The Multisensory Mouth: An investigation into the motivational, affective, and cognitive mechanisms, driving oral behaviours.

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Contents

List of Figures

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

List of Tables

List of Abbreviations

Alum	Aluminium Potassium Sulphate
AON	Anterior Olfactory Nucleus
AQ	Autism Spectrum Quotient
AVI	Alanine-Valine-Isoleucine
CNS	Central Nervous System
ECG	Electrocardiography
EMG	Facial Electromyography
fMRI	Functional magnetic resonance imaging
GCPRs	G-Protein Coupled Receptors
GTS	Genetic taster status
HR	Heart Rate
LMS	Labelled Magnitude Scale
MSI	Multi-Sensory Integration
MVC	Maximal Volitional Contraction
NAcc	Nucleus accumbens
NaCl	Sodium chloride
NST	Nucleus of the solitary tract
OFC	Orbitofrontal cortex
P.T.C.	Phenylthiocarbamide.
PAV	Proline-Alanine-Valine
PEA	Phenyl Ethyl Alcohol
PET	Positron emission tomography
PROP	6-n-propylthiouracil
SSS	Sensory-specific satiety
TRP	Transient receptor potential
VAS	Visual Analogue Scale
VMPFc	Ventromedial prefrontal cortex
VPM	Ventral posterior medial nucleus
VTA	Ventral tegmental area

Abstract

Consumer goods and healthcare companies face significant challenges in effectively marketing their products, particularly in sectors such as food and oral health, where sensory experiences such as taste and smell play a central role in shaping consumer perceptions and purchasing decisions (Purcarea, 2019). One important aspect of product success is understanding how sensory cues influence not only immediate product liking but also long-term preferences and consummatory behaviours (Sagha et al., 2022). However, sensory experiences are not standardised across consumer populations. While cultural factors influence acceptance of certain textures or aromas (Jeong & Lee, 2021), individual differences in taste sensitivity and odour perception, for example, also significantly shape consumer responses to products (Carlson et al., 2018; Cliff & Green, 1996), suggesting a more segmented approach to product development and marketing can be beneficial (Manrique & Zald, 2006).

Difficulties arise, however, in establishing research methodologies which effectively capture individual variations in product perception and enjoyment (Spence, 2015). Traditional consumer methods, such as, focus groups and questionnaires, have limitations not only in their susceptibility to cognitive biases and demand characteristics, that lead to socially desirable or consciously filtered responses, but also in the fact they disrupt natural, on-going behaviours. For example, asking someone to consciously reflect on how much they 'like' something while still consuming it can influence their natural responses (Boesveldt & de Graaf, 2017). Moreover, these methods fail to capture spontaneous and automatic emotional responses to sensory stimuli, which can occur outside conscious perception and are central to understanding authentic consumer behaviour (Mastinu et al., 2022; Kaneko et al. 2018).

To address these limitations, objective, real-time assessment techniques are needed, which capture unconscious emotional and physiological responses to a product's sensory cues. For example, in the oral health sector, understanding how variations in taste sensitivity influence responses to menthol can help in the development of more appealing, segment targeted products. Similarly, physiological insights into how sensory cues influence food choices can guide the development of healthier food products while also helping to identify which sensory attributes resonate most strongly with different consumer segments (McCrickerd & Forde, 2016). Therefore, the studies within this PhD use behavioural and physiological methods to increase understanding of 1) how sensory and perceptual differences influence product

perception and liking and 2) which real-time measures of consumer experience are the best predictors of product enjoyment.

Motivating individuals to purchase or consume certain foods is driven by a complex interplay of psychological and sensory factors. Understanding what drives this motivation is essential for both food manufacturers and marketers, who seek to align their products with consumer desires. However, measuring these motivations presents a significant challenge, as motivation itself is an internal psychological construct that cannot be directly observed. Whilst assessments of the motivational value of food rewards have largely relied on subjective rating scales (Chae et al., 2023; Morquecho-Campos, 2021; Proserpio et al., 2019; Ramaekers et al., 2014; Gaillet et al., 2013; Rolls & Rolls, 1997), these often fail to capture implicit processes and are susceptible to biases (Chong et al., 2016). Behavioural measures, such as food selection, provide more objective insights but are susceptible to demand characteristics, which can subtly influence participants' decisions and obscure genuine motivational effects. To address these limitations, effort-based measures, which quantify motivation by the effort exerted to obtain a reward, offer an objective alternative (Mela, 2006; Pool et al., 2016). Research in both animals and humans has demonstrated that measures like progressive ratio schedules (Zepeda-Ruiz et al., 2020; Velazquez-Sanchez et al., 2015), key pressing (Temple, 2016; Rogers & Hardman, 2015), and grip-force dynamometers (Ziauddeen et al., 2014) can effectively capture changes in motivational state associated with sensory-specific satiety. Specifically, effort decreases for previously consumed foods, while remaining unchanged for novel ones.

One of the central questions addressed in this thesis is whether exposure to ambient food odours produces a motivational priming or satiety effect, and how these effects can be objectively measured. Theories of incentive motivation, (e.g. Berridge & Robinson 1998), distinguish between the mechanisms of 'wanting', a motivational drive to obtain a reward, and liking, the sensory pleasure derived from consumption of a food reward. While 'wanting' is often a non-conscious process driven by external cues, 'liking' represents a conscious hedonic experience felt during and immediately following consumption. Here, employing an effort-based measure of incentive motivation, specifically, a grip-force paradigm, (Study 1, Chapter 3) provides an objective assessment of how olfactory cues influence 'wanting' for congruent foods. The grip-force paradigm allows for the measurement of physical effort exerted to obtain a reward, providing a direct measure of motivation that is less vulnerable to cognitive biases than traditional self-report and food selection methods. This approach builds on earlier studies that

have demonstrated the validity of effort-based tasks in assessing incentive motivation for food (Pessiglione et al., 2007; Ziauddeen et al., 2012), a finding which is replicated in study 2 (Chapter 4). These findings have important implications for food marketing and oral health strategies. For instance, the impact of odour cues, may depend not only on factors such as timing, intensity, or odour type, but also on the methods used to measure consumer responses. A deeper understanding of how to accurately measure consumer motivation for products, could ultimately help companies design more effective product designs and marketing strategies, increasing product selection and consumption.

Beyond understanding how to measure and manipulate consumer motivation for products, it is also important to understand the individual variations in how people perceive products. In the food and personal care industry, aroma and fragrance are important predictors of consumer liking, and drivers of purchase (Milotic, 2003). Existing research suggests humans find it challenging to identify individual odours within even simple mixtures, with performance declining rapidly as the number of components increases beyond three (Le Berre et al, 2007; Laing & Francis 1989) even with extensive training and experience (Livermore & Laing 1996). Possibly due to perceptual phenomena such as odour blending (Le Berre et al, 2010), masking (Stevenson et al, 2007), and synergy (Thomas-Danguin et al, 2014). For instance, in odour blending, different smells fuse to form a unique composite scent, whilst in odour masking, stronger smells suppress weaker ones. However, while research on olfactory mixture perception has provided valuable insights into odour processing, the traditional approach of relying on single volatile mono-molecule odourants (Castro et al, 2021) such as vanillin (Chen et al., 2013) for understanding olfactory processing, may present limitations. This is because, odours encountered in natural settings are typically complex, multi-molecular mixtures that combine to form a unified percept (Thomas-Danguin et al, 2014), such as, roasted coffee (Grosch et al, 2000). As such, standard methods may not fully capture the complexity of natural odour experiences, potentially limiting the ecological validity and applicability of the findings to real-world olfactory perception.

Comparable to the visual domain, where scene-analysis is processed through both local (analytical) and global (configural) perspectives, olfaction also relies on a balance between local and global processing to make sense of complex odour environments (Rokni et al, 2014). Whilst global processing enables us to perceive odour mixtures as unified, cohesive odour objects, capturing the overall character of a smell, local processing allows for the identification of individual components within a mixture (Thomas-Danguin, 2014), such as detecting the

subtle hint of vanilla in a cup of coffee or the various fruity, earthy, or floral notes in wine. However, studies of perceptual scene analysis have predominantly focused on single sensory modalities, without exploring domain-general processing across senses. Evidence from other sensory domains suggests that individual differences in processing styles, such as biases for local versus global processing, can be influenced by both state and trait factors. For example, changes in affective state can influence processing style, with negative affect associated with enhanced local processing and positive affect with enhanced global processing (Gasper & Clore, 2002; de Groot et al., 2015). Additionally, a stable bias for local processing has been observed in autistic individuals and those with higher levels of autistic traits (Neufeld et al., 2019; Happé & Booth, 2008).

As such, a further aim of this thesis (Study 3, Chapter 5) is to increase understanding of the cognitive processes underlying olfactory scene analysis by determining whether ability to identify odour objects against a complex background is predicted by a visual perceptual style. Understanding how these processing styles operate in olfaction, could provide valuable insights for consumer goods companies, supporting the design of targeted marketing strategies or the creation of product variations that appeal to specific consumer segments.

Building on these individual differences in sensory processing, it is also important to consider how genetic differences in oral perception contribute to food preferences and consumption behaviours, which have important implications for food marketing in real-world settings. One example is the variation in sensitivity to the bitter compound 6-n-propylthiouracil (PROP), which categorises individuals as super-tasters, medium-tasters, or non-tasters based on their sensitivity to the bitter tasting compound, 6-n-propylthiouracil (PROP) (Bartoshuk et al., 2003; Bartoshuk et al., 1998; Delwiche et al., 2001). Super-tasters, who have a heightened sensitivity to bitterness, often exhibit stronger aversions to bitter foods, which can influence their overall dietary choices (Bartoshuk, 1991). These genetic differences not only affect the perception of bitter tastes but are also believed to extend to other oral sensations, such as astringency (Pickering & Robert, 2006) and chemesthetic properties (Bartoshuk et al, 1993; Prescott & Swain-Campbell, 2000; Prescott et al, 2004). As a result, individuals with varying taster statuses experience these oral sensations in markedly different ways, leading to a wide range of subjective food experiences. While some research has reported no associations between taster status and food preference (Dinehart et al., 2006; Yackinous & Guinard, 2006; Jerzsa-Latta et al., 1990), indicating that personality traits, culture, and experience can also impact food choices (Tepper et al., 2009), several studies have highlighted the health-related

implications of taster status, particularly in relation to body-mass index (BMI). For example, non-tasters have been found to have higher BMI compared to their super-taster counterparts. Such differences in taste sensitivity and their resulting preferences underscore the need for tailored approaches in understanding taste preferences and consumption behaviours.

To date, a vast majority of consumer research on product liking has relied on subjective measures, such as self-report ratings and questionnaires (Lim, 2011; Cordonnier & Delwiche, 2008; Meiselman & Cardella, 2003). However implicit psychophysiological techniques, such as facial electromyography (EMG), offer a powerful and objective approach for understanding hedonic responses to oral stimuli during consumption. Facial EMG measures subtle muscle activities that occur in response to emotional stimuli, including the facial expressions associated with positive or negative reactions to food. By capturing involuntary facial reactions, such as the activity of the corrugator supercilii (associated with brow lowering) and zygomatic major muscles (associated with smiling or lip corner pulling), facial EMG allows for a more nuanced and accurate understanding of consumer response than subjective ratings can provide (Cacioppo et al., 1992; Dimberg et al., 1990). Specifically, increased activity in the corrugator supercilii has been found to be negatively correlated with perceived pleasantness, while activity in the zygomatic major muscle is positively correlated with positive emotional responses, such as enjoyment (Sato et al., 2020a). An advantage of facial EMG is that it continuously monitors these subtle facial muscle movements without requiring participants to consciously reflect on or interrupt their on-going behaviour, allowing researchers to capture real-time, spontaneous emotional reactions that are unconscious and automatic (Bell et al., 2018; Hebert et al., 2008).

Therefore, a final aim of this thesis (study 4, chapter 6) is to investigate whether PROP Taster Status is predictive of subjective liking of threshold and suprathreshold concentrations of bitter, astringent and chemesthetic compounds, and determine whether facial EMG, can predict individual differences in dis/liking of these stimuli.

The importance of this programme of research lies in its potential to bridge the gap between laboratory-based studies of sensory perception and real-world consumer behaviour. Traditional sensory testing methods, such as self-report questionnaires or basic taste tests, often fail to capture the complexity of consumer responses, relying heavily on conscious introspection and subjective assessments that can be influenced by biases or demand characteristics (Bell et al. 2018; Hebert et al. 2008). By employing objective measures of motivation and affective

response, this thesis aims to increase understanding of how sensory cues influence food-related behaviours. This approach builds on and expands typical consumer and sensory testing by incorporating physiological measures, such as facial EMG, that offer real-time insights into unconscious emotional reactions. For the oral-care and food industries, insights into how sensory cues such as taste and smell shape consumer preferences can inform product development and marketing strategies, leading to more effective targeting of various consumer populations and the development of products that resonate with specific sensory profiles.

Chapter 1. Introduction

1.1 Olfaction - from Receptor to Cortex

The olfactory system can detect and discriminate millions of different volatile molecules, which provide important information about the environment (Genva et al. 2019). The detectability and discriminability of volatile molecules by the olfactory system is facilitated by several key properties inherent to odourant molecules, such as their unique chemical structures, characterised by the specific arrangements of atoms and functional groups, which play a crucial role in determining their odour characteristics (Castro et al. 2021), and their relatively low molecular weight, typically below 300 Daltons, meaning they are volatile and easily dispersed in the air from where they are inhaled into the nasal cavity (Sharma et al. 2019; Zhang et al. 2021). During inhalation, odourant molecules enter the nasal cavity and dissolve within the olfactory epithelium, a specialised tissue covering an area of approximately 2.5cm^2, situated on the upper surface of each nasal cavity and extending a short distance along the lateral wall and nasal septum (Elsaesser & Paysan, 2007). Odourants can reach the nasal epithelium via two routes (Fig 1.1a): (1) *the orthonasal pathway*: the sensation of volatile odourous molecules through inhalation, (2) *the retronasal pathway*: the sensation of odourous molecules emanating from the mouth and back of the throat during eating and drinking (Wilson, 2021; Young, 2023).

The olfactory epithelium contains three distinct cell types: olfactory receptor neurons, supporting cells, and basal cells (Chen et al. 2014) (Figure 1.1b). Olfactory receptor neurons are the primary sensory cells of the nose and are responsible for detecting odours. The supporting cells, often referred to as sustentacular cells, are non-sensory cells that provide structural and metabolic support to the olfactory receptor neurons. The basal cells are stem cells, responsible for the regeneration and replacement of olfactory receptor neurons and supporting cells (Brann & Firestein, 2014; Child et al. 2018). Olfactory receptor neurons extend a dendrite from the apical pole of their cell body to the epithelial surface, forming a knoblike protrusion with numerous cilia extending into the nasal cavity mucus (Crespo et al. 2018). When an odourant molecule binds to its specific olfactory receptor on the cilia of an olfactory receptor neuron, it initiates a cascade of events that leads to the generation of an electrical signal. These olfactory receptors, identified as G-Protein Coupled Receptors (GPCRs) through pioneering research by Buck and Axel (1991), activate a signalling pathway involving G-proteins. GPCRs are a diverse family of cell membrane proteins that play crucial roles in

various cellular signalling processes (Calebiro et al. 2021; Antunes et al. 2014), including the transmission of signals from outside to inside the cell, which results in the opening of ion channels and neuronal depolarisation (Li et al. 2022).

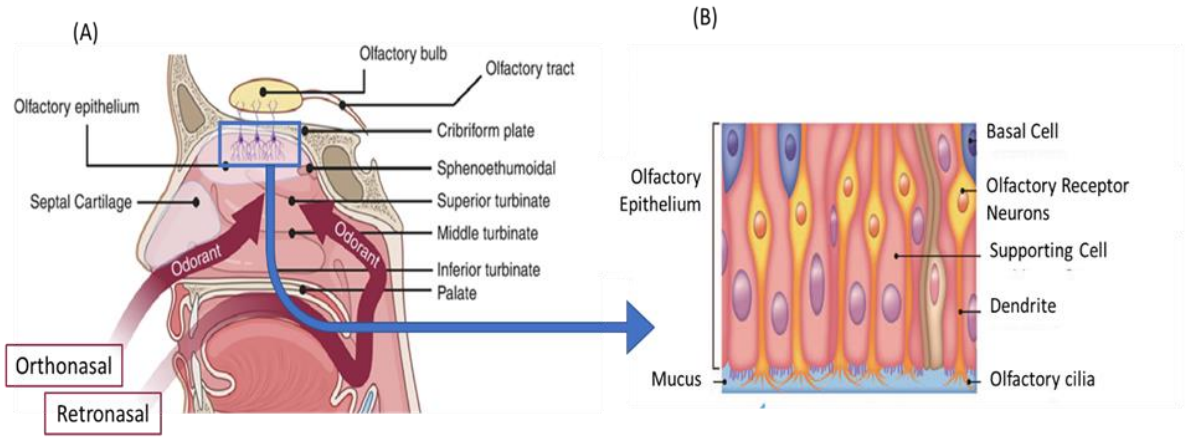

Figure 1.1: *(A) shows a sagittal section of the lateral nasal cavity, depicting the areas involved in the perception of odourants via the orthonasal and retronasal routes. (B) shows the structure of the Olfactory Epithelium (Image adapted from "Anatomy, physiology, and neurobiology of olfaction, gustation, and chemesthesis," by R. B. Jaime-Lara, L. To, and P. V. Joseph, 2021, Sensory Science and Chronic Diseases, Springer, Cham. Open access, licensed under the Creative Commons Attribution 4.0 International License).*

The genes responsible for coding GPCRs exhibit extensive diversity across species, with hundreds of distinct olfactory receptor genes identified in humans (Glusman et al. 2001; Malnic et al. 2004), rodents (Zhang et al, 2002), and canines (Olender et al. 2004). Each gene codes for a unique olfactory receptor protein, enabling the detection and discrimination of a wide array of odourants (Fleischer et al. 2009). Early estimates suggested humans can discern approximately 10,000 odours (Amoore, 1963), though recent studies propose this number may exceed one trillion (Bushdid et al. 2014), a topic of ongoing debate (Gerkin & Castro, 2015; Meister, 2015). Despite the vast diversity in odourants perceived, the actual number that humans or any mammal can distinguish remains uncertain. Notably, recordings from single olfactory receptor neurons, demonstrates that each olfactory receptor neuron responds to more than one odourant and that individual odourants activate unique sets of olfactory receptor neurons (Gonzalez-Kristeller, et al. 2015; Hu, et al. 2020; Kurian et al. 2021; Nara, et al. 2011; Sato-Akuhara, et al. 2016), providing evidence that different odourants, or indeed different concentrations of the same odourant activate a unique combination of olfactory receptor neurons within a species (Kepchia et al. 2017; Niimura et al. 2014). This pattern of

combinatorial receptor coding supports the discrimination of such a vast array of different odourants (Gonzalez-Kristeller, et al. 2015; Hu, et al. 2020; Kurian et al. 2021).

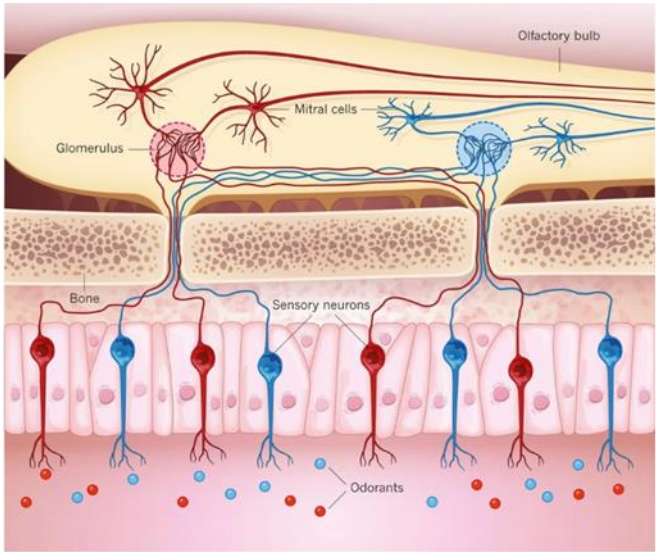

Figure 1.2: *Sensory neurons in the nose are activated by odourants (depicted in blue and red) and transmit this information to mitral cells. The transmission takes place in the glomeruli, each of which receives input from a single type of sensory cell. Mitral cells linked to the same glomeruli are functionally more similar to each other than to mitral cells that connect to other glomerular networks. (Image from "Neuroscience: Circuits drive cell diversity," by N. Urban and S. Tripathy, 2012, Nature, 488(7411), 289–290. Copyright 2012 by Nature Publishing Group. Reprinted with permission).*

The combinatorial code is further enhanced by the convergence of olfactory receptor neurons onto second-order neurons in the olfactory bulb (de March et al. 2020; Kurian et al. 2020). As olfactory nerve fibres carrying information from different receptor types, synapse onto mitral and tufted cells in the olfactory bulb, forming spherical structures known as glomeruli (Figure 1.2), each glomerulus integrates inputs from multiple receptor types (Banerjee et al. 2016) (Figure 1.3). This convergence allows for the preservation of the spatial pattern of activation, wherein distinct odourant identities are represented based on the specific combination of activated receptors. In the olfactory bulb, this preserved spatial pattern of activation serves as a foundational mechanism for integrating and processing sensory inputs from different receptor types. By combining these activation patterns, the olfactory system constructs a cohesive representation of complex, multicomponent odours (Giessel & Datta, 2014). This integrated representation facilitates the discrimination and recognition of complex, multicomponent odours, enabling individuals to discern and respond appropriately to a broad spectrum of olfactory stimuli.

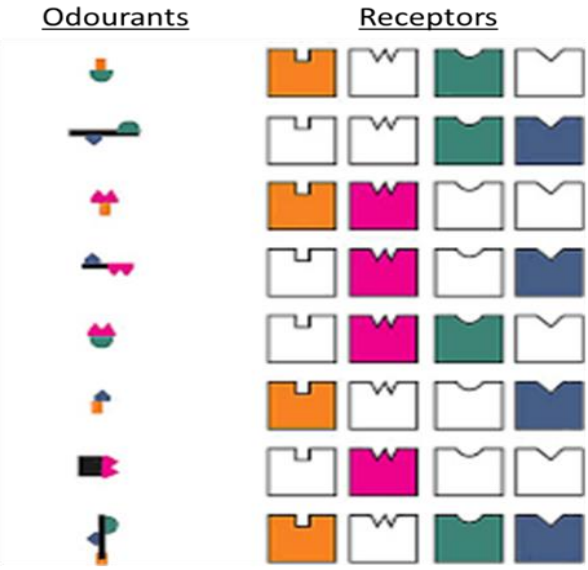

Figure 1.3: *A schematic representation of hypothetical stimulating molecules, with some shared and some distinct molecular features (left). The various patterns of neural activity that would be generated by each molecule across a theoretical population of four receptor cells (right). Each receptor cell expresses a specific receptor protein that is associated with a particular molecular feature. The activated cells for each molecule are highlighted with assorted colours. It is important to note that numerous molecules can activate multiple receptors, and each molecule produces a distinct pattern of activity within the receptor cell population. (Image from "Combinatorial receptor codes for odors," by B. Malnic, J. Hirono, T. Sato, and L. B. Buck, 1999, Cell, 96(5), 713–723. Copyright 1999 by Elsevier. Reprinted with permission).*

Olfaction stands out among sensory systems due to its distinct anatomical arrangement. Unlike other senses, in which sensory information typically travels through the thalamic nucleus prior to reaching the primary sensory cortex (Harvey & Heinbockel, 2018; Zhou et al. 2019), from the olfactory bulb processed olfactory information is transmitted directly to several cortical regions collectively known as the Olfactory Cortex (Courtiol & Wilson, 2015; Harvey & Heinbockel, 2018; Patel & Pinto, 2013). The anterior olfactory nucleus helps co-ordinate bilateral olfactory processing by connecting the two olfactory bulbs, enhancing spatial and temporal resolution. The piriform cortex is essential for decoding complex odour patterns, enabling odour identification, discrimination, and supporting associative learning. The olfactory tubercle integrates olfactory information with other sensory inputs and is involved in reward-related processing and motivational behaviours. The lateral part of the cortical amygdala links odours with emotional and motivational responses, mediating affective dimensions of smell. The anterior entorhinal cortex (EC) acts as a gateway to the hippocampus, linking olfactory signals with memory and spatial navigation, thereby contributing to odour-

associated memories and guiding behaviour based on past olfactory experiences. (Silvas-Baltazar et al. 2023).

Despite the established complexity of olfactory processing, the role of the olfactory bulb itself in this system has been reconsidered in light of recent research. Traditionally, the olfactory bulb was believed to fulfil the role of the thalamus in olfaction, due in part to similarities to thalamic nuclei in both its structure and function (Kay & Sherman, 2007). However, recent research challenges this view, as functional olfactory abilities have been identified in individuals without apparent olfactory bulbs (Rombaux et al. 2006; Weiss et al. 2020). For instance, Weiss et al. (2020) used functional Magnetic Resonance Imaging (fMRI) to demonstrate comparable olfactory perception between individuals with no visible olfactory bulb and those with intact bulbs. Possible explanations for this finding include the notion that even a small, degenerated olfactory bulb may be adequate for maintaining olfactory function or that early loss of the olfactory bulb could lead to compensatory neural adaptation (Licht et al. 2023; Slotnick et al. 2004). Evidence from both motor and sensory systems supports the brain's ability to adapt and compensate for damage through plasticity and regenerative mechanisms (Depner et al. 2014; Jones, 2017; Slotnick et al. 2004). The olfactory system exhibits high plasticity, with adult neurogenesis in the olfactory bulb and olfactory epithelium allowing for adaptation to environmental changes and restoration of function following damage (Cheetham et al. 2016; Lledo & Valley, 2016). Licht et al. (2023) further investigated this concept, reporting preserved olfactory function in mice with diminished olfactory circuitry. They suggested that compensatory mechanisms involving alternative neural pathways, or plasticity within remaining neural networks, may account for retained olfactory abilities in humans with degenerated olfactory bulbs.

It has been proposed that the direct pathway olfactory information has to cortex, bypassing the thalamus, in part explains the ability of odours to impact behaviour outside conscious awareness (Kay & Laurent, 1999). However, although there is no direct relay between the olfactory sensory neurons and the thalamus, the mediodorsal nucleus of the thalamus both receives and sends information to primary as well as secondary olfactory areas, such as the Orbitofrontal Cortex (OFC), where olfactory information is integrated with cognitive and emotional information, contributing to odour perception, memory formation, and decision-making (Rolls, 2023). Thus, the trans-thalamic pathway is functionally operational in humans and likely modulates olfactory attentional processing (Plailly et al. 2008).

1.1.1 Olfaction: The Sense of Smell

The sense of smell plays a significant role in human behaviour and provides us with vital information about the world around us, influencing various social *(i.e., relationships and communal eating)* and non-social aspects *(i.e., food preference, eating behaviour and self-care)* of our lives, perhaps most importantly supporting the identification of edible foods and avoidance of potentially dangerous situations, such as; fire, gas leaks and rotten foods (Boesveldt & Parma, 2021). While it is recognised as a crucial communication channel in many animals (Brai & Alberi, 2017), historically the sense of smell has been considered of limited importance for human behaviour (Doty, 1981; Boesveldt & Parma, 2021; Sharma et al. 2019), with research showing that individuals would be prepared to give-up their sense of smell in place of keeping their mobile phones, an attitude which remains unchanged in spite of the COVID-19 pandemic (Herz & Bajec, 2022). Scientific interest in the human sense of smell surged after two pivotal discoveries: Buck and Axel's identification of the olfactory-receptor superfamily of proteins in rodents (1991) and the Human Genome Project (Venter et al. 2015; Venter et al. 2001). These advancements significantly impacted the field of olfaction and enhanced our understanding of the sense of smell (Glusman et al. 2001; Godfrey, Malnic, & Buck, 2004; Zhang & Firestein, 2002). Building on these discoveries, researchers began to explore the anatomical and genetic differences in olfactory systems between humans and other species. Notably, a larger percentage of the mouse genome is devoted to olfactory receptors compared to humans, with mice having approximately 1100 functional olfactory receptor genes while humans have about 400 (Shephard, 2004). However, humans compensate for this difference with more intricate central processing of olfactory inputs. For example, the size of the human olfactory bulb is relatively larger (60 cubic mm compared to 27 cubic mm in mice), and humans possess more glomeruli for information processing (16 compared to 2 in mice) (McGann, 2017).

Perhaps the most notable difference between human olfactory processing, compared to that of other animals, is that humans hold more intricate cortical regions for interpreting olfactory inputs. This is particularly evident in the case of the OFC, which has a greater structural complexity and size in humans than other mammals as well as being highly interconnected with other regions of the neocortex. (Zelano & Sobel, 2005; Zhou et al. 2019). Consequently, humans are capable of advanced olfactory functions, such as the nuanced

perception and discrimination of a wide array of odours, integration of olfactory information with other sensory inputs, and the ability to form complex associations between smells and memories or emotions (Stevenson & Attuquayefio, 2013). Despite structural differences, both the peripheral and central olfactory system are generally similar in neurobiology and sensory capabilities across mammalian species (McGann, 2017). A range of studies have shown a reliance on olfaction and heightened olfactory ability in humans and non-human primates (McGann, 2017; Porter et al. 2006; Wackermannova et al. 2016), with Laska (2017) reporting that humans have lower olfactory detection thresholds for aliphatic alcohols and aldehydes than mammals traditionally esteemed for their olfactory acuity such as mice, rats and hedgehogs. Humans display inferior olfactory discrimination ability compared to species such as mice and Asian elephants, however, their capacity to distinguish between structurally related odourants appears comparable to species such as squirrel monkeys and honeybees (Rizvanovic et al. 2012). Indeed, it has been demonstrated that humans can follow a scent trail, a critical ability in microsmatic mammals. When tasked with following a chocolate scent, in the absence of visual, auditory and tactile inputs, it was found that with practice, participants improved their tracking accuracy and speed. Additionally, as with scent tracking mammals, using both nostrils simultaneously enhanced tracking performance (Porter et al. 2007). Thus, although human evolution, with adoption of an erect posture, has moved the nose away from the ground, and reduced the size of the nose (as the eyes moved to the middle of the face, supporting depth perception), data indicate that the human sense of smell is in fact much better than originally believed (Laska, 2017; Shepherd 2004).

