) was entered as a continuous moderator (W).

Glucose condition

There was a significant negative association between interoceptive coherence and disinhibited eating (B = -1.823, 95% CI LL -3.190, UL 0.297), and a significant negative association between confidence and disinhibited eating (B = -0.135, 95% CI LL -0.164, UL 0.-0.106). However, the interaction was not significant (B = 0.021, 95% CI LL -0.032, UL 0.075).

Sucralose condition

Disinhibited eating was positively associated with interoceptive coherence (B = 2.721, 95% CI LL 0.487, UL 4.954), and negatively associated with confidence (B = -0.082, 95% CI LL -0.137, UL -0.027). In addition, the interoceptive coherence X confidence interaction (B = 0.073, 95% CI LL 0.036, UL 0.143) was significant (**Figure 10**). In those high in confidence there was a positive association between interoceptive coherence and disinhibited eating (t(26) = 2.371, p =0.014). This effect was diminished in those low in confidence (t(26) = -0.033, p = 0.986).

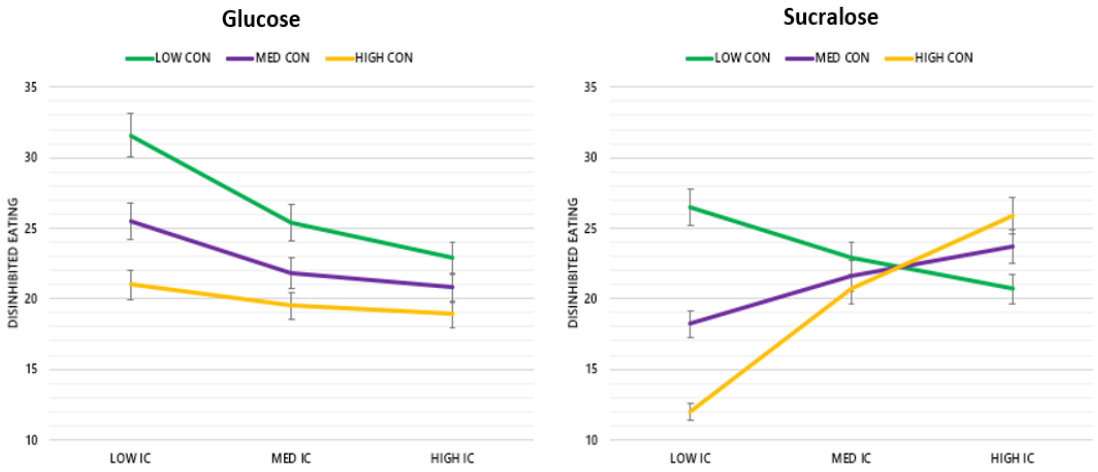


Figure 10: The interaction between expected satiety confidence and interoceptive coherence in the glucose and sucralose conditions.

Note. Data are mean (SE). In the glucose condition, confidence (CON) after tasting was negatively associated with disinhibited eating (B = -0.135, 95% CI LL -0.164, UL 0.-0.106), as was interoceptive coherence (IC) (B = -1.823, 95% CI LL -3.190, UL 0.297). In the sucralose condition confidence (CON) after tasting interacted with interoceptive coherence (IC) to influence disinhibited eating (B = 0.073, 95% CI LL 0.036, UL 0.143). When confidence was high there was a positive association between interoceptive coherence and disinhibited eating (t(26) = 2.371, p=0.014). This effect was diminished in those low in confidence (t(26) = -0.033, p = 0.986).

4.4 Discussion

For the first time, this study aimed to understand individual differences in inferential and cue integration processes underlying subjective satiety in common eating styles that have been associated with risk of developing obesity. To this end we utilised a recently developed paradigm developed from a predictive processing perspective that was able to discern individual differences in the degree to which postprandial satiety is driven by prior expectations rather than incoming sensations (Young *et al*., 2021). We observed that when postprandial sensations were unpredictable (sucralose condition), those high in RE scores developed an 'illusionary' sense of satiety and were more likely to be driven by prior expectations based on visual and orosensory cues when rating their postprandial satiety (Figure 6). Conversely, after sucralose, those scoring high on the DE scale experienced greater levels of 'rebound hunger', which may indicate that they may be more sensitive to surprising interoceptive states (Figure 8). Irrespective of the nature of the drink, those reporting a higher DE score were less confident in using visual cues to predict their subsequent satiety (Figure 7). Notably, those scoring high on the EE scale did not differ in these processes underlying satiety. These findings indicate that DE and RE styles may be understood from a predictive processing perspective which in the future can be used to develop individualised interventions to influence satiety.

A key observation in the present study was that those scoring high on the RE scale were more reliant on their satiety expectations after tasting the sucralose drink leading to an 'illusionary' sense of satiety (Figure 6). Although our population did not have clinically relevant eating concerns, previous research using clinical samples found that those with restrictive eating disorders are characterised by overly precise and inflexible prior beliefs. For example, Khalsa *et al*, (2015) administered either saline or isoproterenol (a peripherally acting beta-adrenergic agonist) to those with anorexia nervosa (AN), before presenting them with a calorically dense meal. Compared to the control group, those with AN reported significantly heightened sensations of palpitations and dyspnea during the saline infusion - despite no observed changes in body state (Khalsa *et al*, 2015). This change in felt interoceptive state, without

concomitant changes in physiology, was interpreted as a cardiorespiratory visceral illusion (Khalsa *et al*, 2015). Similarly, during food image exposure, those with remitted AN had heightened insula activity (an area of the brain thought to be involved with the prediction of internal states) (Oberndorfer *et al*., 2013). The present data may suggest that those with high RE may generate strong expectations about postprandial sensations, and, when internal signals are uncertain, create an 'illusion' of satiety. If future work can replicate these observations, then those with a higher RE score, may be more likely to benefit, in terms of weight loss efforts, from 'sensory enhanced', or 'diet' food products which have been designed to induce expectations of satiety while delivering a low caloric load (McCrickerd, Chambers, Brunstrom, & Yeomans, 2012). These will be important avenues for future research.

In contrast, those scoring high in DE had lower satiety expectation confidence (Figure 7). These observations in part support previous reports of an association between self-control and the ability to predict future interoceptive states. For example, in a study by Walter *et al*. (2020) individuals who expected more dyspnea during an inspiratory breathing-load task were more effective in the down-regulation of food craving using negative future-thinking strategies. In addition, levels of anterior insula activation during the anticipation dyspnea were associated with having more self-control in the craving task (Walter *et al*., 2020).

From the perspective of active inference, the ability to accurately anticipate future bodily needs is linked with guiding adaptive decision making. To achieve this, the brain uses an internal (generative) model to continuously infer and control internal states (Barrett, 2017; Barrett & Simmons, 2015). This model is iteratively updated using sensory feedback from the body (Young *et al*, 2021). If there is a 'mismatch' between the anticipated future state and bottom-up interoceptive feedback, this gives rise to a prediction error which must be minimised (Friston *et al*., 2017; Seth & Friston, 2016; Young *et al*., 2019). One way to achieve this is through instigating 'actions' which bring incoming sensations more in line with top-down expectations i.e., goal-directed behaviour (Seth & Friston, 2016; Tschantz *et al*., 2022; Young *et al*., 2019). Therefore, from an active inference perspective, self-regulated behaviour (including eating behaviour) may reflect being driven by an imperative to minimise prediction errors (through active inference) and achieve congruency between the internal model

and afferent signals (Tschantz *et al*., 2022). It is important to note that in active inference, internal models entail 'policies' that generate expected sensations, which are associated with various degrees of "expected certainty or precision". In this regard, the present observation that those high in DE had lower expected satiety confidence may indicate that they might be characterised by high "expected uncertainty". That is, an *a priori* belief that the interoceptive consequences of one's own action are unpredictable. This could have ramifications for prospective food related decision making, for example, the selection of appropriately satisfying portion sizes, and this should be explored in the future. Whether a lower confidence reported by this population accurately reflects the volatility of their physiological states remains an important question. For example, future research could quantify the within person variability in glucose tolerance to a standardised drink / meal presented on multiple occasions and determine the association with expected satiety confidence in those scoring high in DE. It is possible that dietary interventions designed to reduce interoceptive volatility e.g., low glycaemic load diets, that avoid extreme glucose excursions, may overtime improve expected precision in persons scoring high in DE (Young & Watkins, 2016b), which again could be considered in the future.

Interestingly, the present study also provided evidence consistent with the view that those with high DE ratings are more sensitive to "surprising" internal states. When sucralose was consumed i.e., a sweet taste with no energy, those rating higher DE experienced higher 'rebound hunger' (Figure 9) and had a stronger correlation between changes in blood glucose and changes in hunger. This may indicate that during interoceptive ambiguity, those rating higher in DE may weigh incoming afferent sensations more heavily than prior beliefs when judging their postprandial state. Speculatively, such hypersensitivity to unexpected bodily signals (e.g., hunger) may increase the incentive value of environmental food cues that restore homeostasis; an effect that may explain an increased propensity towards DE (Zaborszky *et al*., 2008b). If future work can replicate and confirm such observations, then for those scoring high in DE, may benefit from avoiding artificially sweetened and 'diet' foods which may create a 'mismatch' between expected and energy content. In the future, longitudinal studies, might use the present findings to develop specific sensory congruent dietary patterns and examine whether that eating style can help in the management of disinhibited eating.

Importantly, a higher DE score did not equate to greater sensitivity to all interoceptive signals. Indeed, there was no association between interoceptive coherence and DE when the sweet taste was followed by a predictable increase in blood glucose i.e., in the glucose condition. One possible explanation for this discrepancy is that sensitivity to expected, and unexpected feedback might depend on different neuromodulators i.e., acetylcholine and norepinephrine respectively (Angela & Dayan, 2005; Zaborszky *et al*., 2008a). Therefore, further exploration of the relative roles of these neurotransmitters in different satiety processes and eating styles, might be profitable.

Indeed, in our exploratory analysis we observed that expected satiety confidence moderated the association between interoceptive coherence and DE but only in the sucralose condition. Figure 10 illustrates the effect - when sensations were predictable (glucose condition), there was a negative association between sensitivity to glucose changes and disinhibited eating, but only in those low in confidence. Conversely when sensations are ambiguous (sucralose condition), there was a positive association between sensory sensitivity and disinhibited eating, but only in those with the highest confidence. Whilst this analysis was exploratory and thus requires careful interpretation, further work exploring how beliefs about the predictability of afferent sensations influence the response to both predictable and unpredictable sensations is warranted. It is possible that such interactions between top-down and bottom-up signalling explain the propensity for DE. Future research combining behavioural interventions and psychophysiological methods (Young *et al*, Harrison *et al*., 2021; 2017) or computational modelling may be able to confirm or refute these ideas (Lawson, Bisby, Nord, Burgess, & Rees, 2021).

4.4.1 Limitations

Limitations of the study should be considered. Firstly, we restricted our sample to young healthy females to reduce variability. However, inevitably this reduces generalisability. Therefore, these effects should be replicated in different populations including males and older adults who may differ in their interoception (Brennan *et al*., 2022; Prentice & Murphy, 2022). Secondly, it is probable that those scoring higher in RE and DE, vary in their habitual diet – this should be considered in the future. Finally,

the validity of the present paradigm needs to be considered. As noted previously (Young *et al*, 2021), satiety is a multifaceted process involving more than just blood glucose. Therefore, it is possible that other interoceptive signals e.g., ghrelin, CCK, GLP-1, and PYY concentrations might also need to be measured, to gain a more accurate understanding of active inference in the context of satiety. In addition, to experimentally manipulate interoceptive volatility the presentation of multiple foods varying in sensory congruity on repeated occasions will be required. This is, in theory, a plausible extension to the present paradigm which could be combined with computational modelling, to gain insight into individual differences in learning rate. In recent years, several psychophysically robust paradigms have been developed (e.g., Harrison *et al*., 2021; Ryan Smith *et al*., 2020; Smith *et al*., 2021). However, in general these either do not assess interoception in a domain relevant to eating behaviour (Harrison *et al*., 2021; Ryan Smith *et al*., 2020), or lack ecological validity and a clearly defined sensory mechanism (Smith *et al*., 2021). Other available tasks / paradigms fail to differentiate between prospective expectation driven processes and those driven by afferent sensations (e.g., Green, Delargy, Joanes, & Blundell, 1997; Schandry, 1981; Van Dyck *et al*., 2016). Here, and in previous publications (Young *et al*, 2021), we have demonstrated that the present approach is able to capture information pertaining to individual differences in satiety processes, from an active inference perspective. In addition, we have taken an ecologically valid approach which may have implications for dietary interventions. In the future, determining how these satiety process vary with age will likely prove profitable.

4.4.2 Conclusion

The present results indicated that eating styles associated with an increased risk of obesity – i.e., RE and DE – may be understood from a predictive processing perspective. Individuals scoring high in DE lacked confidence in their expected satiety. In addition, those with higher DE scores, responded more strongly to an unpredictable, but not a predictable, interoceptive sensation. Conversely, those with a higher RE score had more precise satiety expectations after tasting the sucralose drink leading to an 'illusionary' sense of satiety. These findings could be used in future where dietary interventions is the focus of the work. That is, those reporting a higher RE score might be more likely to benefit from sensory enhanced foods designed to enhance satiety. On the other hand, individuals who score high in DE, who may be

hyper-sensitive to sensory incongruity, might be advised to avoid artificially sweetened products and instead potentially benefit from consuming a diet that reduces interoceptive volatility and uncertainty - an important avenue for future research.

Chapter 5: Study 3

The role of interoception in age and eating behaviour: a structural equation modelling study.

5.1 Introduction

The previous chapters found that eating behaviours associated with an increased risk of obesity, may also be linked with atypical processing of interoceptive information. Yet, recent conceptualisations of interoception define it as a multidimensional concept (Khlasa *et al*., 2018; Garfinkel *et al*., 2015; Murphy *et al*., 2020b). An important aspect of interoception, not yet explored in this thesis is *interoceptive sensibility* (Murphy *et al*., 2020b). This component of interoception represents an individual's self-reported beliefs concerning their perception of bodily signals (Garfinkel *et al*., 2015; Khalsa *et al*, 2018). Whilst this umbrella term was originally developed to describe "the self-perceived tendency to focus on interoceptive stimuli" (Garfinkel *et al*., 2015), it now covers many other features of interoception (e.g., confusion about internal sensations, tendency to focus on internal sensations, trust afforded to internal signals, awareness of positive or negative symptoms, emotional awareness). Furthermore, interoceptive sensibility has been assessed across a variety of domains (domain general e.g., Murphy *et al*. (2020b)) or in just one domain (domain specific e.g., Hunot *et al*. (2016)). This has contributed to conceptual confusion, and a lack of clarity around which aspects of interoceptive sensibility are most important, when it comes to eating behaviour and risk of developing obesity. Although some research has found that domain general interoceptive sensibility was associated with disordered eating (Jenkinson *et al*., 2018), other evidence indicated that appetite specific interoception i.e., hunger/satiety, may be more relevant (Poovey, Ahlich, Attaway, & Rancourt, 2022) - at least in undergraduate samples.

Interestingly, Robinson *et al*. (2021) adopted a recent model proposed by Murphy *et al* (2020). This model was designed to overcome some of the methodological issues in interoceptive research. Of relevance to the present study, Murphy *et al* (2020) identified the importance of clearly describing 'what' interoceptive dimension is being

measured (interoceptive attention or accuracy) (Murphy *et al*., 2020a). Robinson *et al* (2021) explored the association between the two factors of interoceptive sensibility (attention and accuracy) and appetitive traits, in 1657 adults (Robinson, Marty, Higgs, & Jones, 2021). Interoceptive accuracy (i.e., domain general interoception, see **Table 14**) was not associated with trait hunger or satiety responsiveness (i.e., appetite specific interoception, see **Table 14)** but was negatively correlated with emotional overeating. Meanwhile, subjective interoceptive attention (i.e., domain general) was positively associated with trait hunger and satiety responsiveness, as well as a greater propensity to emotionally overeat (Robinson *et al*, 2021). Given the mean (SD) age of the sample in Robinson's study was 37.2 (12.6), it remains unclear whether the association between general- and appetite- specific interoception generalises across younger and older adults.

As discussed in the systematic review (Chapter 2), to date, most studies on interoception and aging have assessed performance accuracy on a domain specific behavioural task (e.g., heartbeat detection). In general, performance on these interoception tasks declines with age (Khalsa *et al*, 2009; Murphy *et al*., 2018a). In addition, in Chapter 3 we reported that older adults had weaker connectivity in the frontoparietal (FPN) and default mode (DMN) networks of the brain that are thought to play key roles in interoception (Kleckner *et al*, 2017). However, little is currently known about how different aspects of interoceptive sensibility changes with age. In addition, it is not known whether any age-related changes in interoceptive sensibility influence eating traits that are associated with an increased risk of obesity in this population.

A hurdle to enhancing understanding in this area, is a lack of a clear conceptual framework, and a limited appreciation of the possible inter-relationships between key concepts (e.g., appetite specific versus general interoception). There is a need to disentangle the components of interoceptive sensibility and clarify how they relate to age, eating styles and body weight (see **Table 14** for definitions of key concepts used in the present study). Therefore, the aim of the present research was to investigate whether the link between age and BMI is influenced by deficits in interoceptive sensibility (attention and accuracy), appetite specific interoception (trait hunger, satiety responsiveness), and eating traits. We hypothesised that (**1**) general interoception (accuracy and attention) would be differentially associated with the

appetitive interoceptive traits of hunger drive and satiety responsiveness; (**2**) age would be associated with poorer interoceptive abilities (**3**) eating traits linked with an increased risk of obesity (emotional overeating, food responsiveness) will be positively associated with hunger drive and negatively associated with satiety responsiveness, and (**4**) specific pathways incorporating the intervening variables: interoceptive sensibility, appetitive specific interoception, and eating traits associated with risk of developing obesity would influence the relationship between age and BMI.

Table 14

Definition of the terms, and the associated explanations of how those concepts are categorised in the present study.

CATEGORY	MEASURE	DEFINITION	QUESTIONNAIRE USED IN PRESENT STUDY	THE EFFECT OF AGE [RELATED MEASURES]
DOMAIN GENERAL INTEROCEPTION	Self-reported interoceptive accuracy	Beliefs or perception of one's own ability to perceive accurately interoceptive signals.	Interoceptive Accuracy Scale (IACC) (Murphy *et al*., 2020b)	↓ IACC scale (Murphy *et al*., 2020)
	Self-reported interoceptive attention	The degree to which interoceptive signals are the object of attention	Interoceptive Attention Scale (IATT) (Gabriele *et al*., 2022)	To the best of our knowledge, the IATT scale has not been used within the context of age to date. **Similar constructs** → Attention regulation (MAIA subscale) (Jennifer Elliott & Gaby Pfeifer, 2022) → Noticing (MAIA subscale) (Nusser, Pollatos, & Zimprich, 2020) ↓ Bodily awareness (BPQ short version) (Murphy *et al*., 2018b). *Link to interoceptive attention: the below measures assess adaptive

				vs maladaptive attentional styles towards bodily experiences ***** Of note: These measures may assess similar constructs however the specific constructs may <u>not</u> be synonymous with the current studies measures.***
DOMAIN SPECIFIC INTEROCEPTION	Hunger drive	The propensity to noticing how frequent one experiences physical hunger sensations (e.g., stomach rumbles)	Adult Eating Behaviour Questionnaire (AEBQ) (Hunot *et al*., 2016)	↓ Trait Hunger (AEBQ) (Cohen, Kakinami, Plourde, Hunot-Alexander, & Beeken, 2021) **Similar constructs**** ↓ reliance on hunger cues (IES-2-HS) (Ahlich & Rancourt, 2022) ↓ Trait hunger (TFEQ) (Gilmour Flint *et al*., 2008b) ↓ Trait hunger (TFEQ) (Antje Löffler *et al*., 2015) ↓ state hunger (VAS) (J. C. Moriguti *et al*., 2000)
	Satiety responsiveness	The propensity to notice and respond to within-meal feelings of fullness (i.e. I often get full before my meal is finished)	Adult Eating Behaviour Questionnaire (AEBQ) (Hunot *et al*., 2016)	→ Trait Satiety Responsiveness (AEBQ) (Cohen *et al*., 2021) **Similar constructs****

				↓ reliance on hunger cues (IES-2-HS) (Ahlich & Rancourt, 2022) ↑ state satiety (VAS) (Kerstin Sturm *et al*., 2004) (9)] → state hunger (VAS) (J. C. Moriguti *et al*., 2000)
APPETITIVE TRAITS	Food responsivity	characterised by a preoccupation with food or a desire to eat often evoked by food related cues (e.g. smelling food makes me want to eat)	Adult Eating Behaviour Questionnaire (AEBQ) (Hunot *et al*., 2016)	↓ Trait Food responsivity (AEBQ) (Cohen *et al*., 2021) **Similar constructs**** ↓ disinhibited eating (Brennan *et al*., 2022) ↓ disinhibited eating (TFEQ) (Antje Löffler *et al*., 2015)
	Emotional Overeating	characterised by eating large amounts of food as a response to, and a form of coping with negative emotions	Adult Eating Behaviour Questionnaire (AEBQ) (Hunot *et al*., 2016)	↓ Trait Emotional Overeating (AEBQ) (Cohen *et al*., 2021) **Similar constructs**** ↓ Emotional eating (DEBQ) (Samuel & Cohen, 2018)
	Emotional Undereating	characterised by purposefully eating less in response to negative emotions	Adult Eating Behaviour Questionnaire (AEBQ) (Hunot *et al*., 2016)	↓ Trait Emotional Undereating (AEBQ) (Cohen *et al*., 2021)

				Similar constructs** ↑ cognitive restraint over eating (TFEQ) (Antje Löffler *et al*., 2015)
	Enjoyment of food	characterised by an appreciation of the pleasures associated with eating	Adult Eating Behaviour Questionnaire (AEBQ) (Hunot *et al*., 2016)	↓ Trait Enjoyment of Food (AEBQ) (Cohen *et al*., 2021) **Similar constructs**** ↓ Taste acuity Hedonic liking (7 point rating scale) e.g. (Kennedy, Law, Methven, Mottram, & Gosney, 2010)
KEY: ↑ = SCORES INCREASE WITH AGE; ⟶ = NO EFFECT OF AGE; ↓ = SCORES DECREASE WITH AGE.				

Abbreviations: BPQ = Body Perception Questionnaire; DEBQ = Dutch Eating Behaviour Questionnaire; IES2-HS = Intuitive Eating Scale – reliance on hunger and satiety cues subscale; MAIA = Multidimensional Assessment of Interceptive Awareness; TFEQ = Three Factor Eating Questionnaire; VAS = Visual Analogue Scale

5.2 Method

5.2.1 Participants

A total of 1006 participants participated in the present online survey. Given that research has previously shown sex differences exist across the various dimensions of interoception (Grabauskaitė, Baranauskas, & Griškova-Bulanova, 2017) and appetite traits (Cornier, Salzberg, Endly, Bessesen, & Tregellas, 2010), the present research controlled for biological sex as a confounding variable by only recruiting females. English speaking adults were recruited from the undergraduate student body at Swansea University, older participants were recruited via email, social media, the community, and the online platform Prolific (www.prolific.co). The sample size was based on previous research that has considered associations between obesity, eating behaviour and interoceptive deficits (Robinson *et al*., 2021). G power 3.1.3 estimated a minimum sample size of 772 participants for sufficient power (85%, $p < 0.05$). The sample comprised solely of female participants given that previous research has documented sex differences in eating behaviour e.g. emotional eating (Anversa *et al*., 2021). Self-reported demographic data was collected, which included age, height, and weight. Body Mass Index (BMI) was calculated as [weight (lb) / height (in)^2]. Participants with an implausible BMI (i.e., > 44) were excluded (23 cases removed in total). There were 545 younger adults (aged 18-35 years) and 392 older adults (aged 56-80 years) (see **Table 15**).

5.2.2 Measures and procedure

5.2.2.1 Interoceptive accuracy / attention scale

To assess the two factors of interoceptive sensibility (attention and accuracy - outlined by Murphey *et al*. 2018; 2020), two self-report measures were used. The Interoceptive Accuracy Scale (IACC) (Murphy *et al*., 2020b) and the Interoceptive Attention Scale (IATT) (Gabriele *et al*., 2022) were used. The IACC measures perceived accuracy for detecting specific physical signals and represents one's belief in the accuracy of one's interoceptive percept. Individuals are asked to report their self-perceived interoceptive accuracy across 21 items (e.g., 'I can always accurately perceive when my blood sugar

is low'). Each item is accompanied by a five-point scale ranging from *strongly agree* (5) to *strongly disagree* (1). Total scores range from 21 to 105, whereby greater self-perceived interoceptive accuracy is reflected in a higher score. A Cronbach's alpha ($\alpha = 0.874$) indicated that the IACC has good internal consistency in the present sample.

The IATT also comprises the same 21 items as the IACC and similarly asks participants to report on a five-point scale ranging from *strongly agree* (5) to *strongly disagree* (1). However, the IATT requires participants to self-report how much time they spend attending to the 21 interoceptive signals. This scale seeks to quantify how much attention is focused on various signals, regardless of whether they are present. For example, 'Most of the time when I am eating, my attention is focused on different tastes'. Cronbach's alpha ($\alpha = 0.927$) indicates that the IATT has good internal consistency in the present sample.

5.2.3 Adult eating behaviour questionnaire (AEBQ).

The Adult Eating Behaviour Questionnaire (AEBQ) (Hunot *et al*., 2016) is a 35-item measure of appetitive traits. Each item requires a self-reported rating along a 5-point Likert scale (1 = "strongly disagree" to 5 = "strongly agree"). Moreover, the AEBQ is made up of eight characteristic appetite traits which are divided into two categories - food approach and food avoidance.

The four *food approach* traits include: Emotional Overeating (five items, e.g. "I eat more when I'm upset"); Enjoyment of Food (three items, e.g. "I look forward to mealtimes"); Food Responsiveness (four items, e.g. "When I see or smell food that I like, it makes me want to eat"); Hunger (five items, e.g. "If my meals are delayed, I get lightheaded"). The four *food avoidance* traits include: Emotional Under-Eating (five items, e.g. "I eat less when I'm angry"); Food Fussiness (five items, e.g. "I am interested in tasting new food I haven't tasted before"); Satiety Responsiveness (four items, e.g. "I often leave food on my plate at the end of a meal"); and Slowness in Eating (four items, e.g. "I am often last at finishing a meal").

The current study focuses on the appetite traits associated with obesity and where plausible age differences may be associated. As informed by the evidence outlined in the introduction. Cronbach's alpha for each subscale are as follows: Enjoyment of Food (α = .879), Emotional Overeating (α = .904), Emotional Undereating (α = .904), Hunger (α = .722), Satiety Responsiveness (α = .766), and Food Responsiveness (α = .742). Cronbach's alpha (α = .647) indicates that the AEBQ has acceptable internal consistency in the present sample given the large sample size and comparison between age groups where eating traits are likely to differ considerably.

5.2.5 Procedure

Firstly, participants provided their written informed consent, detailing their rights as research participants. Participants accessed a link to the secure online survey platform (Qualtrics) and then asked to respond to a series of demographic questions (height, weight, age etc.). Subsequently, participants continued to complete the questionnaires online. Questionnaires were presented to the participants in a set order, attentional checks were distributed throughout each questionnaire (e.g., *Attention Check: Please select "A Moderate amount"*). The procedure took approximately 25 minutes to complete. Ethical approval was gained from the Swansea Psychology Department Ethics Committee and the study was carried out in accordance with the Declaration of Helsinki—Ethical Principles for Medical Research Involving Human Subjects.

5.2.6 Data preparation and analytic strategy.

Of the 1006 participants, only 983 had provided complete and plausible data for the variables of interest in the present study. A multivariate ANOVA was used to detect age group differences (**Table 15**).

To examine whether the age-related differences in BMI may be explained by deficits in general and specific interoception and eating behaviour, a serial mediation regression was conducted using structural equation in IBM® SPSS® AMOS™ 28.0.0.

A bootstrap sample specified at 5000, and a 95% CI was applied. To overcome problems of multicollinearity, variables were mean centred. Additionally, robust standard errors were used to overcome any issues of homoscedasticity. BMI was defined as the outcome variable (Y) and age was defined as a group predictor variable (X). Mediator variables were specified and organised in accordance with previous research, here general interoceptive sensibility (attention and accuracy) was specified as (M_1), specific interoception i.e., trait hunger and trait satiety responsiveness were specified as (M_2), and lastly, eating behaviours i.e., subscales of the AEBQ (e.g., emotional overeating) were specified as (M_3) in the association between age and BMI. A False Discovery Rate (FDR) procedure was used to correct the *p*-values of the univariate tests. Significance was set at an $\alpha = 0.05$ with FDR correction (Yoav & Yosef, 1995). Potential outliers were determined using the Cooks distance diagnostics. To avoid removal of natural variability, we specified a conservative Cook's distance threshold of 0.0042 (Bollen & Jackman, 1985).

5.3. Results

5.3.1 Demographic / group comparisons.

Upon inspection of the data, 23 cases were identified with an implausible BMI (e.g., BMI < 16), these cases were excluded from further analysis. Next, cases exceeding the Cooks' distance threshold of 0.0042 were identified (46 cases in total) and removed from the analysis (N = 937). Descriptive statistics of the sample were calculated using IBM SPSS statistics version 28.0. Compared to older adults, younger adults reported significantly lower interoceptive accuracy (IACC) ($F (1, 935) = 6.90$, $p = .009$, $\eta = .007$) but higher interoceptive attention (IATT) ($F (1, 935) = 60.55$, $p < .001$, $\eta = .061$). Younger adults were more likely to score higher on food approach traits i.e., emotional overeating (EOE) ($F (1, 935) = 31.03$, $p < .001$, $\eta = .032$), enjoyment of food (EOF) ($F (1, 935) = 22.94$, $p < .001$, $\eta = .024$), and responsivity to food cues (FR) ($F (1, 935) = 132.66$, $p < .001$, $\eta = .124$). However, older adults self-reported significantly greater fussiness for food (FF) ($F (1, 935) = 3.89$, $p = .049$, $\eta = .004$), but lower emotional

undereating (EUE) (F (1, 935) = 4.92, p = .027, η = .005) (See **Table 15**). The results indicated no age differences for the trait slowness in eating (SE) (p = .530)

As expected, older adults reported significantly lower trait hunger (H) (F (1, 935) = 76.15, p < .001, η = .075), yet surprisingly, no age differences were observed for trait satiety responsiveness (SR) (F (1, 935) = .178, p = .673, η = .000). Nor did we find any age differences for the trait slowness in eating (SE) (p = .530)

For a detailed overview of sample characteristics - see **Table 15** below.

Table 15

Demographic data of younger and older adult groups (mean and standard deviations [SD])

Participant Characteristics	Younger Adult Group	Older Adult Group	F ratio	*p*-value
Age Group	n = 545	n = 392		
Mean Age (S.D.)	28.19 (4.12)	64.98 (5.16)	-	-
Age Range (years)	18 – 35	56 – 80	-	-
BMI (kg / m^2)	25.86 (4.75)	26.80 (4.58)	9.19	.002*
Healthy 18 – 25	259 (47.52%)	154 (39.29%)	-	-
Overweight 26-30	177 (32.48%)	136 (34.69%)	-	-
Obese 31 – 35	74 (13.58%)	78 (19.9%)	-	-
Severely Obese > 35	35 (6.42%)	24 (6.12%)	-	-
Interoceptive Accuracy	81.80 (9.45)	83.46 (9.66)	6.90	.009*
Interoceptive Attention	49.22 (13.52)	42.20 (13.78)	60.55	< .001**
Hunger	16.12 (3.66)	13.91 (4.06)	76.15	< .001**
Enjoyment of Food	13.21 (2.44)	12.48 (2.09)	22.94	< .001**
Emotional OverEating	15.03 (5.58)	13.00 (5.51)	31.03	< .001**
Emotional UnderEating	14.82 (5.27)	14.05 (5.18)	4.92	.027*
Food Responsiveness	14.10 (3.15)	11.74 (2.99)	132.66	< .001**
Satiety Responsiveness	10.33 (3.34)	10.24 (3.41)	0.178	.673
Food Fussiness	10.23 (4.90)	10.86 (4.64)	3.89	.049*
Slowness in Eating	10.56 (4.00)	10.73 (3.99)	0.40	.530

Note *$p < .05$ ** $p < .001$

Mean and standard deviations for indiividual items of the AEBQ in both samples can be found in Table 23 Appendix D8.

5.3.2 Structural equation model (SEM).

Zero order correlations between all variables are available as supplementary information (See appendix D7). As expected, the total effect of the model showed a significant positive relationship between age and BMI (β = .135, p = .004, LLCI .081, ULCI .186). Full details of the direct and indirect effects that emerged from the SEM can be found in **Table 17** and **Figures 11** and **12**. Key findings are highlighted below.

5.3.2.1 Associations between general and specific interoception.

Table 17 and **Figure 12** show the coefficients associated with specific pathways of the SEM model. Specifically, age was negatively associated with interoceptive attention (β = -.238, LLCI -.288, ULCI -.187), but positively associated with interoceptive accuracy (β = .071, LLCI .017, ULCI .123). There was a positive direct association between interoceptive attention and both hunger drive (β = .314, LLCI .265, ULCI .368) and satiety responsivity (β = .106, LLCI .053, ULCI .165). Meanwhile, interoceptive accuracy was unrelated to hunger drive (β = -.052, LLCI -.109, ULCI .005) and satiety responsivity (β = -.047, LLCI -.103, ULCI .009) (**Table 18**).

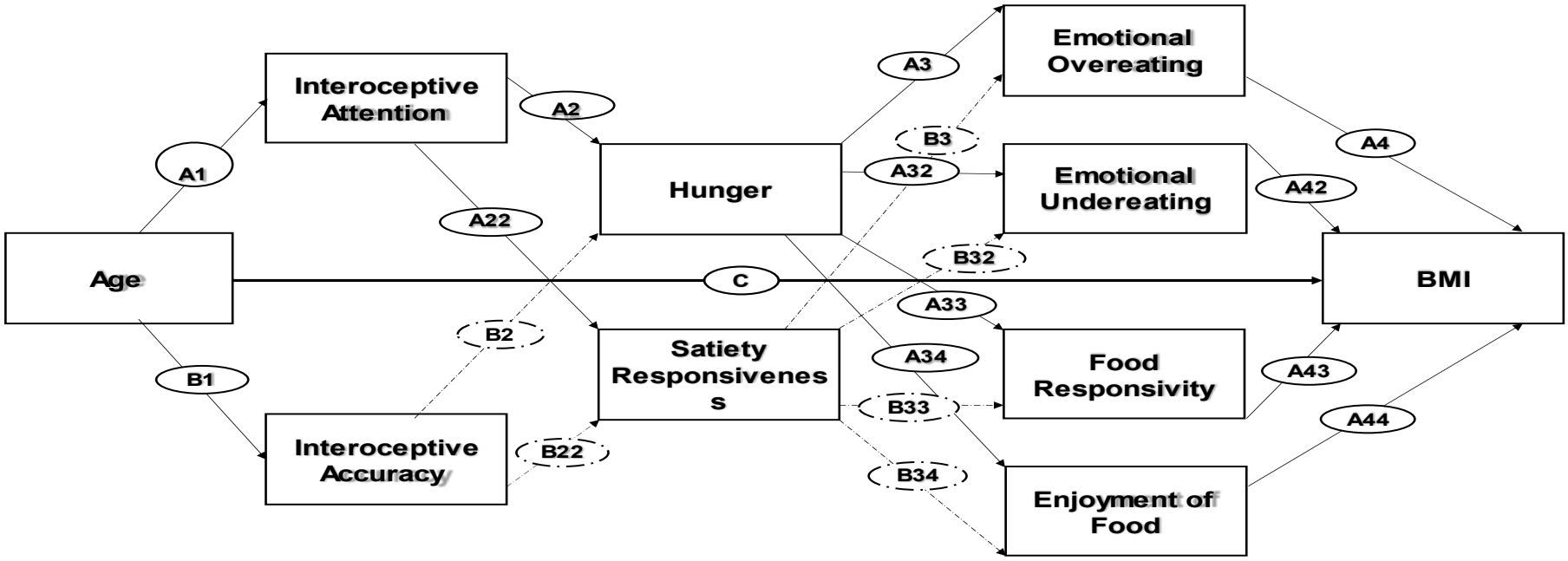
5.3.2.2 Associations between specific interoception and eating style.

As expected, hunger drive was positively associated with food approach traits, including emotional overeating (β = .253, LLCI .198, ULCI .303), food responsivity (β = .548, LLCI .051, ULCI .059), and enjoyment of food (β = .141, LLCI .093, ULCI .193). However, hunger did not influence emotional undereating (β = .027, LLCI -.029, ULCI .081). Likewise, poorer responsiveness to satiety was associated with higher food approach behaviours, including emotional overeating (β = -.224, LLCI -.272, ULCI -.172), food responsivity (β = -.335, LLCI -.372, ULCI -.029), and enjoyment of food (β = -.388, LLCI -.433, ULCI -.338). Meanwhile, satiety responsiveness had a positive direct effect on emotional undereating (β = .321, LLCI .265, ULCI .369). Interestingly, when eating traits were considered in parallel, only

emotional overeating exerted a direct effect on BMI (β = .279, LLCI .219, ULCI .339) (**Figure 12**).

5.3.2.3 Indirect effect of age on BMI through interoception and eating style.

The following indirect effects were also significant: (**1**) age → interoceptive attention → hunger → emotional overeating → BMI (β = -.057, *p* = .003, LLCI -.091, ULCI -.035); (**2**) age → interoceptive attention → satiety responsiveness → emotional overeating → BMI (β = .017, *p* = .002, LLCI .007, ULCI .035); (**3**) age → interoceptive attention → satiety responsiveness → food responsivity → BMI (β = .006, *p* = .036, LLCI 0, ULCI .017). The estimates (user defined estimands) of the specific indirect pathways are summarised in **Table 16** and **Figure 12**. These findings indicated that lower interoceptive attention in older adults may contribute to alterations in the way hunger and satiety are experienced with consequences for eating behaviour and obesity.



2

Figure 11: Serial mediation in (AMOS, v.26). The full structural equation model (SEM) representing all mediating pathways: Age → Interoceptive sensibility dimensions → Hunger / Satiety Responsiveness → Appetite trait → BMI.

[2] Serial mediation structural equation model (n=937). Indirect effects of Age on BMI through domain general interoceptive sensibility, appetite specific interoceptive sensibility, and appetite traits. Standardised effects are presented. Dotted lines depict the pathways via interoceptive accuracy and satiety responsiveness. A/B1 depicts the standardised effects of age on interoceptive attention/accuracy. A/B 2/22 depict the standardised

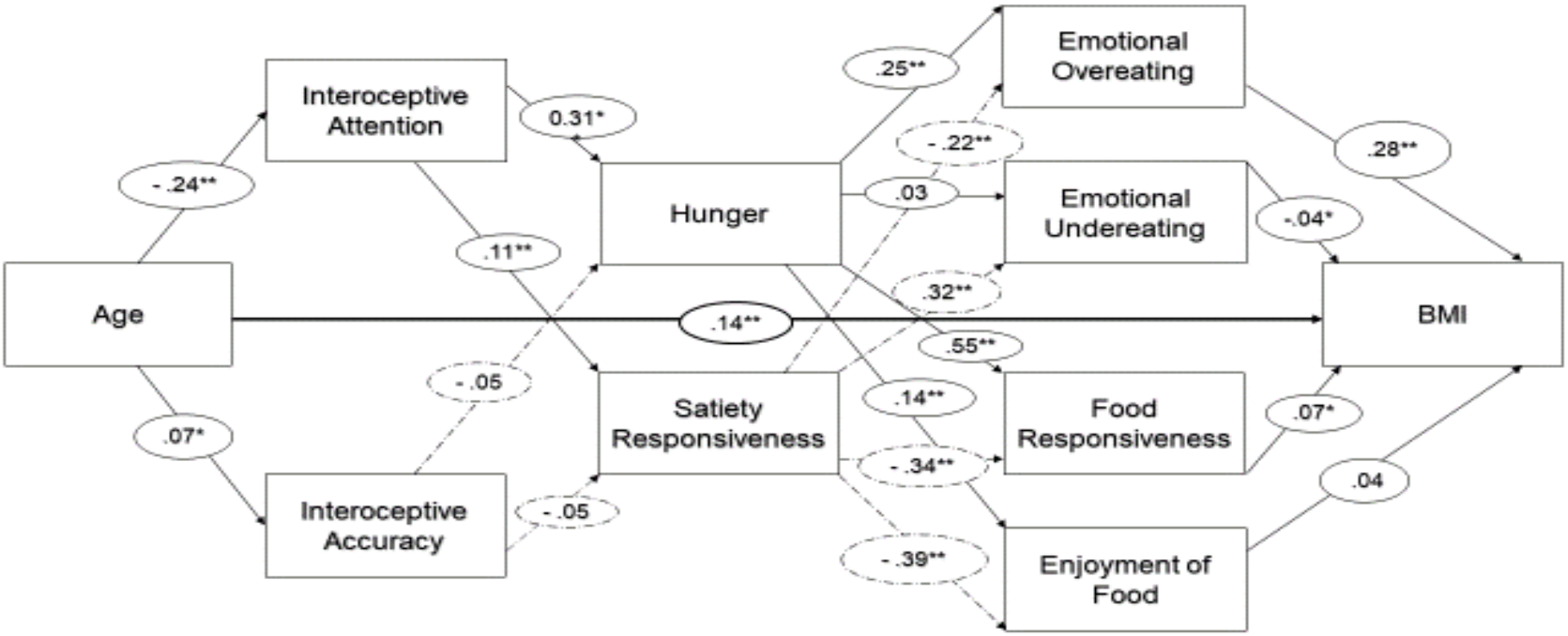


Figure 12: Regression coefficients representing the direct effects per pathway of the SEM.

effects of domain general interoceptive sensibility on appetite specific interoceptive sensibility. A/B 3/32/33/34 depict the standardised effects of appetites specific interoceptive sensibility on the four appetite traits. A4/42/43/44 depict the standardised effects of appetite traits on BMI. The effects on the direct path from Age to BMI (C) depict the direct effect. *P<0.001.

Table 16

Estimates of pathways for all observed variables defined with the structural equation model: the specific indirect effects in the association between age and BMI

Parameter	β	LLCI	ULCI	*P*
Age → IATT→ H→ EOE→ BMI	-0.057	-0.091	-0.035	0.003**
Age → IATT→ H→ EUE→ BMI	0.001	-0.001	0.007	0.284
Age → IATT→ H→ FR→ BMI	-0.030	-0.064	0.002	0.056
Age → IATT→ H→ EoF→ BMI	-0.005	-0.014	0.002	0.211
Age → IATT→ SR→ EOE→ BMI	0.017	0.007	0.035	0.002**
Age → IATT→ SR→ EUE→ BMI	0.004	-0.002	0.014	0.145
Age → IATT→ SR→ FR→ BMI	0.006	0.001	0.017	0.036*
Age → IATT→ SR→ EoF→ BMI	0.004	-0.002	0.015	0.182
Age → IACC→ H→ EOE→ BMI	-0.003	-0.011	0.001	0.131
Age → IACC → H→ EUE→ BMI	0.000	0.001	0.001	0.196
Age → IACC → H→ FR→ BMI	-0.001	-0.008	0.001	0.106
Age → IACC → H→ EoF→ BMI	0.000	-0.002	0.001	0.176
Age → IACC → SR→ EOE→ BMI	0.002	0.001	0.009	0.103
Age → IACC → SR→ EUE→ BMI	0.000	0.001	0.004	0.126
Age → IACC → SR→ FR→ BMI	0.001	0.001	0.005	0.067
Age → IACC → SR→ EoF→ BMI	0.001	0.001	0.005	0.160

Abbreviations: β standardised coefficient, EOE = Emotional Overeating, EoF = Enjoyment of Food, EUE = Emotional Undereating, FR = Food responsiveness, H = Hunger, IACC = Interoceptive Accuracy, IATT = Interoceptive Attention, LLCI = Lower Limit Confidence Interval, SR = Satiety Responsiveness, ULCI = Upper Limit Confidence Interval.