Numerous studies have investigated the human ability to detect, discriminate, and identify monomolecular odourants, which can be influenced by various stimulus level factors including it chemical structure (Keller & Vosshall, 2016; Khan et al. 2007), For example, the molecular configuration, including size, shape, and functional groups, determines how odourants interact with olfactory receptors in the nasal epithelium. Araneda et al. (2000) reports that even minor modifications in the molecular structure of odourants, such as changes in functional groups or slight alterations in the carbon chain length, can shift the pattern of receptor activation. For instance, the addition or removal of a single functional group could result in a different set of olfactory receptors being activated. This change in receptor activation patterns translates directly into a change in the perceived odour. For example, a molecule with a slight structural alteration might be perceived as having a completely different smell, such as shifting from a floral to a fruity scent (Araneda et al. 2000; Laing et al. 2003; Sanz et al. 2008)

While the ability to detect, discriminate, and identify odours are an important facet of olfactory processing, pleasantness is the primary perceptual aspect individuals use to discriminate odours (Khan et al. 2007), with pleasant and unpleasant odourants being evaluated at different speeds (Bensafi et al. 2002) and by separable neural networks, as evidenced in both EEG recordings (Kobal et al. 1992; Masago et al. 2001) and fMRI studies (Gottfried et al. 2002; Anderson et al. 2003; Rolls et al. 2003). Humans can consistently and accurately evaluate odours based on their pleasantness, with ratings influenced by factors such as odour intensity and familiarity (Li et al. 2019; Moss et al. 2016) as well as varying according to gender (Ferdenzi et al. 2019; Seubert et al. 2008). For pleasant odours, hedonic ratings increase as concentration increases, however, for an unpleasant odour, hedonic ratings decrease as concentration increases (Li et al. 2019; Moss et al. 2016), while familiar odours are rated higher in pleasantness compared to unfamiliar odours (Distel et al. 1999; Keller & Vosshall, 2016).

To date, the vast majority of olfactory perception research has only considered orthonasal olfaction, indeed, direct comparisons of orthonasal and retronasal olfactory acuity are difficult to perform (Hannum et al. 2018). Odourants reach the same receptor fields in the olfactory epithelium, regardless of route of delivery, however, there have been reported differences in the perceived sensation and perception (Espinosa Diaz 2004; Hummel & Heilmann 2008; Small & Prescott. 2005; Welge-Lussen et al. 2009). Both human and animal research has found that retronasally presented odourants are typically perceived as less intense than the same odourants presented orthonasally (Espinosa Diaz, 2004; He et al. 2021; Hummel et al. 2005; Pierce & Halpern, 1996; Small et al. 2005), though exceptions have been reported depending on the odourant being used (Heilmann & Hummel 2004; Small et al. 2005), with Small et al. (2005) indicating that the effect is influenced by whether an odourant represents a food. Additionally, adaptation is more pronounced when odourants are delivered orthonasally but not retronasally (Pierce & Simons 2018), this occurs as a result of repeated or prolonged odour exposure, which in turn, induces a decrease in responses or behaviours. Other factors include contextual effects, differences in nasal airflow affecting odour access to the olfactory epithelium, varying trigeminal sensitivities of the respiratory epithelium, and potentially different wiring of olfactory receptor neurons (Hummel et al. 2005). Evidence suggests that orthonasal and retronasal odours may differ in their perceptual qualities (Hummel et al. 2005; Visschers et al. 2006), hedonic responses (Small et al. 2005), and behaviours (Burdach & Doty, 1987; Heilmann & Hummel, 2004). While these findings are consistent with the *'Duality of*

Smell' hypothesis, which proposes that odours perceived through the mouth may have unique sensory properties compared to those perceived from the external environment (Rozin, 1982), further research is needed to fully establish the extent and mechanistic basis of these differences.

While research on olfactory perception has provided valuable insights into odour processing, it often relies on single volatile mono-molecule odourants, such as vanillin (Chen et al. 2013), butanol, and phenyl ethyl alcohol (PEA) (Croy et al. 2009). However, this approach presents challenges, as real-world odours are typically complex multi-molecular mixtures that combine to generate a unitary percept (Thomas-Danguin et al. 2014), such as roasted coffee (Grosch et al. 2000) and red wine (Aznar et al. 2001). As such, the use of mono-molecules in research does not fully capture the complexity of natural odour experiences, potentially limiting the ecological validity and applicability of the findings to real-world olfactory perception.

1.1.2 Odour Mixture Perception

The perception of an odour mixture is not simply a sum of its individual components, rather, factors , (Bierling et al. 2021), such as individual odour intensity, (Atanasova et al. 2005; Thomas-Danguin et al. 2014), odour quality, which is associated with the chemical structure of the odourants (Kaeppler & Mueller, 2013; Sanz et al. 2008; Snitz et al. 2013) and odour pleasantness, (Kermen et al. 2011) all contribute to the overall evaluation of an odour mixture. These factors highlight the complexity involved in the perception of odour mixtures and suggest that understanding the mechanisms behind their integration is crucial for predicting the experience of such mixtures.

However, predicting the quality of an odour mixture is complicated, due to the interactions that arise from the complex chemical signal encoding and processing within the olfactory system (Thomas-Danguin et al. 2014). For example, phenomena such as odour blending (Laing & Willcox, 1983; Tromelin et al. 2020; Thomas-Danguin et al. 2014), masking (Rodriguez-Raecke et al. 2019; Stevenson et al. 2007), and synergy (Miyazawa et al. 2008; Tian et al. 2020), can all influence how we perceive and interpret the overall smell of a mixture. Odour blending occurs when the components of an odour mixture fuse together, creating a single, integrated odour sensation, which is perceived configurally (Thomas-Danguin et al.

2007; Tromelin et al. 2020;). In more complex mixtures, odour synergy can occur, where the quality of the mixture is entirely different from any of its individual components, (Lindqvist et al. 2012; Livermore & Laing, 1998; Miyazawa et al. 2008). Masking, on the other hand, happens when one odour in a mixture reduces the perception of another odour, resulting in the diminished or complete loss of the perception of one or more odour components in the mixture. The presence of certain odourants, or the concentration combination in the mixture, can mask the detection of other odours (Laing et al.1992; Ma et al. 2023). For example, when the concentration of one odour component in a binary mixture is manipulated, and the other is kept constant, the perceived intensity of the constant odour decreases, as the concentration of the manipulated odour increases, indicating a masking effect (Stevenson et al.2007).

Simple molecules, such as single volatile mono-molecular odourants (e.g. vanillin or butanol), often demonstrate predictable effects in terms of masking and blending due to their relatively well-defined and limited interactions (Chen et al. 2013; Croy et al. 2009). These mono-molecular odourants are often used in experimental studies, as their isolated perceptual qualities can be reliably assessed and quantified (Castro et al. 2021). In contrast, complex mixtures, which more closely resemble the odours encountered in real-world environments (e.g. roasted coffee or red wine), are characterised by multi-molecular interactions that can result in emergent perceptual phenomena (Thomas-Danguin et al. 2014). For example, studies have shown that when perceptually iso-intense levels of woody and fruity odours naturally present in wine (e.g. isoamyl acetate/whiskey lactone or ethyl butyrate/whiskey lactone) are combined, a blending effect may occur. This effect can render one or both individual components unidentifiable within the mixture (Thomas-Danguin et al. 2014), illustrating the configural nature of odour perception in complex systems.

Moreover, complex mixtures are more likely to exhibit synergistic effects, where the combined quality of the mixture is entirely distinct from that of any individual component (Livermore & Laing, 1998; Miyazawa et al. 2008). This phenomenon reflects the intricate combinatorial dynamics within such mixtures, which are not typically observed in simpler molecules. For instance, synergy has been noted in mixtures of floral and citrus odours, where the combined perception differs significantly from the individual contributions of each component (Tian et al. 2020; Lindqvist et al. 2012). The inherent differences between simple molecules and complex mixtures underscore the need to investigate both, as they contribute uniquely to the understanding of odour perception and mixture interactions. Simple molecules

offer insights into the fundamental properties of olfactory stimuli, while complex mixtures reveal the dynamic and often unpredictable outcomes of multi-molecular interactions in more ecologically valid contexts (Aznar et al. 2001; Grosch et al. 2000).

Due to these interactions, it is believed that the olfactory system analyses mixtures using configural processing, in which complex mixtures are perceived and interpreted as a unified whole (Coureaud et al. 2022). As such, multiple odourant molecules from the mixture bind to their corresponding olfactory receptors, leading to the activation of multiple receptors simultaneously (Chan et al. 2018; Reddy et al. 2017). The brain then interprets these activation patterns and integrates them with other sensory information to create a coherent perception of the odour mixture (Duchamp-Viret et al. 2023; Koulakov et al. 2007; Thomas-Danguin et al. 2014). However, evidence also suggests that odour mixtures can be processed analytically, where the brain dissects and analyses individual components (Kay et al. 2005). When a complex smell is perceived, the activation patterns across different olfactory receptors provides information about the composition of the odour mixture and contribute to the discrimination of individual components in the overall odour perception (de March et al. 2020; Gottfried, 2010). This specific combination and intensity of receptor activations contribute to the perception of specific odour qualities and the ability to distinguish between different odours within a mixture (Thomas-Danguin et al. 2014). This analytical processing is crucial for identifying specific environmental cues, such as potential threats or food sources, and enables precise behavioural responses (Stevenson & Wilson, 2007; Thomas-Danguin et al. 2014). For instance, when preparing a meal, analytical processing helps identify spoiled foods amidst the complex olfactory environment of multiple food odours, ensuring each component's freshness despite overlapping cues. Ultimately, how an odour mixture is perceived and whether it can be broken down into its individual components depends on a variety of factors. However, the relative perceptual intensity of individual odours is the single most important factor influencing perception of a mixture (Le Berre et al. 2007; Wilson et al. 2021). For example, a 30/70 ratio of ethyl isobutyrate (strawberry) and ethyl maltol (caramel) is identified configurally as pineapple, whilst a 68/32 ratio of the same odourants is not perceived configurally and is not identified as pineapple scent (Le Berre et al. 2007). In general, mixtures of perceptually similar odourants, which bind to overlapping populations of olfactory sensory neurons and produce overlapping activation patterns in the olfactory bulb, are more likely to be perceived configurally, whilst mixtures of perceptually dissimilar odourants are more likely to be perceived elementally (Frederick et al. 2009; Linster & Smith, 1999).

There is further evidence to suggest that olfactory perception is also heavily dependent on learning and memory, in which participants are initially poor at detecting unfamiliar odours from each other but improve rapidly following exposure (see Spence, 2019 for review). Using the same odours as Le Berre et al. (2007), it has been demonstrated that whilst a component odour mixture (strawberry and caramel) was identified configurally as pineapple, repeated exposure to the individual components shifted the perception of the odour mixture from a unified, configural perception to a more separate, analytical perception (Sinding et al. 2015). However, Livermore and Laing (1996), report that even after extensive training and experience, people have difficulty identifying individual odours contained within the simplest of mixtures, with performance declining rapidly with mixtures of more than 3 components (Laing & Francis 1989; Le Berre et al. 2007). Research investigating the ability to discriminate and identify odour mixtures reports that expert oenologists do not display superior performance to untrained individuals during odour detection tasks, though their ability to discriminate and identify specific odours is better (Poupon et al. 2018). Thus, suggesting, that while experience and training may not enhance olfactory discrimination and identification skills (Chambers & Smith 1993; Livermore & Laing 1996; Roberts and Vickers 1994), they could potentially improve detection thresholds (Parr et al. 2002). These findings may be due to a phenomenon known as adaptation, which is caused by repeated or prolonged exposure to an odourant, typically leading to elevated thresholds and reduced responsiveness to suprathreshold stimulation. Essentially, following prolonged exposure, sensory neurons become less responsive to individual components within the mixture, altering how the overall odour mixture is perceived (Kadohisa & Wilson, 2006). For example, using mixtures of benzaldehyde (cherry), maltol (caramel), guaiacol (smoke), and methyl anthranilate (grape-smoke), Frank et al. (2017) reported that identification of odours decreased for components that participants were adapted to, but increased for components that were initially suppressed within the mixture. Thus, suggesting that adaptation resulted in the overall identity of the odour compounds being maintained rather than being broken down into individual molecular features.

Given the evidence of both configural and analytical processing styles in olfaction, it is believed that the olfactory system adopts a dual approach, allowing for the complex integration and interpretation of multiple odourant components, enabling humans to discriminate a vast array of olfactory stimuli (Bushdid et al. 2014). However, to date, the vast majority of odour-mixture research relies on mono-molecular odours (Jinks & Laing 1999; Laing & Francis,

1989; Laing & Glemarec, 1992; Livermore & Laing, 1998; Luckett et al. 2021; Thomas-Danguin et al. 2014), which are not comparable to the odour mixtures encountered in real life environments.

1.2 Gustation: from Receptor to Cortex

When food enters the mouth, food molecules (tastants) are dissolved in saliva and enter taste buds on the tongue which reside in papillae, the bumps on the tongue that give it a rough texture (Spence, 2022). The taste system comprises three types of taste papillae: Circumvallate, foliate and filiform *(Figure 1.4).* Each taste bud contains basal cells which are responsible for the regeneration and turnover of taste bud cells, supporting cells which form a protective barrier and support basal cells, and around 30-100 gustatory (taste) receptor cells arranged in the shape

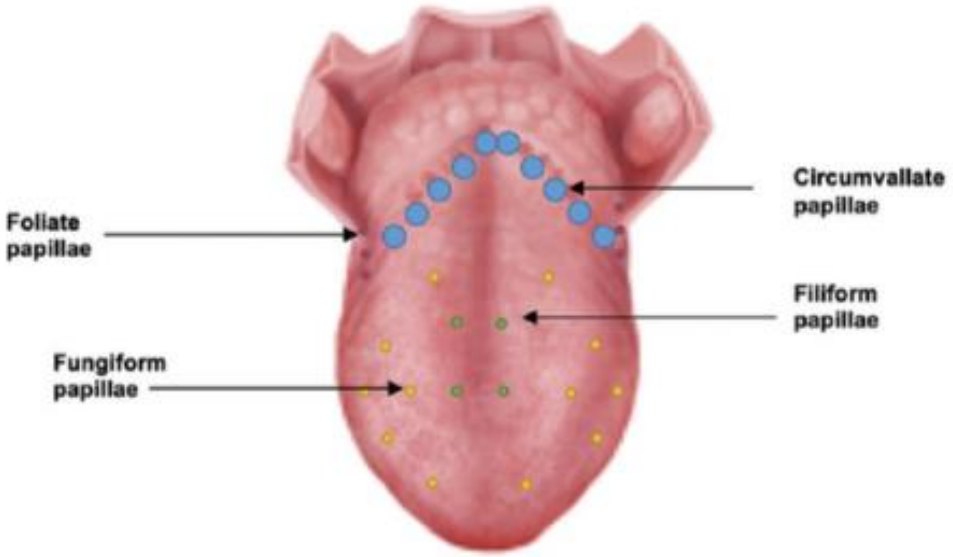

Figure 1.4*: Representation of papillae on the tongue. Raised lingual structures located at the anterior of the tongue's surface are fungiform papillae, each containing approximately 3-5 taste buds. Circumvallate papillae are located at the posterior of the tongue's surface and contain more than 100 taste buds. Located bilaterally in two zones at the sides of the tongue are foliate papillae, each also containing more than 100 taste buds. A fourth type of papillae, filiform, also exist, but do not contain any taste buds. These are responsible for the sensation of touch (Image from "Pigmented Fungiform Papillae of the Tongue in a Saudi Woman," by N. Alzahrani and R. Alharithy, 2018, Journal of Dermatology and Dermatologic Surgery, 22(1), 39–40. Open access, licensed under the Creative Commons Attribution 4.0 International License).*

of a glove with an opening, or taste pore, located at the top (Witt & Reutter, 2015). These receptor proteins are highly specific, including several classes of G protein-coupled receptors (GPCRs) and ion channels, with each responding to a particular taste quality (Yarmolinsky et al. 2009). Taste bud cells are arranged into three main categories, type I cells are known as glial-like cells and do not directly detect taste stimuli, type II cells detect bitter, sweet and

umami tastes, whilst type III cells detect sour stimuli. Salt perception is detected by undefined taste bud cells, though it has been suggested that specialised sodium taste receptor cells, a subset of Type II taste receptor cells, are responsible for this detection (Manguele & Merlo, 2023; Roper & Chaudhari, 2017). Once taste signals are generated within the taste buds, chemicals interact with taste receptor proteins located on the microvilli (small hair-like structures, located upper-side of taste receptor cells) (Chaudhari & Roper, 2010; Kinnamon, 2011). During this transduction, the binding of tastants to receptor proteins triggers intracellular signalling pathways, resulting in the release of neurotransmitters from the taste receptor cells, which are then picked up by specialised nerve fibres known as gustatory afferent fibres (Roper, 2021) *(Figure 1.5).* These neurotransmitters, including adenosine triphosphate and serotonin, act as chemical messengers, initiating the transmission of taste signals (Finger et al. 2005) to the brain via gustatory afferent fibres which are connected to a network of cranial nerves involved in gustatory processing; glossopharyngeal nerve (CN VI), facial nerve (CN VII) or vagus nerve (CN X), depending on the location of the taste bud.

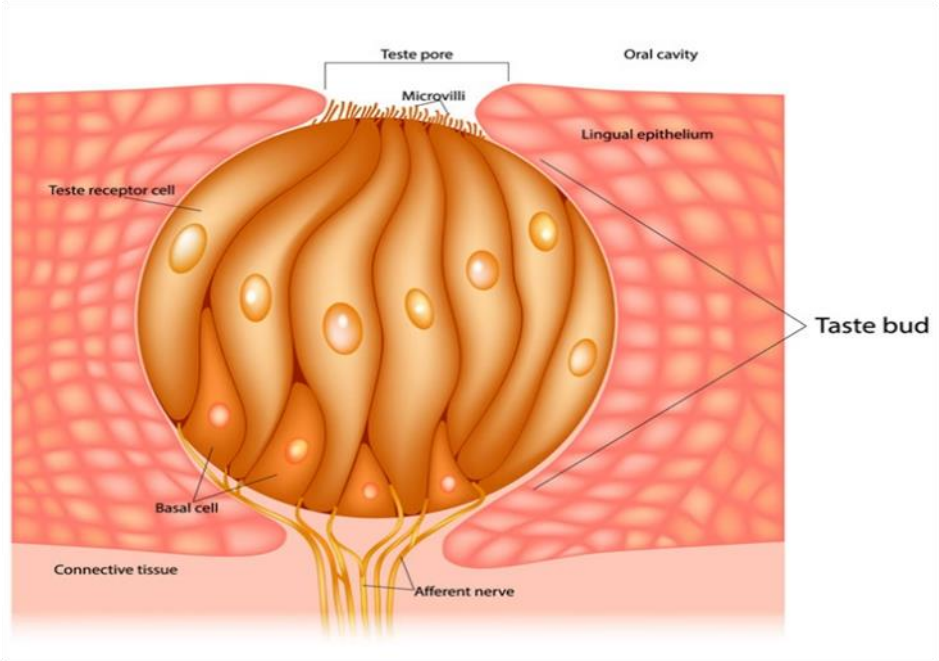

Figure 1.5: *Structure and organisation of the human taste bud. Chemical molecules react with the taste receptor proteins located on the microvilli. Each taste bud (not including filiform) contains taste receptor cells, basal cells and supporting cells. (Image from "The Senses: Smell and Taste," Dana Foundation. Retrieved from https://dana.org/resources/the-senses-smell-and-taste/)*

Taste information is then relayed to the brainstem (Fig 1.6), specifically the nucleus of the solitary tract (NST), which acts as a primary relay centre for taste information processing.

In the NST, taste signals are integrated and processed to extract essential features such as taste quality (Roussin et al. 2008), intensity, and timing (Chen et al. 2011). The gustatory fibres of the facial nerve (chorda tympani) and glossopharyngeal nerve synapse with second-order neurons in the NST, leading to the onward transmission of taste signals to higher brain regions via the Ventral Posterior Medial nucleus (VPM) of the thalamus to the gustatory cortex for further processing (Shepherd, 1995; Teeter & Cagan, 2020). This notion is supported by research reporting that the pattern of neuronal activity across thalamic sub-regions varies according to the intensity of taste stimuli presented (Avery et al. 2019). In a rodent model, neuronal responses to varied taste stimuli revealed that thalamic taste cells exhibited broad tuning and responsiveness to diverse taste qualities (Vogt & Paxinos, 2012).

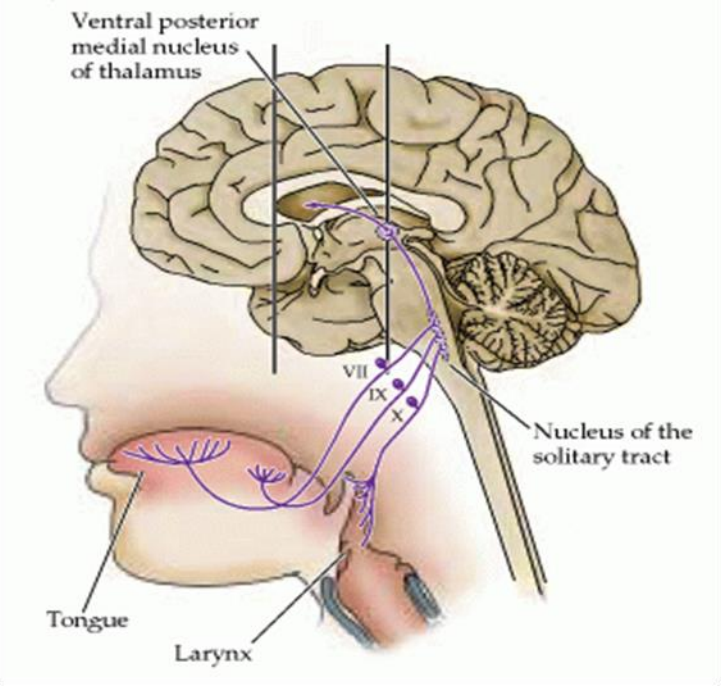

Figure 1.6: *Organisation of the human taste system. Relationship between the taste sensory organs in the oral cavity, three cranial nerves involved in transduction, and taste related domains in the brain. (Image from From "In vivo analysis of the cellular interactions during taste sensory organ assembly in zebrafish (Doctoral dissertation) by M. Soulika, 2014, Université Pierre et Marie Curie-Paris VI).*

The gustatory cortex, located within the insula and the frontal operculum regions, is responsible for processing and integrating taste information, enabling the discrimination and recognition of different taste qualities (de Araujo & Simon, 2009; Small, 2010). Neurons in this region respond selectively to specific taste qualities, forming taste-specific circuits facilitating the identification and discrimination of basic tastes (de Araujo & Simon, 2009; Rolls, 2006). Using fMRI, Avery et al. (2019) investigated brain activity during the tasting of

sweet, salty, sour, and tasteless liquids. They found activation of the primary taste cortex in the bilateral dorsal mid-insula in response to both taste and tasteless (2.5 mm NaHCO3 + 25 mm KCl) stimuli, with no consistent preference for any individual taste. However, decoding revealed distinct taste representations in the mid-insula and regions associated with affect and reward, such as the striatum, orbitofrontal cortex, and amygdala. This suggests taste quality is represented through a distributed neural network involving primary taste cortex and regions processing taste hedonics (Avery et al. 2019).

1.2.1 Gustation: The Sense of Taste

Gustation refers to the sensation elicited when chemicals stimulate taste receptors located in the taste buds, across a large portion of the tongue's dorsum and other parts of the oropharynx, such as the larynx, pharynx, and epiglottis (Spence, 2022) *(Figure 1.7).*

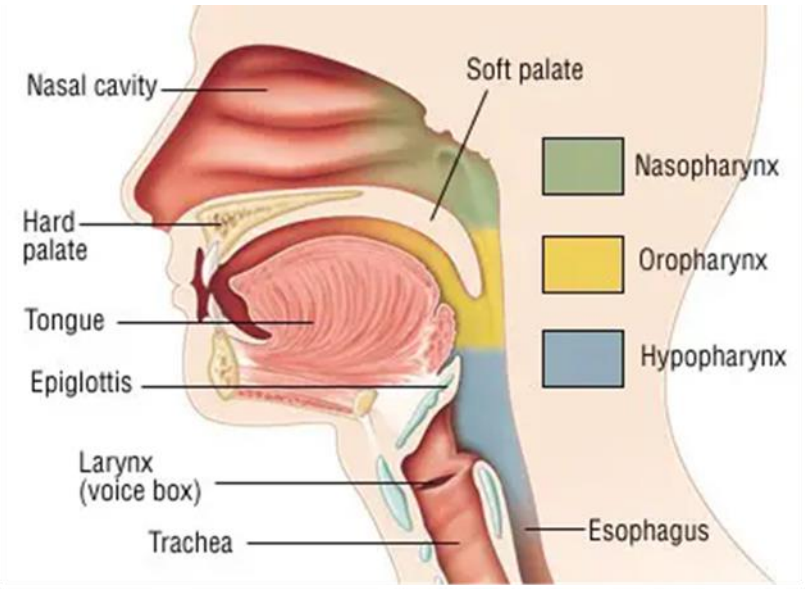

Figure 1.7: *Diagram depicting the Mouth, Pharynx and Esophagus. The dorsum refers to the uppers surface of the tongue, the oropharynx is located in the middle section of the throat, behind the mouth, comprising the soft palate, the side and back walls of the throat, the tonsils, and the back one-third of the tongue. The pharynx is the muscle-lined space connecting the nose and the mouth to the larynx and oesophagus (eating tube). The larynx (voice box) is a cylindrical grouping of cartilages, muscles and soft tissue which contains the vocal cords, and the epiglottis is a flap of soft tissue and cartilage located just above the vocal cords. The epiglottis folds down over the vocal cords to avoid food and irritants from entering the lungs (Image from "Pharynx," I Biologia by Rabiya, 2019. Retrieved from https://ibiologia.com/pharynx/#google_vignette).*

The five basic tastes; sweet, salty, sour, bitter, and umami, each signal important information about the nutrients or physiological properties of ingested substances (Gravina et al. 2013; Toepel & Murray, 2015). Salt tastes signal the presence of Sodium (Na+) and other minerals, which aid in maintenance of water balance and blood circulation. Sour taste is associated with the presence of acids, allowing for the avoidance of ingesting spoiled foods. Sweet taste signals sugars and carbohydrates, usually indicating energy rich nutrients. Umami taste, elicited by L-glutamate and a few other L-amino acids, indicates the protein content in food. Finally, bitter tastes can be a signal of the presence of toxins and poisons (Chaudhari & Roper, 2010). In addition, research using rodents (Pittman, 2010) and humans (Running et al. 2015) has proposed the existence of a sixth sensory quality, termed oleogustus. The term combines the Latin root “oleo”, meaning 'oily' or 'fatty,' with “gustus”, meaning 'taste' (Passilly-Degrace et al. 2014; Running et al. 2015). Prior to the discovery of oleogustus, the perception of fats was mainly attributed to the texture and mouthfeel of foods (Drewnowski, 1990).

In perceiving these tastes, it was once believed that specific regions of the tongue were solely responsible for detecting each taste, an idea commonly known as the ‘tongue map’ (Bartoshuk, 1993). This notion, which posited that sweet was detected at the tip of the tongue, bitter at the back, and sour and salty along the sides, was widely accepted throughout much of the 20th century (Bartoshuk, 1993; Feeney & Hayes, 2014). However, more recent research has shown that this oversimplified model does not reflect the complexity of taste perception, demonstrating that taste receptors for sweet, salty, sour, bitter, and umami are not confined to specific regions but instead, are distributed throughout the tongue and other parts of the oral cavity, including the soft palate and pharynx (Breslin & Huang, 2006; Chandrashekar et al. 2006; Spence, 2022). The hedonic response to these specific taste qualities is dependent on context and concentration and can be influenced by a combination of genetic, environmental exposures and, cultural factors. Genetic variations in taste receptors and their sensitivity to specific taste compounds play a significant role in determining taste perception. For example, variations in the TAS2R38 (bitter taste receptor) gene family are associated with differences in bitterness perception, influencing whether individuals find certain foods or beverages palatable or not (Bartoshuk et al. 1994; Tepper, 1998). Bitter tastes, are generally unpleasant and are thought to signal toxins or unripe food, posing a potential threat (Yanagisawa & Misaka, 2021). Despite this natural aversion, individuals often consume large quantities of bitter foods and drinks. This has been proposed to be due to the presence of other chemicals in these food-stuffs, such as the psychoactive compounds caffeine and alcohol, which enhance feelings of

well-being and thus override the innate rejection response to bitter tastes (Mattes, 1994). Another explanation may be that sugars have been found to suppress bitterness perception in a range of bitter agents, such as potassium chloride (Ben Abu et al. 2018), urea, caffeine, denatonium benzoate, propylthiouracil (Mennella et al. 2014) and quinine (Keast et al. 2004; Mennella et al. 2015), which in addition to providing well-liked sweetness, serves to mask the unwanted bitter taste (Ben Abu et al. 2018; Keast et al. 2004; Mennella et al. 2014). Preference of sweet foods is believed to be universal (Venditti et al. 2020; Ventura & Mennella, 2011), though sweet tastes are generally liked at all concentrations (Minella & Bobowski, 2015; Venditti et al. 2020) high concentrations can be perceived as unpleasant by some (Minella & Bobowski, 2015; Reed et al. 2006). Umami, the taste of monosodium glutamate, thought to signal protein, is considered unpleasant when tasted as a single component (Scinska-Bienkowska et al. 2006; Okiyama & Beauchamp, 1998) though when combined with breastmilk (Yamaguchi & Ninomiya, 1999) and foods such as soup (Masic & Yeomans, 2013), it can enhance the overall palatability of a meal. Salt and sour tastes are often desirable at low and moderate concentrations, though commonly avoided at high concentrations (Reed et al. 2006). Individual differences in taste perception are not limited to the bitter tastes, with variations in sensitivity to sweet and salty tastes also being reported (Hardikar et al. 2017; Venditti et al. 2020), using detection and recognition threshold tests (Joseph et al. 2021; Pugnaloni et al. 2019). Differences in sensitivity have been found to depend on factors such as age (Da Silva et al. 2013; Fukunaga et al. 2005; Kennedy et al. 2010; Wiriyawattana et al. 2018;), gender (Da Silva et al. 2013; Sanematsu et al. 2018; Wardwell et al. 2009), and ethnicity (Dora et al. 2020; Williams et al. 2016). Other external factors which impact an individual's sense of taste, include smoking-status, weight, medical disorder, and medication (Doty et al. 2008; Fischer et al. 2014).