Note *$p < .05$ ** $p < .01$

Table 17

Standardised Total, Direct and Indirect Effects of SEM

	Total Effect				Direct Effect				Indirect Effect			
Parameter	**β**	**Confidence Interval 95%**		***p***	**β**	**Confidence Interval 95%**		***P***	**β**	**Confidence Interval 95%**		***p***
		LLCI	**ULCI**			**LLCI**	**ULCI**			**LLCI**	**ULCI**	
Age → BMI	0.135	0.081	0.186	.004**	0.141	0.087	0.191	.004**	-0.006	-0.013	-0.002	.006**
Age → SR	-	-	-	-	-	-	-	-	-0.028	-0.044	-0.016	.004**
Age → H	-	-	-	-	-	-	-	-	-0.078	-0.103	-0.058	.004**
Age → EOE	-	-	-	-	-	-	-	-	-0.013	-0.022	-0.007	.004**
Age →FR	-	-	-	-	-	-	-	-	-0.033	-0.048	-0.022	.004**
Age → EoF	-	-	-	-	-	-	-	-	0.001	-0.007	0.007	.917
Age → EUE	-	-	-	-	-	-	-	-	-0.011	-0.018	-0.005	.004**
IACC → EOE	-	-	-	-	-	-	-	-	-0.003	-0.025	0.018	.832
IACC → FR	-	-	-	-	-	-	-	-	-0.013	-0.055	0.027	.576
IACC → EoF	-	-	-	-	-	-	-	-	0.011	-0.014	0.037	.497
IACC → EUE	-	-	-	-	-	-	-	-	-0.017	-0.035	0.002	.140
IACC → BMI	-	-	-	-	-	-	-	-	0.001	-0.01	0.01	.938
IATT → EOE	-	-	-	-	-	-	-	-	0.056	0.033	0.084	.004**
IATT → FR	-	-	-	-	-	-	-	-	0.137	0.098	0.176	.004**
IATT → EoF	-	-	-	-	-	-	-	-	0.003	-0.028	0.033	.754
IATT → EUE	-	-	-	-	-	-	-	-	0.042	0.019	0.067	.004**
IATT → BMI	-	-	-	-	-	-	-	-	0.023	0.011	0.037	.006**
SR → BMI	-	-	-	-	-	-	-	-	-0.115	-0.146	-0.084	.004**
H → BMI	-	-	-	-	-	-	-	-	0.113	0.077	0.147	.004**

Abbreviations: β standardised coefficient, EOE = Emotional Overeating, EoF = Enjoyment of Food, EUE = Emotional Undereating, FR = Food responsiveness, H = Hunger, IACC = Interoceptive Accuracy, IATT = Interoceptive Attention, LLCI = Lower Limit Confidence Interval, SR = Satiety Responsiveness, ULCI = Upper Limit Confidence Interval.

Note *$p < .05$ ** $p < .01$

Table 18:

Direct effects, associations between the sequential observed variables as defined within the Structural Equation Model.

Parameter		β	Standard Error	t	95% Confidence Interval LLCI ULCI	LLCI ULCI	Pathway Label
AGE	→ IATT	-0.238	0.885	-7.672	-0.288	-0.187	A1**
	→ IACC	0.071	0.624	2.24	0.017	0.123	B1*
IATT	→ H	0.314	0.009	10.386	0.265	0.368	A2**
	→ SR	0.106	0.008	3.33	0.053	0.165	A22**
IACC	→ H	-0.052	0.013	-1.71	-0.109	0.005	B2
	→ SR	-0.047	0.011	-1.488	-0.103	0.009	B22
H	→ EOE	0.253	0.042	8.399	0.198	0.303	A3**
	→ EUE	0.027	0.039	0.879	-0.029	0.081	A32
	→ FR	0.548	0.02	22.14	0.51	0.59	A33**
	→ EoF	0.141	0.017	4.825	0.093	0.193	A34**
SR	→ EOE	-0.224	0.05	-7.424	-0.272	-0.172	B3**
	→ EUE	0.321	0.046	10.608	0.265	0.369	B32**
	→ FR	-0.335	0.024	-13.549	-0.372	-0.29	B33**
	→ EoF	-0.388	0.02	-13.297	-0.433	-0.338	B34**
EOE	→ BMI	0.279	0.029	9.072	0.219	0.339	A4**
EUE	→ BMI	-0.041	0.03	-1.37	-0.103	0.021	A42
FR	→ BMI	0.069	0.051	2.201	0.008	0.126	A43
EoF	→ BMI	0.041	0.07	1.322	-0.012	0.097	A44
AGE	→ BMI	0.14	0.323	4.673	0.087	0.191	C**

Abbreviations: β standardised coefficient, EOE = Emotional Overeating, EoF = Enjoyment of Food, EUE = Emotional Undereating, FR = Food responsiveness, H = Hunger, IACC = Interoceptive Accuracy, IATT = Interoceptive Attention, LLCI = Lower Limit Confidence Interval, SR = Satiety Responsiveness, ULCI = Upper Limit Confidence Interval.

Note *$p < .05$ ** $p < .01$

5.4 Discussion

The aim of the present study was to determine whether interoception contributes to age-related changes in eating traits and BMI. In particular, the mediating effects of domain general (accuracy and attention) and domain specific (hunger and satiety) interoception were established. Key findings included: (**1**) older adults self-reported poorer interoceptive attention but better interoceptive accuracy, than younger adults. Despite having a higher BMI, older adults also reported lower hunger drive, emotional overeating, food responsivity and enjoyment of food; (**2**) higher self-reported interoceptive attention was associated with a greater hunger drive and responsivity to satiety. However, perceived interoceptive accuracy was not associated with appetite-specific interoception; (**3**) hunger drive was positively associated with emotional overeating, food responsivity and enjoyment of food, whereas satiety responsiveness was negatively associated with the same three eating traits; (**4**) the SEM indicated that the positive association between age and BMI was partially mediated by antagonistic indirect pathways involving interoception and appetitive traits (**Table 17**). Overall, the present findings suggest that reduced interoceptive attention in older adults may protect against weight gain by reducing the propensity towards eating traits associated with an increased risk of obesity.

An important finding was that this study found that age was negatively associated with interoceptive, and positively associated with interoceptive accuracy. Thus, while older adults believe their interoceptive perceptions are accurate, they report paying less attention to them. However, these findings are not in line with some previous research that found older adults report lower interoceptive accuracy (Murphy *et al*., 2020a: Study 5). Yet, in Murphy *et al*.'s study, establishing the effect of age was not a primary aim. Across the sparse literature involving older adults and interoception, age parameters remain poorly defined. For example, in Murphy's study the oldest participant recruited was 56 years old, yet references are made to older adults. Poorly defined samples may explain some inconsistencies. The present study calls for further exploration of the dimensions and factors of interoception in ageing populations.

To the best of our knowledge the present study is the only one to assess interoceptive attention in older adults using the IATT. However, previous research using the Porges

Body Perception Questionnaire similarly found that older adults reported being less aware of their bodily sensations during most situations (Murphy *et al*., 2018b). Given the link between interoception and mental health, the wider implications of the age-related differences require future exploration. However, the present data indicates lower interoceptive attention in older adults, which may have both beneficial and harmful effects regarding eating traits associated with an increased risk of weight gain in later life. For example, older adults had both lower interoceptive attention and a reduced hunger drive, and these two factors were associated (See **Table 16 and 18**). This reduced hunger drive in older adults aligns with evidence suggesting that older adults report lower levels of subjective hunger while fasting (Johnson *et al*., 2020). Some evidence also indicates that older adults have higher postprandial levels of the appetite regulating hormones insulin, leptin, cholecystokinin and peptide-YY (Johnson *et al*., 2020), and a higher satiation during a standardised meal (Sturm *et al*., 2004). Although we found similar reported levels of satiety responsiveness across age groups, we did observe a significant negative association through interoceptive attention (indirect effect) – older individuals reported lower interoceptive attention which was associated with greater satiety responsivity. Future research combining biological and subjective interoceptive measures may be profitable to further explore the link between appetite regulating hormones, satiety responsivity and reduced interoceptive attention in older adults.

Notably, the present pattern of results between general- and appetite-specific interoception indicates that interoceptive attention may be important for understanding eating traits. Specifically, interoceptive attention was positively associated with both hunger drive and satiety responsivity, however, interoceptive accuracy was not. This is consistent with the findings by Robinson *et al* (2021) who reported that in a sample with an average age of 37.2 (12.6) years, interoceptive accuracy was not associated with trait hunger or satiety responsiveness, but interoceptive attention was associated with both (Robinson *et al*., 2021). Notably, the coefficients depicted in **Figure 12** highlight a stronger association between hunger and interoceptive attention, emotional eating, and food responsivity, compared to the associations with satiety responsiveness. Seemingly, hunger drive and interoceptive attention are mediators in the association between age and BMI. This is further highlighted and resulted in the three indirect pathways noted in **Table 16**. Given the consistency of these

observations, future intervention studies may consider interoceptive attention as a viable target for modifying appetitive sensations in older adults e.g., through self-compassion (Young *et al*., 2021) or physical activity (Seabury, Benton, & Young, 2023). For example, some research has highlighted the benefits of mindfulness training on improving interoceptive attention (Li *et al*., 2021). In addition, directing attention to the body (i.e., a body scan intervention) increased feelings of hunger (but not satiety) (Palascha, 2021). Similarly, physical activity interventions have been recommended as a way of ameliorating age-related declines in appetite (Clegg and Godfrey 2018). King *et al* (2009) presented evidence to support a dual-process model of exercise and appetite regulation. Specifically, it was suggested that while exercise may result in an increased hunger drive, it may also increase the satiating efficiency of a meal (King *et al*. 2009). These previous observations suggest that mindful attention to the body and / or exercise could improve interoceptive attention and / or ameliorate reduced hunger in older populations, although currently data in older adults are limited (Clegg and Godfrey 2018), future work will be needed to confirm this. However, while increasing interoceptive attention and hunger drive in frail older adults may prove beneficial (Clegg and Godfrey 2018), the present data suggests that in otherwise healthy older adults, it may be linked with a risk of weight gain. In addition, the overall consequence of these interventions for increasing both hunger and satiety in different populations still needs to be determined. Future research combining interventions and statistical modelling to determine antagonistic indirect pathways might prove profitable in that regard. Overall, it will be important for future intervention studies to consider tailoring interventions depending on desired individual health outcomes.

An important question that remains is whether lower interoceptive attention in older adults is a cause or a consequence of diminished hunger and satiety signalling. For example, computational evidence indicates that when sensory sensitivity is low (or the signal itself is weakened), the result is diminished attentional processing of that sensory channel (in favour of more reliable sources of information) (Mirza, Adams, Friston, & Parr, 2019). However, the fact that older adults in the present study also reported higher levels of interoceptive accuracy suggests that they may have more confidence in the accuracy of their interoceptive percept and therefore argues against this possibility, an important avenue for further work.

In line with previous research, the present study found that older adults tend to experience lower levels of emotionally cued eating (Samuel & Cohen, 2018), food responsivity (Brennan *et al*., 2022), and food enjoyment (Spence & Youssef, 2021), despite having a higher BMI. Importantly, the current study highlighted that differences in the way interoceptive signals are processed, may contribute to these observations. Specifically, spending more time paying attention to interoceptive signals was associated with having higher levels of emotional eating, food responsivity, and food enjoyment. In addition, hunger drive mediated the association between interoceptive attention and both emotional overeating and food responsivity, a similar pattern to that observed in (Robinson *et al*., 2021). As older adults in the present study reported lower interoceptive attention this might explain their reduced propensity towards eating traits associated with a greater risk of weight gain.

Reduced interoceptive attention and lower emotional overeating in older, compared to younger adults, may reflect age-related differences in the degree to which 'bottom-up' interoceptive signalling contributes to emotional experience. Mendes (2010) introduced the idea of maturational dualism, which posits that aging is accompanied by a weakened connection between the body and mind, which influences the way emotions are experienced. Specifically, the ability to perceive internal bodily sensations diminishes as individuals grow older, primarily due to the increased vulnerability of the peripheral nervous system and a resulting decrease in physiological reactivity. In theory, some older adults may become less skilled at recognising the physiological changes that occur when they are emotionally stimulated. In the absence of being able to identify these internal bodily changes, older adults' emotional experiences may become more 'cognitive'. That is, they may rely more on external representations from the present context, prior experience, and knowledge about emotion categories to assess their emotional responses (Barrett, 2017). Furthermore, less intense interoceptive experiences might make it easier to regulate one's emotions (Charles, 2010). This view aligns with observations that emotional regulation improves with age (Orgeta, 2009), and could be relevant to the patterns observed in the present study i.e., explain lower levels of interoceptive attention, hunger, and emotional eating amongst older adults. In support of this suggestion previous research that found heightened interoceptive signalling and decreased meta-cognitive awareness of interoceptive capacities, are characteristic of emotional eaters (Young *et*

al., 2017). As noted earlier, the evidence for older samples is sparse and more research is needed to better understand the associations and mechanisms in older populations.

Regarding BMI, older adults are more likely to be classified as being overweight and obese; an effect confirmed in the present study. However, rather than exacerbating weight gain, the results of our SEM may suggest that reduced interoceptive attention in older adults may be protective. That is, in older adults lower interoceptive attention and hunger were associated with lower food approach eating behaviours and therefore a lower BMI (negative indirect pathway). Crucially, the direct effect, that is the effect of age on BMI after the indirect pathways have been considered, was significant and positive, indicating partial mediation. These findings suggest that other factors besides interoception (e.g., lean muscle mass, basal metabolic rate, other lifestyle factors) may also be implicated with obesity in later life, and therefore should be included in future modelling studies.

5.4.1 Limitations and future directions

Given that the sample consisted of females only, it should be noted that reproductive hormones such as oestrogen, play a key influential role in appetite, obesity, and ageing (Hirschberg, 2012). Some research has shown that during the follicular phase of menstruation reproductive hormones may have an antagonistic effect on energy intake and appetite regulation (Campolier *et al*., 2016; Stelmanska & Sucajtys-Szulc, 2014). Yet, less is known about the luteal phase of menstruation (Kamemoto *et al*., 2022). Furthermore, there is little to no research exploring these ovarian cycle effects in relation to general interoceptive sensibility. Intuitively, experiencing painful and unpleasant menstrual symptoms may correlate with attention to symptoms and self-regulatory abilities (Borlimi *et al*., 2023). Though the measures used in the present study have yet to be explored in relation to menstrual phases and menopause, therefore these associations remain speculative. This research gap may be salient for future exploration, particularly in modelling studies.

The current study benefited from a theoretical framework of the mechanisms underlying eating traits, a large sample size, SEM modelling, well validated and reliable measures, and the recruitment of an under-researched population. The measures adopted here (e.g. AEBQ) have been recommended as a comprehensive

assessment tool for eating traits in older adults (Fostinelli *et al*., 2020). However, limitations require consideration. Firstly, given the cross-sectional design, causality cannot be inferred. Secondly, we concentrated on participants whose birth sex is female, due to sex differences in eating behaviour and interoception. This study should be replicated in male samples. Thirdly, we used self-reporting methods of BMI, the problems and questions of reliability using this method have long been documented. However, some research has found a positive association between reporting inaccuracies and BMI, particularly in adolescent samples (Allison *et al*., 2020). The present research recruited adults only and implausible BMI data was removed. Lastly, the present research may have benefitted from further demographic information e.g., social economic status, ethnicity, health status etc.

5.4.2 Conclusion

The present study indicated a complex pattern of associations connecting age, interoception, appetite and BMI. Older adults had a higher BMI and an indirect pathway involving age-related reductions in interoceptive attention, lower satiety responsivity, and more emotional eating and food responsivity mediated this effect. However, a stronger antagonistic indirect pathway was also present; age-related reductions in interoceptive attention were associated with a lower hunger drive, less emotional eating, and a lower BMI. This may suggest that overall reduced interoceptive attention in older adults may protect against weight gain by lowering hunger and the propensity towards eating traits associated with an increased risk of weight gain / obesity. These findings highlight that the interoceptive mechanisms driving eating behaviour and obesity in older adults may not be the same as in young adults. Further research aimed at understanding the role of interoception will likely shed light on the mechanisms underlying eating traits and risk of obesity and pave the way towards innovative treatment methods. A deeper understanding of the complex mechanisms underlying obesity in this cohort is required to tailor age-related- and novel- therapeutic approaches, with beneficial implications for public health.

Chapter 6 General discussion

6.1 Focus of the thesis.

In most countries, obesity is on the rise. The obesity pandemic has a problematic impact on health as well as a financial burden. Evidence from current and past research suggest that eating behaviour may be a contributor in the obesity pandemic. Yet, the underlying mechanisms are not fully understood, particularly in already vulnerable populations such as older adults. The current thesis sought to identify factors driving eating behaviour associated with an increased risk of developing obesity in older populations with a focus on the potential role of interoception. Interoception was measured using a variety of methods (brain imaging, satiety ratings, self-report questionnaires) and the link to eating styles that may be associated with a higher BMI (i.e., restrained, disinhibited, and emotional eating) was assessed. The inter-relationships between key concepts were determined and how these may differ in younger and older adults was assessed.

6.2 Summary of key findings.

> **Aim 1**: Systematically review the evidence that interoception changes with age and evaluate the evidence that this has consequences for eating behaviour. (Chapter 2).

The integrative systematic review in Chapter 2 identified a general absence of evidence for most interoceptive factors associated with eating behaviour and obesity in older adults. Notably, the strongest body of evidence, where younger and older adults have been compared concerned hunger and satiety. Specifically, there was evidence that younger and older adults reported different levels of subjective state hunger, and a lower trait hunger drive, albeit evidence for differences in satiety was limited (**Table 6**). There was some evidence that this might be related to higher circulating gut hormones such as insulin, leptin, cholecystokinin and peptide-YY (Johnson *et al*., 2020). Beyond appetitive signals, there was also evidence that older adults experience reduced interoception in other domains, for example the cardiac domain (Khalsa *et al*., 2009). (**Table 7**). However, a major limitation of this evidence base was that few

studies had considered whether the association between interoception and eating / bodyweight varied with age. The chapter concluded by presenting a road map to better understand the links between interoception, eating behaviour and bodyweight in this already vulnerable population.

Aim 2a: To examine the neural correlates of disinhibited eating (using resting state fMRI) in younger and older adults who were matched on their BMI (Chapter 3).

In Chapter 3, older and young participants underwent an fMRI scan and completed the Three Factor Eating Questionnaire to assess self-reported levels of disinhibited eating, emotional eating, and cognitive restraint overeating. As expected, younger adults scored higher on the disinhibited- and emotional- eating subscales. However, restraint was similar across both age groups. Notably, older adults compared to young adults, were observed to have weakened connectivity in the frontoparietal- and default mode-networks; networks thought to play an important role in interoception (Barrett, 2016). In addition, associations between functional connectivity and eating behaviour differed between the two age groups. In older adults, disinhibited eating was associated with weaker connectivity in the FPN and DMN—effects that were absent in the younger sample. These findings may reflect changes in interoceptive signalling as part of the ageing process, which may have implications for the processes involved in energy regulation. Thus, further highlighted the importance of studying this under-researched population.

Aim 2b: Using a novel paradigm (that assesses the processes underlying satiety, from the perspective of active inference (Young *et al*., 2021)) to determine whether older and younger adults differ in the degree to which the use expectations versus sensation to inform their postprandial satiety.

Note that due to the COVID 19 pandemic we were unable to recruit older adults into the laboratory. Therefore, the aim of this Chapter was changed to determine whether disinhibited eating effected the degree to which individuals use expectations versus sensation to inform their postprandial satiety (Chapter 4).

In Chapter 4 participants took part in a novel paradigm which required them to consume a glucose (predictable condition) or a sucralose (unpredictable condition)

while rating their expected and actual satiety. Participants also completed the TFEQ. The study identified that when postprandial sensations were unpredictable (after consuming a sensory incongruent drink; sucralose, but not a sensory congruent drink; glucose), those scoring high in dietary restraint were more likely to rely on prior expectations and develop an 'illusionary' sense of satiety. Conversely, those scoring high in disinhibited eating were more sensitive to the incongruent surprising interoceptive state - they experienced higher levels of 'rebound hunger' and had a greater sensitivity to low blood glucose. Irrespective of the nature of the drink, those high in disinhibited eating were less confident in using visual cues to predict their subsequent satiety. These findings provide mechanistic insight to the satiety processes that may underlie common eating styles, which in the future can be extended to understand the processes underlying changes in hunger and satiety in older adults.

Aim 2c: Use Structural Equation Modelling to investigate whether domain general - (interoceptive accuracy and attention (Murphy *et al*., 2020b)) and domain specific - (hunger drive and satiety responsivity (Hunot *et al*., 2016)) interoception mediate the link between age, eating traits and BMI (Chapter 5).

In Chapter 5 younger and older adults completed an online survey that included the interoceptive attention and accuracy scales (Murphy *et al*., 2020b), and the adult eating behaviour questionnaire (Hunot *et al*., 2016). As expected, compared to younger adults, older adults reported lower trait hunger, food responsivity and emotional eating, but similar levels of satiety responsivity. A novel finding was that older adults also reported lower levels of interoceptive attention which was associated with their lower trait hunger. Results from Structural Equation Modelling indicated that interoceptive attention and hunger mediated the association between age and eating traits associated with an increased risk of a higher BMI.