1.2.2 Taster Status

Genetic taster status (GTS) is an inherited relative sensitivity to taste stimulation related to chromosomal expression of the *TAS2R38* gene (Duffy et al. 2004; Calò et al. 2011; Wooding et al. 2004). Variations in the TAS2R38 gene can result in different versions of the receptor protein, known as haplotypes. The most studied haplotypes are PAV (proline-alanine-valine) and AVI (alanine-valine-isoleucine). PAV haplotype carriers tend to be more sensitive to bitter tastes, perceiving bitterness at lower concentrations. In contrast, AVI haplotype carriers have

reduced sensitivity to bitterness and may require higher concentrations of bitter substances to elicit a taste response (Bufe et al. 2005). In the 1930s (Blakeslee & Fox, 1932), it was discovered that approximately 25% of the population are unable to detect the bitter sensation of 6-n-propylthiouracil (PROP) and have 16 times fewer taste buds on the tongue compared to the average individual. They were classified as 'non-tasters' (AVI haplotype carriers). Twenty five percent of the population have a high density of taste buds on the tongue and perceive the bitter sensation PROP as extremely intense and aversive. They were classified as 'super-tasters' (PAV haplotype carriers). The middle 50% of the population who can detect the bitter sensation but perceive it as less intense than 'super-tasters' were classified as 'tasters' (Catanzaro et al. 2013). Historically, research in this area has used sensitivity to the bitter tasting substances phenylthiocarbamide (PTC) and PROP to determine GTS (Bartoshuk et al. 1994; Delwiche et al. 2001, Chang et al. 2006; Hong et al. 2005; Yang et al. 2014). However, due concerns around the toxicity of PTC, PROP is now generally used (Syathirah Hanim, et al. 2020).

Whilst sensitivity to the PROP and PTC has long been associated with variations in the TAS2R38 gene (see Dioszegi et al. 2019 for review), research suggests that TAS2R38 polymorphisms are insufficient to explain the differential bitter responses, and that other genes are also involved, such as the bitter taste receptor genes TAS2R19 and TAS2R31 (Hayes et al. 2015; Reed et al. 2010). Polymorphisms in these taste receptor genes have been reported to lead to differences in taste receptor cell activation, influencing how individuals perceive various taste qualities, beyond that of bitter (Yeomans et al. 2022). A vast amount of research has reported that differences in PROP sensitivity is also associated with differences in liking for specific foods and sensory experiences (Duffy et al. 2004, Tepper, 2008). For example, the increased responsiveness of super-tasters to PROP is believed to translate into increased responsiveness to other oral sensory qualities, (Dinehart et al. 2006; Lanier et al. 2005; Sandell & Breslin, 2006; Tepper et al. 2009; Zhao & Tepper, 2007), including sour tastes (Prescott et al. 2004) astringency (Pickering et al. 2009, Pickering et al. 2004), salt (Hayes et al. 2010), sweetness (Duffy et al. 2004, Hayes & Duffy, 2007), and creaminess (Duffy et al. 1996; Hayes & Duffy, 2007; Kirkmeyer, 2003; Tepper & Nurse, 1997) compared to medium and non-tasters. However, many studies have failed to find an association between PROP GTS and intensity ratings of non-bitter tastants (Deshaware and Singhal, 2017; Drewnowski et al. 1998; Feeney & Hayes, 2014) or liking of real-world foods (Bahauddin et al. 2022; Catanzaro et al. 2013).

In addition to their enhanced sensitivity and aversion to bitter tastes, super-tasters have also reported an increase in oral tactile sensitivity (e.g. from high-fat salad dressings) (Essick et al. 2003; Lanier et al. 2005; Tepper and Nurse, 1997, Yackinous & Guinard, 2001), as well as heightened chemesthetic sensations (e.g. from carbonated drinks, alcohol, ginger, black pepper and chili) (Prescott & Swain-Campbell, 2000). Indeed, increased acceptance of alcohol-related oral sensations has been proposed to contribute to higher consumption of alcoholic beverages and consequently, an increased risk of illness in non-tasters (Guinard et al. 1996, Intranuovo & Powers, 1998). Non-tasters are reported to display greater liking of cruciferous vegetables, coffee, grapefruit juice, high-fat foods (Dinehart et al. 2006, Lanier et al. 2005, Tepper and Nurse, 1998, Villarino et al. 2009) and sweet tastes (Yeomans et al. 2007) compared to super-tasters, which raises concerns about the potential consumption of high-fat and high-sugar foods, which may contribute to weight gain and obesity-related diseases over time, as studies have shown higher BMI and body fat in non-tasters (Goldstein et al. 2005; Tepper & Ullrich, 2002;).

1.3 Oral Somatosensation: From Receptor to Cortex

The oral cavity is innervated with a variety of sensory receptors, such as mechanoreceptors, thermoreceptors, and nociceptors (Lemon, 2021; Sidney & Rainer, 2017). Mechanoreceptors such as Merkel cells and Ruffini endings play essential roles in sensory perception. Merkel cells are epithelial cells located in the basal layer of the epidermis, which connect with nerve endings, forming Merkel cell-neurite complexes that are essential for detecting fine tactile details and texture discrimination. Ruffini endings, on the other hand, are elongated, spindle-shaped mechanoreceptors found in the dermis and subcutaneous tissue. They are sensitive to skin stretch and contribute to the perception of object manipulation and localisation, providing feedback on the position and movement of objects in the mouth. (Johnson, 2001; Sidney & Rainer, 2017). Thermoreceptors are sensory receptors that detect temperature changes and are divided into cold and warm receptors, each associated with specific cutaneous fibres and their endings. Cold receptors are innervated by thinly myelinated A-delta fibres, which transmit signals quickly and have free nerve endings in the superficial layers of the skin, responding to temperatures between 10°C and 35°C. Warm receptors are associated with unmyelinated C-fibres, which conduct signals more slowly and have free nerve endings in the deeper skin layers, responding to temperatures between 30°C and 45°C. Thermal signals are transduced by temperature-sensitive ion channels, such as TRPM8 for cold and

TRPV1/TRPV2 for warm (Leijon et al. 2019; Sidney & Rainer, 2017; Yarmolinsky, 2016). Nociceptors are free nerve endings, which respond to potentially harmful stimuli, including extreme temperatures above 45-50°C and below 5-10°C, and mechanical damage, and are responsible for pain perception, leading to the release of chemicals such as bradykinin, prostaglandins, and substance P (Haggard & de Boed, 2014; Sidney & Rainer, 2017).

When a stimulus is detected by these receptors, it initiates sensory transduction processes, whereby the physical stimulus is converted into an electrical signal, transmitted via the trigeminal system along sensory neurons toward the Central Nervous System (CNS) (Sidney & Rainer, 2017). It was originally suggested that trigeminal activation resulted from non-specific interactions between the chemical compounds of odours and the nerve endings of the trigeminal nerve (Cain & Murphy, 1980, Radil & Wysocki, 1998). However, the discovery of Transient Receptor Potential (TRP) channels, which are a diverse group of ion channels expressed in various cell types, including sensory neurons, (Bandell et al. 2004; Caterina et al. 1997; McKemy et al. 2002; Xu et al. 2008) and are abundantly expressed in sensory neurons on the fibres of the trigeminal nerve (CN V) *(see Figure 1.8)*, fundamentally changed this understanding, in providing evidence that trigeminal stimulation is independent of both olfactory (via CN I) (Friedland & Harteneck 2017), and gustatory processing, with signals transmitted via the glossopharyngeal nerve (CN IX), and the vagus nerve (CN X) (Shepherd, 1995).

The trigeminal nerves, specifically the branches of the fifth cranial nerve (CN V), consisting of the ophthalmic (V1), maxillary (V2), and mandibular (V3) branches (Figure 1.8), play a pivotal role in conveying tactile, thermal, and nociceptive signals, crucial for somatosensation, from various regions of the face, including the skin, mucous membranes, and oral cavity, contributing significantly to the ability to chew, speak, and experience the sensory qualities of ingested substances (Gambeta et al. 2020; Van der Cruyssen & Politis, 2018). For example, the trigeminal receptor TRPAnkyrin 1 (TRPA1) is particularly activated by cinnamaldehyde, the active ingredient in cinnamon, and its activation leads to a sensation of warmth (Legrand et al. 2020; Bandell et al. 2004), whilst eucalyptol, the active ingredient in eucalyptus, instead activates the TRPM8 (Transient Receptor Potentials Melastatin 8) receptor, producing a sensation of freshness (Caceres et al. 2017; McKemy et al. 2002) and inhibits TRPA1 (Stinson et al. 2023). Additionally, capsaicin (Caterina et al. 1997) and camphor

activate the TRPV1 (Transient Receptor Potentials Vanilloid 1) receptor (Takaishi et al. 2015), resulting in burning, stinging, and tickling sensations.

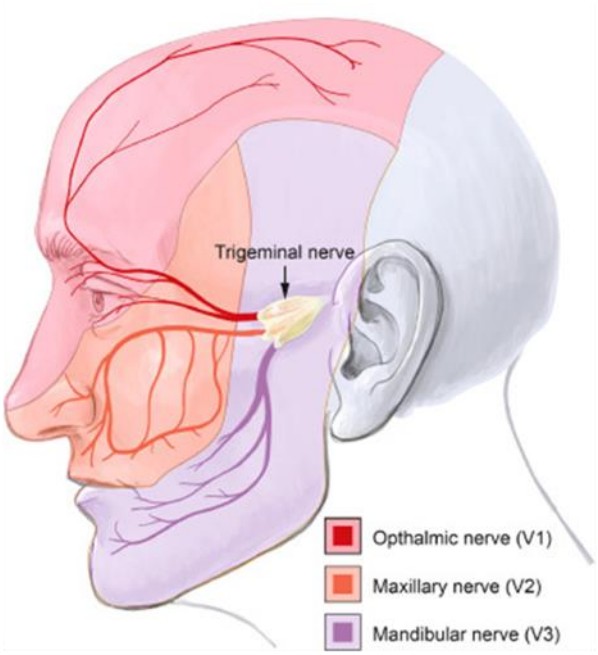

Figure 1.8: *Depicts the three branches of the trigeminal nerve. The ophthalmic nerve (VI) is responsible for providing sensory innervation to the upper part of the face and skull, extending from the region above the palpebral fissure to the eye and portions of the nasal cavity. The maxillary nerve (V2) supplies sensation to various areas, including parts of the nasal cavity, sinuses, maxillary teeth, palate, and the middle section of the face and skull, spanning from above the mouth to below the forehead. The mandibular nerve (V3) is distinct in that it carries both sensory and motor fibres. It is responsible for sensory innervation of the buccal mucosa, mandibular teeth, and the skin below the mouth. Additionally, the motor component of the mandibular nerve (V3) controls all the muscles involved in chewing or mastication. (Image from Trigeminal neuralgia by E. M. Ferneini, 2021, Journal of Oral and Maxillofacial Surgery, 79(11), 2370–2371)*

Sensory signals then travel through the trigeminal nerve root, from the peripheral nerve endings to the CNS (Terrier et al. 2022). The central brainstem components of the trigeminal system include the spinal trigeminal nucleus, the spinal trigeminal tract, and the trigeminal thalamic tract. The spinal trigeminal nucleus is a group of neurons located in the medulla oblongata, and it serves as a primary site for receiving sensory inputs from the trigeminal nerve (Terrier et al. 2022; Van der Cruyssen & Politis, 2017). It is divided into three subnuclei: oralis, interpolaris, and caudalis, each associated with different sensory functions (Olszewski, 1950). The spinal trigeminal tract is a fibre tract which carries somatosensory information from the trigeminal nerve to the brainstem and higher brain regions. It extends to the thalamus, relaying

sensory signals for further processing, allowing for the integration and modulation of somatosensory information before it reaches the cortex (Terrier et al. 2022).

In the perception of smell, the trigeminal system interacts with the olfactory system to contribute to the overall sensory experience. Almost all odourants act as trigeminal agonists at medium to high concentrations (Cometto-Muñiz & Abraham, 2015; Cometto-Muñiz & Cain, 1990; Doty et al. 1978), stimulating both olfactory sensory neurons and trigeminal sensory fibres (Doty et al. 1978). Doty et al. (1978) found that only 5 of 75 odourants, including vanillin and phenyl ethyl alcohol (PEA), were identified by fewer than 15% of anosmics, explaining their widespread use in olfactory research requiring pure olfactory stimuli without trigeminal activation (Chen & Halpern, 2007; Cometto-Muñiz et al. 2005; Stephenson & Halpern, 2008;). The trigeminal nerves, particularly the ophthalmic and maxillary branches, provide somatosensory inputs related to the chemical irritants and thermal properties of odourants (Terrier et al. 2022). The integration of trigeminal inputs with olfactory inputs occurs in the olfactory bulb, which is the first site of processing for smell in the brain. In the olfactory bulb, the trigeminal inputs and olfactory inputs converge, allowing for the combination of sensory information to create a unified perception of smell. From the olfactory bulb, the sensory signals are transmitted to the primary olfactory cortex, which is responsible for the initial processing of smell and plays a crucial role in distinguishing different odourants and their qualities (Terrier et al. 2022; Van der Cruyssen & Politis, 2018). In the perception of taste, the trigeminal system interacts with the gustatory system to contribute to the overall sensory experience of flavour. The trigeminal nerves, particularly the mandibular branch, innervate the oral cavity and provide somatosensory inputs related to touch, temperature, and pain (Haggard & de Boer, 2014). From the taste buds, taste information travels via cranial nerves (including the facial, glossopharyngeal, and vagus nerves) to the brainstem, where trigeminal and taste inputs converge in the NST. The NST receives and integrates signals from both the gustatory system and the trigeminal system before onward relay to the thalamus (Terrier et al. 2022; Van der Cruyssen & Politis, 2018).

1.3.1 Somatosensory Contributions to Oral Processing

The textural attributes of food, such as smoothness, crunchiness, or grittiness, can enhance or detract from its taste, with the interaction between texture and taste involving both peripheral and CNS processes (Rolls, 2010). It is widely believed that texture is often a decisive

factor in food acceptance or rejection, with certain textures being preferred or avoided based on individual sensory experiences. (Jeltema et al. 2015; Rustagi, 2020; Szczesniak, 2002). When the concentration of NaCl in a solution exceeds 0.08%, the perceived intensity of saltiness and sweetness decreases if the solution is viscous and increases in non-viscous solutions (Christensen, 1980; Cook et al. 2002; Koliandris et al. 2010). Similarly, aroma compounds can significantly influence yogurt texture perception, in that yogurts with fatty aromas (coconut and butter) are perceived as thicker, while green aromas (green apple and almond) are perceived as smoother (Kora et al. 2003; Saint-Eve et al. 2004). Mixed aroma compounds reduce thickness and stickiness but enhance smoothness (Saint-Eve et al. 2004).

The perception of temperature in the oral cavity can also influence the overall sensory experience of eating and drinking. For instance, foods and beverages that are served at their optimal temperature are often perceived as more enjoyable and satisfying (Stroebele & De Castro, 2004). Changes in food temperature affect perceptions of taste intensity, for example, sweet tastes are perceived as more intense at higher compared to moderate and low temperatures when tasted alone (Lipscomb et al. 2016; Schiffman et al. 2000), an effect that diminishes when sweetness is combined with other tastes, such as salty and sour (Bonnans & Noble, 1993; Lipscomb et al. 2016). Sourness is perceived as more intense at moderate compared to low and high temperatures (Lipscomb et al. 2016), whilst the perception of salt has been reported an unchanged with temperature variations when mixed with a water solution (Lipscomb et al. 2016), but when added to soup broth, saltiness perception decreased as temperature increased (Kim et al. 2015). This suggests that temperature can directly influence taste perception, but its effects may vary depending on the specific compounds involved. For example, in contrast to other sweeteners such as sucrose, the sweetness of saccharin is not affected by temperature (Green, 2003; Schiffman et al. 2000). The bitterness of caffeine is decreased by cooling, whereas for quinine, the taste threshold increases with heating (Green & Frankmann, 1987).

The trigeminal chemosensory system allows the perception of sensations such as freshness, burning, stinging, or tickling from odourous stimuli (Doty et al. 1978; Laska et al. 1997; Frasnelli et al. 2011), and tactile, thermal, painful and kinaesthetic stimuli arising from oral stimuli (Braud & Boucher, 2019; Cayeux et al. 2023). For example, a sweet drink will induce nociceptive responses and likely be rejected if served extremely hot, whilst usually acceptable and tasty foods, such as fruits or meats, may be rejected if associated with an

abnormal texture, such as sogginess, or unusual odours, since both would indicate the potential presence of toxins (de Araujo & Simon, 2009). Chemical stimuli can induce multiple sensations, with the intensity of the sensation depending on the concentration of the compound. Menthol induces pure cooling at low concentrations but also a burning sensation at higher concentrations (Green & Schoen, 2005; Namer et al. 2005; Proudfoot et al. 2006), the pungency of spices like mustard or chili is due to the trigeminal sensations they trigger in the nasal cavity (Engel et al. 2006; Gerhold & Bautista, 2009; Tremblay & Frasnelli, 2018;), whilst an odourless sensation is often experienced in the nose from carbon dioxide, which is commonly known as a 'pure' odourless trigeminal stimulant, (Cain & Murphy, 1980; Chevy & Klinger, 2014).

Trigeminal sensitivity can be assessed using an odour lateralisation task, which requires identification of the stimulated nostril in a monorhinal stimulation paradigm (Frasnelli et al. 2006; Hummel et al. 2003; Kleemann et al. 2009) and is based on the principle that odour localisation is only possible when the trigeminal nerve is activated (Croy et al. 2014), helping to differentiate the contributions of the trigeminal and olfactory systems. As a result, humans can accurately lateralise mixed olfactory/trigeminal stimuli, which activate both the olfactory and trigeminal nerves (e.g. eucalyptol), but not pure odours which exclusively activate the olfactory nerve (e.g. vanillin) (Croy et al. 2014; Frasnelli et al. 2009; Kellman et al. 2009; Kobal et al. 1989). Whilst the association of olfactory/trigeminal perception is well studied, the interactions between taste and trigeminal perception have not been given the same attention (Cayeux, 2023; Labbe et al. 2008).

1.4 Multisensory Integration and the Chemical Senses

Whilst taste and smell are distinct sensory modalities with their own receptor organs, they often integrate to create the overall sensory experience of flavour (Pocock et al. 2017). The trigeminal system contributes to this integrated experience (Cayeux, Saint-Leger & Starkenmann, 2023; Green & Nachtigal, 2012). The International Standards Organisation (ISO 5492, 2008) defines flavour as a: "*Complex combination of the olfactory, gustatory and trigeminal sensations perceived during tasting. The flavour may be influenced by tactile, thermal, painful and/or kinaesthetic effects*". Flavour perception is the way our brain represents the taste of food while we are eating. Whilst there is limited evidence of for the brain regions

involved in the integration of the chemical senses, studies using fMRI and Positron Emission Tomography (PET) in both in primates (Rolls & Baylis, 1994) and humans (Dalton et al. 2000 ; De Araujo et al. 2003; Mizoguchi et al. 2016; Rolls, 2006), have reported that when a combination of stimuli (taste, odour, trigeminal) are presented together in congruent combinations, synergistic activation of the OFC is evident, in that there is greater activation in response to combined mixtures, compared to the sum of each stimulus presented independently, an effect that is significantly reduced when stimuli are incongruent. These interactions are demonstrated by the overlapping activation patterns resulting from independent stimulation of the olfactory and gustatory senses. Thus, though the flavour of foods and drinks appear to emerge from the tongue, it is in-fact a holistic, multi-sensory perceptual construct in which each of these sensory modalities contributes to the construction of a unitary flavour percept (Verhagen & Engelen 2006), with perception depending significantly on the specific combination of the stimuli being used (Spence, 2016).

Multisensory integration (MSI) refers to the process by which the brain combines information from multiple sensory modalities, to form a unified and coherent perceptual experience. Rather than processing sensory information from each modality in isolation, the brain actively combines and integrates these inputs to generate a more accurate and comprehensive understanding of the environment (Idris et al. 2022; Stein et al. 2014; Stein & Meredith, 1994). For several decades, multisensory integration has been defined and investigated according to the three '*central principles of multisensory integration*', specifically, the '*spatial'* rule, the '*temporal'* rule, and the principal of '*inverse effectiveness'* (Stein et al. 2014; Wallace et al. 1998). The '*spatial'* rule describes how multisensory integration is often stronger or more prevalent when the constituent unisensory stimuli are presented from approximately the same location. The '*temporal'* rule is similar in that it describes an effect for stimuli that are presented simultaneously, whilst the '*temporal binding window'* has been defined as the range of temporal asynchronies within which two stimuli are perceived as being presented simultaneously (Meredith et al. 1987; Stein et al. 2014), with the strength of MSI reducing significantly as the temporal asynchrony of two stimuli increases beyond 100ms (Meredith et al. 1987; Spence & Squire, 2003). The principle of '*inverse effectiveness'* describes an inverse relationship between multisensory integration and unisensory responsiveness, multisensory enhancement is large for weak unimodal stimuli and decreases with increasing stimulus intensity (Meredith & Stein 1983; Ohshiro et al. 2011). '*Inverse effectiveness'* typically manifests as a transition from super-additivity (more than the sum of

the unisensory responses) to subadditivity, as the modality-specific stimuli themselves become more potent (Stein et al. 2009). These principles, however, are not universally applicable under all conditions. For example, research has shown that spatial congruence is not always necessary for MSI, as integration can still occur when stimuli are spatially disparate but temporally aligned or semantically related. Spence (2013) indicates that highly congruent stimuli, such as auditory and visual components of speech, can be effectively integrated even when presented from disparate locations. This phenomenon has been observed in the 'ventriloquist effect', where auditory stimuli are perceived as originating from the location of a corresponding visual stimulus, despite a spatial mismatch (Keetels & Vroomen, 2008). Additionally, the dominance of one sensory modality in a task, such as vision in audiovisual interactions, can reduce the reliance on spatial alignment (Soto-Faraco et al. 2005). Similarly, the temporal binding window can vary across modalities and contexts. Certain tasks or environmental conditions can lead to a broader or narrower temporal window, and integration can still occur outside this window if the stimuli are semantically or contextually congruent (Spence, 2013; Talsma et al. 2012). For example, temporally asynchronous auditory and visual stimuli in speech perception may still be integrated when semantic congruence provides a strong contextual anchor, as seen in studies of audiovisual speech integration (Stevenson & Wallace, 2013). In addition, the principle of inverse effectiveness, which posits that integration is strongest when unisensory stimuli are weak, is also not absolute. The relationship between stimulus intensity and multisensory integration is not linear and can be influenced by factors such as attention, task demands, and prior experience (Spence, 2013; Talsma et al. 2012). For instance, strong unisensory stimuli can sometimes enhance integration when they are semantically congruent or when the task requires a high level of sensory precision. Furthermore, the transition from super-additivity to subadditivity, often cited as characteristic of inverse effectiveness, is not always observed and may depend on the specific neural mechanisms or sensory systems being studied (Fetsch et al. 2013; Spence, 2013).

In support of the '*central principles of multisensory integration'*, several studies have evidenced the generalisability of these rules to the chemical senses *(smell, taste, and trigeminal sensations)*. Research investigating the influence of *'temporal'* dynamics of flavour perception using odour-taste combinations, has found that holding a sub-threshold concentration of saccharine in the mouth reduces detection thresholds for a sweet almond aroma. In contrast, when participants expectorated the saccharine solution prior to sampling the odour, detection thresholds were unaffected (Dalton et al. 2000; Pfeiffer et al. 2005), demonstrating flavour

perception is influenced by the temporal congruency between odour and taste stimuli. Isogai and Wise, (2016) looked to determine whether modulation of taste by retronasal odour is dependent on temporal congruency, with onset of odour presentation ranging from two seconds before taste delivery to two seconds after taste delivery onset. Enhancement of taste intensity was greatest with simultaneous onset of taste and odour. These findings were later supported in a study using a number of '*spatial'* and '*temporal'* manipulations to investigate the effect of simultaneous and successive presentation of benzaldehyde on the taste threshold of a saccharin solution. Olfactory and gustatory stimuli were presented either simultaneously or with a temporal delay. Results showed a significant increase in taste enhancement when the odour was presented simultaneously to the swallowing of the taste solution. If the odour was presented simultaneously with the taste, it lowered the threshold of saccharin detection, however, when taste presentation preceded odour presentation, the effect disappeared. (Djordjevic et al. 2004; Pfeiffer et al. 2005; Sakai et al. 2001). However, Sakai et al. (2001) indicate that the simultaneous presentation of odour and taste enhances sweetness perception regardless of whether an odour is delivered orthonasally or retronasally. This suggests that temporal congruence, is more important for taste/odour integration than spatial congruence, such as whether the odour and taste originate from the same flavour or food object.

Research has examined these principles on the perception of odour, taste and trigeminal interactions and found that, stimulus congruency (e.g. strawberry odour and sucrose) (Djordjevic et al. 2004) increased the perceived intensity and pleasantness compared to when the stimuli were incongruent (e.g. water chestnut and sweetness) (Prescott, 2004). Other research has examined how the localisation of trigeminal stimuli if affected by the simultaneous presentation of olfactory stimuli, reporting that that localisation accuracy for weak air-puffs was below 75% when presented alone, improving to around 85% when both stimuli were delivered to the same nostril, but not when delivered to opposite nostrils (Karunanayaka et al. 2020). Many studies have highlighted the suppressive or masking effect of chemesthetic compounds on taste perception (Delwiche, 2004; Cowart, 1987; Lawless & Stevens, 1984; Simons et al. 2002). For example, Koskinen et al. (2003) reported that menthol decreases the sweetness and increases the sourness of lemon-flavored yoghurt. Capsaicin can have sweetness reducing (Prescott & Stevenson, 1995), and salt reducing (Hunter et al. 2023) effects in food (such as soup), with spilanthol (a fatty acid amide) enhancing salt perception (Xu et al. 2018).

In support of the ‘Temporal binding window’, in which strength of MSI reduces significantly as the temporal asynchrony of two stimuli increases, Lim and Johnson (2012) found that when an odour was presented alongside a congruent taste, there was a significant increase in the perceived intensity of the odour in the oral cavity and on the tongue, suggesting that the more similar the odour and taste were in congruency, the more likely participants experienced "oral referral," perceiving the odour as if it originated from within the mouth. This phenomenon of oral referral has been reported not only when odours are presented retronasally (Ashkenazi & Marks, 2004) but also orthonasally (Stevenson & Mahmut, 2011). For example, Stevenson, Oaten and Mahmut (2011) presented odours orthonasally to participants who were simultaneously holding taste solutions, water, or nothing in their mouth. They found that the odour was perceived as being in the mouth when holding a taste solution compared to when holding water or nothing. Similarly, Gotow and Kobayakawa, (2022) presented one of two odours orthonasally (Cherry Tree or Soy Sauce) with a saline solution. When presented with the congruent condition (Soy sauce & saline), participants reported perceiving a soy sauce odour in their mouth, however, none of the participants reported oral referral under the incongruent condition (Cherry tree & saline). As such, when the odour and taste were congruent, participants were more likely to perceive them as being spatially proximate (both in the oral cavity), even though they were presented at different spatial locations (odour in the nasal cavity and taste in the oral cavity). These findings support similar reports using audio–visual experiments, in which two stimuli exhibited greater temporal bindings windows when presented from the same spatial location than when presented from different spatial locations (Zampini et al. 2005).

Taken together, the results of these studies highlight the notion that the MSI of the chemical senses depends on their spatial and temporal congruence (Dalton et al. 2000; Djordjevic et al. 2004; Pfeiffer et al. 2005; Sakai et al. 2001). Though, it remains uncertain whether this effect is primarily driven by gustatory or olfactory signals independently or if it results from the combination of both sensory inputs. Therefore, considering the significance of "*spatial*" and "*temporal*" factors in MSI in oral perception, it is expected that when odours are perceived through the orthonasal pathway in combination with taste, there may be neural competition (Small et al. 2004). This competition could arise due to orthonasal olfaction primarily activating the olfactory system, potentially conflicting with the simultaneous processing of gustatory signals. On the other hand, when odours are perceived through the retronasal route in combination with taste, multisensory integration is expected to occur more

seamlessly, possibly due to the notion that retronasal olfaction is closely linked to the gustatory system and the overall experience of flavour (Lim & Green, 2007; Rozin, 1982; Small & Green, 2011). Additionally, in a study using fMRI to examine how odour perception differs depending on route on delivery, it was found that retronasal, but not orthonasal odours, activate the somatosensory cortex, indicating a connection between olfactory and gustatory sensations (Small et al.2005). Comparison of brain activity between orthonasal and retronasal routes revealed differential activation in regions such as the insula/operculum, thalamus, hippocampus, amygdala, and orbitofrontal cortex. Orthonasal delivery elicited stronger responses in certain brain areas to chocolate, while retronasal delivery showed heightened responses in other brain areas, suggesting that neural processing varies based on whether an odour is perceived as a food flavour or an external smell (Lim & Green, 2008; Small et al. 2005;). Thus, suggesting we respond, perceptually and hedonically, not to discrete tastes, odours, and tactile sensations, but to flavours constructed from a synthesis of these sensory signals (Prescott, 2004). The activation of the somatosensory cortex by retronasal odours implies that the somatosensory system processes not only the chemical properties of food but also its physical characteristics, which are essential for a complete sensory experience.