6.3 Theoretical integration

Disinhibited eating and interoception

Across all three experimental chapters an interesting pattern emerged that may suggest an association between disinhibited eating and imprecise or uncertain beliefs about interoceptive outcomes. In Chapter 4 those high in disinhibited eating were less

confident in their expectations of satiety (**Figure 7**). We suggested that interpreting this finding within the framework of active inference would imply an association between disinhibited eating and higher "expected uncertainty". That is, an *a priori* belief that the interoceptive consequences of one's own (interoceptive) actions are unpredictable. There may also be a link with the findings in Chapter 3 that lower connectivity in the frontoparietal and default mode networks in the brain was associated with higher levels of disinhibited eating (**Figures 3 and 4**). The frontoparietal network (FPN) is suggested to have several metacognitive roles including the prediction, filtering and modification of salient afferent signals (Barrett, 2017). In addition, the default mode network (DMN) may be involved in the representation of the brains internal model, that is used by the FPN to inform predictions about sensory inputs (Barrett, 2017). Together, these findings suggest a possible link between higher expected uncertainty, disinhibited eating, and a deficit in neural engagement, of the FPN and / DMN. Further exploration is needed to confirm such a link. Indeed, there is evidence suggesting that the FPN responds to prior uncertainty (Taghizadeh *et al*., 2020). For example, manipulating the variance of expected rewards, independently of the value of the rewards, affected frontoparietal information transmission in monkeys (Taghizadeh *et al*., 2020). Our suggestion may also align with the Hierarchical Modular Adaptive Interoception Control (IMAC) model (Fermin, Friston, & Yamawaki, 2022). This model was developed to explain how discrete modules within the insula (granular, dysgranular and agranular) form reciprocal connections with the prefrontal cortex and striatum (modulated by the acetylcholinergic and dopaminergic systems). These networks are suggested to mediate higher order (conscious) interoceptive representations that explain lower order interoceptive representations. Crucially, the IMAC model hypothesises that cholinergic connections between the PFC and anterior insula (parts of the FPN) provides the capability to flexibly modify and update prior "metaceptions" (i.e., higher- or third- order interceptive representations) (Fermin *et al*., 2022). In the current thesis, expected satiety confidence (or expected uncertainty) might be one such meta-cognitive representation. Future research that combines the methodologies used in Chapters 3 and 4 might be able to confirm this suggestion and help identify the neural underpinnings of expected uncertainty in people who report higher disinhibited eating.

Interestingly, in Chapter 5, interoceptive attention (i.e., time spent attending to internal signals) emerged as a domain general interoceptive variable predicting hunger drive and satiety responsiveness, and in turn emotional over eating, food responsivity and BMI (**Figure 11**) *(note that in the AEBQ; hunger drive and food responsivity represent separate dimensions whereas in the TFEQ disinhibited or uncontrolled eating combines aspects of both these scales – discussed further in the next section).* Notably, from a predictive processing perspective, one way that may increase the precision (i.e., reduce uncertainty) of an interoceptive channel is by paying attention to it (Friston *et al*., 2017; Pezzulo, Rigoli, & Friston, 2015; Seth & Friston, 2016; Young *et al*., 2021). As such, it is not surprising that those who reported spending more time attending to internal sensations also reported feeling more appetitive sensations (i.e., hunger and satiety), and consequently more emotional overeating and food responsivity. In the first instance this effect (i.e., higher interoceptive attention (and therefore less uncertainty) = more hunger and food responsivity) might be viewed as contradicting our suggestion that disinhibited eating is positively associated with interoceptive uncertainty. However, it is important to differentiate different kinds of interoceptive attention. For example, attention may be repeatedly drawn to ambiguous internal states to try and resolve uncertainty. This can result in a heightened self-focus that is not necessarily adaptive (Mehling, 2016). Alternatively, attention may be flexibly controlled to selectively accentuate / attenuate particular sensory channels in a context dependant manner (Mehling, 2016). Future research would benefit from incorporating various attentional measures.

It is plausible that in Chapter 5 the positive associations between interoceptive attention, hunger, and food responsivity represent the hypersampling (i.e., increased attention) of internal states to resolve interoceptive uncertainty with varying degrees of success. Indeed, this interpretation would also be consistent with the finding in Chapter 4 that those high in disinhibited eating experienced more rebound hunger after consuming sucralose; a sensory incongruent drink that presumably resulted in a surprising and ambiguous interoceptive state. In Chapter 4, we suggested that during interoceptive ambiguity, those high in disinhibited eating may weigh (i.e., assign precision to, or attend to) incoming afferent sensations more heavily than prior beliefs when judging their postprandial state. Such hypersensitivity to unexpected bodily signals (e.g., blood glucose that signals energy and associated feeling of hunger) may

increase the incentive value of environmental food cues that restore homeostasis (i.e., restore blood glucose back to the 'expected' level); an effect that may explain an increased propensity towards disinhibited eating. Whilst these suggestions are at present very speculative and based on associative findings, future research that attempts to differentiate between anxiety driven hypervigilance to internal sensations (where attention is 'drawn' to 'surprising' afferent sensations) and the ability to adaptively control top-down attention to flexibly accentuate / attenuate selective sensory channels might provide evidence to support this model further. In addition, future research might also consider exploring how different types of interoceptive attention are associated with functional connectivity in the brain. Based on the present findings in Chapter 3 and 5, we would expect flexible attentional control to interoceptive signals to be positively associated with FPN connectivity; while anxiety driven hypervigilance afferent states to be negatively associated with FPN connectivity, although future research will need to confirm this.

An important caveat to any interpretation concerning interoceptive sensibility is that just because an individual reports spending time attending to interoceptive states does not mean that this reflects reality. In fact, a common observation in the interoception literature is that individuals tend to lack insight into their interoceptive abilities (Garfinkel *et al*., 2015), and this might be particularly apparent in those with eating styles associated with an increased risk of obesity (Young *et al*., 2017). Therefore, future research might consider alternative ways of assessing interoceptive attention such as through ecological sampling of behaviour.

Aging, interoception and eating.

A growing body of research using a variety of methods supports a role for interoception (beyond appetitive sensations) in eating behaviour (see Martin *et al*., 2019), body weight and obesity (see Robinson *et al*., 2021). However, much like other areas of eating behaviour research (Chapter 3) the focus has been predominantly on younger adults. Using both neuroimaging and self-report methods this thesis found not only that older adults may differ from younger adults in the processing of internal signals e.g., lower interoceptive attention (Chapter 5) and lower FPN connectivity (Chapter 3), but also that this might have implications for their eating behaviour i.e.,

disinhibited, and emotional overeating. Specifically, older adults with a higher FPN connectivity had lower levels of disinhibited eating (Chapter 3). In addition, older adults with lower interoceptive attention had a lower hunger drive and less food responsivity (Chapter 5). These observations may suggest that more time spent attending to interoceptive signals might reflect attempts to resolve uncertainty caused by a failure of higher-level neural circuits to appropriately modulate the precision of interoceptive expectations. If these assumptions are correct, lower interoceptive attention in older adults might reflect the learned propensity to attend elsewhere for information regarding appetitive decisions. That is, in the face of irreducible interoceptive ambiguity and failed attempts to increase the precision of internal signals by increasing attention one may eventually seek alternative sources of information to inform appetitive choice. Clearly, whilst these interpretations fit well within the active inference framework and may explain the present pattern of associations across all three studies, they should be considered speculative, given that these patterns are based on associative findings, yet they do pave the way directing future research. Nonetheless, they raise interesting questions regarding the type of intervention that may be most profitable for altering eating behaviour in older adults. For example, attempts to increase interoceptive attention may inadvertently increase interoceptive ambiguity, hunger, and disinhibited and emotional eating in older samples. Therefore, attempts to restore older adult interoceptive attention to resemble younger adult interoceptive attention may not be the best strategy. Conversely, attentional control or bias modification training which recruits regions of the FPN (Carlson *et al*., 2022; Hakamata *et al*., 2018) could prove helpful. The associations presented in the current thesis bring into question the effectiveness of evidence-based interventions that have been developed with young adults in mind. Given that interoceptive processes alter as we get older, it remains unclear whether older populations will benefit from existing interventions. This is concerning given that older populations tend to be vulnerable to poor health and are the most likely age category to be diagnosed with obesity.

6.4 Limitations of the present research and future research recommendations

Firstly, responsivity to hunger sensations is a fundamental aspect of disinhibited eating. For example, some items of the TFEQ disinhibited eating subscale reflect

feelings of hunger, e.g., “I am always hungry enough to eat at any time”. Therefore, items relating to food responsivity e.g., “When I smell a delicious food, I find it very difficult to keep from eating, even if I have just finished a meal” tend to load onto the same construct as hunger drive (Anglé *et al*., 2009b). In Chapters 3 and 4 this made it difficult to determine which aspects of eating behaviour were associated with interoception. Therefore, in Chapter 5 we incorporated the use of the AEBQ (Hunot *et al*., 2016), to probe a wider range of eating traits. During the development of the AEBQ the hunger and food responsivity scales (which contain very similar items to the TFEQ disinhibited eating scale) showed a strong association but a confirmatory factor analysis confirmed that separating these factors provided the best model fit (Hunot *et al*., 2016). Despite using slightly different scales the current research found similar patterns, i.e., that otherwise healthy community dwelling older adults scored lower on food responsivity and disinhibited eating across the various studies. One possibility is that these scores reflect altered interoceptive processing in older populations. Future studies that pinpoint the mechanisms underlying reduced hunger and uncontrolled eating in older persons, and more generally, may prove useful.

Secondly, cross-sectional methods and associative findings are limited in terms of making any conclusions regarding causality. This presents a particular challenge in determining the cause of interoceptive dysfunction in older adults. For example, lower interoceptive attention might reduce feelings of hunger or lower interceptive attention might be the consequence of not being able to rely on sensations of hunger to inform dietary decisions, though at present these remain associative interpretations. Longitudinal research will be needed to differentiate between these possibilities. Due to the research restrictions imposed during the pandemic, BMI was captured via self-report methods in study 3. Whilst those with an implausible BMI were removed, self-report methods are susceptible to errors and bias. Lastly, as mentioned throughout the various sections of the current thesis, research tends to overly rely upon BMI. Future research may benefit from adopting various other markers of obesity such as body fat percentage and waist circumference, particularly in older adults who are likely to differ in body composition, compared to younger adults.

Whilst in Study 1 of the current thesis diet quality was accounted for, it was found that older adults reported a better-quality diet, compared to younger adults. However, diet was not controlled for in subsequent investigations. Diet quality is methodologically

problematic in research, yet more evidence is required to better understand age differences in diet composition.

Dietary style has been linked to some aspects of interoception (Young *et al*., 2022b). Whilst in Study 1 (Chapter 3) of the current thesis diet quality was accounted for, due to an already complex model and paradigm in studies 2 (Chapter 4) and 3 (Chapter 5) diet was not considered. Nonetheless, older adults reported a better-quality diet, compared to younger adults (Chapter 3). More research is underway to explore how habitual diet (for example, the habitual consumption of sweet foods) might influence different components of interoception (for example, beliefs about the satiating properties of sweet drinks).

Obesity is influenced by a complex network of factors (Hall *et al*., 2011). Regrettably, accounting for all, well known, risk factors of weight gain and obesity such as habitual sleep deprivation (Benedict *et al*., 2012; St-Onge *et al*., 2012), and impulsivity (Coveleskie *et al*., 2015) is beyond the scope of the present thesis. Future research might consider how these factors influence interoception and eating behaviour.

Additionally, future research should account for recent weight loss or significant reductions in fat percentage across participants. Such factors have been linked with improvements in self-efficacy, mood, cognitive control, and quality of life (Prehn *et al*., 2017). All of which have been extensively linked to the function of central hubs of the DMN and FPN; e.g. food motivation regions (Nakamura & Ikuto., 2017; Honea *et al*., 2016; Sugiura, 2016). Furthermore, future research might consider different kinds of dietary restraint i.e. flexible versus rigid restraint (Westenhoefer *et al*., 2013) which could be differentially related to these brain networks and interoception.

6.5 Restrictions on data collection due to the COVID 19 pandemic

Whilst older adults were already neglected in eating behaviour research this was further exacerbated during the pandemic. Here strategies were carefully considered for safety purposes; however online research was the only option available during the uncertainty of lockdowns. The exception was Study 1 (Chapter 3) which was conducted pre-pandemic.

Nonetheless, it is important to consider issues related to inclusivity, particularly with an often-overlooked cohort. The use of online resources is limited within older populations as research has shown that only 15% of older adults have any interest in engaging with online activity. Of those already online, almost 80% reported that a perceived lack of I.T. skills was a barrier to internet usage (Age UK, 2020). These statistics are likely to be greater in areas of lower socioeconomic status. Therefore, access to online resources, confidence in use of online materials as well as demographic areas are important considerations for determining how well older adults are represented in research. However, the current research was able to match sample sizes (younger vs older adults) in Study 1 (Chapter 3). Also, a large sample was recruited in Study 3 (Chapter 5) exceeding a sample size pre-determined by statistical power (i.e., G-power). Even so, restrictions prevent us from recruiting an older sample into Study 2 (Chapter 4).

6.6 Concluding remarks.

The present research considered age differences in the interoceptive mechanisms underlying eating behaviour. The thesis utilised neuroscientific, behavioural, and self-report methods to triangulate the question and tap into different interoceptive components. Overall, the findings highlighted that healthy community-dwelling older adults report a lower hunger drive, food responsivity, disinhibited and emotional overeating despite having a higher BMI (Chapters 2 to 5). This may be related to differences in the way older adults process interoceptive signals. The research presented here found that older adults might have a lower self-reported tendency to attend to internal signals (Chapter 5), and reduced activity in interoceptive networks of the brain (Chapter 3). In younger adults, disinhibited eating was also associated with lower expected satiety confidence and a higher rebound hunger. Based on the other findings in this thesis we would expect older adults with less disinhibited eating to be more confident in and driven by prior satiety expectations and research is now underway to determine if this is the case. Overall, the findings herein illustrate the value in understanding interoceptive contributions to eating behaviour beyond the gut-brain axis and across different populations. In time, this line of research might facilitate the development of personally tailored behavioural and dietary interventions

to reduce eating behaviours associated with an increased risk of weight gain and obesity in vulnerable populations.

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Appendices

Appendix B1: Chapter 3 study 1 Summary table of studies investigating the association between obesity, eating behaviour, and network connectivity using both intrinsic and extrinsic methods.

Table 19

A Summary of studies exploring the relationship between obesity and functional networks

Author	Design	Technique	Measures	(N)	Age	Gender	Findings	Comments	Confounders
(Bo-Yong *et al*., 2016)	CS Intrinsic RS (10 RSNs)	Group ICA (48 ICs)	**TFEQ**	82 BMI-HW:22.0 (1.7) Non-HW: 30.9 (3.8) Obese	Healthy Weight: 29.8 (9.9) Non HW: 33.2 (10.1)	50M:32F both sexes combined and not controlled No sig diff between groups.	FPN showed significant correlation with TFEQ-D scores. FPN and cerebellum networks showed high correlation with BMI	FPN= RSN9 (IC 25) bilateral middle orbitofrontal gyrus; inferior frontal gyrus; superior- and inferior-parietal lobule; and supramarginal gyrus.	Adult self-report scores for psychiatric conditions were excluded.
(Ding *et al*., 2020)	CS Intrinsic RS (4 RSNs) Within and Between network connection.	Group ICA (30-ICs)	Yale Food Addiction Scale Self-reported levels of craving for High vs Low cal	70 BMI OB: 39.2 ± 0.9 Severely OB NW: 20.9 ± 0.4	Obese(OB): 28.3 ± 1.7 HW: 26.1 ± 1.2 Ages weight matched	32M:38F Sexes weight matched, but not controlled. No significant differences between groups	OB exhibited decreased FC strength in the VMPFC and PCC/precuneus in the DMN. Decreased FC strength in the dACC and increased FC in	Increased interactions (SN and FPN), highlighting a key role of the SN in altered FNC in OB. Used a novel LAGS analysis	Clinical interviews for Anxiety and Depression severity scores, were used as covariates. T2 diabetes and hypertension included.

	Functional Connectivity FC						the bilateral INS in the SN. Decreased FC in the DLPFC and AG in the FPN	Eyes closed - less reliable.	
(Park *et al*., 2018)	Cross correlational Intrinsic (8 RSNs) Multimodality imaging: Static and dynamic connectivity	Group ICA (16 ICs)	Waist Hip Ratio ED Examination Questionnaire: (restraint, eating/ shape/ weight concern)	274 BMI: Ab-OB: 31.4 (5.0) Obese NonAb OB: 29.8 (4.4) Overweight	Age added as a covariate. Abdominal OB: 54.9 (17.2) Non-Ab OB: 40.8 (19.1)	116M:158F Gender combined and uncontrolled for.	FC in FPN and ECN showed significant inter-group differences between people with ab and non-ab OB.	The **corona radiata** (limbic-thalamo-cortical circuitry) and the **cerebral peduncle** (fiber tracts from motor, temporal, PFC and parietal cortices) yielded significant associations with ED behaviours.	OVERLAP WITH EDs BMI variable of no interest

(McFadden *et al*., 2013)	Longitudinal Intrinsic (Network masks)	ICA (20 ICs)	**TFEQ** 6-month exercise intervention Fat mass and %body fat Leptin concentration	12 BMI: 33.3 ±4.3 Obese	38.2 ±9.5	7M: 5F Gender combined and uncontrolled for.	Significantly decreased DMN activity in the precuneus associated with fat mass loss and decreased hunger. DE mean score: 7.9(Baseline), 7.5(post-exercise)	No control group Eyes open. No change in SN	Craving and Mood Questionnaire served as a variable of no interest. Diet was explored via a 3day/week diary entry but excluded from reported analyses.
(Legget *et al*., 2016)	Longitudinal Intrinsic: Between-network Effective connectivity using Granger causality analysis.	ICA (50 ICs)	TFEQ 6-month exercise intervention Leptin concentration Fat mass & %body fat	10 BMI: 33.6 ± 1.4 Obese	38.2 ± 3.2	5M: 5F	Reductions in outgoing and incoming connectivity from the PCC to other DMN components, and sensory networks. Outgoing changes from the PCC to CEN.	Eyes open Refinement in monitoring, re-allocation of neuronal resources, and improved cognitive functioning	Craving and Mood Questionnaire served as a variable of no interest. Active dieting, Psychiatric disease and ED excluded from sample.

(Sadler *et al*., 2018)	Experimental Intrinsic	ICA (1. 25 ICs; 2. 100 ICs)	Twin study (weight discordant vs concordant)	282 BMI: 28.1 (5.6) Overweight	29.7 ± 3.5	34%M : 66%F)	Higher BMI twin showed stronger connectivity between DMN, SN, CEN and Cerebellar networks. Connectivity patterns represent weight variability	An unrelated control group selected to match the discordant twin sample on both BMI and gender.	Heritability. A mixed linear model showed no between group or within pair differences in measures of Major depressive episodes and number of symptoms
(Beyer *et al*., 2017)	Cross sectional Intrinsic (6 RSNs) multivariate model selection approach followed by univariate analyses.	ICA (18 ICS)	Cognitive function BMI Older healthy adults. Obesity related co-morbidities	521 Replication sample=191 BMI= 27.5 ± 4.1 Over-weight. Covariate	70.1 ± 3.8 Covariate	291M:230F 95M:96F Gender combined but controlled for as a covariate	Higher BMI is associated with decreased posterior DMN connectivity. Obesity precedes connectivity differences	FC patterns: independent of age, sex, obesity co-morbidities, this remained stable in replication analyses. Posterior DMN connectivity correlated with executive function.	Controlled for depression score, but his did not significantly contribute to the model

(García-García *et al*., 2013)	Cross sectional Intrinsic (6 RSNs)	ICA Dual regression	Hunger Cognitive function	34 BMI: 36.5 ± 6.3 Severely obese	33.89 ± 6.69	12M:22F	FC strength of the putamen nucleus (SN) was increased in the OB. Correlations between activation of the SN and mental slowness. (basal ganglia circuits modulate rapid processing of information)	Participants were in a eucaloric state which may explain no FC alterations observed in the DMN (self-monitoring), majority of studies require prolonged fasting.	Anxiety and depression matched (HADS). High triglyceride and cholesterol levels also excluded from sample
(Shapiro *et al*., 2019)	Cross sectional Intrinsic	ICA (26 ICs) Seed based	eating in the absence of hunger (EAH) paradigm hedonically motivated disinhibited eating behaviour	18 BMI: -0.63	5.8 (0.5)	7M:11F combined but sex controlled as covariate	Alterations in CEN, SN, DMN, and reward network functional circuitry begin early in the life course and may underlie the risk for later life obesity via overeating. EAH is stable over time.	A temporality observed measure of disinhibited eating behaviour along with neurobiology before onset of obesity	Did not account for child developmental changes during the 6 month testing gap.

(Rucker & Ikuta, 2019)	Cross sectional Intrinsic	Voxel-wise connectivity analysis ROI-ROI connectivity analysis	Pituitary Gland (PG)	494 BMI: 27.32 ± 6.35 Overweight Covariate Ethnically diverse sample	43.46 ± 20.81 covariate	184M: 310F combined but sex controlled as covariate	OFC showed positive FC with the PG and inverse association with the BMI in its connectivity to the PG. OFC has been shown to be responsible for disinhibition of eating.	Dysconnectivity between the PG and dopaminergic regions (putamen, hippocampus) implicate dopaminergic modulation between the PG and these regions that influences body weight.	*Regions of DMN (vmPFC) and SN(Insula) positively correlated with PG. CEN (dlPFC) and SN (ACC) negatively correlated with PG
(Lips *et al*., 2014)	Cross sectional Intrinsic	Seed based connectivity analysis	T2 Diabetes Glucose intolerance Fasting	58 BMI: 43.8 (3.2) Morbidly obese	49.2 (6.22)	All female sample 80% postmenopausal.	OB group: Stronger hypothalamic connectivity with the mPFC and the dorsal striatum. The amygdala was differentially connected to the right insula. Food intake barely affected connectivity between regions.	strong hypothalamic-insula connectivity in lean individuals in the food-wanting phase and a reduction after food intake. Observes insensitivities in OB group.	Age and BMI controlled for

(Wijngaarden *et al*., 2015)	Cross sectional Intrinsic	Seed based connectivity analysis	48 Hour fast	24 BMI: 35.4 (1.2) Severely obese	31 (3) Covariate	4M:20F combined but sex controlled as covariate	At baseline, stronger connectivity between hypothalamus and L.insula in OB and weaker Amygdala connectivity with the vmPFC. After prolonged fasting, connectivity of the hypothalamus with the (dACC) increased in lean but decreased in OB.	Contrasting PCC findings as compared to previous literature.	Did not control for menstrual phase or contraceptive use
(Coveleskie *et al*., 2015)	Cross sectional Intrinsic	Seed based connectivity analysis	Reward network NAcc volume	50 (31 = control group) BMI: Range 26–38 Over weight – Severely obese	27.05 (7.03)	All female sample *Pre-menopausal	High BMI had greater connectivity of the left NAcc with bilateral ACC and right vmPFC in a MF band and with the left ACC in a HF band.	alterations within the extended reward network, (Inhibitory cortical control) mechanisms that can lead to hedonic driven ingestive behaviors, as opposed to metabolic aspects	Excluded diagnosed ED and mood disorders, diabetes, as well as bariatric surgery. Age and BMI controlled for.