1.5 Motivation

Concepts of motivation seek to explain how internal and external factors drive an individual to initiate and sustain goal-directed behaviour (Bandhu et al. 2024; Simpson & Balsam, 2015). Internal factors primarily encompass physiological needs (hunger, thirst) and emotional states (positive, negative), which stimulate individuals to engage in behaviours aimed at maintaining homeostasis. For example, it has been shown that increased hunger significantly enhances motivation to seek out and consume food (Lowe et al. 200), whilst positive emotions (pleasure) drive individuals toward rewarding activities and negative emotions (fear, anxiety) lead to avoidance of potentially distressing situations (Ballard et al. 2017). In addition, external factors, including both social (praise, recognition) and non-social (financial) incentives, can also significantly influence behaviour.

1.5.1 Homeostatic drive theory of Motivation

Homeostatic drive theory (Hull, 1943) focuses on the internal factors which influence motivation, particularly those related to physiological needs and the maintenance of homeostasis. According to this theory, when there is a deviation from an optimal internal state, a drive is activated, which motivates individuals to engage in behaviours that will restore balance. For example, the internal states of hunger and thirst create a physiological imbalance, triggering motivation to engage in ingestive behaviours aimed at restoring homeostasis (Hull, 1943). In support of this theory, low levels of blood glucose (Campfield & Smith, 2003) and increased levels of the hormone ghrelin are seen prior to meal initiation and associated with feelings of hunger (Cummings et al. 2001). With levels of both returning to homeostatic baseline post-food consumption. In one of his seminal experiments, Hull (1943), compared the behaviour of three groups of rats in navigating a maze. The first group always received food at the end of the maze, leading to immediate learning. The second group, which never received food, showed no incentive to learn and wandered aimlessly, however, the third group, initially without food for the non-reward phase (10 days), quickly learned to navigate the maze once food was introduced in the reward phase (11th day). As such, Hull (1943) reported that rats in the third group, exhibited a higher motivation to learn and complete the maze during the reward phase compared to the non-reward phase (Hull, 1943).

Despite the importance of these physiological factors in food consumption, research has shown that individuals often consume more food than required to meet metabolic demands (Reichelt et al. 2015). Furthermore, consumption is frequently initiated in the absence of any significant drop in glucose levels (Bilman, van Kleef & Van Trijp, 2015; Hlaing & Liabsuetrakul, 2016;). In such cases, many other internal (e.g. stress and dietary goals) and external factors (e.g. food availability and social context) influence eating behaviour (Plassmann et al. 2021). At a sensory level, the sight, smell or taste of food can be sufficient to initiate food seeking and consummatory behaviours (Bilman et al. 2015; Felton & Gibson, 2012; Lowe & Butryn, 2007), such observations led to the conclusion that hedonically laden sensations, such as sweet tastes, are rewarding and motivating even in the absence of a deficit induced motivational drive (Berridge & Robinson, 1998).

1.5.2 Theories of Incentive Motivation

Theories of incentive motivation were developed to address the limitations of drive reduction theories (Bandura, 2005; Bandhu et al. 2024; Deci, 1972; Deci, 1991). In contrast to drive reduction models, they acknowledge the importance of both internal drive states and hedonic value to motivated behaviour, with physiological states modulating both the incentive value of, and sensory pleasure derived from, the consumption of primary rewards (such as foods and drink) as well as of the motivational salience of environmental reward cues (e.g. sight and smell of the food) associated with them.

A key example of this framework is the Incentive Salience Theory developed by Berridge and Robinson (1998) has proven to be particularly influential in the field of affective neuroscience. This theory dissociates, both neurally and psychologically, two components of reward, liking and wanting. Here, liking refers to the sensory pleasure triggered by the receipt of a reward, typically assessed post-consumption, such as the hedonic enjoyment experienced when consuming food or other rewards. This type of liking reflects the affective response to the actual experience of reward consumption. In contrast, '*wanting',* (or incentive salience), refers to the motivational value of the same reward and the environmental cues associated with it (Figure 1.9). Evidence that these are separate constructs originates from animal studies investigating the neural basis of reward processing, in which, '*wanting'* is generated by mesolimbic dopamine systems originating from the midbrain that project to various limbic structures, such as the prefrontal cortex, orbitofrontal and insula regions, to generate incentive salience. Whilst 'Liking is mediated by hedonic hotspots within the nucleus accumbens, ventral palladium, OFC, Insula and parabrachial nucleus regions of the mesocorticolimbic circuitry, where manipulation of opioid, orexin, endocannabinoid systems have been found to enhance positive orofacial expressions to sucrose taste (Berridge & Valenstein, 1991; Reynolds & Berridge, 2002; Smith & Berridge, 2005; Wyvell & Berridge, 2000).

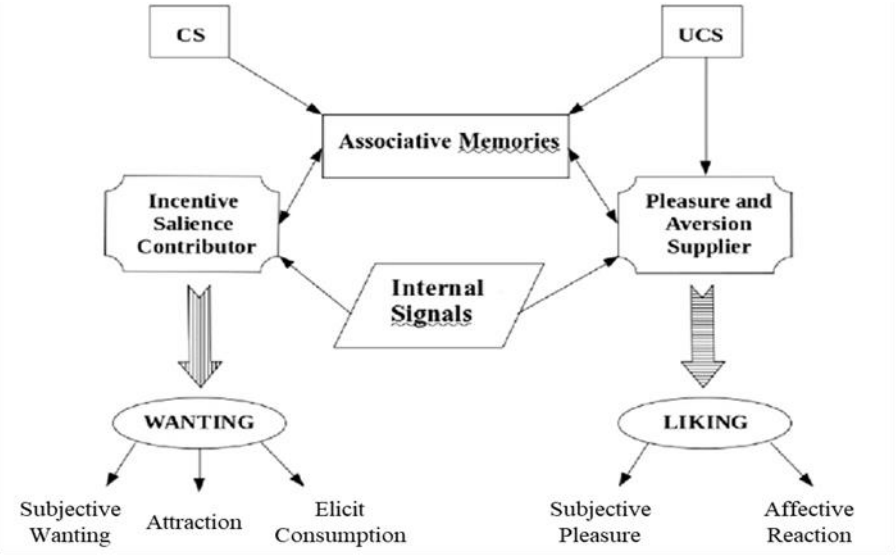

Figure 1.9: *Incentive salience model of incentive motivation, in which Liking and Wanting correspond to separate psychological and neurological systems. (Image from Transitionality in addiction: A "temporal continuum" hypothesis involving the aberrant motivation, the hedonic dysregulation, and the aberrant learning by E. Patrono, A. Gasbarri, C. Tomaz, & H. Nishijo, 2016, Medical Hypotheses, 93, 62–70).*

This dissociation of constructs is most commonly observed when dopaminergic manipulations affect the motivational '*wanting'* but not the hedonic liking of a food's incentive value. For example, dopamine suppression reduces the incentive value of sweetness and sucrose, as measured by changes in lickometer measures of ingestive behaviour (Galistu & D'Aquila, 2012; Reynolds & Berridge, 2002; Wyvell & Berridge, 2000) and suppression of other appetitive food seeking behaviours (Reynolds & Berridge, 2002; Wise, 2006; Wyvell & Berridge, 2000). However, taste reactivity responses to a consumed food, are not diminished by these same dopamine inhibitors (Peciña et al. 1997; Reynolds & Berridge, 2002; Wyvell & Berridge, 2000), thus showing that dopamine is not essential for the hedonic impact of food pleasure but is necessary for their incentive motivation value. In a study by Wyvell and Berridge (2000), amphetamine (a dopamine reuptake inhibitor) was microinjected into the nucleus accumbens shell of rats to assess its impact on reward-related behaviours. Rats, trained to press levers for sucrose and conditioned to associate a Pavlovian reward cue with sucrose, showed increased lever pressing in response to the reward cue after amphetamine treatment, indicating enhanced motivation. However, this increase in 'wanting' did not correspond with changes in 'liking,' as taste reactivity tests revealed no alteration in pleasure from sucrose.

Building upon this distinction, the theory of Incentive Salience is largely grounded in evidence from behavioural neuroscience, where animal models have been used to investigate the neural mechanisms underlying wanting and liking. For example, behavioural measures such as the nose poking (Berridge & Aldridge, 2000; Flagel et al. 2009; Piantadosi, Yeates & Floresco, 2020; Robinson et al. 2014) and lever pressing tasks (Saunders et al. 2018; Marshall et al. 2020; Salamone et al. 2007) are widely used in animal studies to measure incentive salience, or '*wanting'*, of rewards. In these tasks, rodents are trained to perform a specific action, to obtain a reward. The frequency and intensity of these behaviours are then considered quantitative indicators of motivational drive. In contrast, liking is often measured using taste reactivity, which is a method for measuring the liking of a substance by recording the hedonic (liking) or aversive (disliking) orofacial responses of rats to various tastants. For example, sucrose induces appetitive reactions, while bitter quinine results in aversive reactions (Kiefer et al. 1990; Berridge, 2000). Consistent reactions to the specific hedonic value of different tastants, along with the associated changes in neural activity, support its effectiveness as a measure of liking (Castro & Berridge, 2014; Holland et al. 2008).

Although animal studies have significantly advanced our understanding of the neural mechanisms underlying incentive motivation, translating these findings to humans remains a considerable challenge (Weinstein, 2023). To date, empirical assessment of incentive salience (wanting) has primarily relied on self-report scales (Chae et al. 2023; Gaillet et al. 2013; Morquecho-Campos, 2021; Proserpio et al. 2019; Ramaekers et al. 2014; Rolls & Rolls, 1997), which assess a participant's subjective experience of wanting rewards, particularly in the context of food. However, such self-report measures primarily capture conscious expectations an individual holds about the pleasantness of a reward and may not fully capture underlying cognitive and neural processes involved in implicit, unconscious '*wanting'* (Berridge, 1997; Berridge & Robinson, 2008). This limitation highlights the need for a more nuanced approach to studying incentive motivation, as proposed by Berridge (2008). Specifically, Berridge's framework emphasises that a comprehensive assessment should incorporate three key elements: '*wanting'* (incentive motivation), liking (hedonic pleasure) and the physiological state of the individual (Berridge & Robinson, 2016). From this perspective, wanting is determined by the interaction between an individual in a particular physiological state and the perception of a reward associated cue (e.g. sight, or smell) and should be evaluated by motivational drive i.e., the amount of effort exerted in order to acquire the reward. It is therefore suggested that a promising approach to measuring food '*wanting'* concerns tasks in which the

participant, analogous to rodent studies, perform an instrumental response to obtain food reinforcement (Mela, 2006), such as pressing a key (Rogers & Hardman, 2015; Temple, 2016) or squeezing a grip-force dynamometer (Ziauddeen et al. 2014). Such effort-based measures of incentive motivation can objectively quantify wanting (Bindra, 1974, Bolles, 1972; Mela, 2006; Pool et al. 2016), with the level of effort expended thought to be proportional with the anticipated value of the reward when conditions are favourable, such as when the reward is highly motivating or when effort is perceived as reasonable relative to the reward's value. However, empirical evidence suggests that the relationship between effort and reward may not always be straightforward, as it is influenced by factors such as the subjective value of the reward, task difficulty, individual differences in motivation, and environmental or contextual influences (Mela, 2006; Pool et al. 2016). For instance, in certain cases, the effort required may outweigh the reward's perceived value, leading to reduced motivation or effort expenditure (Richter et al. 2016). Additionally, individuals may demonstrate variable effort expenditure based on prior experiences (Urdan & Kaplan, 2020), task difficulty (Richter et al. 2008), or emotional states (Blakemore et al. 2017), indicating that effort-based motivation is context-dependent rather than fixed.

Thus, in investigating the impact of physiological state, such as hunger and satiety, on motivation for food rewards, effort-based measures have gained attention in assessing wanting of rewards in humans. For instance, in a task employed by Epstein et al. (2003), participants played a game to earn snack food points by pulling a joystick, with increasing effort required for additional points. The study revealed that food-deprived participants exerted more effort and worked longer to earn snack food compared to those who were satiated. Similarly, several studies have used grip force to study the influence of hunger state on the willingness to exert effort to obtain food rewards. Here, consistent with studies in rodents, exerted effort is greater during a hungry compared to satiated state (Pirc et al. 2019; Ziauddeen et al. 2011). However, the relationship between deprivation and effort is not strictly linear. Granger et al. (1969) observed that while performance typically improves with longer deprivation, this trend reverses at extreme levels. For example, running speed increased with dehydration up to 48 hours but declined after 60 hours, likely due to depleted energy reserves or physiological disorganisation from overactivation. This curvilinear relationship between deprivation and performance highlights the potential for reduced effort and performance at extreme levels of need.

Moreover, this state-dependent modulation of drive is evident even when visual reward cues are not consciously perceived, as demonstrated by Ziauddeen et al. (2011), where effort exerted to gain rewards was modulated by hunger, even in the absence of conscious visual cue recognition. This suggests, in line with incentive salience theory, that modulations of effort for consumed food can occur outside conscious awareness, as the motivational drive is primarily influenced by internal states of deprivation rather than external cues alone (Berridge & Robinson, 1998). The complexity of the deprivation-effort relationship becomes evident in the fact that at certain levels of deprivation, excessive activation may lead to reduced performance due to overexertion and resource depletion. This phenomenon is consistent with findings in both animal models and human studies, where moderate deprivation can enhance motivation and performance, but extreme deprivation may lead to a breakdown in effort as the body's reserves are exhausted.

Central to the theory of incentive salience is the fact that exposure to a reward, or an environmental cue associated with a reward, can prime incentive motivation, even in the absence of any physiological drive (Berridge & Robinson, 1998). Consistent with the theory, goal-priming effects occur when exposure to a reward cue (such as visual images or odour cues) enhances the response to a subsequent stimulus (like food), often without conscious awareness (Biswas & Szocs, 2019; Gaillet et al. 2013; Proserpio et al. 2019). This phenomenon suggests that external cues can activate a mental representation of a goal, thereby increasing motivation and effort towards obtaining congruent rewards. This concept has been evidenced in the priming literature using both visual (Gaillet et al.2013) and olfactory (Biswas & Szocs, 2019) food cues, demonstrating that external cues, whether at a conscious or non-conscious level (Smeets & Dijksterhuis, 2014; Ziauddeen et al. 2012), activate a mental representation of a goal, and in turn, increases motivation and behaviour for congruent foods (Bargh et al. 1996).

Similar to 'wanting', subjective measures have traditionally served as the primary means of assessing hedonic liking in humans (Hellemann & Tuorila, 1991, Sidel et al. 1972, Vickers & Mullan, 1997). Tools such as the Food Liking Questionnaires (József Tóth et al. 2023; Wanich et al. 2018) and hedonic rating scales (Finlayson et al. 2007; Lim, 2011; Visalli et al. 2023) are commonly employed to gauge an individual's preference and anticipated enjoyment of various foods. However, it is suggested that, in measuring liking, timing is crucial (Berridge & Robinson, 2016), and that, in order to capture the hedonic reaction, measures must be taken either during, or immediately following reward consumption, and similar to wanting, can also

be influenced by an individual's current physiological state (Berridge & Robinson, 2016). Furthermore, due to the self-report measures primarily capturing conscious aspects of hedonic experiences it has been argued they do not necessarily reflect the same cognitive and neural processes as innate, evolutionarily conserved, oro-facial expressions to taste stimuli (Berridge, 2000).

In contrast to these subjective measures, research analysing facial expressions in response to taste stimuli provides more direct evidence of hedonic reactions. Similar to animals, human facial expressions are influenced by the taste quality, with pleasant tastes (such as sweet and savoury) eliciting positive facial expressions such as lip-licking and smiling, while unpleasant tastes (such as bitter and sour) produce negative reactions such as grimacing and nose wrinkling (Danner et al. 2014; de Wijk et al. 2012; Weiland et al. 2010; Wendin et al. 2011). However, criticisms of orofacial expressions as a measure of hedonic response highlight the inherently subjective interpretation of expressions and the difficulty in capturing subtle or involuntary responses may limit the reliability and accuracy of this method. In contrast, numerous psychophysiological studies have demonstrated that facial electromyography (EMG) is an effective, objective tool, for capturing the valence and quality of emotional responses to a wide range of affective stimuli (Beyts et al. 2017; Cannon et al. 2017; Cacioppo et al. 1992; Larsen et al. 2003; Sato et al. 2008; Sato et al. 2020a, Sato et al. 2020b; Sato et al. 2021). Specifically, EMG activity recorded from the corrugator supercilii (associated with brow lowering) and zygomatic major muscles (associated with lip corner pulling) are negatively and positively correlated with valence ratings, respectively (Cacioppo et al. 1992; Dimberg et al. 1990). For instance, a study measured subjective ratings of valence and arousal along with facial EMG, while participants viewed emotional-scenes and food images. They found that subjective valence ratings had a linear negative association with corrugator supercilii activity and a positive association with zygomatic major activity (Sato et al. 2020a). This relationship has further been supported in response to oral stimuli, in which participants display an increase in corrugator activity in response to unpleasant tastes, such as quinine, caffeine, whilst zygomaticus activity is more activated in response to pleasant stimuli, such as sucrose (Armstrong et al. 2017; Beyts et al. 2017; Cannon et al. 2017; Sato et al. 2008; Sato et al. 2020). While EMG is an effective tool for capturing muscle activity related to hedonic responses to both pleasant and unpleasant stimuli, it has been suggested that this measure should not be considered a direct marker of pleasantness. As highlighted by Richter and Slade (2017) and further discussed in the context of facial EMG by Sato et al. (2020), physiological responses

such as facial EMG can be influenced by a variety of factors beyond emotional valence, including effort (de Morree & Marcora, 2010), attention (Porges & Raskin, 1969), and fatigue. These additional factors confound the inference of these physiological changes as unique indicators of hedonic response. Therefore, while facial EMG can reflect physiological responses to affective stimuli, its interpretation as a marker of pleasantness requires careful consideration and further validation. As noted in the literature, these measures should be understood as reflecting physiological outcomes of emotional responses, but not necessarily as specific, one-to-one markers of pleasantness (Cacioppo et al. 2000).

Aims and Objectives

This thesis focuses on the role olfactory and oral perception play in shaping our consummatory experiences, preferences, and food seeking behaviours. Investigation in this area is important to health research, shaping understanding of individual differences in food selection, consumption, and other dietary behaviours. It is also informative for food and drink manufacturers who want to understand the factors which drive consumers to select one product over another as well as which measures of consumer experience are the best predictors of product enjoyment and repeat purchasing.

Concepts of motivation provide a framework for investigating the psychological processes by which external stimuli, internal physiological and affective states, and cognitive processes interact to guide real world behaviour. Central to the concept of incentive motivation is hedonic reward (liking), the sensory pleasure derived from consumption of rewarding items. **Liking** a reward, such as a food, is a key affective driver of future behaviour. That is, through the process of conditioned reinforcement, stimuli associated with sensory pleasure acquire an incentive value and elicit goal-directed approach behaviour, termed **wanting**, aimed at obtaining the predicted reward.

Ambient food odours are conditioned stimuli that, through their incentive value, have been reported to prime goal-directed behaviour. However, some studies report that both conscious and non-conscious exposure to ambient odours can instead induce satiety effects, reducing self-reported expected liking and the probability of an associated food being selected for consumption.

The Aim of study 1 was to determine whether exposure to ambient food odours produces a goal priming or a satiety effect and to establish whether any such motivational changes could be detected through an effort-based measure of wanting - thus extending previous use of subjective reports and choice tasks which can be affected by demand characteristics and dietary habits.

The Aim of study 2 was to establish whether, as previously reported, grip force is a reliable measure of wanting by demonstrating that reductions in incentive drive induced by satiety can be detected through changes in effort expended to obtain them.

Individual differences in approach motivation have been widely reported. Individual differences in perceptual processing are also known to affect the detection, salience and

ultimately behaviour elicited by sensory cues in our environment. In the real world, ambient odours are rarely encountered in isolation, thus the brain must segregate motivationally relevant odour objects, typically comprised of 10s-100s of individual volatiles, from the complex olfactory background they are encountered against. While the cognitive basis of olfactory scene analysis has received little attention to date, state and trait differences in the processing of visual scenes are well documented.

The Aim of study 3 was to determine whether a local processing advantage in the visual domain is associated with superior ability to dis-embed component odour objects from within a multicomponent mixture. Such findings give insight into the domain general and domain specific cognitive processes underlying olfactory processing.

Oral processing of food stuffs is a multisensory process where gustatory, olfactory and somatosensory cues combine to generate a unitary percept termed flavour. Individual differences in affective responses to flavours are widely reported and are affected by cultural, personality and other demographic factors. Genetic Taster Status, an inherited relative sensitivity to taste stimuli, reflecting individual variation in the density of fungiform papillae on the tongue, is predicted to impact not just sensitivity to tastants but also to the somatosensory and chemesthetic properties of oral stimuli. However, to date studies are limited and findings mixed.

The Aim of study 4 was to determine whether facial EMG, an established measure of affective responses to sensory stimuli, can be used to differentiate between PROP Super-tasters and Non-tasters in their affective responses to threshold and suprathreshold bitter, astringent and chemesthetic compounds. Such an implicit measure of immediate liking has advantages over traditional ratings scales which are vulnerable to demand characteristics and require interruption of the hedonic response for completion.

Chapter 2: General Methods

2.1: Ambient Odour Presentation

A wide variety of methodological approaches have been used in priming studies to present ambient food odours, such as scented clothing (Chae et al. 2023), freshly baked food (Coelho et al. 2009; Fedoroff et al. 2003; Ferriday & Brunstrom, 2011; Jansen et al. 2003; Larsen et al. 2012), active sniffing (Rolls & Rolls, 1997; Ramaekers, 2014; Zoon et al. 2016) and odour dispersion (Gaillet-Torrent et al. 2014; Morquecjo-Campos & Boesveldt, 2021; Proserpio et al. 2019; Ramaekers et al. 2014). The findings in the extant literature are mixed and it has been suggested that stimulus level factors, such as nature of exposure, timing and food-odours used, may differentially affect whether priming or satiety effects are observed (Abeywickrema et al. 2014; Oey, Peng, 2022).

In Study One, a diffuser was used to disperse the test odours. Diffuser methods are widely used (Biswas and Szocs, 2019; Chambaron et al. 2015; de Wijk et al. 2018; de Wijk & Zijlstra, 2012; Gaillet-Torrent et al. 2014; Morquecho-Campos et al. 2020; Morquecho-Campos et al. 2021; Proserpio et al. 2017; Proserpio et al. 2019; Sulmont-Rossé et al. 2018; Ramaekers et al. 2014; Zoon et al. 2014) as it allows for experimenter control over the timing, concentration, and duration of odour exposure.

Figure 2.1: *The mini scent diffuser used for dispersing ambient food odours at a non-conscious level. Mini Dispenser purchased from AromaPrime.com. (Image from Aromaprime. Retrieved 23/01/24, from https://aromaprime.com/.)*

For initial pilot testing, a Dry Scent Diffusion System was purchased from AromaCo.co.uk. This relied on scent cartridges, with cartridges containing different odours sitting side-by-side in the machine. In preliminary tests, it became evident that the two test odours (chocolate and orange), though dispensed separately, were contaminated by the other odour block. Thus, the delivered odours always had a Chocolate-Orange character. In addition, this system, designed for large exhibition spaces, was not optimal for delivery of a subtle ambient odour in a small test space as required for this study. Ultimately, *'Mini Dispensers'* from AromaPrime.com *(Figure 2.1)* were used. Two systems were purchased, one for each odour, in order to avoid contamination.

Initially a range of indulgent *(Doughnut, Double Chocolate, Chocolate Cake)* and non-indulgent *(Strawberry, Orange, Banana, Pineapple, Orange, Raspberry)* food associated aroma oils were tested. From these the Orange and Chocolate were selected as they were judged by various raters, to provide the most realistic perceptions of the target foods. In determining the effectiveness of these odours, two pilot tests were conducted. During pilot test one *(methods and results outlined in chapter 3.1.2)* odours were presented in amber glass jars. The aim of the pilot test was to ensure that the selected odours were identifiable, and matched in terms of pleasantness, intensity, familiarity, edibility, expected liking. Participants were instructed to open each jar in turn, smell the contents and rate the perceived odour on a set of 12cm Visual Analogue Scales (VAS), one for each descriptor. Following this, Pilot Study Two consisted of the odours being dispersed in two equally sized laboratory rooms *(which would be used as the odour dispersion rooms in the main study).* One room contained the Seville Orange Odour, one room contained the Double Chocolate Odour, two additional rooms were used as controls, no odour was diffused in them. Upon entering each room, participants were required to rate the odours on the same VAS scales as used in Pilot Study One, with an additional question asking whether they were able to detect an odour in the room. From these tests, timing and duration of odour diffusion were determined.

2.2: Incentive Motivation

This work is grounded in a model of Incentive Motivation, the Incentive Salience Theory (Berridge, 1989). According to this theory, the brain contains two distinct systems: one system responsible for hedonic pleasure, or "liking," and another separate yet interconnected system responsible for "wanting,". Liking refers to the pleasure or enjoyment experienced when receiving a reward, reflecting its hedonic value. "Wanting," however, can be implicit

(unconscious and Pavlovian) or explicit (conscious and goal-oriented). Implicit *wanting (denoted by italics),* involves unconscious motivational responses triggered by cues predicting rewards, while explicit wanting involves conscious, cognitive desires with specific goals (Berridge & Robinson, 1998).

When measuring these constructs in humans, wanting is often assessed using subjective measures (Chae et al. 2023; Gaillet et al. 2013; Morquecho-Campos, 2021; Proserpio et al. 2019; Ramaekers et al. 2014; Rolls & Rolls, 1997) or evaluations (Biswas & Szocs, 2019). However, such measures are not believed to be valid assessments of non-conscious, implicit level motivations (Berridge & Robinson, 1998; Pool et al. 2016). In animals, implicit *wanting*, has typically been assessed using behavioural measures such as the nose poking (Berridge & Aldridge, 2000; Flagel et al. 2009; Piantadosi et al. 2007; Robinson et al. 2014) and lever pressing tasks (Crocker & Cardinal, 2017; Clark et al. 2013; Salamone et al. 2007; Saunders et al. 2018;), where the frequency and intensity of responses reflect motivation to obtain a reward (Robinson et al. 2014; Saunders et al. 2018).Correspondingly, it has been suggested that the effort exerted through grip-force can provide a more objective measure of *wanting* in humans (Pirc et al.2019; Ziauddeen et al. 2014). For example, Ziauddeen et al. (2011), adopted the use of a grip-force dynamometer to measure motivation for food related images, presented either for 200ms (conscious) or 33ms, (non-conscious). They reported a significant sensory-specific satiety, in that, participants applied less force to win the food they had just consumed and more effort to win the other food option, evident for both conscious and non-conscious trials. It is, however, possible that this reduction in motivation for a consumed food could be influenced by the presence of variety, which increases food intake through sensory-specific satiety (Embling et al., 2021). As variety in sensory characteristics (e.g., taste, texture, and smell) is introduced, the appeal of the initial food decreases relative to alternatives, therefore, increasing motivation toward other foods (Hetherington et al., 2006). This shift is consistent with the findings of Rolls and colleagues (1981), who demonstrated that food variety can enhance consumption by offering diverse sensory experiences. Therefore, the decline in motivation for the initially consumed food may not only reflect a sensory-specific satiety effect, but also the attraction of alternative sensory inputs, reinforcing the role of variety in food-seeking behaviours (Rolls et al., 1981).

Further, "liking" which can only be captured during or immediately after the consummatory phase of reward attainment is typically measured in humans using either

subjective ratings of pleasure or enjoyment using self-report scales, or, more rarely, physiological measures such as facial Electromyography (fEMG) to assess positive facial expressions, such as smiling (Cannon et al. 2017; Danner et al. 2014; de Wijk et al. 2012; Weiland et al. 2010; Wendin et al. 2011).

Studies 1 *(Chapter 3)* and 2 *(Chapter 4)* replicated the main features Ziauddeen et al. (2011), by using a MLT004/ST Grip Force Dynamometer (*adinstruments.com*), a pre-calibrated strain-gauge based isometric transducer (Image 2.2), in order to measure motivation for food related images.

Figure 2.2: *The MLT004/ST Grip Force Transducer, a pre-calibrated strain-gauge based isometric transducer with a linear response in the 0-800 N range was used to measure grip-force. (Image from From ADInstruments. Retrieved 18/01/2024, from https://www.adinstruments.com/products/grip-force-transducer)*

In Studies 1 (Chapter 3) and 2 (Chapter 4), following the methodology of Ziauddeen et al. (2012), a Grip-Force Dynamometer *(Image 2.2)* was used as an implicit measure of incentive motivation to directly measure the impact of brief, odour exposure (Study 1) and food consumption (Study 2) on motivation for food related images, as well as actual food choices. Full methodological details can be found in Chapter 3.4.3.2.

2.3: Facial Electromyography (EMG)

In Study Four, facial Electromyography (EMG) was used to measure individual differences in 'liking' of oral stimuli (Berridge & Robinson, 1998) (full methodological details can be found in Chapter 6.6.1.1. In the context of food reward, sweet and pleasant tastes elicit positive facial 'liking' expressions (such as tongue protrusions & lip smacking), whilst bitter

and unpleasant tastes elicit facial 'disliking' expressions (such as gaping & nose wrinkling), characteristics which are homologous in humans and animals (Berridge, 2000). This notion has been evidenced in research analysing video data of facial expressions (Danner et al. 2014; Wijk et al. 2012; Weiland et al. 2010; Steiner et al. 2001), during the consumption of liquid stimuli. Unlike video analysis, EMG has been found to capture the subtle and often imperceptible muscle contractions that correspond to emotional reactions, thereby providing a sensitive measure of hedonic responses to oral stimuli, even when overt facial expressions are minimal (Armstrong et al. 2017; Cannon et al. 2017; Sato et al. 2020).

Facial EMG measures spontaneous electrical activity of muscles from the body surface with a high temporal resolution and produces a stochastic signal the amplitude of which reflects the intensity of muscle activations beneath the skin's surface. Despite there being at least five muscles that are considered essential for the facial expression of basic emotions (Waller et al. 2008), facial EMG research has primarily often focussed on the Corrugator Supercilli (CS), which is located above the brow, toward the nose, and is associated with negative affect, and the Zygomaticus Major (ZM), which runs across the cheek, from the corner of the mouth to the ear lobe activity of which is typically associated with positive affect (Pawling et al. 2017; Epstein, 1990; Larsen et al. 2003; Tan et al. 2012) (Figure 2.3). Research has widely established the effectiveness of EMG activity in relation to discriminating responses to positive and negative faces (Wingenbach et al. 2018), touch (Pawling et al. 2017), pictures, sounds and words (Larsen et al. 2003; van Berkum et al. 2020), food (Sato et al. 2020) and odour stimuli (Armstrong et al. 2007). Whilst it is typically shown that ZM and CS muscles have a differential relationship whereby increased activity in one is associated with a decrease in the activity of the other (Cacioppo et al. 1986; Larsen et al. 2003), it is important to note that factors such as attention, effort, and cognitive processing can also influence muscle activity, obscuring the interpretation of EMG as a direct marker of emotional valence.

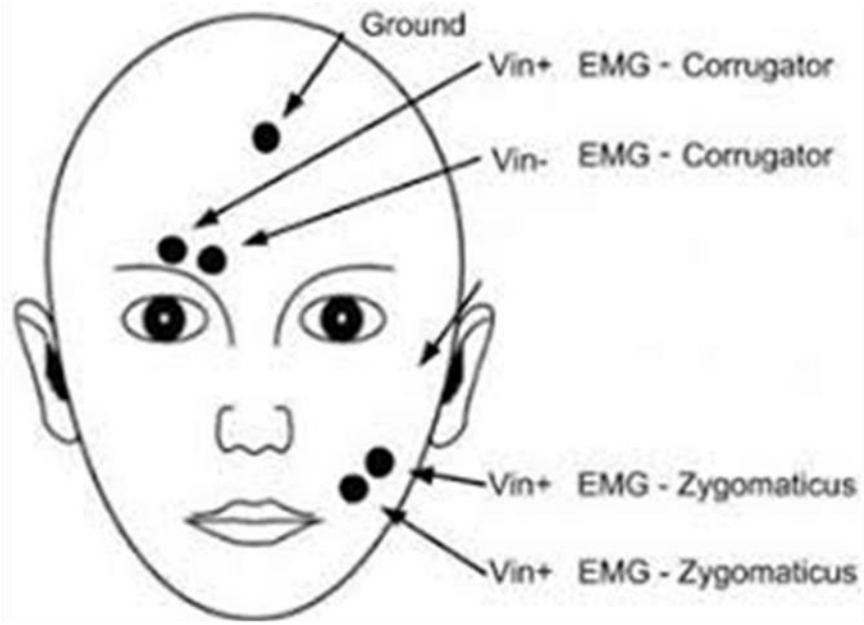

Figure 2.3: *Location of the EMG electrodes used for measuring muscle activity from the Corrugator Supercilli and Zygomaticus major. Zygomaticus major activity was measured by placement of two electrodes on the cheek, running from the corner of the mouth toward the earlobe. Corrugator Supercilli was measured by placement of two electrodes placed above the let brow. One ground electrode placed near the hairline, acts as a reference electrode (Image adapted from "Computing emotion awareness through galvanic skin response and facial electromyography," by J. H. Westerink, E. L. Van den Broek, M. H. Schut, J. Van Herk, and K. Tuinenbreijer, 2008, Probing experience: From assessment of user emotions and behaviour to development of products (p. 159). Springer).*

2.4: Genetic Taster Status

Genetic Taster Status (GTS) refers to an individual's sensitivity and perception of taste and is often used to categorise individuals into either Super-Tasters, Medium-Tasters or Non-Tasters, based on their ability to detect bitter thiourea compounds such as phenylthiocarbamide (PTC) and its chemical derivative, 6-n-propylthiouracil (PROP) (Bartoshuk, 1991). This genetic variation in bitter taste perception is believed to contribute to differences in food preferences, in which individuals identified as Super-Tasters perceive PTC and PROP to be intensely bitter, Medium-Tasters perceive them as moderately bitter, whereas Non-Tasters perceive these compounds to be weak or tasteless (Bartoshuk et al. 1994; Bartoshuk et al. 1998; Delwiche et al. 2001; Yang et al. 2014). Among bitter taste receptors (T2Rs), the TAS2R38 gene encodes a receptor protein that plays a crucial role in detecting bitter tastes, with genetic variations influencing the structure and function of the receptor, thereby affecting an

individual's ability to perceive and react to bitter compounds. Specifically, variations in TAS2R38 determine whether an individual will be a Super-Taster, Medium-Taster, or Non-Taster by altering the receptor's sensitivity to bitter molecules such as PTC and PROP (Bartoshuk, 2000; Kim et al. 2003).

Such variation in oral perception reflects the fact PROP tasters have a higher density of gustatory papillae and taste pores (Bartoshuk et al. 1994; Bartoshuk, 2000; Essick et al. 2003; Zhou et al. 2021) on their tongues than Non-Tasters (Dietsch et al. 2019). Approximately half of the population are believed to be Medium-Tasters, and a quarter Super-Tasters, with females being more likely than males to be Super-Tasters (Bartoshuk et al. 1994). Though it is widely accepted that this increase in the number of fungiform papillae on the tongue is associated with increased sensitivity to bitter tastants (Bartoshuk et al. 1994; Bartoshuk, 2000; Essick et al. 2003; Zhou et al. 2021), the association with enhanced sensitivity to trigeminally mediated, chemesthetic, thermal and tactile sensations (Essick et al. 2003), such as astringency (Pickering & Robert, 2006) and capsaicin (Green, 2003) and menthol (Cliff & Green, 1996), is much less understood (see also Eldeghaidy et al. 2011). As such, understanding how GTS affects responses to chemesthetic and astringent stimulation can provide insights into why individuals prefer certain foods over others and how they experience food textures and flavours differently. For instance, individuals with lower sensitivity to bitter tastes may consume more bitter vegetables, associated with health benefits, while those with heightened sensitivity may need alternative strategies to incorporate these foods into their diet (Costanzo, 2023).

GTS can be determined via quantification of the density of the fungiform papillae on the tongue using a blue-dye method (Bartoshuk et al. 1994; Duffy et al. 2004; Eldeghaidy et al. 2018; Essick et al. 2003; Nachtsheim & Schlich, 2013). This technique involves staining of the tongue with food colouring, providing visual contrast between the fungiform papillae (which remain pink) and the filiform papillae (dyed blue) - meaning they are countable (Figure 2.4) (Duffy et al. 2004; Essick et al. 2003). Following capture of a high-quality digital image, fungiform papillae are counted over a small region of the anterior tongue using a 5–10 mm circular template. It has been suggested that this method of counting is subjective, with inconsistencies in papillae density when different assessors count the same tongue image, however, Nuessle et al. (2015) proposed the '*Denver Papillae Protocol'* as a standardised method to characterise fungiform papillae, and found that with this specialised training, variability significantly decreased (Nuessle et al. 2015). The absence of a standardised

approach to measuring fungiform papillae density contributes to inconsistencies across studies (Eldeghaidy et al. 2018).

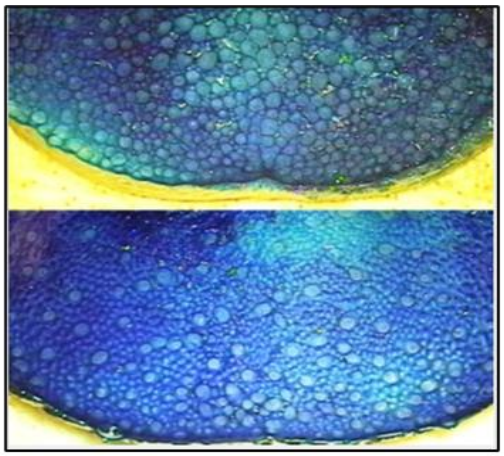

Figure 2.4: *Blue-dye method for measuring Taster Status. The tongue is stained with a blue food-dye in order to provide a contrast between the fungiform papillae (which remains pink) and the filiform papillae (dyed blue). A high-quality digital image is then obtained, which allows fungiform papillae to be identified over a small region of the anterior tongue using a 5-10mm circular template. (Image from "Measurement of gustation: From clinical to population-based methods," by V. B. Duffy, S. Rawal, and J. E. Hayes, 2021, Sensory science and chronic diseases: Clinical implications and disease management (p. 75). Springer).*

GTS is also widely assessed using subjective ratings. Originally this was done using a procedure in which individuals evaluated five supra-threshold concentrations each of PROP (0.032–3.2 mM) and NaCl (10 mM–1 M) (Bartoshuk et al. 1994) using magnitude estimation and are classified by visually comparing the taste response to PROP with that to NaCl. Those who rate NaCl higher in intensity than PROP are classified as Non-Tasters, those who rated PROP higher than NaCl were classified as Super-Tasters, with Medium-Tasters providing similar ratings to NaCl and PROP. In attempt to simplify the protocol, Tepper and Christensen, (2001) compared the assessment of GTS using two methods; a three-solution method, which required individuals to taste three samples each of PROP (0.0032, 0.32 and 3.2 mmol/l) and NaCl (sodium chloride) (0.01, 0.1, 1.0 mol/l) and rate the perceived intensity on a Labelled Magnitude Scale (LMS) (Figure 2.5) (Green et al. 1993), and a one-solution method, which carried the same procedure, though required the rating of only one PROP solution (0.32 mmol/l) and one NaCl solution (0.1 mol/l). It was reported that both the three-solution and one-solution methods reliably classify subjects by PROP taster status (Tepper et al. 2001).

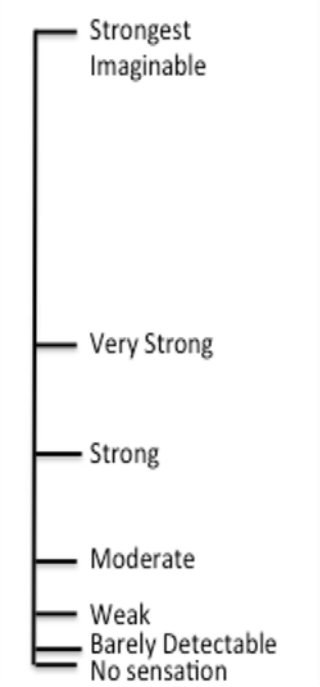

Figure 2.5: *Labeled Magnitude Scale (LMS; Green et al., 1993). This scale allows individuals to mark the perceived intensity of a sensation, with the top labeled "strongest imaginable" — specifically, the strongest oral sensation they can imagine, whether from oral health care products, foods, or any sensation they consider the most intense. The bottom of the scale is labeled "no sensation," indicating the absence of any perceptible sensation. Participants are free to place their rating anywhere along the line, with no restriction to the anchor points. (Image from "Evaluating the 'Labeled Magnitude Scale' for measuring sensations of taste and smell," by B. G. Green, P. Dalton, B. Cowart, G. Shaffer, K. Rankin, and J. Higgins, 1996, Chemical senses, 21(3), p. 326).*

A key feature of these methods is the use of the LMS or evaluating the samples. The LMS is a psychophysical tool used to measure perceived intensity of sensory stimuli and is used widely in taste perception research. This involves the use of numerical cut-off scores and features verbal descriptors (e.g. "barely detectable," "moderate," "very strong"), placed at quasi-logarithmic intervals, it allows for sensitive and accurate ratings across a wide range of intensities. Measuring 0-165mm from the base of the scale, non-tasters are classified as those who rate intensity 0-20, medium-tasters ratings fall between 20–100, and super-tasters rate 100-165 (Green et al. 1993).

This method was further refined by Zhao, Kirkmeyer, and Tepper (2003) using PROP and NaCl impregnated filter papers, rather than solutions. In the three-paper method, participants evaluate three concentrations of PROP and three concentrations of NaCl on a LMS (Green et al. 1993), as per the original method. In the one-paper method, individuals evaluate a single concentration of PROP (either 0.50 mmol/L, 0.42 mmol/L, or 0.32 mmol/L) and NaCl

(0.1 mol/L) in the same way as the three-paper method. Findings confirmed that both the three-paper and one-paper method were a reliable screening tool for assessing taster status. However, for the one-paper method, taster groups could not be separated with PROP at 32 mmol/l or 42 mmol/l, with discrimination of the taster groups only being achieved when the concentration was increased to 50 mmol/l (Zhao, Kirkmeyer, and Tepper., 2003).

In Study 4, following the methodology of Zhao et al. (2003), the one-paper method was used to measure taster status. Full details can be found in Chapter 6.5

2.5: Odour Identification Task

Odour identification tests involve presenting a series of suprathreshold odours to assess a participant's ability to accurately identify them, typically using a 4-alternative forced choice method with visual cues (Doty, 2018; Hummel et al. 1997). This type of forced-choice testing, in which participants must choose an answer even if nothing is smelled is widely used (Brumm et al. 2023; Moein et al. 2023; Sulmont-Rosse et al. 2005). Whilst some tests allow for an additional response category in which participants can report an answer of 'no odour', these are susceptible to malingering in clinical settings, in which individuals may report the absence of an odour, in order to falsely report or exaggerate olfactory impairments (Doty & Crastnopol, 2010).

The University of Pennsylvania Smell Identification Test (UPSIT) (Doty et al. 1984) and The Burghart Sniffin' Sticks test (Hummel et al. 1997), are two widely used clinical measures of olfactory function. The UPSIT, developed by Richard Doty at the University of Pennsylvania in the 1980s (Doty et al. 1984), is a standardised, four-alternative test of olfactory identification utilising a scratch-and-sniff method, consisting of 40 chemically micro-encapsulated odour patches that release an odour when scratched. The UPSIT focusses on the ability of individuals to identify a number of odourants at the suprathreshold level (Eibenstein et al. 2005). The Burghart Sniffin Sticks test was developed by Professor Hummel at the Burghart Medical Technology company in Germany (Hummel et al. 1997), in order to create a standardised and comprehensive assessment tool of olfactory function. The test comprises a collection of twelve odourised pens, each containing a scent associated with foods/flowers/household items. Participants are presented with these pens and are required to sniff them and then identify and differentiate the odours.

Whilst most research using these methods, focusses on the identification of single odours, methods have been adapted in which emphasis has been put on the ability to identify component odours within mixtures, using similar forced-choice procedures. For example, an adapted version of the Sniffin' Sticks test, termed the Sniffin Sticks Odour Mixture Identification Test (SSomix), is based on the identification of single odourants in both binary and ternary mixtures. (Liu et al. 2020). Whilst the development of this standardised mixtures test is relatively new, other research has adopted similar approaches (Chan et al. 2018; Livermore & Laing, 1996; Poupon et al. 2018), however often the stimuli used in such studies lack ecological validity as odour objects encountered in the real world are typically themselves multi-component mixtures, not mono-molecules. Walker et al. (2020) adopted a four-alternative-forced choice procedure to test identification of ecologically relevant, multi-component odours such as marzipan and chocolate cake within binary *(2 odours)* and ternary mixtures *(3 odours).* This complexity better represents the natural olfactory environment, providing a more accurate and realistic assessment of individual odour identification abilities (Thomas-Danguin et al. 2014).

Study2, adopted the same methodology used by Walker et al. (2020) in order to investigate odour mixture perception, using six food-related fragrances: blackcurrant, chocolate cake, cola bottles, marzipan, orange, and strawberry. Full methodological details can be found in Chapter 5.3.2.1.

2.6: Measures of Visual Processing Style

Individuals often attend to and process visual information from two different perspectives, deemed global processing and local processing (Navon, 1977). Global processing involves perceiving the overall Gestalt of a stimulus, focusing on the broader context or big-picture aspects. In contrast, local processing involves attending to specific details within a stimulus, emphasising a narrower and detail-oriented approach (Kimchi, 1992; Navon, 1977).

The NAVON task is designed to examine how individuals process visual stimuli that contain both a global shape or letter and smaller local elements (Navon, 1977). The main purpose of the NAVON task is to examine how participants prioritise or process global and local information and can be used to investigate the concept of perceptual interference, where incongruent global and local information may compete for attention and influence response times and accuracy. NAVON involves the presentation of a large letter *(global level)* composed

of smaller letters *(local level)* in which the global and the local letters are either congruent (e.g. *global S &local Ss or global H &local Hs*) or incongruent (e.g. *global H & local Ss or global S &local Hs*). Individuals are instructed to identify either the local or global target on successive blocks. A large body of research indicates that neurotypical adults show a global bias, as measured by a faster reaction times and greater accuracy to global than local targets on incongruent trials (Chamberlain et al. 2017; Lachmann et al. 2014; Navon, 1981). However, individual differences in processing style and ability exist, with enhanced local processing reported in autistic participants (Bolte et al. 2007, D'Souza et al. 2016; Gerlach et al. 2017), as well as in artists and musicians (Chamberlain et al. 2017), and across cultures (Davidoff et al. 2008; Lao et al. 2013). Temporary changes in affective state also influence the preference for local or global stimuli (Fredrickson & Branigan, 2005; Srinivasan & Hanif, 2010), thus, suggesting that an individual's visual processing style is malleable rather than static.

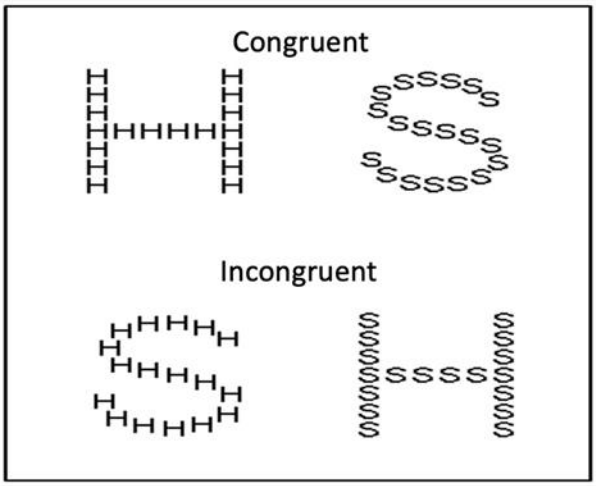

Figure 2.6*: Illustrates the 4 stimulus types from the Navon task. Trials are equally split into global (identify the large letter) and local (identify the small letter) trial, with equal presentations of congruent and incongruent stimuli. (Image adapted from Navon letters and composite faces: Same or different processing mechanisms? by D. Fitousi and O. Azizi, 2023, Frontiers in Psychology, 14, 1219821. https://doi.org/10.3389/fpsyg.2023.1219821. Open access).*

The Block Design Task (Wechsler, 1981) is a neuropsychological test commonly used to assess visual-spatial skills and cognitive abilities. It is a subtest of the Wechsler Intelligence Scale for Children (WISC) and the Wechsler Adult Intelligence Scale (WAIS), which are widely used intelligence tests. This task requires individuals to recreate a global image using local parts. Throughout this task, participants are presented with a set of red and white blocks,

each consisting of two red, two white and two diagonally striped faces, and are required to recreate specific patterns or designs using the blocks. The patterns can range from simple arrangements to more complex designs. Though not as widely used, Autistic individuals (Bolte et al. 2008; Muth et al. 2014; Shah & Frith, 1993), as well as those with other neurodevelopmental disorders (Cardillo et al. 2017; Jacobson et al. 2005) display superior performance, indicating a bias for local processing on the Block Design task. It is however suggested that successful completion of the Block Design Task can be influenced by fine motor skills and hand-eye co-ordination, and as such, difficulties in these areas can impact performance, even if an individual has strong local-global processing abilities (Cardillo et al. 2017).

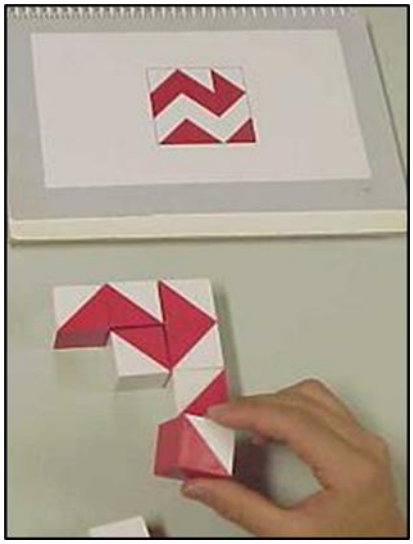

Figure 2.7: *Illustrates the Block Design task, in which individuals are required to replicate 2D patters using 3D blocks. The number of blocks required to recreate thee designs, increases incrementally as trials progressed, from 4-9. (Image from Finite Geometry by S. H. Cullinane, 2004, Finite Geometry Online (http://finitegeometry.org/sc/gen/bdes/).*

Based on these methodologies, Study 3 study opted to use both the NAVON Task and the Block Design Task to assess local-global processing style. Whilst the NAVON Task primarily tests perceptual processing and attentional control, assessing how individuals perceive and prioritise global versus local elements within visual stimuli (Navon, 1977), the Block Design Task assesses visual-spatial skills, including the ability to perceive and manipulate local elements (individual blocks) to reproduce a global pattern or design accurately (Wechsler, 1981). Together, these tasks provide a comprehensive assessment of how individuals process visual information across different cognitive domains. Full methodological details can be found in Chapter 5.3.3.1 *(NAVON Task)* and 5.3.3.2 *(Block Design Task).*

Chapter 3. No evidence for goal priming or sensory-specific satiety effects following exposure to ambient food odours.

The study reported in this Chapter, combined with the study reported in Chapter 4, has been published in the journal Appetite.

https://www.sciencedirect.com/science/article/pii/S0195666324005348

3.1 Abstract

Sensory-specific satiety (SSS) describes a decline in the hedonic value of a food after it has been consumed relative to a food, with differing sensory properties, that has not been consumed. Implicit wanting of the consumed food has also been shown to decline. Several studies have reported that brief exposure to food odours can also produce a SSS effect, in the absence of consumption, selectively reducing hedonic ratings and subsequent food choices. In contrast, other studies have reported goal priming effects of ambient odours. The aim of the present study was to determine whether exposure to ambient food odours would selectively reduce implicit motivation for associated foods. Participants (N=40) were randomly assigned to a high (*chocolate)* or low *(orange)* calorie odour group and completed two blocks of an incentive force task. One block was completed immediately before and the other immediately after odour exposure. A grip-force transducer was used to measure exerted effort to win food prizes. The prizes were depicted in visual images presented at two durations – 200 and 33ms. A mixed ANOVA containing three within subject factors: Block *(one, two)*, Image *(Orange, Chocolate)* and Duration *(33ms, 200ms)* and one between subject factor: Group *(Orange Odour, Chocolate Odour),* was used to measure differences in exerted effort. While participants exerted greater effort to win high calorie, indulgent, than low calorie, non-indulgent foods, no significant satiety or priming effects were found following ambient odour exposure. While this finding could be explained by factors such as odour concentration, as well as the timing and nature of odour exposure, it raises questions about the robustness of previously reported odour induced satiety and priming effects.

3.2 Introduction

Rewards are desired, appetitive, and positive outcomes of motivated behaviour (Matyjek et al. 2020). Humans, like all animals, are innately driven to seek out and consume primary rewards, to satisfy their physiological needs (Smiejers et al. 2022). Cues in the environment can initiate motivated behaviours, both consciously and unconsciously, through their acquired association with primary rewards (Anselme & Robinson, 2016; Berridge, 2018; Morales & Berridge, 2020;), evidenced in the priming literature where presentation of visual cues increases motivation for, and goal-directed behaviour towards associated rewards (Blanchfield et al. 2014; Friese et al. 2006; Friese et al. 2008; Legget et al. 2022; Spence, 2016). Though visual food primes (e.g. tv advertisements, billboards) are widely understood to increase motivation for associated foods, the impact of olfactory primes on food consumption is less clear (Biswas & Szocs, 2019; Finlayson, King & Blundell, 2008; Mas, Brindisi, Chabanet & Chambaron, 2020; Proserpio et al. 2019; Rolls & Rolls, 1997).

Whilst odours are part of the flavour percept during food consumption (retronasal olfaction) (McCrickerd & Forde, 2016; Small, 2012), prior to ingestion, odours can alert us to foods in our environment (orthonasal olfaction) and prime consummatory behaviour (Boesveldt & Graaf, 2017; McCrickerd & Forde 2016). For example, explicit exposure to ambient food odours for 20 minutes *(e.g. banana, chocolate, tomato soup, and bread)* selectively increased appetite for the cued food (Ramaekers et al. 2014). Indeed, people do not have to be consciously aware of an odour for it to be an effective prime. In fact, since the sense of smell adapts rapidly to stimulation, reducing the perceived intensity of an odour (Dalton, 2000), implicit odours may act as more effective primes that sub-consciously drive behaviour (Boesveldt & de Graaf, 2017; Gaillet et al. 2013; Morquecho-Campos, 2021; Proserpio et al. 2019; Ramaekers et al. 2014). In support of this, Gaillet et al. (2013) reported that implicit exposure to ambient fruit odours for 15 minutes led to more subsequent choices of fruit-and vegetable-based foods from a menu.

However, exposure to food odours has also been reported to induce not only priming effects, but also sensory-specific satiety effects (See, Zhang & Spence, 2023, for review). This widely replicated phenomenon refers to the reduced hedonic and motivational value of a food following consumption. (Rolls et al. 1981). There is some indication that exposure to food odours can elicit sensory-specific satiety, without requiring foods to enter the gastrointestinal

system (Biswas & Szocs, 2019; Coelho et al. 2008; Rolls & Rolls, 1997). For instance, explicitly smelling a banana or chicken odour for five minutes, reduced subsequent ratings of both pleasantness and intensity (Rolls & Rolls, 1997), indicating food odours can satiate desire to consume associated foods. Furthermore, restrained eaters implicitly exposed to a food odour subsequently consumed less of the cued food than non-exposed restrained eaters (Coelho et al. 2008). Similarly, Biswas and Szocs (2019) implicitly exposed people to either an indulgent (unhealthy) or un-indulgent (healthy) ambient odour, across various locations (laboratory, supermarket, school). It was reported that exposure to an indulgent, high calorie food associated odour for over two minutes, resulted in more healthy, lower-calorie food selections, indicative of a sensory-specific satiety effect, while, in contrast, brief exposure (<30secs), produced a priming effect, as individuals opted for food options congruent with the odour they were exposed to.

Such mixed findings on the motivational effects of food odours may be explained by methodological variations in the nature and duration of odour exposure. For example, explicit retronasal exposure for five minutes has been shown to induce satiety effects (Rolls & Rolls, 1997), while explicit orthonasal exposure for ten and twenty minutes resulted in increased appetite for odour congruent foods (Jansen et al. 2003; Ramaekers 2013). Consistently, non-conscious exposure to ambient odours for ten to twenty minutes has been reported to prime congruent food choice (Proserpio et al. 2019; Gaillet-Torrent et al. 2014; Gaillet et al. 2013) and enhance both appetite ratings (Ramaekers et al. 2014) and food cue reactivity (Mas et al. 2020). While, in contrast, Biswas and Szocs (2019) reported priming effects after only thirty seconds of implicit exposure to an ambient food odour, with exposure of two minutes or more reducing selection of odour congruent foods. Meanwhile, Morquecho-Campos (2021) did not find any effect on appetite, preference, or intake after implicit exposure of three minutes. Taken together, reports that extended exposure to ambient food odours primes non congruent food choices (Biswas & Szocs 2019; Chae et al.2023) stand in contrast to the majority of the extant literature.

The incentive salience theory of motivation distinguishes neurally and psychologically between the motivational drive to obtain a reward (wanting) and the hedonic pleasure derived from its consumption (liking) (Robinson & Berridge 2003). Operationally, liking is measured as an explicit affective response to reward during, or immediately after, consumption while wanting is a measured as motivation to obtain a future reward and can be either implicit or

explicit (Berridge 1989; Pool et al. 2016). Results from both animal and human studies demonstrate that sensory specific satiety effects are apparent, not just in affective measures of food liking (Berridge 1991; Rolls et al.1981) but also in motivational assessments of food wanting, manifested as a selective decrease in drive to obtain a consumed food (Balleine & Dickinson 1998; Havermans 2009; Saelens & Epstein 1996; Ziaudden et al.2014). In animals, wanting is typically measured in instrumental behavioural tasks such as progressive ratio-schedules, where motivation is assessed as the amount of effort expended to obtain food (Zepeda-Ruiz et al. 2020; Velazquez-Sanchez et al. 2015; Kendig et al. 2013). In equivalent tasks, human participants are asked to perform actions such as pressing a response key (Temple, 2016; Rogers & Hardman, 2015) or squeezing a grip-force dynamometer (Ziauddeen et al. 2014). Here, the goal is to assess the value of the food at the moment of the response. For example, Ziauddeen et al. (2014) found that participants exerted less effort to win a visually cued food after they had consumed it to satiety, while there was no change in effort exerted to obtain a food that hadn't been consumed. This sensory-specific decrease in incentive motivation was apparent whether the food images were presented at a conscious or non-conscious level, suggesting that modulations of effort for the consumed food occurred outside conscious awareness. Whilst effort-based measures of incentive motivation have been shown to objectively measure wanting (Bindra, 1974, Bolles, 1972; Mela, 2006; Pool et al. 2016). Cacioppo and Tassinary (1990) proposed a framework categorising physiological measures based on their specificity and generality, arguing that most are outcomes rather than direct markers of psychological states. Outcomes exhibit a one-to-many relationship, where a physiological measure may reflect a psychological state but is also influenced by factors such as fatigue, attention, or cognitive effort. Thus, indicating, that effort-based measures, while valuable for examining incentive motivation, are not exclusive indicators of motivation (Richter & Slade, 2017). Despite their limitations, these measures provide a robust means of quantifying motivational states in contexts such as sensory-specific satiety, where effort changes align with shifts in reward value (Ziauddeen et al. 2014). Thus, effort-based tasks continue to serve as effective tools for examining the dynamic processes underpinning incentive motivation.