(Avery *et al*., 2017)	Cross sectional Intrinsic	Seed based connectivity analysis (Seed: dorsal mid-Insula)	pre vs. post-meal functional connectivity Hunger and pleasantness ratings Various interoceptive states	52 BMI: 35.3(3.6) Severely obese	37.3(8)	18M:33F combined but sex controlled as covariate	Between fasted and fed scans OB exhibited a significant increase in FC between the mid-insula and dorsal striatum dependent upon pleasantness rating. Decreases in interoceptive hunger showed decreased connectivity between the dorsal mid-insula and OFC.	The OFC, in concert with the amygdala and mediodorsal thalamus, represents the real time value of stimuli in the environment or behavioural outcomes, informed by homeostasis	Age/ gender/ education/ ED and depression symptoms excluded
(Nakamura & Ikuta, 2017)	Cross sectional Intrinsic	Seed based connectivity analysis (Seed: Caudate)	**TFEQ** Restrained eating, BMI, CAUDATE	185 BMI: 26.1 ± 5.48 Over-weight	37.4 ± 19.4	111M:74F combined but sex controlled as covariate	RE showed a robust inverted U-shaped relationship with BMI (peak: 29.9 Overweight). Higher caudate-precuneus FC was associated with lower obesity preventive tendency, inhibiting the processes to cognitively prevent obesity	precuneus (DMN) volume has been found to be associated with general self-efficacy	Age BMI

(Gupta *et al*., 2018)	Cross sectional Intrinsic	Seed based connectivity analysis (Seed: Caudate)	Gender BMI low frequency bands	86 BMI: F=25.60 (5.79); M=25.62 (3.32) Overweight	29.84 ± 7.45	43:43 separate samples	(F): increased BMI was associated with reduced slow-5 FC (**left globus pallidus /putamen and emotion and cortical regulation regions). Greater prevalence of Emotional Eating (M): increased with medial frontal cortex. **Basal Ganglia (reward network)	Sex similarities: increased BMI was associated with increased slow-4 connectivity between right globus pallidus/bilateral putamen and emotion regulation and sensorimotor-related regions	Menstrual cycles, BMI, Anxiety/Depression scores
(Figley *et al*., 2016)	Cross sectional Intrinsic	Seed based Whole-brain voxel-wise analyses Functional and structural imaging data	BMI Body fat % White matter volume Averaged within network connectivity: SN CEN DMN	32 BMI: 24 Healthy weight Body fat %: 23	28.7 ± 9.7	16M:16F combined but sex controlled as covariate Sig gender differences: Males have higher BMI and lower BF%	Differences in BMI and BFP were not correlated with FC throughout the DMN-Kullmann *et al*. calculated FC strengths of each region separately and then reported regions for which connectivity was significantly increased.	Higher BMI and BFP were associated with increased FC throughout the SN Reduced DMN, ECN, and SN white matter volumes Eyes open	age, gender, and total intracranial volume

(Prehn *et al*., 2017)	Experimental Intrinsic	Seed based connectivity analysis (Seed: Caudate)	12-week calorie restricted (CR) Weight loss program, Older adults	37 BMI: 34.7 (4.3) Obese	61 (6)	Female only sample Post-menopausal,	significant increase in RSFC between hippocampus and left precuneus and left angular gyrus decrease in RSFC was found between hippocampus and right IFG extending to the insular cortex	CR: reductions in olfactory cortex, left postcentral gyrus, and cerebellum/vermis -the bottom-up appetitive network (IAw, eating behaviour, energy needs, approach appetizing stimuli)	Age, Handedness, Blood pressure, blood glucose. depressive symptoms (BDI)
(Contreras-Rodríguez *et al*., 2017)	Longitudinal Intrinsic	Seed based connectivity analysis	12 WEEK diet counselling session Food craving Impulsivity/ habit learning measures	81 BMI: 30.5 (3.63) Obese	33.6 (6.16)	38M:43F combined but sex controlled as covariate	Increased FC between the V.striatum and Mpfc/ parietal cortices and between the D.striatum and the somatosensory cortices. Reduced FC between the V.striatum and the dACC, insula, and lateral OFC.	D.striatal connectivity positively correlates with food craving and predicts BMI gains after 12 weeks, supporting the food addiction model.	AGE, GENDER, EDUCATION

(Lepping *et al*., 2015)	Longitudinal Intrinsic	Seed based connectivity analysis	Bariatric surgery Weight loss via behavioural methods pre/post meal	28 BMI: 40.65 (1.86) Morbidly obese	40.2 (8.1)	7M:21F combined but sex controlled as covariate	Behavioural dieters exhibited increased connectivity between left precuneus/superior parietal lobule (SPL) and bilateral insula Bariatric patients exhibited decreased connectivity between these regions	increased attention to hunger signals (SN-Interoception) following surgery Increased attention to satiety (DMN-Self-referential processing) signals following diet.	Groups were not selected via random assignment. Groups were not matched for comorbid conditions, such as diabetes Major depression and specialist diets excluded.
(Y. Zhang *et al*., 2017)	Longitudinal Intrinsic	**Graph Theory** Local and Global Functional Connectivity Density Seed based connectivity analysis	Bariatric surgery pre/post op	41 BMI: 40(6.5) Morbidly obese	27.8 (6.9) Age controlled as covariate	21M:21F combined but sex controlled as covariate	significant reduction in gFCD for VMPFC, right DLPFC, and right insula, post-surgery. Food addiction score positively correlated with change in gFCD in VMPFC	after surgery VMPFC had stronger FC to left DLPFC and weaker FC to HIPP/PHIPP PCC/precuneus had stronger FC with right caudate and left DLPFC (Food desire and reward)	Depression /anxiety severity measured by clinician. Self-reported food addiction measured completed.

(Baek *et al*., 2017)	Cross sectional Intrinsic	**Graph theory** (multi-echo ICA used as de-noise method)	Obesity and BED (Research Diagnostic Criteria from DSM4)	80 BMI: 33.4 (3.9) Obese	42.7(11.1) Age controlled for, regressed out.	42M:38F 65% of the obese group were male. No significant difference between groups. Controlled for as a covariate	Obesity is associated with global and local network efficiency and decreased modularity. Decreased FC cortico-striatal/cortico-thalamic networks Network alterations were primarily associated with obese severity.	Observations dovetail with theories of automatic inflexible habitual behaviours implicating the putamen	OVERLAP WITH ED BDI scores showed no significant correlations with global network metrics but significantly different between groups
(Doucet *et al*., 2018)	Cross sectional Intrinsic	**Graph Theory** (638 nodes) Within and between network connectivity	Twins Regional Taste Intensity test and on the Flanker Inhibitory Control and Attention Task	496 BMI: 26.6 Unevenly distributed weight classes (underweight – Obese)	29 Demographic data obtained from the Human Connectocome Project	Gender ratio unspecified. combined but sex controlled as covariate	Elevated BMI was associated with reduced within network FC and increased between network FC of sensory-driven networks (SMN, VN) and internally guided networks (DMN, CEN), implicating increased attention to sensory stimuli	siblings discordant for obesity did not differ in DMN connectivity, it is likely that changes in this network may follow rather than drive increases in BMI	Hypotheses-driven analyses related to age, sex, smoking status), and alcohol use

(Ming-Chou *et al*., 2018)	Cross sectional Intrinsic	**Graph Theory** PPI	Pre-Bariatric surgery Executive functions	17 BMI: 37.99 ± 5.40 Severely obese	33 (8.9)	7M:10F	OB patients, identifying the salience of appetitive cues (the precuneus and the MidOG) may be associated with poor inhibitory control and cue-evoked craving (SN) may be associated with poor affective decision-making.	amplitude of low frequency fluctuations	
(Verdejo-Román *et al*., 2017)	Cross sectional Extrinsic	**Graph Theory** (8 nodes) Correlational PPI	Food and Monetary rewards Excess weight: BMI and body fat%	76 BMI: 30.4 (3.69) Obese	33.6(6.23)	35M:41F combined but sex controlled as covariate	Contrast between high palatable vs plain food showed significant activation in the occipital cortex middle and lateral orbitofrontal gyri (SN) and precuneus (DMN).	FC showing reduced coupling (food task) in OB, predominantly linked frontal lobe nodes, striatal, insula and parietal regions. Important for regulation, valuation, attention, and interoception.	Controls were matched for age, sex, education and income

(Isabel García-García *et al*., 2015)	Cross sectional **Extrinsic and Intrinsic**	**Graph Theory** **Seed based**	Hunger	41 BMI: 35.9 (5.83) Severely Obese	33.6(5.61)	15M:26F	obese participants show a diminished functional connectivity of the middle frontal gyrus (SN) and the lateral occipital cortex with the entire brain network.	reduced functional integration, i.e., diminished information exchange effecting selective attention, working memory, inhibitory control and monitoring.	Control group were comparable in age, sex distribution, years of education, anxiety, depression and toxic habits
(Mehl *et al*., 2019)	Randomised control Trial **Extrinsic and Intrinsic**	PPI Seed based connectivity analysis Seed: Angular Gyrus	TFEQ Cognitive bias modification training approach healthy and avoid unhealthy foods	33 BMI: 35.57 (4.63) Severely obese	28 (5)	15M:18F combined but sex controlled as covariate	CBM resulted in a diminished approach bias towards unhealthy food, decreased activation in the rAG, increased activation in the ACC. Relatedly, FC between the rAG and right superior frontal gyrus increased.	AG is part of a junction linking 2 brain networks integrating external (sensory) vs. internal (memory, social-oriented stimuli) information	BMI and age Mood measured on a VAS (Good- bad mood) TFEQ and Mood not reported in analysis

(S. Frank *et al*., 2013)	Cross sectional **Extrinsic and Intrinsic**	Group spatial ICA (18 ICs)	TFEQ Obesity, Gastric Bypass surgery; High/low cal food cues	31 BMI: 40.2 (2.8) Morbidly obese	42.6(4)	focus just on female	Obesity non surgery group showed strongest FC in frontal regions of DMN during RS and cerebellum. However task did involve a high cognitive load.	DE and hunger score significantly higher in OB. HW and surgery group showed similarities in eating scores	subclinical mood and sleep disorders were not excluded
(Kullmann *et al*., 2013)	Cross sectional Extrinsic (5 networks)	ICA (6 ICs) FNC	TFEQ POMS (depression, fatigue, anger, and vigour) Fasting glucose and insulin Object recognition task	24 BMI: 30.46 ± 1.77 Obese	24.7 (2.42) Age serves as a covariate.	12M:12F both sexes combined and not controlled	Higher FC in the inferior occipital gyrus, ACC (SN), MPFC, and precuneus (DMN). Increased FNC between the temporal visual association and SN DE showed a trend between groups.	Evidence supporting the top-down deficiencies driving the overconsumption of food. Use of external stimuli high/low calories food images.	No significant differences between groups on 4 mood states

(I. García-García *et al*., 2013)	Experimental Extrinsic	ICA (3 ICs) Plus a less sensitive regional analysis.	Food/non-food/rewarding/neutral visual stimuli Hunger	37 BMI: 34.9 (4.78) Obese	34.8 (4.5)	13M:24F combined but sex controlled as covariate	Deactivation of the DMN in response to rewarding stimuli (food and non-food). Neutral stimuli was linked with activation of the DMN and deactivation of occipital and frontal areas. Overall reduced connectivity strength in OB.	Hunger served a continuous covariate. Smoking and Alcohol consumption patterns included no significant differences for **fruit and veg frequency.**	Anxiety and depression matched (HADS). BED excluded. Controlled for motivational variables, time of scan and menstrual phase. #Did not measure visual acuity.
(Tregellas *et al*., 2011)	Experimental Randomised cross over design Extrinsic	ICA	Diet conditions: eucaloric and overfed. Maintained 5% weight loss.	42 BMI: 27.5(2.6) Overweight	27.5(2.6)	20M:32F both sexes combined and not controlled	Increased activity of the DMN in reduced obese subjects. Overfeeding increases activation of the network in lean individuals. Parietal cortex activity is associated with measures of appetite.	Mean body fat difference between groups 12.1%	Menstrual cycle phase controlled (follicular phase) Diet was controlled but solely based on calorie and balanced macronutrients

(A. Dietrich *et al*., 2016)	Cross sectional Extrinsic	PPI Seed-based connectivity analysis	**TFEQ** Craving/regulating	43 BMI: 27.5 (5.3) Overweight	26.7 (3.5)	All female sample	BMI correlated with the left putamen, amygdala and insula (inverted U-shaped manner). FC between the putamen and dlPFC correlated (+) with BMI. DE correlated (-)with the strength of FC between dmPFC, amygdala, and caudate.	self-monitoring (dmPFC) or eating-related strategic action planning (caudate) and salience processing (amygdala) might be hampered with high Disinhibition	Measures of mood /habitual dieting unaccounted for.
(Kube *et al*., 2018)	Cross sectional Extrinsic	PPI Seed-based connectivity analysis	OBESITY probabilistic reinforcement learning task PREDICTION ERROR (PE)	42 BMI: 35.4 (4.5) Severely obese	29.5 (5.6)	21M:21F combined but sex controlled as covariate	individuals with obesity exhibit aberrant value representations of monetary losses in the mPFC. A decreased motivational significance of negative action consequences impacting decision making.	Maintenance of eating behaviour can be strongly determined by perception and motivational significance of health(over eating) consequence	Control group comparable with respect to gender, age, education, and working memory performance. Depression symptoms and smoking status excluded. Working memory controlled for.

(Stoeckel *et al*., 2009)	Cross sectional Extrinsic	PPI Seed-based connectivity analysis. S.E.M	graph Connectivity: NAc, AMYG, and OFC High/Low calories visual food cues	24 BMI: 30.8 – 41.2 Obese-Morbidly obese	27.8(6.2)	All female sample	greater activation of the reward system and differences in the interaction of regions within this network, may contribute to the relatively increased motivational value of foods in obese individuals.	reduced connectivity from AMYG to OFC and NAc and increased connectivity in OFC → NAc	Controlled for age, ethnicity and menstrual phase.
(Atalayer *et al*., 2014)	Cross sectional Extrinsic	PPI Seed-based connectivity analysis Seeds: amygdala and ventral striatum	high and low-ED foods in both fasted and fed states Obese Gender Difference in FC (emotion and reward)	31 BMI: 36.5 (5.55) Severely obese	35(6.9)	17M:14F separate samples	OB (F) fed state: the AMG showed greater FC with angular gyrus and precentral gyrus. Also IFG and dmPFC (cognitive control). No significant gender/BMI interactions (fasting).	Greater FC of emotion and reward- regions with sensory processing, cognitive control, motor planning/ execution reflects greater neural compensation (DE increasing over time)	BED as measured by EDE-Q served as a covariate Sub clinical eating behaviour was not measured *Speculatively findings are associated with emotional eating

(Susan Carnell, Benson, Pantazatos, Hirsch, & Geliebter, 2014)	Cross sectional Extrinsic	PPI Seed-based connectivity analysis Seeds: midbrain/ VTA and cerebellum	high and low-ED food visual and auditory cues	20 BMI: 32.9 (5.3) Obese Body fat%: 41.4 ± 6.7	22.4 (2)	All female sample	greater FC with the midbrain/VTA in response to conjoined VIS and AUD –high vs. low-ED food cues in the cerebellum	Roles of the midbrain/VTA and putamen in reward, motivation and learning of appetitive behaviours, results indicate relatively greater appetitive neural responses to high-ED food cues among obese women.	Sample contained participant with binge eating symptoms. ED and psychological disorders excluded (measure unspecified)
(Geha *et al*., 2017)	Cross sectional **Extrinsic And Intrinsic**	Global Brain Connectivity Seed-based: GBC Hubs	TFEQ DEBQ	30 BMI: 35.3 (0.9) Severely obese	27.7 (1.7)	4M: 26F	Decreased global FC in vm/vlPFC, Insula, caudate nucleus. Global FC increased in dorsal attentional networks, premotor, superior parietal lobule and visual cortex. Decreased DMN & CEN.	Increased disinhibition and increased emotional eating with increasing BMI BMI strongest predictor of Global Brain Connectivity	Age and hunger controlled for

(Nummenmaa *et al*., 2012)	Cross sectional Extrinsic fMRI and PET	PPI Seed-based connectivity analysis Effective connectivity	Obesity High/low calorie	35 BMI: 43.9 (3.74) Morbidly obese Body fat%: 48.3	43.97 (3.74)	Gender unspecified.	OB failed to activate cortical inhibitory regions (dlPFC and OFC), in response to appetizing food. Caudate nucleus showed increased FC with the amygdala and posterior insula in OB whilst viewing appetizing vs bland foods.	Effective connectivity indicates abnormally high input from AMY and post' insula, dysfunctional inhibitory control (PFC) may account for abnormal stimulus-response learning and incentive motivation (d.caudate nucleus)	Covariates: age, height and blood pressure
(Tuulari *et al*., 2015)	Cross sectional Extrinsic	PPI Seed-based connectivity analysis	Craving regulation	41 [27:14] BMI: 41.4 (3.9) Morbidly obese	42.1 (9.3)	Female only sample	OB stronger FC of the cognitive control network (SMA and precuneus), with regions involved in conflict monitoring (anterior cingulate cortex) and arousal control (thalamus)	OB during appetite control, showed diminished responses in the frontal cortices,dorsal striatum. Imaginary eating - responses diminished in the insular cortex.	Healthy controls contributed 34% of the sample

(Weygandt *et al*., 2013)	Longitudinal Extrinsic	PPI Seed-based connectivity analysis	12-week dietary protocol (Calorie restriction Nutritional counselling and Physical exercises) Delayed gratification / Cue reactivity	16 BMI: 34.5 (3.2 Obese	43 (23.2) Age and BMI-covariates	3M:13F combined but sex controlled as covariate	stronger connectivity of the DLPFC and the VMPFC is associated with healthier food choices and positively correlated with dietary. Simultaneous negatively correlated with impulsivity.	Pre diet impulse control predicted dietary success.	Diet protocol: 8-week formula diet portions followed by 4 weeks of 3 meals a day minimalizing carbohydrate intake. All disorders excluded, assessed via 2X clinical psychology screenings
(Kahathuduwa, Davis, O'Boyle, Boyd, *et al*., 2018)	Randomised control trial Extrinsic	PPI Seed based connectivity analysis (Seed: dlPFC)	TFEQ, Food Craving Inventory; Power of Food Scale; Yale Food Addiction 3 wk meal replacement TMR shakes vs. calorie restricted 1120Kcal/day	32 BMI: 35.1 (3.8) Severely obese Body fat mass: 38.7 ± 11.5	31.3 (11.9)	12M:16F combined but sex controlled as covariate	dlPFC cortex was increased in the MR indicating that calories restriction may be increasing overall executive control over ingestion, often observed in RE.	The dlPFC, negatively modulating (suppressing) the food cue reactivity in the Nucleus Accumbens. TMR may enhance negative modulatory effects on the left OFC, right insula and bilateral amygdala.	Menstrual phase, BMI, Body Fat Mass, BP **body fat mass controlled to observe differential brain influences related to type of diet, reflecting neurocognitive changes distinguishing intentions to regulate eating.

(Hinkle *et al*., 2013)	Randomised control trial Extrinsic	PPI Seed based connectivity analysis (Seed: Hypothalamus)	Reduced weight maintenance, Leptin repletion, Obesity	10 BMI: 39.9 (8.2) Severely obese	36.8(6.5)	2M:8F	Weight loss increased FC of hypothalamus with visual and attention areas. Leptin repletion increased FC hypothalamus with the insula and the central and parietal operculae but decreased FC with the OFC, frontal pole, and dorsal ACC.	Reintegration of hypothalamic functional circuitry (frontal reward+ emotion) areas. An up-regulation of neural sensitivity to food cues following weight loss, partially reversed by leptin repletion.	macronutrient content, exercise and the social environment that food is administered
(Filbey & Yezhuvath, 2017)	Randomised control trial Extrinsic	PPI Seed based connectivity analysis (Seed: right Inferior Frontal Gyrus)		34 BMI: 30.7 (6.3) Obese	32.6 (10.6)	13M:21F	BMI was related to decreased BOLD response during inhibitory control in temporal and insular lobes (attentional and salience processing). Trait impulsivity mediates the relationship between BMI and neural response.	Significant positive connectivity between the rIFG seed region and the left PCC (DMN), positive association between BMI and FC between the rIFG(DMN) and rMFG (SN)	BMI, Impulse Sensation Seeking Scale (ImpSS) Controlling for ImpSS illustrates that the effects of BMI on brain response during inhibitory control is in part due to impulsive personality.

Table 19

Summary of studies exploring the relationship between eating styles, disordered eating and functional networks.