These objective measures have not so far been used to test the effects of ambient odour exposure on incentive motivation for associated foods (Cereghetti et al. 2020, Pool et al. 2015). Thus, to further explore the psychological mechanisms underlying previously reported odour priming and satiety effects, the current study used grip force as an objective measure of

incentive motivation (Ziauddeen et al.2012; Ziauddeen et al.2014) to investigate the effect of brief, odour exposure on appetitive motivation. In-line with incentive models of motivation, it is hypothesised that brief, five-minute, exposure to an ambient food odour will result in a priming effect, with participants displaying selective enhancement of motivation for congruent food images following odour exposure, and that this variation in motivation would be evident at both a conscious and non-conscious level. In addition, participants will be asked to make an unobserved explicit food selection at the end of the study. It is hypothesised that odour exposure will increase selection of the primed over the non-primed food.

3.3 Pilot Testing

Pilot testing to select odour and visual stimuli was conducted using staff members at Liverpool John Moores University. The participants of these preliminary experiments differed from those involved in the main experiment. In determining the odours to be used throughout the study, several stimuli were purchased *(AromaPrime.com)*, from which Seville Orange and Double Chocolate were selected as the most appropriate, in-line with the indulgent and non-indulgent options reported by Biswas and Szocs (2019).

3.3.1 Pilot 1: Odour Identification

3.3.1.1: Methods

A total of 14 participants volunteered to take part in the first pilot test. A 200µl *(4 drops from a Pasteur pipette)* sample of the Seville Orange and Double Chocolate aroma oils (from *AromaPrime.com*) were deposited onto small filter papers (*GE Healthcare Whatman TM 55mm diameter, Fisher Scientific*), and placed inside separate sealed amber glass jars. Participants were asked to open and smell each jar and rate each odour on a 12cm Visual Analogue Scales (VAS) measuring intensity, pleasantness, familiarity, edibility and expected liking categories (Appendix 1). Participants were also asked whether they were able to identify the odour.

3.3.1.2: Pilot 1 Results

For Identification, answers were considered to be correct if they fell within a '*citrus*' category for the Orange odour and within a Cocoa/Chocolate category for the Chocolate Odour. For the Orange Odour, 78.6% *(n=11)* of participants were correct in their identification *(Orange=50%, Lemon=28.6%)* and 92.9% *(n=13)* were able to correctly identify the Chocolate odour *(Chocolate=64.3%, Cocoa=28.6%).*

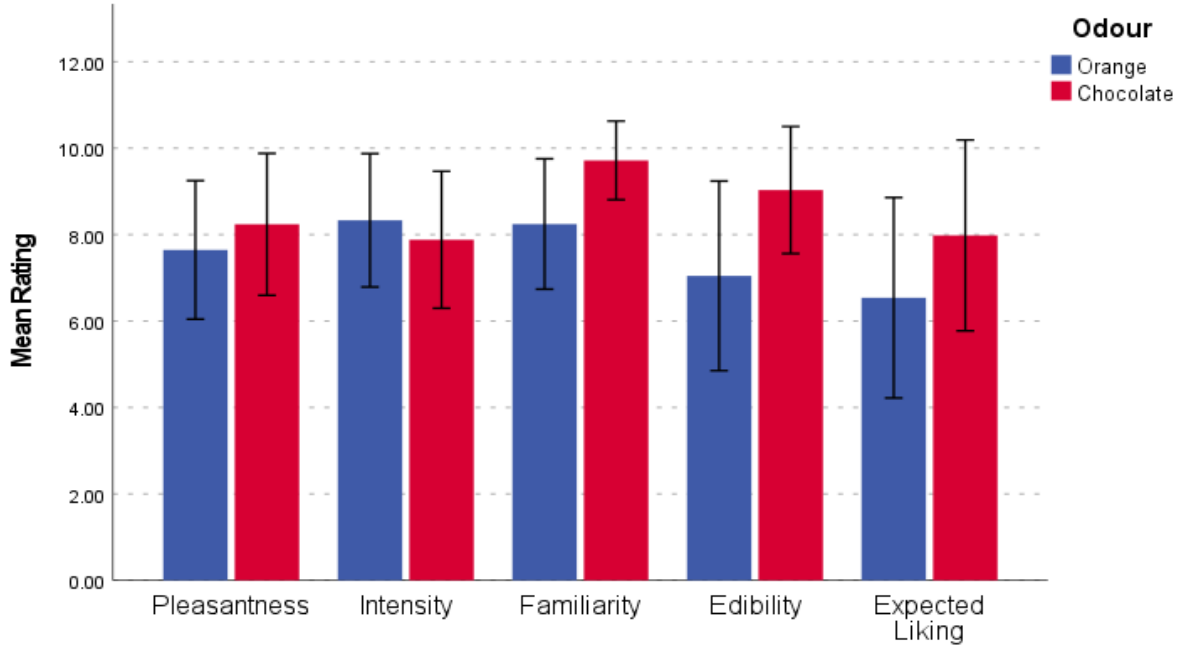

Figure 3.1: *Category ratings for Orange and Chocolate odours used during pilot testing. There were no significant differences in ratings of Pleasantness, Intensity, Familiarity, Edibility and Expected Liking for the Double Chocolate and Seville Orange odours. Error bars show 95% CI.*

Chocolate odour was rated higher on average for Pleasantness, Familiarity, Edibility and Expected Liking, whilst Orange was rated as more Intense *(Figure 3.1)*, however, a series of paired samples t-test indicated ratings for each of the descriptor categories did not significantly differ from each other *(ps>.05).*

3.3.2 Pilot 2: Odour Detection & Concentration

3.3.2.1 Method

A second pilot test was conducted, to determine the quantity of ambient odour to be used. A total of 19 faculty members were asked (*one-by-one*) to enter each of the four rooms in any order they wished. One room contained the Seville Orange Odour, one room contained the Double Chocolate Odour, and two rooms were used as controls and contained no odour. Twenty minutes prior to entering the odour rooms, 200µl of the aroma oil was placed onto the centre of an absorbent pad, which was then placed inside the diffuser and dispersed across the test room for sixty seconds. The diffuser was then removed from the room. Upon entering each room, participants were required to complete a questionnaire (Appendix 2), which asked whether they were able to detect an odour. If an odour was detected, they were asked to rate it

on a series of VAS measuring intensity, pleasantness, familiarity, edibility and expected liking. Participants were also asked whether they were able to identify the odour.

3.3.2.2: Pilot 2 Results

For detection and concentration of the Seville Orange Odour, 100% of participants were able to detect an odour in the room, with 52.6% correctly identifying the odour as being either Orange *(21.1%)*, Lemon *(5.3%)*, Citrus *(21.1%)* or Mandarin *(5.3%)*. Those who incorrectly identified the odour, described it as either Air-Freshener *(5.3%)*, Strawberries *(5.3%)*, Wood *(5.3%)* or Unknown *(31.6%)*.

For the Double Chocolate Odour, 84.2% *(n=16)* of participants were able to detect an odour in the room, with 62.5% *(n=10)* being able to correctly identify the odour as being either 'Chocolate' or 'Cocoa'. Those who incorrectly identified the odour, described it as either Smokey Bacon, Yeast or Unknown. 15.8% *(n=3)* of participants were unable to detect an odour.

For both control rooms, in which no odours were dispersed, 47.4% (n=9) of participants reported being able to detect an odour in room 1, and 31.6% *(n=6)* in room 2, however, other than one participant reporting the detection of Cocoa in Control room one, no other participants were able to describe what the odour was. This detection of odour in the control rooms may have been for one of two reasons; first: it is possible that odour molecules have lingered on participants when switching between rooms, second: demand characteristics may have been evident here as participants were not made aware that two rooms contained no odour, therefore, they may have assumed that they were supposed to detect an odour.

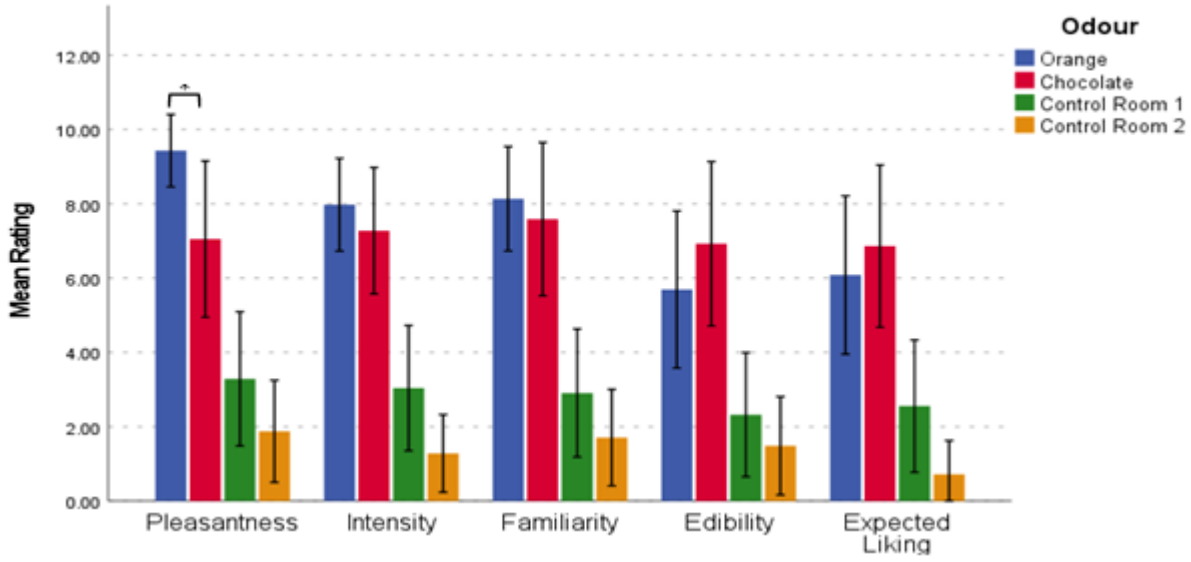

Figure 3.2: *Category ratings for Orange, Chocolate and Control odour rooms. Both food odour rooms were consistently rated higher for all descriptors, compared to the control rooms. Error bars show 95% CI. * denotes sig level<.05*

A one-way ANOVA revealed a significant main effect of room, in which Odour rooms were consistently rated higher than Control rooms for all descriptor categories $F(3,360)=72.09$, $p<.001$, $\eta_p^2=.38$ *(Figure 3.2).* However, there was no significant effect of category rating, in that ratings for each of the descriptor categories did not differ significantly from each other $F(4,360)=2.62$, $p>.05$, $\eta_p^2=.03$. In examining ratings for odour rooms alone, using t-tests adjusted for multiple comparisons, ratings for each of the descriptor categories did not differ from each other (ps>.05), other than for Pleasantness, where Orange was rated as significantly more pleasant than Chocolate *t (18)=2.32, p<.05*, a mean difference of 2.38.

3.3.3 Pilot 3: Image Perception

3.3.3.1: Method

3.3.3.1.1 Image preparation

All task images *(Figure 3.3)* were sourced from non-copyright online platforms and prepared using Adobe Photoshop. They were formatted to 500 x 500 pixels and had the same luminance and opacity, with all edges being blurred to reduce any sharp contrast between the image and the masked background.

3.3.3.1.2 Mask Image Preparation

Mask images were created using MATLAB by randomly scrambling all images and merging them to create ten composite mask images *(example shown in Figure 3.3).* Masking is a widely used and powerful way of studying visual processes to reduce (or eliminate) any influence from previous or upcoming primes (Elgendi et al. 2018).

3.3.3.1.3 Image Perception Task

During the Image Perception Pilot task, a forced choice procedure consisting of 30 trials was adopted. Three stimuli *(one from each category; Orange, Chocolate, Control)* were used *(Image 3.3),* which were displayed at three durations 17ms (short), 25ms (mid) & 34ms (long), to determine whether any duration could be considered subliminal.

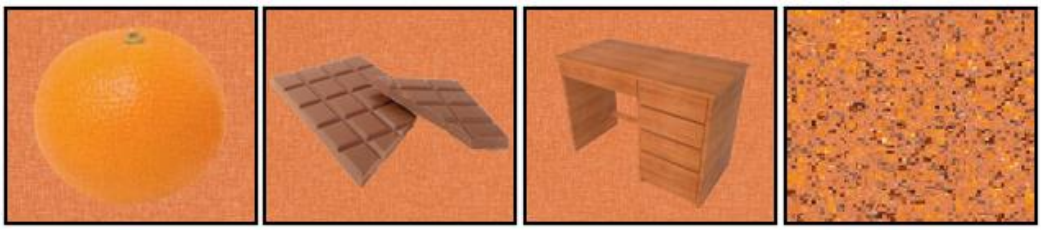

Figure 3.3: *Stimuli (one from each category, Orange, Chocolate & Control) and Mask screen used throughout the pilot task.*

During each trial, participants were presented with a Mask screen, followed by a Stimuli screen and then a second Mask screen. They were then shown a response screen which consisted of two images; the image just presented for that trial and a second randomly selected image. Using keys Z and M on the keyboard, participants were required to decide which of the two images they had just seen *(Image 3.4)*. The order of placement for the correct image on this screen was randomised across trials (50% right/left).

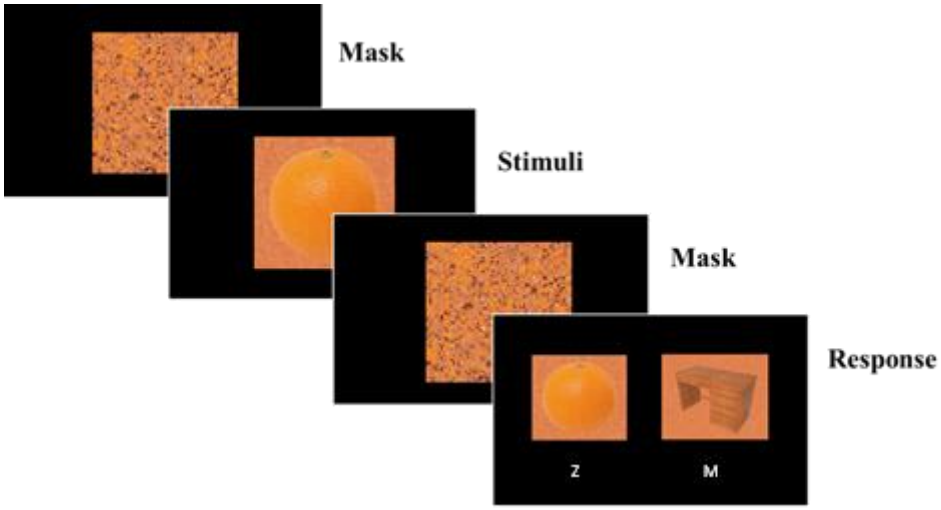

Figure 3.4: *Order of presentation for each trial of the forced choice discrimination task: Mask Image, Stimuli Image, Mask Image, Forced Choice Response screen. Participants were required to determine which of the 2 images on the response screen, matched the image for that specific trial.*

3.3.3.2: Pilot 3 Results

Due to the refresh rate of the monitor, actual presentation times differed slightly from proposed presentation times. The total proposed presentation time for each complete trial was 500ms, however, this ranged from 497.23ms-506.37ms (M=501.80). The stimuli presentation times differed: short (17.56ms), mid (26.69ms) & long (39.98ms).

To determine whether any of the presentation times were at a subliminal level, a Chi-Squared test was conducted between Response Accuracy and Duration. All expected cell frequencies were greater than five. The association between Image Condition and Response Accuracy was significant, $\chi^2(2) = 23.05$, $p<.05$, in that images were correctly identified 82.1% of the time during the short-duration, 87.9% of the time during the mid-duration and 98.6% of the time during the long-duration. However, regardless of presentation time, all images were correctly identified on the majority of trials. The Chocolate Bar (97.1%) and Control (98.6%) images were correctly identified more than the Orange image (72.9%). Overall, participants correctly identified images 89.5% of the time, thus signifying that the images were not in-fact at a subliminal level.

Based on the results of the image perception pilot, it was determined that the Orange image would be carried over and used in the main task, however, the images used for the chocolate stimuli and control stimuli were replaced. This was due to participants reporting that the sharp

edges of the images in both these categories resulted in them being more identifiable. While the images were not subliminal, the concern was that the distinct shape of the stimuli might influence recognition, and therefore, we replaced the Control and Chocolate images with images of the same form (round) to minimise any potential bias.

Although our study aimed to replicate the experiment by Ziauddeen et al. (2014), which involved both subliminal and supraliminal images, it became evident that while the monitors we employed had a refresh rate capable of supporting presentation times below Ziauddeen's threshold of 33ms, achieving a presentation time of 17.56ms, this duration was still insufficient to achieve true subliminal presentation. However, whilst the primary aim of the study was to determine the effectiveness of grip force as an objective measure of incentive motivation, we remained interested in whether varying presentation duration (long vs. short) affected exerted effort. As such, trials will hereafter be referred to as long-duration and short duration, rather than supraliminal and subliminal. (*Detailed information on new images and presentation times are reported main task methods section 3.4.2.3).*

3.4 Materials and Methods

3.4.1 Participants

38 participants (24 female) were quasi-randomly assigned to either Orange (*N=18, 18-58 years old; M = 32.95, SD = 12.79; f=12*) or Chocolate (*N=20, 18-60 years old; M = 30.90, SD = 12.89; female n=12*) odour exposure groups. Age was not reported by one participant in the Orange group. Participants were recruited from the student population at Liverpool John Moores University via the use of posters placed around the Campus. The University's Psychology Research Participant Panel was also used to recruit individuals from the wider public. People were excluded from participating if they had any respiratory problems, food intolerances or allergies. The experimental protocol was approved by the Ethics Committee at Liverpool John Moores University (19/NSP/062). Participants received a £10 shopping voucher to thank them for their time.

A power analysis was conducted using G-Power (Faul et al. 2007). Using the ANOVA: Repeated Measures, within-between interaction option with two groups and two measurements, a sample of 38 was required to detect a small-medium effect size (f = .25) with 85% power and an alpha level of 0.05.

3.4.2 Materials

3.4.2.1 Odour Stimuli

In line with a previous study reporting satiety effects of ambient food odour exposure (Biswas & Szocs 2019), one indulgent (high-calorie) and one non-indulgent (low-calorie) food associated odour was selected for the study. The final selection of Double Chocolate and Seville Orange aroma oils (*AromaPrime.com)* was based on pilot testing (n=13) which confirmed, during explicit exposure (odour presented on filter papers in glass jars), that both odours were identifiable and did not differ significantly in terms of ratings of perceived pleasantness, intensity, familiarity, or edibility.

3.4.2.2 Odour Dispenser

Twenty minutes prior to the participant entering the odour exposure room, 200µl (4 drops from a Pasteur pipette) of the aroma oil were pipetted onto individual quarters of filter paper (GE Healthcare Whatman TM 55mm diameter, Fisher Scientific), placed into the top of a mini scent diffuser (AromaPrime.com) and dispersed for 60 seconds. The diffuser was then removed from the room. Trial and error, coupled with experimenter judgment, were systematically used to determine the timing and concentration of the aroma oil to achieve the desired ambient odour conditions. This iterative process ensured that the odour was sufficiently subtle to avoid immediate detection upon entering the room, while still being identifiable when attention was directed to it. The protocol used during piloting, resulted in intensity ratings of approx. 7, on a 0-10 VAS, when dispersed in the test rooms, while odours were not reliably detected when attention was not directed towards them.

3.4.2.3 Visual Images

Task Images were sourced from non-copyright online sources and prepared using Adobe Photoshop. They were formatted to 500 x 500 pixels and had the same luminance and opacity, with all edges being blurred to reduce any sharp contrast between the stimuli image and the masked background. In line with the task design used in Ziauddeen et al. (2012) study, to minimise direct motor specification effects, different images were used for the long (200ms) and short (33ms) presentation trials *(see Figure 3.5A).* All test images were randomly scrambled using MATLAB. A random combination of pixels from each image were then merged using MATLAB, to create ten composite mask images *(*see Figure 3.5B*).* These were then randomly selected across all trials for both the pre- and post-stimuli mask.

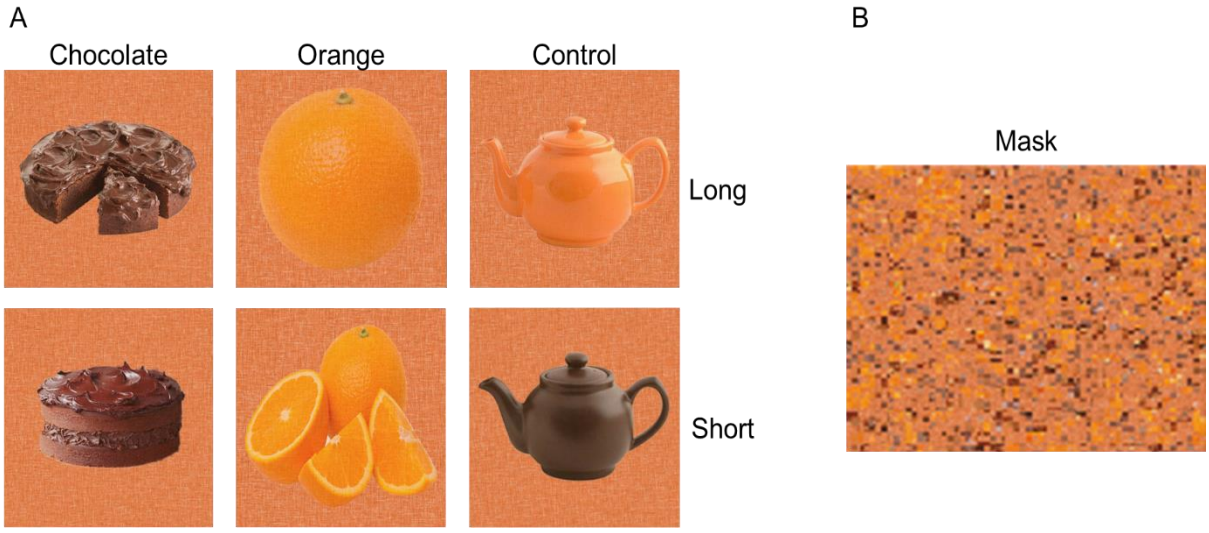

Figure 3.5: *(A) Visual Stimuli used in the Grip-Force Task; two images were used for each category (Chocolate, Orange, Control). The top three images were presented for the Long-duration trials (200msec) and bottom three images were used for the Short-duration trials (33 msec). (B) An example of one of the mask images used.*

3.4.3 Measures

3.4.3.1 Food Preference Questionnaire

Prior to attending the laboratory, participants completed a Food Preference questionnaire presented online via Qualtrics survey software (Qualtrics.com). As shown in Table 3.1, this asked whether they followed a particular diet (e.g. vegetarian/vegan), their snack preferences (e.g. for sweet or savoury foods), general eating habits and any food intolerances/allergies. Information gathered from this questionnaire was used to ensure participants were eligible to take part in the study, could consume the foods being presented, and did not have any relevant dietary restrictions or allergies. These data were not used in any subsequent analysis.

Table 3.1: *Questions contained within the Food Preference Questionnaire. Questions are shown on the top line of each row, with response options shown on the bottom line of each row.*

1	**What do you eat?** (1) Omnivore (meat & fish), (2) Piscivore (fish not meat), (3) Vegetarian, (4) Vegan
2	**Do you have food allergies or other important diet restrictions?** (1) Yes, (2) No
3	**Do you eat snacks between meals?** (1) Yes, (2) No, (3) Occasionally

4	**If so, what are your favourite snacks?** (1) Sweet (unhealthy), (2) Savoury (unhealthy), (3) Spicy, (4) Sweet (healthy), (5) Savoury (healthy)
5	**Do you enjoy spicy/hot foods?** (1) Yes, (2) No, (3) Occasionally
6	**Do you eat desserts after a meal?** (1) Yes, (2) No, (3) Occasionally
7	**If so, what type of desserts do you prefer?** (1) Sweet – unhealthy (e.g. cakes), (2) Sweet – healthy (e.g. fruit), (3) Savoury (egg, cheese & crackers)
8	**Is it important to you that you consume 5 portions of fruit/vegetables per day?** (1) Yes, (2) No, (3) Occasionally
9	**Do you by choice, refrain from eating any specific types of food?** (1) Yes, (2) No, (3) Occasionally
10	**If so, which foods do you refrain from eating?** (1) Sweet (unhealthy), (2) Savoury (unhealthy), (3) Spicy, (4) Sweet (healthy), (5) Savoury (healthy)

3.4.3.2 Grip-Force Task

Experiment generator software E-prime 3.0 (v3.0.3.80) was used to create the task (modified from Ziauddeen et al. 2012). All images were presented on a 19-inch monitor (resolution: 1280 × 1024; refresh rate: 60Hz). The monitor was set up to be approximately 50cm from the participants and at eye level.

A MLT004/ST Grip Force Dynamometer (*adinstruments.com*), a pre-calibrated strain-gauge based isometric transducer with a linear response in the 0–800 N range and accuracy of ± 5% of reading (MLT004/ST Grip Force Transducer, ADInstruments, Dunedin, New Zealand) was used to measure grip-force at a sampling rate of 1000 Hz (Image 2.2). To set up the measure, the Grip Force Dynamometer was plugged into a Pod port on the front of the PowerLab. When force is applied to the device, an output calibrated in units of Newtons was recorded in LabChart. Prior to starting the task, the device was placed on the table in front of the participant, on either their left or right side *(depending on whether they were left or right-handed)* and they were asked to hold it in their hand in order to become comfortable and familiar with it.

Prior to starting the task, all participants provided a measure of their maximum grip-force by applying as much effort as possible onto the transducer three times. The Maximum of these three trials was then taken as the participant's Maximal Volitional Contraction (MVC) (Ziauddeen, 2014). Whilst the response screen was only visible for 1000ms during each trial, exerted effort was measured for a total of 4500ms to ensure the full grip response was captured, even if it extended beyond the visible response period. This extended measurement window allowed for a comprehensive assessment of effort exertion, including any delayed or prolonged responses, ensuring that no data was truncated prematurely.

The data collected during the 4500ms window was binned into 100ms intervals, providing a total of 45 data points per trial. Binning allowed for initial visual inspection of the time course of grip response data, facilitating the examination of the quality of effort exertion over time. This finer temporal resolution helped to smooth the data and provided insights into the dynamics of effort. For the final analysis, these bins were collapsed to focus on the maximum grip force during the exertion period.

The trial design is shown in Figure 3.6. Each trial consisted of a fixation cross which was presented for 200ms, followed by a mask screen presented for 200ms, a stimulus screen depicting either chocolate cake (indulgent), an orange (non-indulgent) or a teapot (control stimuli), was presented for either 33ms (short-presentation) or 200ms (long-presentation). A second mask screen was then presented for either 300ms (short-presentation) or 100ms (long-presentation), followed by a response screen, which cued participants to respond with the grip-force transducer. Lastly, a fluid level screen was presented for 3000ms, the purpose of this was to provide visual feedback that a response has been recorded, however, participants were made aware that the visual guides were not always accurate and should only be taken as an estimate of the exerted force. This fluid level was in-fact set at three randomised levels and was not directly associated with the participant's exerted effort. The purpose of the different timings of the second mask screen was to ensure the total trial time was consistent across long and short presentation trials (4700ms).

Participants first completed 6 practice trials, followed by two identical test blocks. Each block comprised 13 long-presentation and 13 short-presentation trials per stimuli (78 trials per block). Within each block, stimuli were presented in a randomised order for each participant. The images used during the practice trials were the same as those used during the main task.

Participants were instructed *"In order to win the food items, you need to squeeze the handgrip in line with how much you want each item – so, the more you want the reward shown, the harder you squeeze".* The food items presented in the images were the specific rewards participants could win, and they were aware that their effort would determine their chances of winning those particular items.