Author	Design	Technique	Measures	N	Age	Gender	Findings	Comments	Confounders
(Boehm *et al.*, 2014)	Cross sectional Intrinsic	ICA (26 ICs) 10 RSNs	Interoceptive awareness, Anorexia Nervosa (AN) symptomatology Clinical measures: All subjects assessed for eating-related psychopathology, Eating disorder-specific psychopathology and personality dimensions	70 Un-medicated BMI: AN:14.8 ±1.26 HW: 20.8 ±2.72	AN: 16.1 (2.56) HW: 16.2 (2.64)	All female sample Eumenorrheic Control group recruited from schools or universities.	Increased FC in the fronto-parietal network No group differences in FC in the SN. Anterior insula, (part of the ventral neurocircuit), more strongly connected to the DMN in AN.	Subthreshold AN controls also have RSN characteristics similar to AN. RSN characteristics are expressed along a continuum, representing a vulnerability factor rather than a consequence of AN. However, cannot discount symptom denial in AN	Comorbid conditions assessed by clinician and medical records Groups were matched for age and similar exclusion criteria applied. Regular binge eating was part of the exclusion criteria

(Zhao *et al.*, 2017)	Cross sectional Intrinsic	ICA Seed based connectivity analysis	TFEQ	99 BMI: 27.18 ± 0.58 **Over weight**	35.1 ± 1.14	62M:37F	positive correlation of the activities of the lateral OFC and disinhibition to eating is consistent with the idea that hyper-activation of the motivation system contributed to food anticipation and intake	DE positively correlated with ALFF in several brain regions within the frontal cortex, cingulate, and cerebellum Disinhibited eating scores generally low for the sample (slightly higher than that reported of AN patients)	age, gender, and handedness
(Lee *et al.*, 2014)	Cross sectional Intrinsic	Seed based connectivity analysis (Seed: dorsal ACC)	Eating Disorders: AN, BN EDI-2 Interoceptive Accuracy	58 BMI: AN: 16(1.7), BN 21.6(2.3), Ctrl: 19.9(1.9)	AN=16(1.7) BN= 21.6(2.3) Controls= 19.9(1.9) All subjects underwent DSM4 clinical interviews.	Female only sample Recruited from an eating disorder clinic. HC were volunteers from the community.	AN: greater synchronous activity (dACC and retrosplenial cortex) BN: greater synchronous activity (dACC and mOFC) ED: stronger FC (dACC and precuneus)	FC of the dACC and precuneus might be associated with the disorder-specific rumination on dieting, body weight and shape.	Movement parameters were added as first-level covariate, and age, education, BDI, BAI and BMI scores were added as second-level covariates.

(Stopyra *et al.*, 2019)	Cross sectional Intrinsic	ICA (20 ICs) Seed based connectivity analysis (Seed: dorsal ACC)	Binge Eating Disorder BED Bulimia Nervosa BN DEBQ	113 BMI: BED: 32.6(13.1) Obese BN:21.3(2.99)	BED: 38.4 (13.1) BED control: 39.4 (10.5) BN: 27.5 (10.6) BN Control: 26.9 (6.6);	Gender ratio unspecified combined but sex controlled as covariate	BN: greater synchronous activity (dACC and bilateral retrosplenial cortex) correlated with the quantity of weekly binges BED: stronger FC (dACC and somatosensory cortex.	Eyes closed Contradictory findings regarding the vmPFC but could be explained by hemispheric laterality, patient group (left/emotional) region more affected. *Overlap with obesity	Education, age, gender, BMI and depressive symptoms (assessed using the BDI) matched
(Benson, 2020)	Cross sectional Intrinsic	Seed based connectivity analysis	Development markers of BN Loss of control eating (LOC) weight concern (WC)	155 BMI: 24.63 ± 5.35 Healthy weight	14.28 ± 2.62	44M:111F combined but sex controlled as covariate	LOC group showed less connectivity (frontoparietal network to the PCC) and decreased connectivity between the superior frontal gyrus (SFG) and (PPC) and decreased connectivity between the brain steam and insula.	LOC eating is related to dysfunction in connectivity between a control network and regions related to self-awareness or self-reflection, and WC is related to dysfunction in connectivity of somatosensory to visual processing region	Depression and anxiety symtomology controlled for.

(Martín-Pérez *et al.*, 2019)	Cross sectional Intrinsic	Seed based correlational analysis (seed: lateral and medial Hypothalamus)	DEBQ, Emotional Eating Excess weight, Salivary cortisol (Trier Social Stress Task),	104 BMI percentile: NW: 52.35 (24.35); EW: 93.98(3.98)	NW: 15.29 (1.75) EW:14.64(1.78)	36M:68F combined but sex controlled as covariate	EW: higher FC between the LHypothalamus and the lateral OFC, the ventral striatum, the anterior insula higher connectivity between the MH, which contributes to inhibit eating behaviours	LH−midbrain network also showing a positive association with emotional eating in the EW group.	Age subject-specific number of outlier volumes
(S. Chen *et al.*, 2016)	Cross sectional Intrinsic	Seed based connectivity analysis (Seed: DLPFC) Voxel mirrored homotropic	Restrained eating RE BN symptoms	47 BMI: RE:21.1 (2.38); Controls:21.0 (2.5) Healthy weight	RE: 20.74 (1.51); Ctrl: 21.04(1.85	All female sample Chinese sample	Decreased RSFC between the right DLPFC and regions associated with reward estimation – the (VMPFC) and (PCC).	BN-REs showed reduced FC in appetite inhibition regions and altered FC in reward regions, may explain why some REs fail to control hedonically-motivated feeding.	Age, BMI, fasting time, hunger level and menstrual cycle phase

(Lavagnino *et al*., 2014)	Cross sectional Intrinsic	Seed based connectivity analysis (Seed: paracentral lobule) Voxel mirrored homotropic	BN EDI-2 Interoceptive Accuracy	34 BMI: 21(2) BN; 22(2)	BN:23(5); Controls: 23(3)	All female sample	reduction in the functional connectivity of the somatosensory network in BN subjects	No significant differences in the within-network rs-FC of the other networks (executive, salience, DMN) in BN patient	age, BMI depressive symptoms
(Canna *et al*., 2017)	Cross sectional Intrinsic	Seed based connectivity analysis (Seed: paracentral lobule) Voxel mirrored homotropic	AN BN inter-hemispheric spectral coherence Slow 5 band	44 BMI: AN:16.8(1.6);HW: 21.1(1.6)	AN= 25.3 (1.6); BN=27.2(2); HW= 26.1(3.5)	All female sample 15 AN and 13 BN patients and 16 healthy controls (HC)	AN: exhibited reduced VMHC in cerebellum, insula, and precuneus, BN: showed reduced VMHC in DLPFC and OFC	loss of inter-hemispheric connectivity in regions implicated in self-referential, cognitive control and reward processing	Age Illness duration

(Wang *et al*., 2017)	Cross sectional Intrinsic	Graph Theory global and regional topological properties	BN, within network connectivity EDI-2	88 BMI: BN: 21(2.6) Controls: 20.5(1.4)	BN 22(3.4); Ctrl: 23.1(3.4)	All female sample Community recruited control All subjects completed EDI and	higher nodal strength in sensorimotor and visual regions and the precuneus, but lower nodal strength in several subcortical regions (insula, amygdala, putamen, thalamus)	dysfunctional integration among large-scale, distributed brain regions/networks.	age, education and mean values of Frame wise Displacement Mood disorders excluded Hamilton depression/anxiety scales
(G. K. W. Frank *et al*., 2016)	Cross sectional Extrinsic	Effective dynamic connectivity White matter connectivity strength	AN, BN, Sucrose solution- sweet taste perception, Homeostasis Reward EDI-3 Temperament and Character Inventory Sensitivity to Punishment and Reward Questionnaire	77 BMI: AN=16.23(1.09); BN=23.56(5.89); HW=21.61(1.21)	AN=23.23(5.26); BN=24.64(3.22); HW=24.39(3.49)	All female sample Community recruited All subjects participated in DSM4 clinical interviews	AN and BN had greater structural connectivity in pathways between insula, OFC and ventral striatum, but lower connectivity from OFC and amygdala to the hypothalamus	AN: additional negative correlation with connectivity strength between thalamus, hypothalamus and insula (sweet taste perception	Age was matched, BMI, Pleasantness Perception. Depression and anxiety measured

(Geliebter *et al*., 2016)	Cross sectional Extrinsic	PPI Seed based connectivity analysis (Seed: dorsal ACC)	Low vs High energy dense food Binge eating vs non binge eating groups DEBQ Questionnaire on Eating and Weight Patterns	20 BMI: 27.4(5.8), 27.7(7.2)HW Over weight	Binge: 22.1(2.3); HW: 21.3(0.6)	All female sample	more activation than the non-BE group in the dACC, with no activation differences in the striatum or OFC Binge eaters also scored higher on EE.	hyper-responsivity in the dACC as well as increased coupling with insula, cerebellum, and supramarginal gyrus	BMI Depression score Body fat %
(Bohon & Stice, 2012)	Cross sectional Extrinsic	PPI Seed based connectivity analysis (Seed: Amygdala)	BN Anticipatory, receipt of milk shake	61 BMI: 23.93(2.82) BN: 23.19(2.42)HW	20.3 (1.9)	All female ethnically diverse sample Diagnostic interviews	greater relation of amygdala activity to activation in the left putamen and insula during anticipation in the bulimia group. The opposite pattern was found for the taste of milkshake	significant positive correlation between brain activation in the putamen, caudate, and pallidum in response to anticipated receipt of milkshake and negative affect, no significant relation between brain activity and negative affect in healthy controls	BMI Age Did not control for handedness Mood was measured using Positive and Negative Affect Schedule (Regressor)

(Neveu *et al.*, 2018)	Cross sectional Extrinsic	PPI Seed based connectivity analysis (Seed: DLPFC) 4 x GLM	BN Unhealthy vs healthy food choices Self-rating tastiness of foods goal directed processes	61 BMI: 19.9(2.5)BN; 21.3(2.36)HW	24(3.87)BN; 23(2.7)HW 6 participants had diagnosed comorbid conditions (OCD, phobias and MDD)	All female ethnically diverse sample Control group: free of any eating disorder and diet	vmPFC activity correlated with health, choice and taste ratings. dlPFC was more coupled with the vmPFC during uncontrolled than controlled choices	connectivity between the left dlPFC and the vmPFC is critical in the development of self-control and in the improvement of anxiety and major depressive disorders .	Menstrual cycle randomly allocated to morning or afternoon assessments to account for circadian variations

Appendix B2: Chapter 3 study 1 Three Factor Eating Questionnaire

The Three-Factor Eating Questionnaire

Please read each statement and select from the multiple choice options the answer that indicates the frequency with which you find yourself feeling or experiencing what is being described in the statements below.

1. When I smell a delicious food, I find it very difficult to keep from eating, even if I have just finished a meal.
Definitely true (4)/ mostly true (3)/ mostly false (2)/ definitely false (1)
2. I deliberately take small helpings as a means of controlling my weight.
Definitely true (4)/ mostly true (3)/ mostly false (2)/ definitely false (1)
3.When I feel anxious, I find myself eating.
Definitely true (4)/ mostly true (3)/ mostly false (2)/ definitely false (1)
4. Sometimes when I start eating, I just can't seem to stop.
Definitely true (4)/ mostly true (3)/ mostly false (2)/ definitely false (1)
5. Being with someone who is eating often makes me hungry enough to eat also.
Definitely true (4)/ mostly true (3)/ mostly false (2)/ definitely false (1)
6. When I feel blue, I often overeat.
Definitely true (4)/ mostly true (3)/ mostly false (2)/ definitely false (1)
7. When I see a real delicacy, I often get so hungry that I have to eat right away.
Definitely true (4)/ mostly true (3)/ mostly false (2)/ definitely false (1)
8. I get so hungry that my stomach often seems like a bottomless pit.
Definitely true (4)/ mostly true (3)/ mostly false (2)/ definitely false (1)
9. I am always hungry so it is hard for me to stop eating before I finish the food on my plate.
Definitely true (4)/ mostly true (3)/ mostly false (2)/ definitely false (1)
10. When I feel lonely, I console myself by eating.
Definitely true (4)/ mostly true (3)/ mostly false (2)/ definitely false (1)
11. I consciously hold back at meals in order not to weight gain.
Definitely true (4)/ mostly true (3)/ mostly false (2)/ definitely false (1)

12. I do not eat some foods because they make me fat.
Definitely true (4)/ mostly true (3)/ mostly false (2)/ definitely false (1)
13. I am always hungry enough to eat at any time.
Definitely true (4)/ mostly true (3)/ mostly false (2)/ definitely false (1)
14. How often do you feel hungry?
Only at meal times (1)/ sometimes between meals (2)/ often between meals (3)/almost always (4)
15. How frequently do you avoid "stocking up" on tempting foods?
Almost never (1)/ seldom (2)/ moderately likely (3)/ almost always (4)
16. How likely are you to consciously eat less than you want?
Unlikely (1)/ slightly likely (2)/ moderately likely (3)/ very likely (4)
17. Do you go on eating binges though you are not hungry?
Never (1)/ rarely (2)/ sometimes (3)/ at least once a week (4)
18. On a scale of 1 to 8, where 1 means no restraint in eating (eating whatever you want, whenever you want it) and 8 means total restraint (constantly limiting food intake and never "giving in"), what number would you give yourself?

Revised 18-Item (Karlsson et. Al. 2000)

Appendix B3: Chapter 3 study 1 Profile of Mood states BiPolar scale

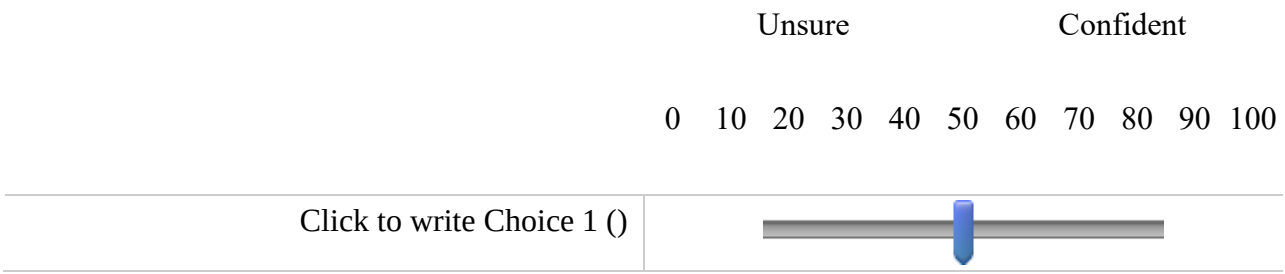
Q1 How do you feel right now?

	Anxious Composed 0 10 20 30 40 50 60 70 80 90 100
2 ()	

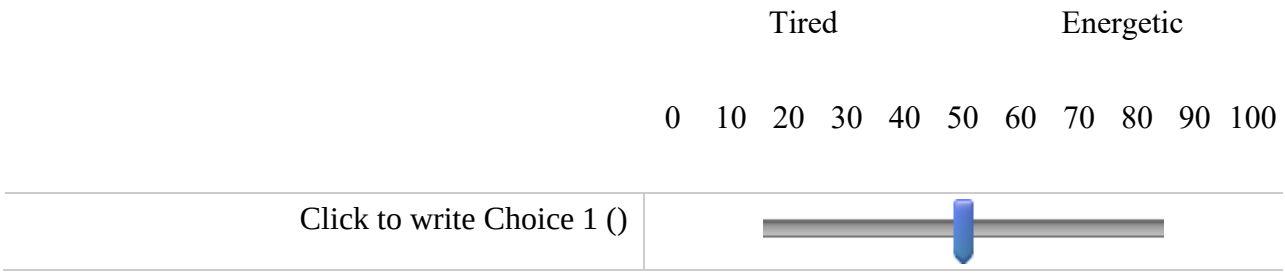
Q2 How do you feel right now?

	Hostile Agreeable 0 10 20 30 40 50 60 70 80 90 100
Click to write Choice 1 ()	

Q3 How do you feel right now?



Q4 How do you feel right now?



Q5 How do you feel right now?

Confused Clearheaded

	0 10 20 30 40 50 60 70 80 90 100
Click to write Choice 1 ()	

Q6 How do you feel right now?

	Depressed Elated 0 10 20 30 40 50 60 70 80 90 100
Click to write Choice 1 ()	

Appendix B4: Chapter 3 study 1 Food Frequency Questionnaire

This questionnaire asks for some background information about you, especially about what you eat. Please estimate your average food use as best you can, and please answer every question - do not leave ANY lines blank. For each food there is an amount shown, either a "medium serving" or a common household unit such as a slice or teaspoon. Please click the circle corresponding to how often, **on average**, you have eaten the specified amount of each food **during the past year.**

Meat and fish (medium serving)

	Never or less than once/month (1)	1-3 per month (2)	Once a week (3)	2-4 per week (4)	5-6 per week (5)	Once a day (6)	2-3 per day (7)	4-5 per day (8)	6+ per day (9)
Beef: roast, steak, mince, stew, or casserole (1)	○	○	○	○	○	○	○	○	○
Beefburgers (2)	○	○	○	○	○	○	○	○	○
Pork: roast, chops, stew, or slices (3)	○	○	○	○	○	○	○	○	○
Lamb: roast, chops, or stew (4)	○	○	○	○	○	○	○	○	○
Chicken or other poultry e.g. turkey (5)	○	○	○	○	○	○	○	○	○
Bacon (6)	○	○	○	○	○	○	○	○	○
Ham (7)	○	○	○	○	○	○	○	○	○
Corned beef, Spam, luncheon meats (8)	○	○	○	○	○	○	○	○	○
Sausages (9)	○	○	○	○	○	○	○	○	○

Savoury pies, e.g. meat pie, pork pie, pasties, steak & kidney pie, saussage rolls (10)	○	○	○	○	○	○	○	○	○
Liver, liver paté, liver sausage (11)	○	○	○	○	○	○	○	○	○
Fried fish in batter, as in fish and chips (12)	○	○	○	○	○	○	○	○	○
Fish fingers, fish cakes (13)	○	○	○	○	○	○	○	○	○
Other white fish, fresh or frozen, e.g. cod, haddock, plaice, sole, halibut (14)	○	○	○	○	○	○	○	○	○
Oily fish, fresh or canned, e.g. mackerel, kippers, tuna, salmon, sardines, herring (15)	○	○	○	○	○	○	○	○	○
Shelfish, e.g. crab, prawns, mussels (16)	○	○	○	○	○	○	○	○	○

Fish roe, taramasalata (17)	○	○	○	○	○	○	○	○	○

Q1.4

Bread and savoury biscuits (one slice or biscuit)

	Never or less than once/month (1)	1-3 per month (2)	Once a week (3)	2-4 per week (4)	5-6 per week (5)	Once a day (6)	2-3 per day (7)	4-5 per day (8)	6+ per day (9)
White bread and rolls (1)	○	○	○	○	○	○	○	○	○
Brown bread and rolls (2)	○	○	○	○	○	○	○	○	○
Wholemeal bread and rolls (3)	○	○	○	○	○	○	○	○	○
Cream crackers, cheese biscuits (4)	○	○	○	○	○	○	○	○	○
Crispbread, e.g. Ryvita (5)	○	○	○	○	○	○	○	○	○

Q1.5 **Cereals (one bowl)**

	Never or less than once/month (1)	1-3 per month (2)	Once a week (3)	2-4 per week (4)	5-6 per week (5)	Once a day (6)	2-3 per day (7)	4-5 per day (8)	6+ per day (9)
Porridge, Readybrek (1)	○	○	○	○	○	○	○	○	○
Breakfast cereal such as cornflakes, muesli etc (2)	○	○	○	○	○	○	○	○	○

Q1.6 **Potatoes, rice, and pasta (medium serving)**

	Never or less than once/month (1)	1-3 per month (2)	Once a week (3)	2-4 per week (4)	5-6 per week (5)	Once a day (6)	2-3 per day (7)	4-5 per day (8)	6+ per day (9)
Boiled, mashed, instant, or jacket potatoes (1)	○	○	○	○	○	○	○	○	○
Chips (2)	○	○	○	○	○	○	○	○	○
Roast potatoes (3)	○	○	○	○	○	○	○	○	○
Potato salad (4)	○	○	○	○	○	○	○	○	○
White rice (5)	○	○	○	○	○	○	○	○	○
Brown rice (6)	○	○	○	○	○	○	○	○	○
White or green pasta, e.g. spaghetti, macaroni, noodles (7)	○	○	○	○	○	○	○	○	○
Wholemeal pasta (8)	○	○	○	○	○	○	○	○	○
Lasagne, moussaka (9)	○	○	○	○	○	○	○	○	○

Pizza (10)	○	○	○	○	○	○	○	○	○

Q1.7 **Dairy products and fats**

	Never or less than once/month (1)	1-3 per month (2)	Once a week (3)	2-4 per week (4)	5-6 per week (5)	Once a day (6)	2-3 per day (7)	4-5 per day (8)	6+ per day (9)
Single or sour cream (tablespoon) (1)	○	○	○	○	○	○	○	○	○
Double or clotted cream (tablespoon) (2)	○	○	○	○	○	○	○	○	○
Low fat yogurt, fromage frais (125g carton) (3)	○	○	○	○	○	○	○	○	○
Dairy dessert (125g carton) (4)	○	○	○	○	○	○	○	○	○
Cheese, e.g. Cheddar, Brie, Edam (medium serving) (5)	○	○	○	○	○	○	○	○	○
Cottage cheese, low fat soft cheese (medium serving) (6)	○	○	○	○	○	○	○	○	○
Eggs as boiled, friends, scrambled, etc. (one) (7)	○	○	○	○	○	○	○	○	○

Quiche (medium serving) (8)	○	○	○	○	○	○	○	○	○
Low calorie, low fat salad cream (tablespoon) (9)	○	○	○	○	○	○	○	○	○
Salad cream, mayonnaise (tablespoon) (10)	○	○	○	○	○	○	○	○	○
French dressing (tablespoon) (11)	○	○	○	○	○	○	○	○	○
Other salad dressing (tablespoon) (12)	○	○	○	○	○	○	○	○	○

Q1.8 **The following on bread or vegetables...**

	Never or less than once/month (1)	1-3 per month (2)	Once a week (3)	2-4 per week (4)	5-6 per week (5)	Once a day (6)	2-3 per day (7)	4-5 per day (8)	6+ per day (9)
Butter (teaspoon) (1)	○	○	○	○	○	○	○	○	○
Block margarine, e.g. Stork, Krona (teaspoon) (2)	○	○	○	○	○	○	○	○	○
Polyunsaturated margarine (tub), e.g. Flora, sunflower (teaspoon) (3)	○	○	○	○	○	○	○	○	○
Other soft margarine, dairy spreads (tub), e.g. Blue Band, Clover (teaspoon) (4)	○	○	○	○	○	○	○	○	○
Low fat spread (tub), e.g. Outline, Gold (teaspoon) (5)	○	○	○	○	○	○	○	○	○
Very low fat spread (tub) (teaspoon) (6)	○	○	○	○	○	○	○	○	○

Q1.9 **Sweets and snacks (medium serving)**

	Never or less than once/month (1)	1-3 per month (2)	Once a week (3)	2-4 per week (4)	5-6 per week (5)	Once a day (6)	2-3 per day (7)	4-5 per day (8)	6+ per day (9)
Sweet biscuits, chocolate, e.g. digestive (one) (1)	○	○	○	○	○	○	○	○	○
Sweet biscuits, plain, e.g. Nice, ginger (one) (2)	○	○	○	○	○	○	○	○	○
Cakes e.g. fruit, sponge, home baked (3)	○	○	○	○	○	○	○	○	○
Cakes e.g. fruit, sponge, ready made (4)	○	○	○	○	○	○	○	○	○
Buns, pastries e.g. croissants, doughnuts, home baked (5)	○	○	○	○	○	○	○	○	○
Buns, pastries e.g. croissants, doughnuts, ready made (6)	○	○	○	○	○	○	○	○	○

Sponge puddings, home baked (7)	○	○	○	○	○	○	○	○	○
Sponge puddings, ready made (8)	○	○	○	○	○	○	○	○	○
Milk puddings, e.g. rice, custard, trifle (9)	○	○	○	○	○	○	○	○	○
Ice cream, choc ices (10)	○	○	○	○	○	○	○	○	○
Chocolates, single or squares (11)	○	○	○	○	○	○	○	○	○
Chocolate snack bars e.g. Mars, Crunchie (12)	○	○	○	○	○	○	○	○	○
Sweets, toffees, mints (13)	○	○	○	○	○	○	○	○	○
Sugar added to tea, coffee, cereal (teaspoon) (14)	○	○	○	○	○	○	○	○	○
Crisps or other packet snacks, e.g. Wotsits (15)	○	○	○	○	○	○	○	○	○

Peanuts or other nuts (16)	○	○	○	○	○	○	○	○	○

Q1.10 **Soups, sauces, and spreads**

	Never or less than once/month (1)	1-3 per month (2)	Once a week (3)	2-4 per week (4)	5-6 per week (5)	Once a day (6)	2-3 per day (7)	4-5 per day (8)	6+ per day (9)
Vegetable soups (bowl) (1)	○	○	○	○	○	○	○	○	○
Meat soups (bowl) (2)	○	○	○	○	○	○	○	○	○
Sauces, e.g. white sauce, cheese sauce, gravy (tablespoon) (3)	○	○	○	○	○	○	○	○	○
Tomato ketchup (tablespoon) (4)	○	○	○	○	○	○	○	○	○
Pickles, chutney (tablespoon) (5)	○	○	○	○	○	○	○	○	○
Marmite, Bovril (teaspoon) (6)	○	○	○	○	○	○	○	○	○
Jam, marmalade, honey (teaspoon) (7)	○	○	○	○	○	○	○	○	○
Peanut butter (teaspoon) (8)	○	○	○	○	○	○	○	○	○

Q1.11 **Drinks**

	Never or less than once/month (1)	1-3 per month (2)	Once a week (3)	2-4 per week (4)	5-6 per week (5)	Once a day (6)	2-3 per day (7)	4-5 per day (8)	6+ per day (9)
Tea (cup) (1)	○	○	○	○	○	○	○	○	○
Coffee, instant or ground (cup) (2)	○	○	○	○	○	○	○	○	○
Coffee, decaffeinated (cup) (3)	○	○	○	○	○	○	○	○	○
Coffee whitener, e.g. Coffee-mate (Teaspoon) (4)	○	○	○	○	○	○	○	○	○
Cocoa, hot chocolate (cup) (5)	○	○	○	○	○	○	○	○	○
Horlicks, Ovaltine (cup) (6)	○	○	○	○	○	○	○	○	○
Wine (glass) (7)	○	○	○	○	○	○	○	○	○
Beer, lager, or cider (half pint) (8)	○	○	○	○	○	○	○	○	○
Port, sherry, vermouth, liqueurs (glass) (9)	○	○	○	○	○	○	○	○	○

Spirits, e.g. gin, brandy, whisky, vodka (single) (10)	○	○	○	○	○	○	○	○	○
Low calorie or diet fizzy soft drinks (glass) (11)	○	○	○	○	○	○	○	○	○
Fizzy soft drinks, e.g. Coca cola, lemonade (glass) (12)	○	○	○	○	○	○	○	○	○
Pure fruit juice (100%) e.g. orange, apple juice (glass) (13)	○	○	○	○	○	○	○	○	○
Fruit squash or cordial (glass) (14)	○	○	○	○	○	○	○	○	○

Q1.12 **Fruit (for seasonal fruits marked *, please estimate your average use when the fruit is in season)**

	Never or less than once/month (1)	1-3 per month (2)	Once a week (3)	2-4 per week (4)	5-6 per week (5)	Once a day (6)	2-3 per day (7)	4-5 per day (8)	6+ per day (9)
Apples (1 fruit) (1)	○	○	○	○	○	○	○	○	○
Pears (1 fruit) (2)	○	○	○	○	○	○	○	○	○
Orange, satsumas, mandarins (1 fruit) (3)	○	○	○	○	○	○	○	○	○
Grapefruit (half) (4)	○	○	○	○	○	○	○	○	○
Bananas (1 fruit) (5)	○	○	○	○	○	○	○	○	○
Grapes (medium serving) (6)	○	○	○	○	○	○	○	○	○
Melon (1 slice) (7)	○	○	○	○	○	○	○	○	○
*Peaches, plums, apricots (1 fruit) (8)	○	○	○	○	○	○	○	○	○
* Strawberries, raspberries, kiwi fruit (medium serving) (9)	○	○	○	○	○	○	○	○	○

Tinned fruit (medium serving) (10)	○	○	○	○	○	○	○	○	○
Dried Fruit, e.g. raisins, prunes (medium serving) (11)	○	○	○	○	○	○	○	○	○

Q1.13 **Vegetables - fresh, frozen, or tinned (medium serving)**

	Never or less than once/month (1)	1-3 per month (2)	Once a week (3)	2-4 per week (4)	5-6 per week (5)	Once a day (6)	2-3 per day (7)	4-5 per day (8)	6+ per day (9)
Carrots (1)	○	○	○	○	○	○	○	○	○
Spinach (2)	○	○	○	○	○	○	○	○	○
Broccoli, spring greens, kale (3)	○	○	○	○	○	○	○	○	○
Brussels sprouts (4)	○	○	○	○	○	○	○	○	○
Cabbage (5)	○	○	○	○	○	○	○	○	○
Peas (6)	○	○	○	○	○	○	○	○	○
Green beans, brown beans, runner beans (7)	○	○	○	○	○	○	○	○	○
Marrow, courgettes (8)	○	○	○	○	○	○	○	○	○
Cauliflower (9)	○	○	○	○	○	○	○	○	○
Parsnips, turnips, swedes (10)	○	○	○	○	○	○	○	○	○

Leeks (11)	○	○	○	○	○	○	○	○	○
Onions (12)	○	○	○	○	○	○	○	○	○
Garlic (13)	○	○	○	○	○	○	○	○	○
Mushrooms (14)	○	○	○	○	○	○	○	○	○
Sweet peppers (15)	○	○	○	○	○	○	○	○	○
Beansprouts (16)	○	○	○	○	○	○	○	○	○
Green salad, lettuce, cucumber, celery (17)	○	○	○	○	○	○	○	○	○
Water Cress (18)	○	○	○	○	○	○	○	○	○
Tomatoes (19)	○	○	○	○	○	○	○	○	○
Sweetcorn (20)	○	○	○	○	○	○	○	○	○
Beetroot (21)	○	○	○	○	○	○	○	○	○

Coleslaw (22)	○	○	○	○	○	○	○	○	○
Avocado (23)	○	○	○	○	○	○	○	○	○
Baked beans (24)	○	○	○	○	○	○	○	○	○
Dried lentils, beans, peas (25)	○	○	○	○	○	○	○	○	○
Tofu, soya meat, TVP, Vegeburger (26)	○	○	○	○	○	○	○	○	○

Q1.14 Are there any **OTHER** foods which you ate more than once a week?

○ Yes (1)

○ No (2)

Q1.15 **If yes,** please list the food, usual serving size, and number of times eaten each week below.

_____

Q1.16 What type of milk did you most often use? **(Select one only)**

- ○ Full cream, silver (1)
- ○ Skimmed/blue (2)
- ○ Dried milk (3)
- ○ Semi-skimmed, red/white (4)
- ○ Channel Islands, gold (5)
- ○ Soya (6)
- ○ None (7)
- ○ Other, specify (8) _____

Q1.17 How much milk did you drink each day, including milk with tea, coffee, cereals etc?

- ○ None (1)
- ○ Quarter of a pint (2)
- ○ Half a pint (3)
- ○ Three quarters of a pint (4)
- ○ One pint (5)
- ○ More than one pint (6)

Q1.18 Do you usually eat breakfast cereal (excluding porridge and Ready Brek mentioned earlier)?

- ○ Yes (1)
- ○ No (2)

Q1.19 **If yes,** which **brand** and **type** of breakfast cereal, including muesli, did you usually eat? (List the one or two types most often used)

_____

Q1.20 What kind of fat did you most often use for frying, roasting, grilling etc? **Select one only**

- ○ Butter (1)
- ○ Lard/dripping (2)
- ○ Vegetable oil, please give specific type e.g. corn, sunflower (3) _____
- ○ Solid vegetable fat (4)
- ○ Margarine (5)
- ○ None (6)

Q1.21 What kind of fat did you most often use for baking cakes etc? **Select one only**

- ○ Butter (1)
- ○ Lard/dripping (2)
- ○ Vegetable oil (3)
- ○ Solid vegetable fat (4)
- ○ Margarine, please give name or type e.g. Flora, Stork (5) _____
- ○ None (6)

Q1.22 How often did you eat food that was fried at home?

- ○ Daily (1)
- ○ 4-6 times a week (2)
- ○ 1-3 times a week (3)
- ○ Less than once a week (4)
- ○ Never (5)

Q1.23 How often did you eat fried food away from home?

- Daily (1)
- 4-6 times a week (2)
- 1-3 times a week (3)
- Less than once a week (4)
- Never (5)

Q1.24 What did you do with the visible fat on your meat?

- Ate most of the fat (1)
- Ate some of the fat (2)
- Ate as little as possible (3)
- Did not eat meat (4)

Q1.25 How often did you eat grilled or roast meat? (state the number of times per week)

_____

Q1.26 How well cooked did you usually have grilled or roast meat?

- ○ Well done/dark brown (1)
- ○ Medium (2)
- ○ Lightly cooked/rare (3)
- ○ Did not eat meat (4)

Q1.27 How often did you add salt to food while cooking?

- Always (1)
- Usually (2)
- Sometimes (3)
- Rarely (4)
- Never (5)

Q1.28 How often did you add salt to any food at the table?

- Always (1)
- Usually (2)
- Sometimes (3)
- Rarely (4)
- Never (5)

Q1.29 Did you regularly use a salt substitute (e.g. LoSalt)?

- ○ Yes, please specify which brand: (1) _____
- ○ No (2)

Q1.30 Have you taken any vitamins, minerals, fish oils, fibre, or other food supplements during the past year?

- ○ Yes (1)
- ○ No (2)
- ○ Don't know (3)

Q1.31 **If yes**, please complete the table below. If you have taken more than 5 types of supplements please put the most frequently consumed brands first. Click **one** circle per line to show how often on average you consumed supplements.

	Never or less than once a month (1)	1-3 per month (2)	Once a week (3)	2-4 per week (4)	5-6 per week (5)	Once a day (6)	2-3 per day (7)	4-5 per day (8)	6+ per day (9)
Name and brand 1: (1)	○	○	○	○	○	○	○	○	○
Name and brand 2: (2)	○	○	○	○	○	○	○	○	○
Name and brand 3: (3)	○	○	○	○	○	○	○	○	○
Name and brand 4: (4)	○	○	○	○	○	○	○	○	○
Name and brand 5: (5)	○	○	○	○	○	○	○	○	○

Appendix B5: Chapter 3 study 1 – consent form

Consent Form

Project title: Weaker Connectivity in Resting State Networks is Associated with Disinhibited Eating in Older Adults**.**

Name and Contact details of the principal researcher:

Anthony Brennan - [redacted]

		Participant initial
1.	I (the participant) confirm that I have read and understand the information screen for the above study	
2.	I understand that my participation is voluntary and that I am free to withdraw at any time, without giving any reasons.	
3.	I understand what my role will be in this research, and all my questions have been answered to my satisfaction.	
4.	I understand that I am free to ask any questions at any time before and during the study.	
5.	I have been informed that the information I provide will be safeguarded.	
6.	I am happy for the information I provide to be used (anonymously) in academic papers and other formal research outputs.	
7.	I am willing for my data to be recorded.	

8.	I understand that I can request that a copy of the Participant Information Sheet be sent to me by email.	
9.	I agree to the researchers processing my personal data in accordance with the aims of the study described in the Participant Information Sheet.	
10.	I agree for my anonymous, de-identified data to be made freely available to other researchers if further research is required.	
11.	I understand that should I close the study browser before completion that I will not be debriefed on the study. I understand that I can contact the researcher (on the email address above) to be signposted to support services should I be distressed.	
12.	I agree to participate in this study that is utilizing the functional magnetic resonance imaging (fMRI) laboratory. While at the fMRI lab, I am aware that I will be screened for MRI precautions and have a sequence of MRI scans performed	

If you agree with all statements listed above, click YES.

If you disagree with any of the statements above, click NO and you will be taken to the end of this survey.

This study is being conducted by Swansea University, College of Medicine, Health and Life Science.

Thank you for your participation in this study. Your help is very much appreciated.

Appendix B6: Chapter 3 study 1 – information sheet

PARTICIPANT INFORMATION SHEET

Project Title: Weaker Connectivity in Resting State Networks is Associated with Disinhibited Eating in Older Adults

You are being invited to take part in a research project. Before you decide whether or not to participate, it is important for you to understand why the research is being conducted and what it will involve. Please read the following information carefully.

What is the purpose of the research?
Functional MRI allows investigators to study how the brain works by detecting brain activity in a resting state. The goals of this protocol are (1) to collect images of the brain whilst you are resting, we are looking to identify connectivity patterns within specific brain regions that are associated with age and eating behaviours.

Who is carrying out the research?
The data are being collected by Anthony Brennan studying for a PhD in Psychology under the supervision of Dr Hayley Young in the Department of Psychology, Swansea University. The research has been approved by the Research Ethics Committee in the Psychology Department, Swansea University.

What happens if I agree to take part?
We will ask you to fast for 12 hours before your fMRI scan appointment. While at the fMRI lab, you will be screened for MRI precautions and have a sequence of MRI scans performed. Functional MRI involves lying on a table which then moves into a hollow machine (the magnet). The actual MRI examination of your body will take from 1 to 3 hours, and you will be asked to remain as still as possible during the entire period. Small hand and foot movements are allowed in between scans (you will know you are being scanned because you will hear loud knocking noises), but it is essential that your head remains in the same position during the entire time you are in the scanner. You will hear knocking noises and will be able to talk with the operator or researcher through an intercom at various points during the scanning session. You will also be able to trigger an audible alarm at any time. While you are lying in the scanner, you will not be asked to perform any tasks. The scanner will be operated and images will be acquired.
Once the scan has been completed we will ask you to complete a series of questionnaires which ask about your eating behaviour and current mood

We are also asking permission to store your fMRI image data obtained during the scanning session in a database for future research studies related to brain structure and function

Data Protection and Confidentiality
Your data will be processed in accordance with the Data Protection Act 2018 and the General Data Protection Regulation 2016 (GDPR). All information collected about you will be kept strictly confidential. The researcher/research team will only view your data. All electronic data will be stored on a password-protected computer file held by the researchers. Your consent information will be kept separately from your responses to minimise risk in the event of a data breach.

The data that will be collected for this study will be anonymous and it will not be possible to identify and remove your data later if you decide to withdraw from the study.

What will happen to the information I provide?
An analysis will be conducted to form part of our report at the end of the study and may be presented to interested parties and published in scientific journals. Note all the information presented in any reports or publications will be anonymous and unidentifiable.

Is the participation voluntary and what if I wish to later withdraw?
Your participation is entirely voluntary – you do not have to participate if you do not want to. If you decide to participate, but later wish to withdraw from the study, then you are free to withdraw at any time, without giving a reason and without penalty. However, we will not be able to withdraw your data once the questionnaires have been submitted, given that all responses are anonymous and we will not know which data relates to you.

Data protection and privacy notice
The data controller for this project will be Swansea University. The University Data Protection Officer provides oversight of university activities involving the processing of personal data and can be contacted at the Vice Chancellor's Office.

Your personal data will be processed for the purposes outlined in this information sheet.
Standard ethical procedures will involve you providing your consent to participate in this study by completing the consent form provided to you or by ticking the box provided, if consent is collected with an online survey.

The legal basis that we will rely on to process your personal data will be processing is necessary for the performance of a task carried out in the public interest. This public interest justification is approved by the College of Human and Health Sciences Research Ethics Committee, Swansea

University.

The legal basis that we will rely on to process special categories of data that will be processed is necessary for archiving purposes in the public interest, scientific or historical research purposes or statistical purposes.

How long will your information be held?
Data will be preserved and accessible for a minimum of 10 years after completion of the research.

What are your rights?
You have a right to access your personal information, to object to the processing of your personal information, to rectify, to erase, to restrict and to port your personal information. Please visit the University Data Protection webpage for further information regarding your rights. Any requests or objections should be made in writing to the University Data Protection Officer: University Compliance Officer (FOI/DP), Vice-Chancellor's Office, Swansea University, Singleton Park, Swansea, SA2 8PP; Email: dataprotection@swansea.ac.uk.

How to make a complaint?
If you are unhappy with the way in which your personal data has been processed, you may in the first instance contact the University Data Protection Officer using the contact details above. If you remain dissatisfied, then you have the right to apply directly to the Information Commissioner for a decision. The Information Commissioner can be contacted at: Information Commissioner's Office, Wycliffe House, Water Lane, Wilmslow, Cheshire, SK9 5AF; http://www.ico.org.uk.

If you have any other questions about the research, please do not hesitate to contact us at:

Anthony Brennan
[redacted]
School of Psychology
Swansea
University

Dr Hayley Young
[redacted]
School of Psychology
Swansea
University

Appendix B7: Chapter 3 study 1 - debrief form

DEBRIEF FORM

Weaker Connectivity in Resting State Networks is Associated with Disinhibited Eating in Older Adults.

Thank you for taking part in our research! Now that your contribution has finished, let me explain the rationale behind this work.

We are interested in exploring age related changes within the neural networks associated with disordered eating, as well as the associated mechanisms which may be driving aberrant eating.

Previous research has shown that obesity related eating styles and disordered eating are linked with altered connectivity with the prefrontal cortex. In this research, I am looking at age related changes in connectivity within networks associated with interoception to assess how closely linked these are with influencing eating behaviour. If you would like more detailed information on this topic please contact Anthony on the below email for further reading.

Your information will be used to run analyses and produce publishable manuscripts, data will remain anonymous and stored securely, held for no longer than is necessary.

If you feel affected by issues raised by this research and would like to discuss any concerns, please contact the study Supervisor on the details provided below. If you feel this piece of research may have health implications for you, we advise you to contact your GP (family doctor).

If you have any other questions about the research, please do not hesitate to contact us at:

Anthony Brennan

[redacted]

School of Psychology

Swansea University

Dr Hayley Young

[redacted]

School of Psychology

Swansea University

Appendix B8 Chapter 3 Study 1 The association between Emotional eating (EE) and Network Connectivity

Frontoparietal Network (FPN).

No outliers were identified from this analysis. Overall, the model was significant $R^2 = 0.384$, $F(6,33) = 3.425$, $p = 0.010$, accounting for 38% of variance in FPN connectivity. Expectedly, OA had lower FPN connectivity (β = -0.557, $p = 0.003$, LLCI -0.905, ULCI -0.210). No associations were found between FPN and EE (β = -0.059, $p = 0.694$, LLCI -0.360, ULCI 0.242), BMI (β = 0.067, $p = 0.661$, LLCI -0.241, ULCI 0.375), Mood (β = -0.098, $p = 0.548$, LLCI -0.424, ULCI 0.229) and Diet (β = -0.051, $p = 0.741$, LLCI −0.361, ULCI 0.259). Likewise, no significant associations were found between FPN connectivity and EE in younger adults (β = -0.184, $p = 0.338$, LLCI -0.568, ULCI 0.201) nor in OA (β = 0.066, $p = 0.767$, LLCI -0.385, ULCI 0.518).

Default Mode Network (DMN).

One additional outlier was identified and removed from this analysis, exceeding the cooks distance threshold of 0.2 (0.25). Overall, the model was significant $R^2 = 0.330$, $F(6,32) = 2.632$, $p = 0.035$, accounting for 33% of variance in DMN connectivity. Again, OA were found to have lower DMN connectivity (β = -0.573, $p = 0.003$, LLCI -0.939, ULCI -0.207). No associations were found between DMN and EE (β = -0.159, $p = 0.321$, LLCI -0.480, ULCI 0.162), BMI (β = -0.111, $p = 0.497$, LLCI -0.441, ULCI 0.219), Mood (β = 0.066, $p = 0.694$, LLCI -0.273, ULCI 0.405) and Diet (β = 0.119, $p = 0.469$, LLCI −0.212, ULCI 0.450). Likewise, no significant associations were found between DMN connectivity and EE in YA (β = -0.190, $p = 0.339$, LLCI -0.589, ULCI 0.209) nor in OA (β = -0.126, $p = 0.611$, LLCI -0.627, ULCI 0.375).

Appendix B9 Chapter 3 Study 1: Fisher r-to-z transformation

Table 21

Fishers' r-to-z transformation

Coefficients of YA and OA in the association between DMN connectivity and disinhibited eating

YA r_a	OA r_a	Z	*p*
.132	-.465	1.83	.067

Coefficients of YA and OA in the association between FPN connectivity and disinhibited eating

YA r_a	OA r_a	Z	*p*
-.292	-.492	.68	.497

Abbreviations: DMN = Default Mode Network, FPN = FrontoParietal Network, OA = Older adults, YA = younger adults

Appendix C2: Chapter 4 study 2 - Participant consent form

Consent Form

Project title: Individual differences in sensory and expectation driven interoceptive processes: a novel paradigm with implications for disordered eating and obesity.