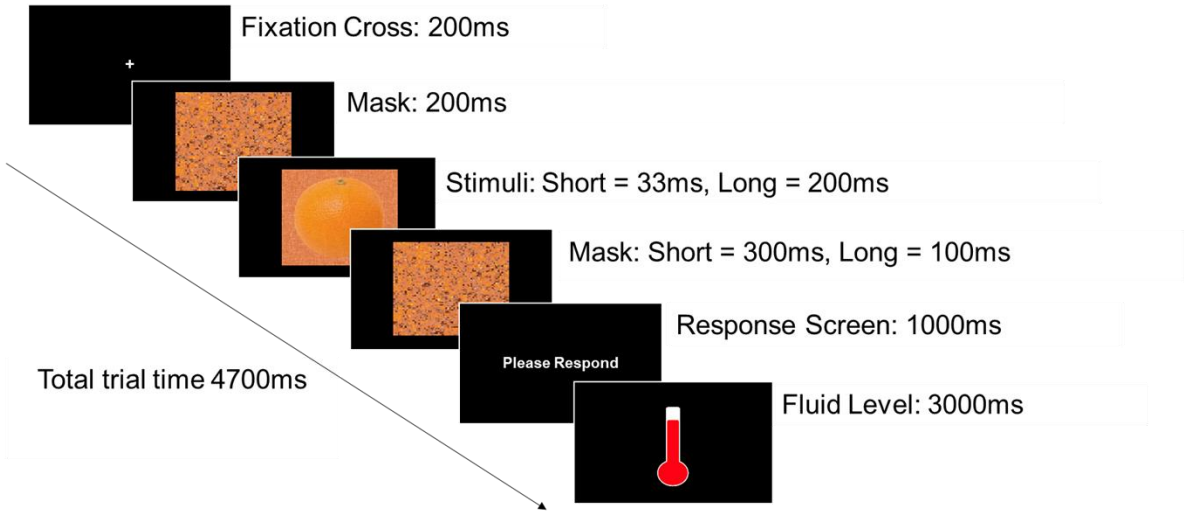

Figure 3.6: *Task Diagram showing order and duration of screens presented during each short-presentation (SP) and long-presentation (LP) trial. On each trial participants were presented with a fixation cross, followed by a mask, a stimulus was then displayed for either 33 or 200 msec, followed by a second mask, a response screen then cued the participant to respond on the grip-force transducer. Finally, a fluid level screen provided visual feedback to the participant that a response had been recorded.*

3.4.3.3 Odour Exposure

Between blocks one and two of the grip force task, participants were taken to the test room where the odour had been diffused. Participants were not told about the odour. They spent five minutes there completing a reading comprehension task (taken from Ngllife.com) which consisted of a ~500-word piece of text and 8 multiple-choice questions related to the text. The piece was chosen as it was affectively neutral and contained no food related content. Data from this task was not intended for analysis and was merely used as a distractor during odour exposure.

3.4.3.4 Forced Choice Discrimination Task

This task measured participant awareness of the images used in the Grip-Force task and comprised 30, 33ms masked presentations in a randomised order. The images used in this task were the same six images used in the main task, the presentation timings were the same as those used for the short-presentation trials in the main task. During each trial, participants were presented with a mask screen, followed by a stimulus screen and then a second mask screen. They were then shown a response screen which consisted of two images; the image just presented for that trial and a second randomly selected image. Using keys Z and M on the keyboard, they were required to indicate which of the two images was the one just presented. Position (left or right) of the correct image on this screen was counterbalanced across trials.

3.4.3.5 Food Choice

At the end of the experiment, participants were asked to select a food item: either a fresh orange (*ASDA Grower's Selection Satsumas*) or a chocolate cake slice (*Mr Kipling Chocolate Slice - Individually wrapped*), which they were able to take away with them as a reward for participating. As prior research has found that participants are more likely to change their eating behaviour if they believe their food intake is being monitored, (Robinson et al. 2014), the food selection was completed in another room, out of sight of the experimenter. Participants were directed to the food choice room upon completion of the tasks. Two dishes were positioned in the room prior to participants entering, one consisting of oranges and the other chocolate slices. Different quantities were used to reduce the likelihood of participants anticipating that their food choice would be identified. All food selections were recorded after each participant left the lab. Individuals who followed a vegan/vegetarian diet were provided with a suitable alternative.

3.4.4 Procedure

Prospective participants were informed they were investigating motivation for food related images and food choices. Once a participant agreed to take part in the study, an e-mail containing a link to the Food Preference Questionnaire was forwarded for completion prior to attending the laboratory. On the scheduled test day, participants were asked not to eat or drink anything, apart from water, for at least 3hrs prior to arriving, and to refrain from smoking for 1hr prior to testing. Upon entering the laboratory, participants were asked to place their personal belongings, including their mobile phone, to one side. They were then provided with

a paper version of the information sheet and instructed to read it carefully prior to being verbally briefed and offered the opportunity to ask any questions. Once the participant was happy with the instructions, they were asked to sign a consent form. Participants then provided a measure of their MVC using the grip-force transducer, before completing the practice trials on the task. Once the participant was happy, they continued to complete block-one of the grip-force task.

Following completion of the first block, participants were told that they were required to take a five-minute break in another room where they completed the reading comprehension task. The room had previously been diffused with either the Chocolate or Orange odour without the participant's knowledge. On returning to the test room, participants completed block-two of the grip-force task followed by the Forced Choice Discrimination Task. Upon study completion, participants were asked whether they noticed anything about the room they completed the reading comprehension task in. This allowed them the opportunity to make the researcher aware of whether the odour was perceived. They were then presented with a debrief sheet which informed them of the full details of the study including the odour exposure. In addition, participants were verbally debriefed on the true purpose of the study including why they were not made aware of the odour exposure prior to participation. They were then told that they were able to collect an item of food from the next room to take with them should they wish to do so.

3.4.5 Data Analysis

Prior to analysis, data from one participant was removed as they wore a face mask throughout testing. Thus, 37 participants were included in the analysis, 18 in the orange and 19 in the chocolate group.

Grip-Force data was exported from LabChart to Microsoft Excel. Data from the Forced Choice Discrimination Task was exported using E-DataAid. All data was transferred to SPSS (IBM Corp. Released 2013. IBM SPSS Statistics for Mac, Version 23.0) for analyses. Upon checking each participant's data, it was clear that several participants did not exert any effort on some trials. However, due to the instructions given to the participant, this was expected, and no data was removed as a result. Following this, it was evident that, on some trials, where a participant had either not exerted any grip or failed to respond during the measurement period,

the transducer recorded negative values, possibly due to the absence of force or a decrease in force from a previous state. Such negative values resulting from non-responses can distort the dataset, as such, data were transformed to a positive value by adding 10 Newtons. Likewise, to ensure all grips were handled in the same manner, the same transformation was applied to the MVC values. To calculate each participant's MVC, the maximum force recorded during each 4500ms sampling period was extracted, and the maximum of these values over the three trials taken as their MVC.

A mixed ANOVA with follow up pairwise comparisons was conducted, with Block (One, Two), Image (Control, Chocolate, Orange) and Duration (Long, Short) as within subject factors and Group (Chocolate, Orange) as a between participant factors. Following the methods of Ziauddeen et al. (2011), all grip-force scores were then normalised based on each participant's MVC. The force exerted during the response period was measured as a percentage of the difference between the baseline and the MVC: (trial value/MVC value)*100.

Secondly, to compare effort exerted for food stimuli, before and after odour exposure, the second stage of the analysis focused on exerted effort for the food items only. Thus, again following the methods of Ziauddeen et al. (2011), the normalised scores obtained in the first analysis were standardised by subtracting category specific control trial responses from category specific food trial responses *(*e.g.,'Block1_Control_Short, was subtracted from Block1_Chocolate_Short*)*. A mixed ANOVA was then conducted with Block (One, Two), Image (Chocolate, Orange) and Duration (Long, Short) as within participant factors and Group (Chocolate, Orange) as a between participant factor.

The Forced Discrimination data was analysed using a Chi-Square test, between Image Condition and Response Accuracy. To compare the proportions of 'Orange*'* food choices versus 'Chocolate*'* food choices, data were analysed using binomial logistic regression on the proportion of participants in each group selecting an orange.

All data fulfilled the assumptions for parametric analysis and there was homogeneity of variances for all conditions, as assessed by Levene's test. In cases where data did not meet the assumptions of sphericity, greenhouse geisser correction was applied. To address the risk of an inflated Type I error, Bonferroni correction for multiple comparisons was applied.

3.5 Results

3.5.1 Exerted Effort: Main effect of Image type

Initial analyses were conducted to determine whether exerted effort varied depending on the presumed motivational value of the depicted food stuffs.

A repeated measures ANOVA revealed a significant main effect of Image on exerted effort (F (2, 74) = 12.26, p<.001, η_p^2 =.25). As shown in Figure 3.7, participants applied significantly less force on Control trials compared to either Chocolate (p<.001) or Orange trials (p<.01). Effort did not significantly differ between Orange and Chocolate trials (p=.06).

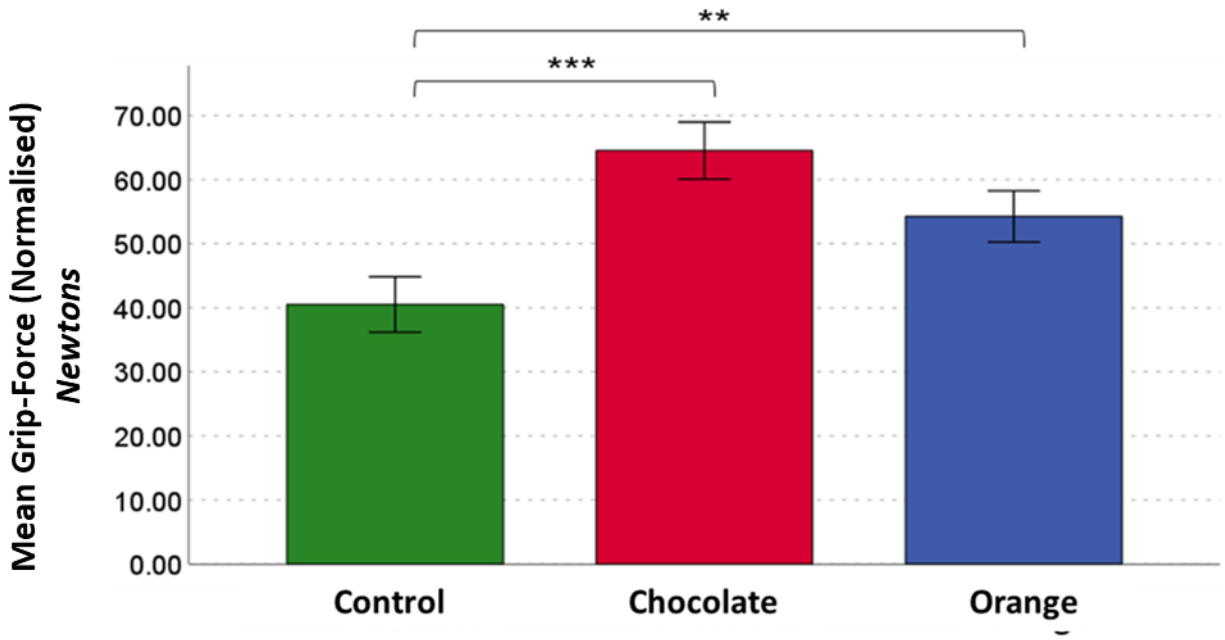

Figure 3.7: *Mean Grip-Force applied for each image type, across both Block One and Block Two (collapsed data) of the Grip-Force task. Exerted effort was significantly greater for food images compared to control images in both studies. *** denotes sig level <.001, ** denotes sig level <.01. Error bars indicate 95% CI.*

3.5.2 Exerted Effort –Main effects of Block and Duration

There was significant main effects of Block (F (1, 36) = 4.39, p<.05, η_p^2 =.11) and Duration (F(1, 36) = 13.58, p<.001, η_p^2 =.27) reflecting the fact participants exerted greater force in block-one compared to block-two, and for long compared to short duration images. There was no interaction between Block and Image (F(2, 74)=.39, p=.68, η_p^2 =.01), however,

there was a significant interaction between Image and Duration (F(2, 72)=6.17, p=.004, η_p^2 =.14), which reflects the fact duration only had an effect on force exerted for Chocolate (p<.01) and Orange Images (p<.01), effort for Control Images did not differ across long and short duration trials (p=.73). See Figure 3.8.

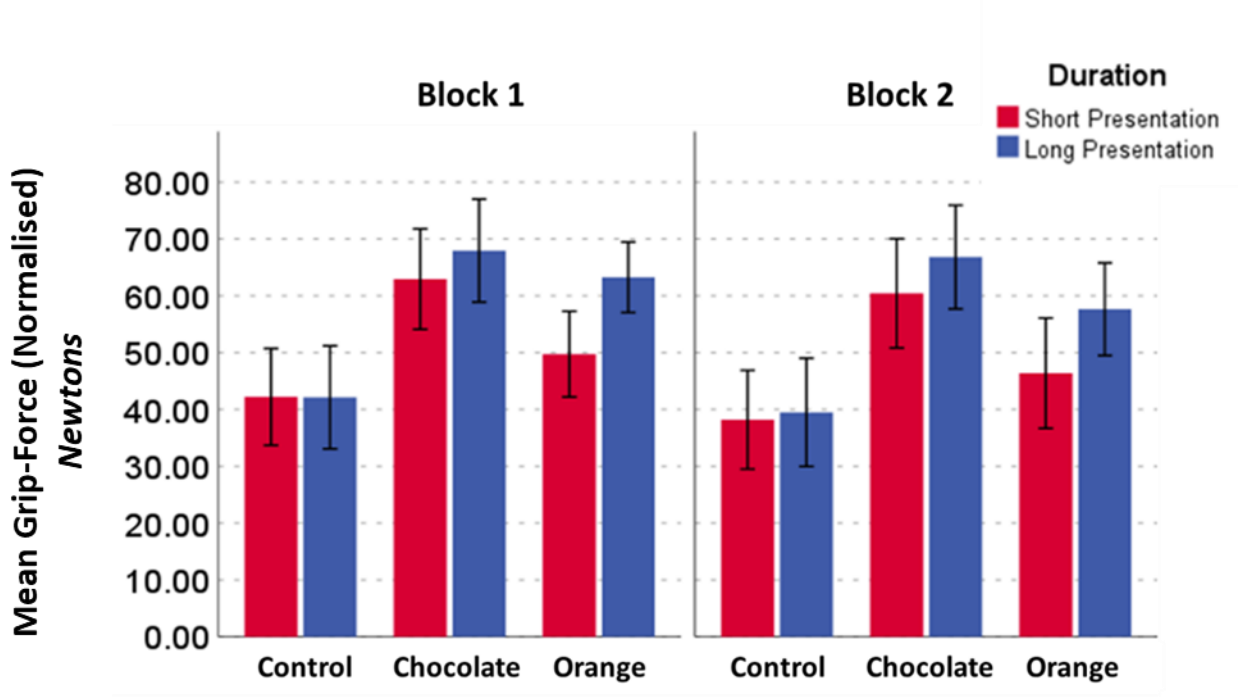

Figure 3.8: *Mean Grip-Force applied for each condition of the grip-force task (Control, Chocolate, Orange). Red bars represent Mean Grip-Force for Short Duration trials (33 msec), and blue bars represent Mean Grip-Force for Long Duration trials (200 msec). Block One is shown on the left figure and Block Two is shown on the right. Error bars indicate 95% CI.*

3.5.3 Effect of Odour Exposure on exerted effort.

To determine whether there was any change in exerted effort for Food Images following Odour Exposure, a mixed ANOVA was conducted using standardised scores of effort exerted for food images minus effort exerted for control images, thus accounting for the general decrease in effort observed in block 2 compared to block 1. Here, within participant factors were Block (Block 1 & 2) Image (Chocolate, Orange) and Duration (Long, Short) and the between participant factor was Group (Orange, Chocolate).

There was no main effect of Group (F (1, 35)=2.34, p=.14, η_p^2=.06) or Block (F(1, 36)=.01, p=.94, η_p^2=.00). There was, however, a significant main effect of Image (F (1, 36)=5.78, p=.001, η_p^2=.14). As shown in Figure 3.9, participants applied greater force for Chocolate compared to Orange images. There was also a significant effect of Duration (F (1,

36)=13.81, p<.001, η_p^2=.28), with greater force applied for Long compared to Short-Duration images. There were no interaction effects with respect of the Group (*ps*>.05).

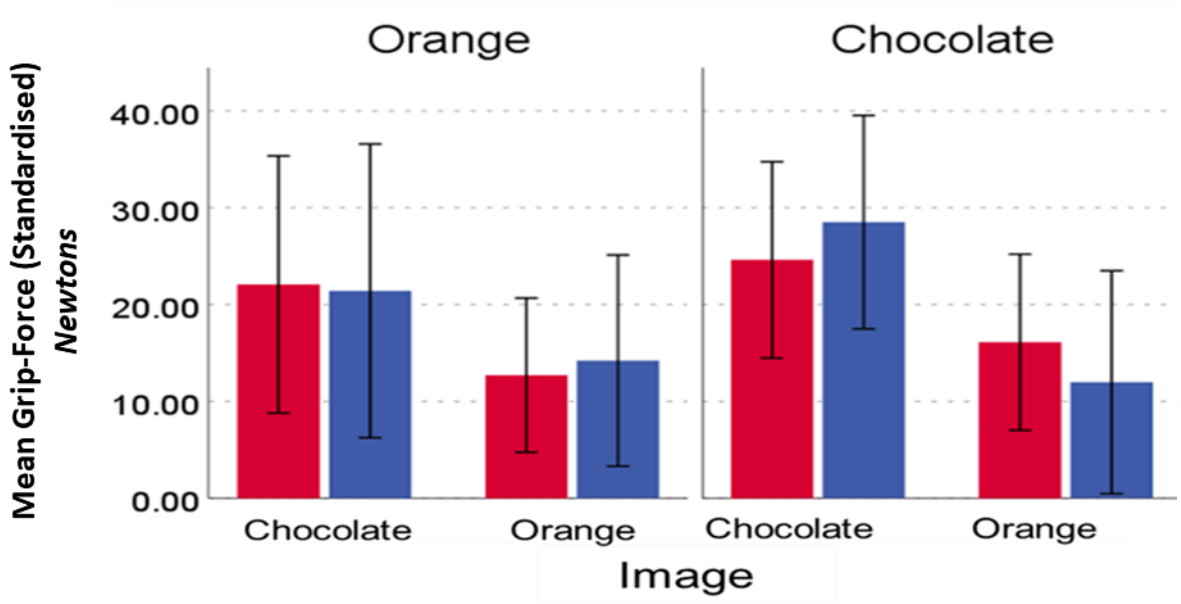

Figure 3.9: *Standardised Grip-Force applied for each food condition of the grip-force task (Chocolate, Orange). Red bars represent Mean Grip-Force for block-one trials and blue bars represent Mean Grip-Force for block-two trials. Exerted effort did not change from block one to block 2. Error bars indicate 95% CI.*

3.5.4 Forced-Choice Discrimination

To determine whether images presented at the short-duration were at a subliminal level, a Chi-Squared test was conducted between Image Condition and Response Accuracy. The association between Image Condition and Response Accuracy was not significant, $\chi 2(2) = 4.31$, p=.12. Images were correctly identified 95.9% of the time (Control images 95.7%, Chocolate images 97.6%, Orange images 94.6% accuracy).

3.5.5 Food Choice

It was found that overall, 41.2% of participants chose Orange as their gift, whilst 58.8% chose Chocolate as their gift. There was no significant effect of Group on these selections (Wald $\chi 2(1) = 2.26$, p=0.13). (Figure 3.10).

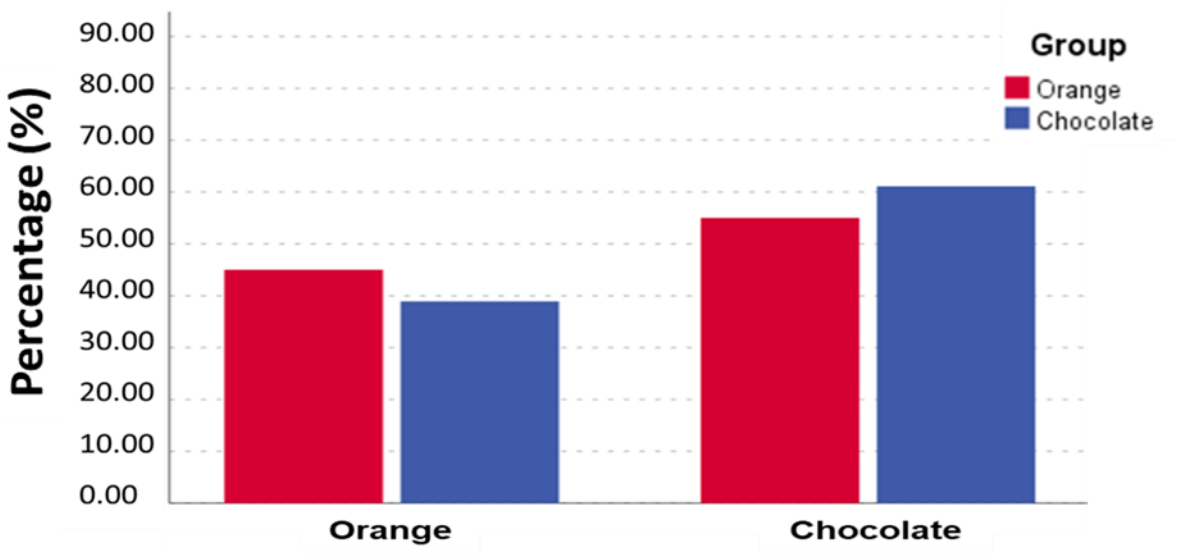

Figure 3.10: *Percentage of food choice (Orange vs. Chocolate). The bars represent the percentage of participants in each food group who selected either Orange or Chocolate. The red bars represent participants in the Orange food group, while the blue bars represent participants in the Chocolate food group. The bars on the left show the percentage of participants selecting Orange, and the bars on the right show the percentage selecting Chocolate.*

3.6 Discussion

The aim of this study was to determine whether implicit exposure to ambient food odours influenced motivation for congruent foods, using grip-force as a measure of incentive motivation. The lack of any effect of odour exposure on motivation for congruent foods contrasts with previous reports of odour priming (Gaillet et al. 2013; Proserpio et al. 2019; Ramaekers et al. 2014), where non-conscious, ambient odour exposure for between 10-20 minutes has been reported to influence food choice (Gaillet et al. 2013; Gaillet-Torrent et al. 2014; Proserpio et al. 2019), as well as enhance appetite ratings (Ramaekers et al. 2014) and food cue reactivity (Mas et al. 2020). While the short exposure duration of just 5 minutes in the present study could potentially explain the null result, several recent studies have suggested that ambient odours can induce priming effects after one minute or less (Biswas & Szocs; 2019; Chae et al. 2023), while satiety effects on food selection were reported following two minutes (Biswas & Szocs; 2019) and five or more minutes of ambient odour exposure in both laboratory and real-world settings (Chae et al. 2023; Gaillet et al. 2013). However, here, exposure to either indulgent or non-indulgent ambient odours did not result in any change in objectively measured incentive motivation towards the associated foods.

Previous studies reporting priming or satiety effects following odour exposure have utilised subjective measures (Biswas & Szocs, 2019; Chae et al. 2023; Gaillet et al. 2013; Morquecho-Campos, 2021; O'Doherty et al. 2000; Proserpio et al. 2019; Ramaekers et al. 2014; Rolls & Rolls, 1997). In contrast, the present study used an objective measure of incentive motivation (Berridge & Robinson, 1998; Pool et al. 2016) which has been established to be sensitive to the detection of classic sensory-specific satiety effects (Arumae, 2019, Ziauddeen et al. 2012). Whilst satiety effects were not evident following odour exposure, consistent with previous literature (Ziauddeen et al. 2012), fasted participants did display a greater level of motivation, indexed by greater expended grip-force, when they were presented with food images, compared to control images, and toward long-duration compared to short-duration food images. Thus, despite potential influences from factors such as fatigue and attention (Cacioppo & Tassinary, 1990), participants did modulate the grip-force applied depending on the motivational salience of the visual cue presented.

In contrast to previous grip-force studies which have reported visual stimulus presentations times of 50ms or less as subliminal (Pessiglione et al. 2006; Ziauddeen et al.

2012), participants in the present study were able to accurately identify all test stimuli when presented for 33ms in a forced-choice discrimination task. This is consistent with the wider visual processing literature which indicates that for stimuli to be considered subliminal, presentation times should not exceed 16.66ms (Ionescu, 2016; Potter et al. 2014). This perceptual threshold however can be dependent on a number of factors, such as the type (picture/texture) and direction (forward/backward/sandwich) of masking technique used (Wernicke, 2014; Potter et al. 2014), as well as the temporal delay (Bacon-Mace et al. 2005; Harris et al. 2011; Nakamura & Murakami, 2021) and contrast (Harris et al. 2011; Haynes & Rees, 2005; Wernicke & Mattler, 2019) between stimulus and mask. In the present study we replicated the stimulus presentation and masking timings and techniques previously reported by Ziauddeen et al. (2012) whose participants performed at chance level on the forced choice discrimination test of awareness. Differences in monitor refresh rates and visual stimuli used could potentially explain this difference. While monitors with a refresh rate of 60Hz, as used here, have been used for subliminal stimulus presentation, a higher refresh rate and shorter presentation time may have been necessary with the present stimuli (Baumgarten et al.2017).

While the primary outcome measure was incentive motivation, to be consistent with previous odour priming studies, we also included a secondary food choice measure. The method of food choice in the current study was two-alternative forced-choice, while previous studies have used buffets (Morquecho-Campos et al. 2021), menus (Proserpio et al. 2017, Proserpio et al. 2019), as well as supermarket and cafeteria settings (Biswas & Szocs, 2019), where participants have a wider range of items to choose from. Forced-choice procedures are thought to offer insight into the immediate motivation behind selecting a specific food product over others (Finlayson et al. 2008), whereas selections from a wider array of choices may more strongly reflect dietary habits and goals (Appelhans et al. 2017). One possible explanation for the lack of effect of odour priming on food selection in the present study is timing. Here, approximately 30 minutes elapsed between odour exposure and food-choice selection, whilst participants in other studies selected food options either during or immediately following odour exposure (Biswas & Szocs, 2019; Gaillet et al. 2013; Proserpio et al. 2019). Also, though participants were instructed not to consume food for three hours prior to attending the testing session, no measurements of subjective hunger were taken during the study. Given physiological state is a significant determinant of expended motivational effort (Pirc et al. 2019) and food selection (Koster, 2009), this should be addressed in future priming studies.

One of the biggest challenges in olfactory priming studies is control of stimulus concentration (Smeets & Dijksterhuis, 2014). For priming effects to occur the intensity of the odour should not be high enough to be consciously perceived, though not so low that it cannot be detected at all (Loersch & Payne 2011; Morquecho-Campos et al. 2021; Smeets & Dijksterhuis, 2014). However, other research suggests that supraliminal odours can also act as effective primes. For instance, Forster and Spence (2018) found that while supraliminal odours can influence perception and behaviour, attentional demands can prevent individuals from detecting important olfactory information. This indicates that olfactory awareness is strongly influenced by where and how attention is directed. Therefore, it is important to consider both subliminal and supraliminal odours when examining priming effects. Whilst some studies do attempt to quantify the intensity of the odour e.g., below 50 on a 0-100 VAS (Morquecho-Campos et al. 2021; Proserpio et al. 2019), others merely state that intensity was low (Chae et al. 2023; Coelho et al. 2009; Gaillet et al. 2013; Gaillet-Torrent et al. 2014; Mas et al. 2019). In preparation for the present study, two pilot tests were conducted. The protocol used resulted in intensity ratings of approximately 7, on a 0-10 VAS, when dispersed in the test rooms, while odours were not reliably detected unless attention was directed towards them. In the study itself, only two participants reported noticing an odour prior to debriefing. Taken together, it seems unlikely our stimuli were too low in intensity to have a priming effect or so high that the aims of the study were obvious to participants. Future, cross-laboratory collaborations that determine best practice guidelines for odour dispersal, quantification and reporting would be beneficial to the field. For example, room size, air temperature, as well as air flow and air exchange rates will impact odour concentration making precise replication of protocols challenging.

The present study does come with limitations, for example, whilst the method of odour dispersion supports the published literature, the intensity of the odours may have contributed to the lack of priming and/or satiety effects. Loersch and Payne (2011), indicate that when intensity of odours is too strong, priming is unlikely to take place. Whilst every care was taken to control the intensity of the odours by conducting two pilot tests, participants of these tests were made aware that odours were present, possibly increasing perceived intensity. Future work should look to pilot odours using methods of non-conscious exposure, in order to determine subliminal intensity levels. Whilst much research reports priming effects following exposure of 10-20 minutes (Gaillet et al. 2013; Gaillet-Torrent et al. 2014; Mas et al. 2020; Proserpio et al. 2019; Ramaekers et al. 2014), it is possible that the exposure time of five

minutes in the current study was too brief to induce priming or satiety effects. The decision to expose participants to the ambient odour for a duration of five minutes in the current study was due to an attempt to replicate the findings of Biswas and Szocs (2019), where priming and satiety effects were reported after brief exposure of ~30seconds and prolonged exposure of two minutes, respectively. As such, future research should look incorporate both long and short exposure times in order to determine any differing effects. The use of indulgent (Chocolate) and non-indulgent (Orange) odours were again, chosen for replication of Biswas and Szocs (2019), with the specific matching of odours to images, replicating the methods of Ziauddeen et al. (2012), where foods consumed matched those used within the grip-force task. Much previous research (Chambaron 2015; Gaillet-Torrent et al. 2014; Mas et al. 2020; Proserpio et al. 2019; Ramaekers et al. 2014; Zoon et al. 2014), though not all (Chae et al. 2023; Coelho et al. 2009), has opted for food categories based on nutritional content (high/low energy) or food groups (sweet/savoury), as opposed to odours being directly congruent to images. In order to try and replicate previous priming effects, odours and images could be separated into these categories (for example, multiple savoury food images could be used alongside a savoury odour) in order to determine the impact of (sweet/savoury) odours on motivation for congruent foods. While the present study was powered to detect small-medium effects with 85% power, it could be that it was underpowered to detect what are likely to be small effects of odour exposure on incentive motivation. Therefore, future studies should utilise larger samples. Lastly, the instructions provided asked participants to express their desire for the reward through the intensity of their effort, possibly converting the task into a self-reported indication of "*wanting*." This may have introduced a level of bias, as participants could consciously modify their effort based on their perceived level of desire for the food item. However, the observed variation in grip force between long- and short-duration images suggests that participants' responses were influenced by more than just conscious self-reporting, potentially reflecting an underlying motivational process. Thus, it is important to note that while the task was designed to measure the implicit motivation or "*wanting*" of a reward, the instruction could have led participants to interpret the task more explicitly, potentially influencing their responses in a way that does not fully reflect an indirect measure of motivation. This issue highlights a key challenge in using effort-based measures to study intrinsic motivation, as external cues, including task instructions, can inadvertently shift the task from an implicit to a more explicit self-report measure. Future research could refine the instructions to avoid directly linking the intensity of the effort to the level of desire for the reward. This would help preserve

the indirect nature of the measure, ensuring it remains a more objective reflection of effort rather than a conscious self-assessment.