Name and Contact details of the principal researcher:

Anthony Brennan - [redacted]

		Participant initial
1.	I (the participant) confirm that I have read and understand the information screen for the above study	
2.	I understand that my participation is voluntary and that I am free to withdraw at any time, without giving any reasons.	
3.	I understand what my role will be in this research, and all my questions have been answered to my satisfaction.	
4.	I understand that I am free to ask any questions at any time before and during the study.	
5.	I have been informed that the information I provide will be safeguarded.	

6.	I am happy for the information I provide to be used (anonymously) in academic papers and other formal research outputs.	
7.	I am willing for my data to be recorded.	
8.	I understand that I can request that a copy of the Participant Information Sheet be sent to me by email.	
9.	I agree to the researchers processing my personal data in accordance with the aims of the study described in the Participant Information Sheet.	
10.	I agree for my anonymous, de-identified data to be made freely available to other researchers if further research is required.	
11.	I understand that should I close the study browser before completion that I will not be debriefed on the study. I understand that I can contact the researcher (on the email address above) to be signposted to support services should I be distressed.	

If you agree with all statements listed above, click YES.

If you disagree with any of the statements above, click NO and you will be taken to the end of this survey.

This study is being conducted by Swansea University, College of Medicine, Health and Life Science.

Thank you for your participation in this study. Your help is very much appreciated.

Appendix C3: Chapter 4 study 2 debrief form

DEBRIEF FORM

Project title: Individual differences in sensory and expectation driven interoceptive processes: a novel paradigm with implications for disordered eating and obesity.

Thank you for taking part in our research! Now that your contribution has finished, let me explain the rationale behind this work.

We are interested in developing a further understanding of how expectations of interoceptive processes such as fullness and eating behaviour are related. Along with testing the validity of a novel paradigm.

Previous research has shown that obesity related eating styles and disordered eating are linked with poorer accuracy of signals within the body. In this research, I am looking at different aspects of internal awareness to assess how closely linked these are with influencing eating behaviour. If you would like more detailed information on this topic please contact Anthony on the below email for further reading.

Your information will be used to run analyses and produce publishable manuscripts, data will remain anonymous and stored securely, held for no longer than is necessary.

If you feel affected by issues raised by this research and would like to discuss any concerns, please contact the study Supervisor on the details provided below. If you feel this piece of research may have health implications for you, we advise you to contact your GP (family doctor).

If you have any other questions about the research, please do not hesitate to contact us at:

Anthony Brennan

[redacted]

School of Psychology

Swansea University

Dr Hayley Young

[redacted]

School of Psychology

Swansea University

Appendix D1: Chapter 5 study 3 Participant information sheet.

PARTICIPANT INFORMATION SHEET

Project Title: The Role of Interoception in Age-Related Obesity: A Structural Equation Modelling Study.

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You are being invited to take part in a research project. Before you decide whether or not to participate, it is important for you to understand why the research is being conducted and what it will involve. Please read the following information carefully.

What is the purpose of the research?
This research is interested in investigating bodily awareness and eating behaviour. You will be asked a series of questions about your feelings, aspects of body awareness, and eating behaviours.

Your participation in this study will take approximately thirty minutes.

Who is carrying out the research?
The data are being collected by Anthony Brennan studying for a PhD in Psychology under the supervision of Dr Hayley Young in the Department of Psychology, Swansea University. The research has been approved by the Research Ethics Committee in the Psychology Department, Swansea University.

What happens if I agree to take part?
Firstly, we will ask for some background information such as your age and gender. We will then present you with a series of questionnaires which measure your eating behaviour and awareness of bodily sensations.

Data Protection and Confidentiality
Your data will be processed in accordance with the Data Protection Act 2018 and the General Data Protection Regulation 2016 (GDPR). All information collected about you will be kept strictly confidential. The researcher/research team will only view your data. All electronic data will

be stored on a password-protected computer file held by the researchers. Your consent information will be kept separately from your responses to minimise risk in the event of a data breach.

The data that will be collected for this study will be anonymous and it will not be possible to identify and remove your data later if you decide to withdraw from the study.

What will happen to the information I provide?
An analysis will be conducted to form part of our report at the end of the study and may be presented to interested parties and published in scientific journals. Note all the information presented in any reports or publications will be anonymous and unidentifiable.

Is the participation voluntary and what if I wish to later withdraw?
Your participation is entirely voluntary – you do not have to participate if you do not want to. If you decide to participate, but later wish to withdraw from the study, then you are free to withdraw at any time, without giving a reason and without penalty. However, we will not be able to withdraw your data once the questionnaires have been submitted, given that all responses are anonymous and we will not know which data relates to you.

Data protection and privacy notice
The data controller for this project will be Swansea University. The University Data Protection Officer provides oversight of university activities involving the processing of personal data and can be contacted at the Vice Chancellor's Office.

Your personal data will be processed for the purposes outlined in this information sheet.
Standard ethical procedures will involve you providing your consent to participate in this study by completing the consent form provided to you or by ticking the box provided, if consent is collected with an online survey.

The legal basis that we will rely on to process your personal data will be processing is necessary for the performance of a task carried out in the public interest. This public interest justification is approved by the College of Human and Health Sciences Research Ethics Committee, Swansea University.

The legal basis that we will rely on to process special categories of data that will be processed is necessary for archiving purposes in the public

interest, scientific or historical research purposes or statistical purposes.

How long will your information be held?
Data will be preserved and accessible for a minimum of 10 years after completion of the research.

What are your rights?
You have a right to access your personal information, to object to the processing of your personal information, to rectify, to erase, to restrict and to port your personal information. Please visit the University Data Protection webpage for further information regarding your rights. Any requests or objections should be made in writing to the University Data Protection Officer: University Compliance Officer (FOI/DP), Vice-Chancellor's Office, Swansea University, Singleton Park, Swansea, SA2 8PP; Email: dataprotection@swansea.ac.uk.

How to make a complaint?
If you are unhappy with the way in which your personal data has been processed, you may in the first instance contact the University Data Protection Officer using the contact details above. If you remain dissatisfied, then you have the right to apply directly to the Information Commissioner for a decision. The Information Commissioner can be contacted at: Information Commissioner's Office, Wycliffe House, Water Lane, Wilmslow, Cheshire, SK9 5AF; http://www.ico.org.uk.

If you have any other questions about the research, please do not hesitate to contact us at:

Anthony Brennan
[redacted]
School of Psychology
Swansea
University

Dr Hayley Young
[redacted]
School of Psychology
Swansea
University

Appendix D2: Chapter 5 study 3 Participant consent form

Consent Form

Project title: The Role of Interoception in Age-Related Obesity: A Structural Equation Modelling Study.

Name and Contact details of the principal researcher:

Anthony Brennan - [redacted]

		Participant initial
1.	I (the participant) confirm that I have read and understand the information screen for the above study	
2.	I understand that my participation is voluntary and that I am free to withdraw at any time, without giving any reasons.	
3.	I understand what my role will be in this research, and all my questions have been answered to my satisfaction.	
4.	I understand that I am free to ask any questions at any time before and during the study.	
5.	I have been informed that the information I provide will be safeguarded.	
6.	I am happy for the information I provide to be used (anonymously) in academic papers and other formal research outputs.	
7.	I am willing for my data to be recorded.	

8.	I understand that I can request that a copy of the Participant Information Sheet be sent to me by email.	
9.	I agree to the researchers processing my personal data in accordance with the aims of the study described in the Participant Information Sheet.	
10.	I agree for my anonymous, de-identified data to be made freely available to other researchers if further research is required.	
11.	I understand that should I close the study browser before completion that I will not be debriefed on the study. I understand that I can contact the researcher (on the email address above) to be signposted to support services should I be distressed.	

If you agree with all statements listed above, click YES.

If you disagree with any of the statements above, click NO and you will be taken to the end of this survey.

This study is being conducted by Swansea University, College of Medicine, Health and Life Science.

Thank you for your participation in this study. Your help is very much appreciated.

Appendix D3: Chapter 5 study 3 Participant debrief form

DEBRIEF FORM

Project title: **The Role of Interoception in Age-Related Obesity: A Structural Equation Modelling Study.**

Thank you for taking part in our research! Now that your contribution has finished, let me explain the rationale behind this work.

We are interested in developing a further understanding of how awareness of bodily sensations (both general and specific) and eating behaviour are related.

Previous research has shown that obesity related eating styles and disordered eating are linked with poorer awareness of signals within the body. In this research, I am looking at different aspects of internal awareness to assess how closely linked these are with influencing eating behaviour. If you would like more detailed information on this topic please contact Anthony on the below email for further reading.

Your information will be used to run analyses and produce publishable manuscripts, data will remain anonymous and stored securely, held for no longer than is necessary.

If you feel affected by issues raised by this research and would like to discuss any concerns, please contact the study Supervisor on the details provided below. If you feel this piece of research may have health implications for you, we advise you to contact your GP (family doctor).

If you have any other questions about the research, please do not hesitate to contact us at:

Anthony Brennan

[redacted]

School of Psychology

Swansea University

Dr Hayley Young

[redacted]

School of Psychology

Swansea University

Appendix D4: Chapter 5 study 3 Adult Eating Behaviour Questionnaire
Adult Eating Behaviour Questionnaire

	1 Strongly Disagree (1)	2 Disagree (2)	3 Neither Agree nor Disagree (3)	4 Agree (4)	5 Strongly Agree (5)
I love food. (1)	○	○	○	○	○
I often decide that I don't like a food, before tasting it. (2)	○	○	○	○	○
I enjoy eating. (3)	○	○	○	○	○
I look forward to mealtimes. (4)	○	○	○	○	○
I eat more when I'm annoyed. (5)	○	○	○	○	○
I often notice my stomach rumbling. (6)	○	○	○	○	○

I refuse new foods at first. (7)	○	○	○	○	○
I eat more when I'm worried. (8)	○	○	○	○	○
If I miss a meal I get irritable. (9)	○	○	○	○	○
I eat more when I'm upset. (10)	○	○	○	○	○
I often leave food on my plate at the end of a meal. (11)	○	○	○	○	○
I enjoy tasting new foods. (12)	○	○	○	○	○
I often feel hungry when I am with someone who is eating. (13)	○	○	○	○	○

I often finish my meals quickly. (14)	○	○	○	○	○
I eat less when I'm worried. (15)	○	○	○	○	○
I eat more when I'm anxious. (16)	○	○	○	○	○
Given the choice, I would eat most of the time. (17)	○	○	○	○	○
I eat less when I'm angry. (18)	○	○	○	○	○
I am interested in tasting new food I haven't tasted before. (19)	○	○	○	○	○

I eat less when I'm upset. (20)	○	○	○	○	○
Attention Check: Please select "Disagree" (21)	○	○	○	○	○
I eat more when I'm angry. (22)	○	○	○	○	○
I am always thinking about food. (23)	○	○	○	○	○
I often get full before my meal is finished. (24)	○	○	○	○	○
I enjoy a wide variety of foods. (25)	○	○	○	○	○

I am often last at finishing a meal. (26)	○	○	○	○	○
I eat more and more slowly during the course of a meal. (27)	○	○	○	○	○
I eat less when I'm annoyed. (28)	○	○	○	○	○
I often feel so hungry that I have to eat something right away. (29)	○	○	○	○	○
I eat slowly. (30)	○	○	○	○	○
I cannot eat a meal if I have had a snack just before. (31)	○	○	○	○	○

I get full up easily. (32)	○	○	○	○	○
I often feel hungry. (33)	○	○	○	○	○
When I see or smell a food that I like, it makes me want to eat. (34)	○	○	○	○	○
If my meals are delayed I get light-headed. (35)	○	○	○	○	○
I eat less when I'm anxious. (36)	○	○	○	○	○

Appendix D5: Chapter 5 study 3 Interoceptive Attention Scale (IATT)

The Interoceptive Attention Scale (IATS)

Below are several statements regarding how much attention you pay to specific bodily sensations? Please rate on the scale how much attention you think you pay to each specific sensation. Think about how you feel during most situations in your daily life, rather than at a specific point in time. For example, if you often think about your heart beating, feeling hungry or needing the toilet then you would rate your attention to these sensations as high. In contrast, if you don't often think about your heart rate, how hungry you are or whether you need the toilet then you would rate your attention to these sensations as low.

Please only rate how much **attention** you pay to these sensations **regardless of how well you think you can perceive them**. For example, if you often feel you need the toilet but when you go to the toilet you realise you don't need to, you should still rate your attention to this signal as high. Do not worry about how often you think the sensation is **truly** happening inside your body – we would like to know how much of the time you pay attention to these sensations

The questions ask about your attention to feelings coming from inside your body. For example, if the question asks about temperature, it is referring to sensations you notice internally without using your hand to feel how warm your skin is, and if it asks about your heartbeat, it is referring to feelings you notice inside your body without taking your pulse.

1. Most of the time my attention is focused on whether my heart is beating fast.
2. Most of the time my attention is focused on whether I am hungry
3. Most of the time my attention is focused on whether I am breathing fast
4. Most of the time my attention is focused on whether I am thirsty or dehydrated
5. Most of the time my attention is focused on whether I need to urinate
6. Most of the time my attention is focused on whether I need to defecate
7. Most of the time when I am eating, my attention is focused on different tastes
8. Most of the time my attention is focused on whether I am nauseated or need to vomit
9. Most of the time my attention is focused on whether I need to sneeze
10. Most of the time my attention is focused on whether I need to cough
11. Most of the time my attention is focused on the temperature of my body (feeling hot or cold)

12. Most of the time my attention is focused on whether I am sexually aroused
13. Most of the time my attention is focused on whether I need to pass wind
14. Most of the time my attention is focused on whether I need to burp
15. Most of the time my attention is focused on whether my muscles are tired or sore
16. Most of the time my attention is focused on whether I am in pain after I am hurt or injured
17. Most of the time my attention is focused on whether I am in pain (that is not caused by injury)
18. Most of the time my attention is focused on whether my blood sugar is low
19. Most of the time when someone is touching me, my attention is focused on whether it is pleasant / affectionate
20. Most of the time my attention is focused on whether touch or materials feel ticklish on my body
21. Most of the time my attention is focused on whether my body feels itchy

Scale: Strongly Agree (5), Agree (4), Neither agree nor disagree (3), Disagree (2), Disagree Strongly (1)

Appendix D6 : Chapter 5 study 3 Interoceptive Accuracy Scale

Below are several statements regarding how accurately you can perceive specific bodily sensations. Please rate on the scale how well you believe you can perceive each specific signal. For example, if you often feel you need to urinate and then realise you do not need to when you go to the toilet you would rate you accuracy perceiving this bodily signal as low.

Please only rate how well you can perceive these signals without using external cues, for example, if you can only perceive how fast your heart is beating when you measure it by taking your pulse this would not count as accurate internal perception.

1. I can always accurately perceive when my heart is beating fast [F1]
2. I can always accurately perceive when I am hungry [F1]
3. I can always accurately perceive when I am breathing fast [F1]
4. I can always accurately perceive when I am thirsty [F1]
5. I can always accurately perceive when I need to urinate [F1]
6. I can always accurately perceive when I need to defecate [F1]
7. I can always accurately perceive when I encounter different tastes [F1]
8. I can always accurately perceive when I am going to vomit [F1]
9. I can always accurately perceive when I am going to sneeze [F2]
10. I can always accurately perceive when I am going to cough [F2]
11. I can always accurately perceive when I am hot / cold [F1]
12. I can always accurately perceive when I am sexually aroused [F1]
13. I can always accurately perceive when I am going to pass wind [F2]
14. I can always accurately perceive when I am going to burp [F2]
15. I can always accurately perceive when my muscles are tired/sore [F1]
16. I can always accurately perceive when I am going to get a bruise [F2]
17. I can always accurately perceive when I am in pain [F1]
18. I can always accurately perceive when my blood sugar is low [F2]
19. I can always accurately perceive when someone is touching me affectionately rather than non-affectionately [F1]

20. I can always accurately perceive when something is going to be ticklish [F2]
21. I can always accurately perceive when something is going to be itchy [F2]

Scale: Strongly Agree (5), Agree (4), Neither agree nor disagree (3), Disagree (2), Disagree Strongly (1)

Appendix D7 Chapter 5 Supplementary information: Zero order correlations.

Table 22a:

Zero-order Correlations between BMI and all SEM variables (R values)

	AGE	IATT	IACC	H	SR	EOE	EUE	FR	EOF	BMI
AGE	1	-.253	.095	-.300	-.018	-.169	-.087	-.345	-.120	.077*
IATT	-.253	1	-.047	.316	.108	.130	.095	.223	-.008	-.018
IACC	.095	-.047	1	-.067	-.052	-.117	.038	-.023	.229	.014
H	-.300	.316	-.067	1	-.086	.270	-.001	.564	.173	.001
SR	-.018	.108	-.052	-.086	1	-.244	.319	-.374	-.397	-.153**
EOE	-.169	.130	-.117	.270	-.244	1	-.604	.475	.180	.321**
EUE	-.087	.095	.038	-.001	.319	-.604	1	-.216	-.172	-.242**
FR	-.345	.223	-.023	.564	-.374	.475	-.216	1	.481	.183**
EOF	-.120	-.008	.229	.173	-.397	.180	-.172	.481	1	.111**
BMI	.077	-.018	.014	.001	-.153	.321	-.242	.183	.111	1

Table 22b:

Zero-order Correlations between BMI and all SEM variables (*p* values)

	AGE	IATT	IACC	H	SR	EOE	EUE	FR	EOF	BMI
AGE	-	<.001	.003	<.001	.573	<.001	.007	<.001	<.001	.016
IATT	<.001	-	.139	<.001	<.001	<.001	.003	<.001	.795	.562
IACC	.003	.139	-	.037	.102	<.001	.237	.472	<.001	.663
H	<.001	<.001	.037	-	.007	<.001	.976	<.001	<.001	.987
SR	.573	<.001	.102	.007	-	<.001	<.001	<.001	<.001	<.001
EOE	<.001	<.001	<.001	<.001	<.001	-	<.001	<.001	<.001	<.001

EUE	.007	.003	.237	.976	<.001	<.001	-	<.001	<.001	<.001
FR	<.001	<.001	.472	<.001	<.001	<.001	<.001	-	<.001	<.001
EOF	<.001	.795	<.001	<.001	<.001	<.001	<.001	<.001	-	<.001
BMI	.016	.562	.663	.987	<.001	<.001	<.001	<.001	<.001	-

Abbreviations: BMI = Body Mass Index, EOE = Emotional Overeating, EOF = Enjoyment of Food, EUE = Emotional Undereating, FR = Food responsiveness, H = Hunger, IACC = Interoceptive Accuracy, IATT = Interoceptive Attention, SR = Satiety Responsiveness.

Note *$p < .05$ ** $p < .001$

Appendix D8 Chapter 5 study 3: Mean (SD) values for individual items of the AEBQ

Table 23

Means and standard deviations of the individual items grouped by age subscale of the AEBQ.

AEBQ Subscale	Item	Younger Adults Mean (S.D)	Older Adults Mean (S.D)
Enjoyment of Food	I love food	4.51 (.816)	4.14 (.809)
	I enjoy eating	4.41 (.917)	4.27 (.694)
	I look forward to meal times	4.27 (1.005)	4.03 (.914)
Food Fussiness	I often decide that I don't like a food, before tasting it	2.40 (1.303)	2.36 (1.208)
	I refuse new foods at first	2.00 (1.191)	2.01 (1.097)
	I enjoy tasting new foods	3.97 (1.087)	3.77 (1.044)
	I am interested in tasting new food I haven't tasted before	3.95 (1.098)	3.70 (1.108)
	I enjoy a wide variety of foods	4.17 (.987)	4.02 (.988)
Emotional Overeating	I eat more when I'm annoyed	3.20 (1.369)	2.53 (1.259)
	I eat more when I'm worried	3.03 (1.436)	2.80 (1.389)
	I eat more when I'm upset	3.54 (1.395)	2.84 (1.354)
	I eat more when I´m anxious	2.78 (1.386)	2.73 (1.295)
	I eat more when I'm angry	2.64 (1.204)	2.40 (1.135)
Hunger	I often notice my stomach rumbling	3.13 (1.142)	2.67 (1.143)
	If I miss a meal I get irritable	3.67 (1.231)	2.87 (1.247)
	I often feel so hungry that I have to eat something right away	3.14 (1.160)	2.78 (1.190)
	I often feel hungry	3.32 (1.017)	2.87 (1.012)
	If my meals are delayed I get light-headed	2.90 (1.226)	2.69 (1.198)
Satiety Responsiveness	I often leave food on my plate at the end of a meal	2.30 (1.234)	2.11 (1.104)
	I often get full before my meal is finished	3.08 (1.095)	2.81 (1.129)
	I cannot eat a meal if I have had a snack just before	2.30 (1.018)	2.65 (1.133)
	I get full up easily	2.69 (1.118)	2.70 (1.084)
Food Responsivity	I often feel hungry when I am with someone who is eating	3.45 (1.073)	2.94 (1.059)
	Given the choice, I would eat most of the time	3.34 (1.276)	2.38 (1.192)
	I am always thinking about food	3.11 (1.160)	2.41 (1.074)

	When I see or smell food that I like, it makes me want to eat	4.17 (.798)	4.00 (.741)
Slowness in Eating	I often finish my meals quickly	3.36 (1.190)	3.11 (1.257)
	I am often last at finishing a meal	2.58 (1.267)	2.77 (1.245)
	I eat more and more slowly during the course of a meal	2.64 (1.090)	2.49 (1.055)
	I eat slowly	2.64 (1.172)	2.69 (1.212)
Emotional Undereating	I eat less when I'm worried	3.03 (1.341)	2.81 (1.280)
	I eat less when I'm angry	2.97 (1.194)	2.74 (1.149)
	I eat less when I'm upset	2.84 (1.335)	2.86 (1.304)
	I eat less when I'm annoyed	2.73 (1.134)	2.61 (1.104)
	I eat less when I'm anxious	3.10 (1.330)	2.79 (1.228)