In conclusion, there was no effect of ambient odour exposure on motivation nor on food selection. This contrasts with previous reports of odour priming following ~5 minutes of ambient odour exposure (Chae et al. 2023; Morquecho-Campos, 2021) and recent reports of sensory-specific satiety effects on food selection after the same exposure time, in both real world and laboratory settings (Biswas & Szocs, 2019). Further research is needed to determine whether stimulus level factors, such as timing, intensity or character of the food odours differentially affect behaviour (Abeywickrema, Oey, Peng, 2022; Smeets & Dijksterhuis, 2014). However, inconsistent findings, along with other null effects (Morquecho-Campos, 2021; Zoon et al. 2014) highlight issues of reproducibility of the odour priming literature (Cesario, 2014) and reinforce the need for detailed methodological reporting and replication.

Chapter 4. The effect of high and low-calorie Food Consumption on Incentive Motivation

The study reported in this Chapter, combined with the study reported in Chapter 3, has been published in the journal Appetite.

https://www.sciencedirect.com/science/article/pii/S0195666324005348

4.1 Abstract

Food consumption often leads to a SSS effect, in which hedonic value and motivation for the consumed food reduces, compared to a food with differing sensory properties, that has not been consumed. Building on from the previous study, which looked to determine whether implicit exposure to ambient odours, would selectively reduce incentive motivation for congruent foods images. The aim of the present study was to determine whether food consumption would selectively reduce implicit motivation for congruent foods. Participants (N=39) were randomly assigned to a high calorie, indulgent *(chocolate)* or low calorie, non-indulgent *(orange)* food group and completed two blocks of an incentive-force task. One block was completed immediately before and the other immediately after food consumption. A grip-force transducer was used to measure effort exerted effort to win food prizes. The prizes were depicted in visual images presented at for either a long *(200ms)* and or short duration *(33ms)* levels. A mixed ANOVA containing three within subject factors: Block *(one, two)*, Image *(Orange, Chocolate)* and Duration *(33ms, 200ms)* and one between subject factor: Group *(Orange, Chocolate)*, was used to measure the change in exerted effort from block-one to block-two. Significantly greater effort was initially exerted to win the indulgent than the non-indulgent food. Exerted effort following food consumption resulted in a classic sensory-specific satiety effect, in that, force exerted for chocolate images declined significantly following chocolate consumption, in the absence of any decline in grip exerted for orange stimuli. Food consumption evidentially induces satiety effects, in which exerted effort to obtain consumed foods diminishes following consumption. Thus, demonstrating that objective measures, such as the grip-force paradigm used here, are sensitive to changes incentive motivation.

4.2 Introduction

Motivation can be measured by determining the amount of effort an individual is willing to put in to obtaining rewards (such as foods) (Chong et al. 2016, Pool et al. 2016), which often requires a great deal of cognitive/physical effort in order to acquire them, and the amount of effort is largely dependent on the value of the reward (Berridge, 2012; Chong et al. 2016; Kringelbach et al. 2012; Lowe & Butryn, 2007; Ziauddeen et al. 2012). Incentive models of motivation differentiate between the consummatory aspect of reward, which is consciously perceived as hedonic pleasure (liking), and the appetitive aspect of reward which, in foraging animals, manifests behaviourally as exploratory and approach behaviours ('*wanting*') (Berridge, 2007; Berridge & Aldridge, 2000). When considering food rewards, the distinction between liking and '*wanting*', is believed to be influenced by an individual's physiological state (Pirc et al. 2019), as when in a state of hunger, the reward value of food items is generally higher, compared to when in a satiated state (Berridge, 2012, Schultz, 2015, Ziauddeen et al. 2012). This suggests that manipulations of food reward, such as the phenomenon of sensory-specific satiety, is likely to result in a decrease in both food liking and food wanting (Havermans et al. 2009; Mela, 2001).

The term sensory-specific satiety refers to the reduced pleasantness and the decrease in motivation for a food as it is eaten, relative to other uneaten foods which possess different sensory qualities (Rolls et al. 1981). This phenomenon is thought to promote both the termination of an eating episode and the tendency to resume eating when different foods become available (Abeywickrema et al. 2022). In exploring this concept using animal models, rats have been found to display a reduction in hedonic taste reactivity to foods and solutions such as sucrose or chow, after having been pre-fed congruent diets (Berridge, 1991; Myers, 2017; Reichelt et al. 2016; Reichelt et al. 2014;). In measuring this same effect in humans, there appears to be a consistent relative decrease in subjective ratings of both the desire to eat and expected pleasantness of various foods, following the consumption of congruent foods (Brunstrom & Mitchell, 2006; Carnell et al. 2014; Finlayson et al. 2008; Rolls & Rolls, 1997; Stevenson et al. 2023; Yeomans et al. 2019). However, these approaches have limitations, as subjective measures are believed tap into the explicit conscious form of wanting rather than implicit incentive salience form of '*wanting'* (Mela, 2006). While individuals may be able to accurately determine their explicit wanting and liking for food items, the same cannot be said

for accurately estimating implicit wanting for food items, as this involves the fundamental motivational aspects of seeking rewards (Arumae et al. 2019).

However, a person's immediate, spontaneous response to a food cue is believed to reflect the core process of *'wanting'* (Mela, 2006). As such, behavioural measures can provide insights into the intrinsic desire for food items beyond what is consciously reported. Just as in animal studies, work-for-food tasks have shown a selective decrease in motivation for sated foods compared to non-sated foods (Balleine & Dickinson, 1998; Balleine & O'Doherty, 2010), motivational effort has also been used to measure satiety effects in humans, using methods such as number of button presses (Havermans et al. 2009), or force exerted using a grip-force transducer (Pirc et al. 2019; Ziauddeen et al. 2012). Whilst it has been suggested that grip-force measures should be interpreted with caution, as effort exertion may also be influenced by factors such as fatigue or cognitive load rather than solely reflecting motivation (Cacioppo & Tassinary, 1990), their widespread use demonstrates a robust correlation between reward value and exerted effort (Pessiglione et al. 2006; Schmidt et al. 2010; Ziauddeen et al. 2014). This has been evidenced in various areas of motivation, such as measuring the value of monetary rewards (Pessiglione et al. 2006), food consumption in restrained eaters (Koningsbruggen et al. 2012), food rewards in obese individuals (Mathar et al. 2015) and motivation for food items following food consumption (Ziauddeen et al. 2012). In adopting this method of measuring incentive motivation following consumption of foods, research has shown a clear, selective decrease in exerted effort for foods that have been eaten to satiety (Pirc et al. 2019; Ziauddeen et al. 2012).

It is therefore evident from previous literature, that behavioural measures of incentive motivation, such as the grip-force paradigm, are reliable in capturing a participant's motivational state, by measuring level of force exerted to acquire rewards. As such, it seems likely that the absence of odour exposure induced priming/satiety effects in the previous study reflects uncertainties around odour exposure methodologies, as opposed to a lack of sensitivity of the grip-force task. To determine this was the case, the current study, following the same grip-force task procedure as the previous study, investigated whether the grip-force paradigm was sensitive in detecting classic sensory-specific satiety effects following food consumption. It was hypothesised that food consumption would result in a satiety effect, with participants exerting a selective decrease in exerted effort for consumed, but not unconsumed foods, in the second block of the task. In addition, food consumption should result in incongruent food

choice, in that, individuals will choose a food reward incongruent to the food consumed during the task.

4.3 Materials and Methods

4.3.1 Participants

39 participants (*female=24),* were randomly assigned to either Orange (*N=18, 18-50 years old; M = 24.89, SD = 6.64; f=14*) or Chocolate (*N=21, 18-60 years old; M = 24.33, SD = 7.55; female n=12*) food consumption groups. Participants were recruited from the student population at Liverpool John Moores University via the use of posters placed around the Campus. The University's Psychology Research Participant Panel was also used to recruit individuals from the wider population. People were excluded from participating if they had any respiratory problems, food intolerances or allergies. The experimental protocol was approved by the Ethics Committee at Liverpool John Moores University (19/NSP/062). Participants received a £10 shopping voucher to thank them for their time.

A power analysis was conducted using G-Power (Faul et al. 2007). Using the ANOVA: Repeated Measures, within-between interaction option with two groups and two measurements, a sample of 38 was required to detect a small-medium effect size (f = .25) with 85% power and an alpha level of 0.05.

4.3.2 Materials

4.3.2.1 Visual Images

The Task Images used were consistent with those used in Chapter 3. Details can be found in 3.4.2.3.

4.3.3 Measures

4.3.3.1 Food Preference Questionnaire

The Food Preference Questionnaire was consistent that used in Chapter 3. Details can be found in 3.4.3.1.

4.3.3.2 Grip-Force Task

The Grip-Force Task was consistent with that used in Chapter 3. Details can be found in 3.4.3.2.

4.3.3.3 Food Consumption

Fixed portions of either ten fresh satsumas (*ASDA Grower's Selection*) or ten chocolate cake slices (*Mr Kipling Chocolate Slice*) were placed on a paper plate in a room separate to that of the grip-force task. Participants were directed to the food consumption room and instructed "please consume as much food as you wish during this five-minute period. Please do not leave the room until instructed to do so by the researcher". Participants were unaware that the portion size was recorded both before and after the consumption stage to determine food intake. After leaving the labs, the researcher returned to the food consumption room and recorded food intake by counting the number of missing items from the plate. Individuals in the chocolate group who followed a vegan/vegetarian diet were provided with a suitable alternative.

4.3.3.4 Forced Choice Discrimination Task

The Forced Choice Discrimination Task was consistent with that used in Chapter 3. Details can be found in 3.4.3.4.

4.3.3.5 Food Choice

Food choice procedure was consistent with those used in Chapter 3. Details can be found in 3.4.3.5.

4.3.4 Procedure

Prospective participants were informed they were investigating motivation for food related images and food choices. Once a participant agreed to take part in the study, an e-mail containing a link to the Food Preference Questionnaire was forwarded for completion prior to attending the laboratory. On the scheduled test day, participants were asked not to eat or drink anything, apart from water, for at least 3hrs prior to arriving, and to refrain from smoking for 1hr prior to testing. Upon entering the laboratory, participants were asked to place their

personal belongings, including their mobile phone, to one side. They were then provided with a paper version of the information sheet and instructed to read it carefully prior to being verbally briefed and offered the opportunity to ask any questions. Once the participant was happy with the instructions, they were asked to sign a consent form. Participants then provided a measure of their MVC using the grip-force transducer, before completing the practice trials on the task. Once the participant was happy, they continued to complete block-one of the grip-force task.

Following completion of the first block, participants spent five-minutes in another room where they consumed either oranges or chocolate cake. Upon returning to the test room, participants completed block-two of the grip-force task followed by the Forced Choice Discrimination Task. They were then presented with a debrief sheet which informed them of the full details of the study. They were then told that they were able to collect an item of food from the next room to take with them should they wish to do so.

4.3.5 Data Analysis

All data analysis procedures were identical to that used in the odour exposure analysis. Prior to initial screening of the Grip-Force data, responses for 2 participants were removed; one participant was removed as they failed to eat any food during the food consumption stage of the task, and one participant was removed as they reported that they exerted effort only for the control images, due to their desire for a cup of tea.

All data fulfilled the assumptions for parametric analysis and there was homogeneity of variances for all conditions, as assessed by Levene's test. In cases where data did not meet the assumptions of sphericity, greenhouse geisser correction was applied. To address the risk of an inflated Type I error, Bonferroni correction for multiple comparisons was applied.

4.4 Results

4.4.1 Exerted Effort: Main effect of Image type

Initial analyses were conducted to determine whether exerted effort varied depending on the presumed motivational value of the depicted food stuffs.

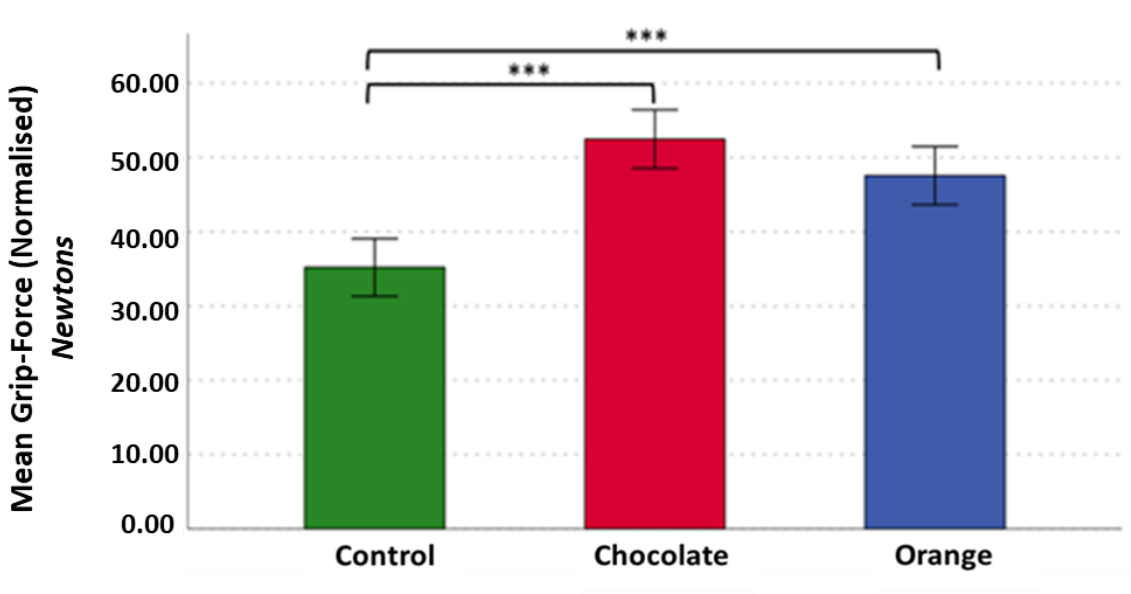

Figure 4.1: *Mean Grip-Force applied for each image type, across both Block One and Block Two (collapsed data) of the Grip-Force task. Exerted effort was significantly greater for food images compared to control images. *** denotes sig level <.001, ** denotes sig level <.01. Error bars indicate 95% CI.*

A Repeated measures ANOVA revealed a significant main effect of Image (F= (2, 72) = 13.72 ,p<.001, η_p^2=*.276*). As shown in Figure 4.1, participants applied significantly greater force on Food trials compared to Control trials. Effort did not significantly differ between Orange and Chocolate trials (p>.05)

4.4.2 Exerted Effort –Main effects of Block and Duration

There was a significant main effect of Block (F (1, 36) = 17.37, p<.001, η_p^2=*.326*) and Duration (F(1,36)=5.97, p=.02, η_p^2=*.14*) in that, participants exerted greater force in block-one compared to block-two, and for long compared to short duration images. In addition, a significant interaction between Block and Image was found (F (2,72)=3.83, p=.03, η_p^2=*.096*), in that there was a significant decrease in effort for chocolate images (p<.001) but not orange images (p>.05) or control images (p>.05), from block 1 to block 2, irrespective of stimulus presentation duration *(Figure 4.2).*

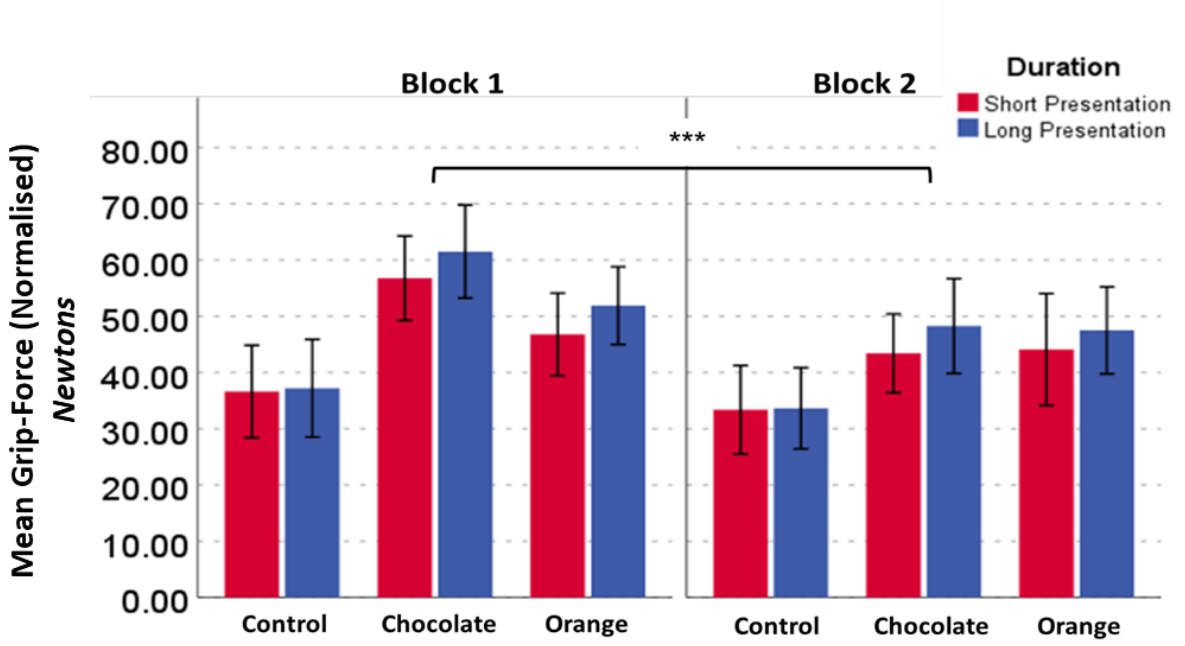

Figure 4.2: *Mean Grip-Force applied for each condition of the grip-force task (Control, Chocolate, Orange). Red bars represent Mean Grip-Force for Short Duration trials (33 msec), and blue bars represent Mean Grip-Force for Long Duration trials (200 msec). Block One is shown on the left of each figure and Block Two is shown on the right. Error bars indicate 95% CI.*

4.4.3 Effect of Food Consumption on exerted effort.

To determine whether there was any change in exerted effort for Food Images following Food Consumption, a mixed ANOVA was conducted using standardised scores of effort exerted for food images minus effort exerted for control images, thus accounting for the general decrease in effort observed in block 2 compared to block 1. Here, within participant factors were Block (Block 1 & 2) Image (Chocolate, Orange) and Duration (Long, Short) and the between participant factor was Group (Orange, Chocolate).

There was a significant interaction between Group, Block and Image ($F(1,35)=7.47$, $p=.01$, $\eta p2=176$). As shown in figure 4.3, there was a significant decrease in force applied for chocolate images from block 1 to block 2, regardless of duration, and this was specific to the chocolate group – therefore suggesting a sensory-specific satiety effect.

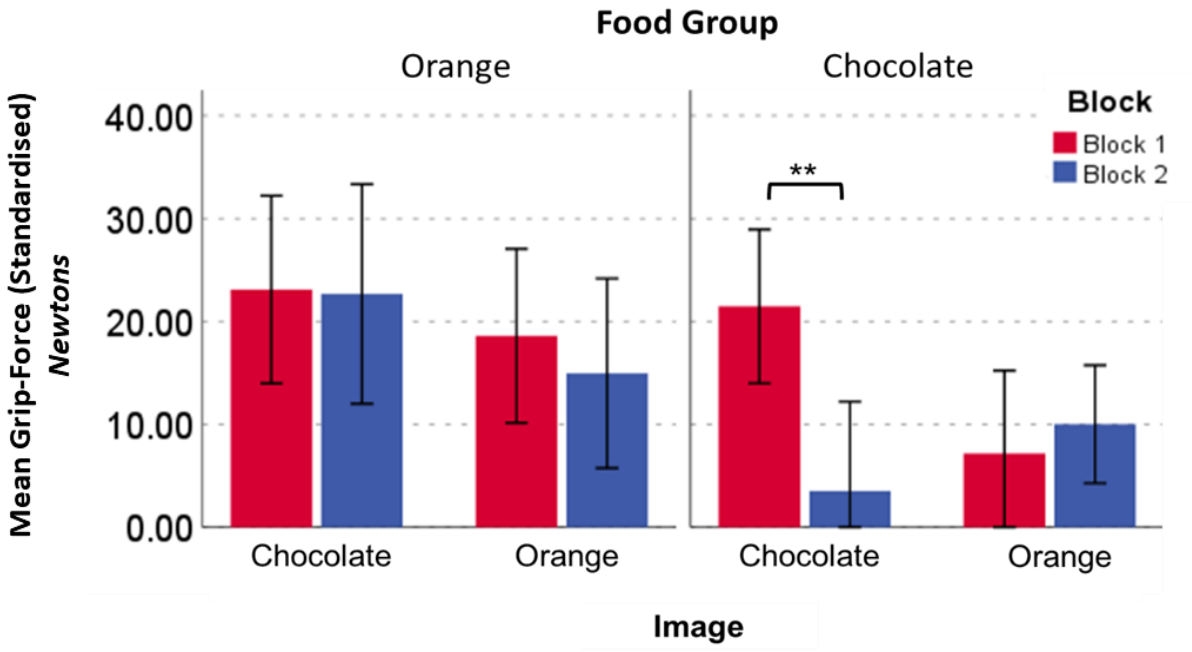

Figure 4.3: *Standardised Grip-Force applied for each food condition of the grip-force task (Chocolate, Orange). Red bars represent Mean Grip-Force for block-one trials, and blue bars represent Mean Grip-Force for block-two trials. Exerted effort did not change from block one to block 2. Error bars indicate 95% CI.*

4.4.4 Forced-Choice Discrimination

To determine whether images presented at the short-presentation time, were at a subliminal level, a Chi-Squared test was conducted between Image Condition and Response Accuracy. All expected cell frequencies were greater than five. The association between Image Condition and Response Accuracy was not significant, $\chi 2(2) = 3.95$, $p > .05$. As shown in Figure 4.4, Control images were identified with 94.7% accuracy, Chocolate images with 97.6% accuracy and Orange images with 97.6%. Overall, images were correctly identified 96.1% of the time.

4.4.5 Food Choice

In determining whether there was an effect of food group, on food choice, it was found that overall, 59.5% of participants chose Orange as their gift. There was a significant satiety effect of food group on these selections (Wald $\chi 2(1) = 121.02$, $p < .001$), with 85% of participants in the Chocolate group, choosing Orange as their gift and 70.6% of participants in the Orange group, choosing Chocolate as their gift.

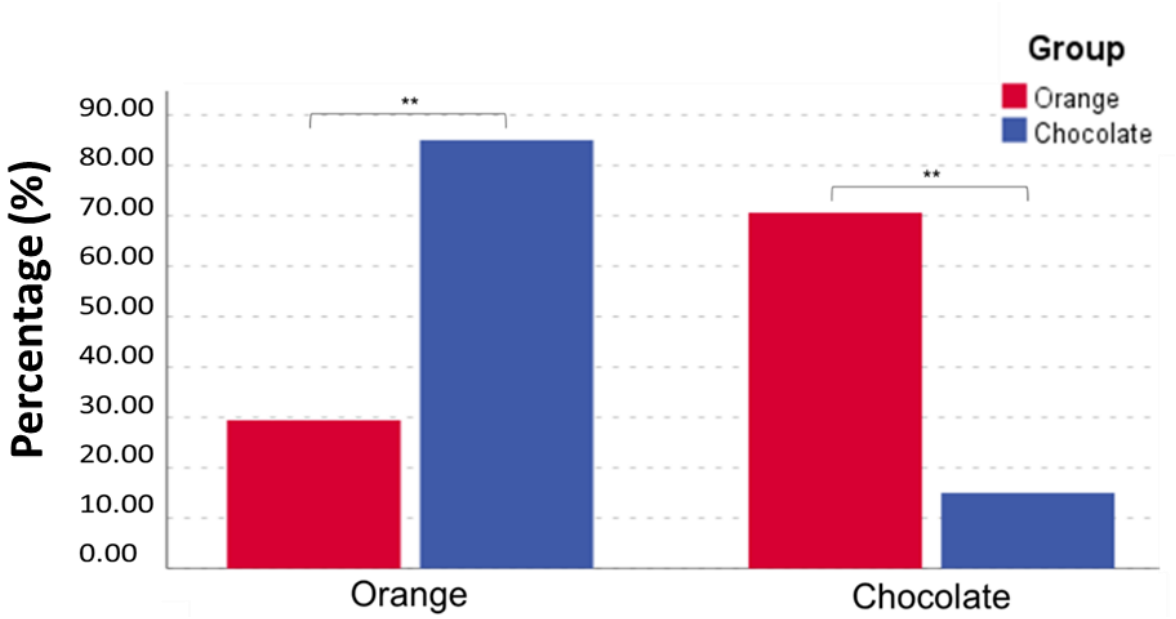

Figure 4.4: *Percentage of food choice (Orange vs. Chocolate). The bars represent the percentage of participants in each food group who selected either Orange or Chocolate. The red bars represent participants in the Orange food group, while the blue bars represent participants in the Chocolate food group. The bars on the left show the percentage of participants selecting Orange, and the bars on the right show the percentage selecting Chocolate. ** denotes significance ($p < 0.01$).*

4.5 Discussion

The current study aimed to determine whether food consumption impacted motivation for congruent foods, using a Grip-Force as a measure of incentive motivation. Based on previous literature, it was hypothesised that food consumption would result in a satiety effect, with participants exerting more effort for images of incongruent foods, and that this variation in motivation would be evident at both a conscious and non-conscious level. The reported results support these hypotheses, in that, prior to food consumption, greater effort was exerted for food items compared to non-food items. Exerted effort following food consumption resulted in a classic sensory-specific satiety effect, in that, force exerted for chocolate images declined significantly following chocolate consumption, in the absence of any decline in grip exerted for orange images. In addition, in both groups, food consumption resulted in more incongruent food choices – that is, significantly more individuals opted for the food item which was incongruent to the food they had consumed.

This satiety effect is in line with previous literature (Ziauddeen et al. 2012), and supports the notion that metabolic state, sensory properties of consumed foods and the availability of incongruent foods, can work together to drive motivated behaviours outside conscious awareness (Bijleveld et al. 2010; Ziauddeen et al. 2012). This same effect, however, was not seen in the group who consumed oranges. This disparity may be due to the fact the satiety value of food is believed to be associated with a number of objective and subjective aspects, such as, energy density, macronutrients, perceived healthiness (Buckland et al. 2015). Individuals in the chocolate condition consumed an average of 274kcal per person, whereas, in the orange condition participants consumed an average of only 53.44kcal per person, as such, those in the orange condition may not have reached the same level of satiety as those in the chocolate group. Research highlights that two foods, consumed in equal amounts, may have distinct effects on satiety if their macronutrient compositions differ, with high-protein, high-fibre and high-fat foods delivering greater satiety effects than energy matched foods with lower levels of protein, fibre and fat (Astbury et al. 2010, Bertenshaw et al. 2009). The decision to use non-matched macronutrient orange and chocolate food options in the current study, is in-line with the work of Biswas and Szocs, (2019), who directly compared indulgent (high calorie) and non-indulgent (low-calorie) items. This contrasts with classic sensory-specific satiety studies which typically use two high-calorie foods such as full-fat chocolate milk (Pirc et al. 2019), pizzas and cheesecake (Ziauddeen et al. 2012).

Another aim of this study was to evaluate the applicability of the grip-force paradigm in assessing incentive motivation. In-line with previous literature (Chong et al. 2016; Mathar et al. 2015; Pessiglione et al. 2006; Schmidt et al. 2010; Ziauddeen et al. 2012), in which rapid, spontaneous responses reflect implicit 'wanting' (Mela, 2006), the present results demonstrate that the grip-force method captured variations in effort exerted in response to food rewards. These responses are thought to be less susceptible to biases inherent in self-report measures, which emphasise explicit wanting, involving both cognitive and conscious processes (Berridge, 2009). It is important to acknowledge however, that the current study did not independently validate grip force as a measure of intrinsic motivation using an established manipulation. Instead, the findings demonstrate its utility in capturing motivational variations in response to food stimuli. Future research should explicitly test the validity of grip force by employing well-established and widely accepted manipulations of intrinsic motivation.

In addition, other limitations of the current research should be addressed. The difference in the average caloric intake between the chocolate and orange conditions may have affected the observed satiety effects. Consuming foods with varying satiety impacts could introduce bias in interpreting motivation changes. As such, future research should incorporate a wider range of food items, including those with varied nutritional profiles, to better understand the generalisability of the findings. Whilst every effort was made to ensure images on the short-duration trials were at a subliminal level, results of the pilot testing, determined that images were in-fact at a supraliminal level. Future research should explore different methods and technologies to present visual stimuli truly subliminally. This could involve using higher refresh rate monitors or more advanced masking techniques to ensure that stimuli remain below the threshold of conscious perception.

In conclusion, this study successfully replicated previous reports of sensory-specific satiety effects on motivation as measured using grip-force, which were also accompanied by changes in food selection behaviour. This provides evidence that the use of objective measures, such as the grip-force use within this and the previous study (Chapter 3), are in fact, effective measures of motivation, in which the magnitude of expected reward correlates with the amount of physical effort exerted. As such, it would appear that lack of priming or satiety effects in the previous study, may be attributed to the methodological decisions made around the odour

exposure, further highlighting issues of reproducibility of the odour priming literature (Cesario, 2014).

Chapter 5: Olfactory Scene Analysis - Does analytical visual processing predict superior identification of component odours in a complex mixture?

The study reported in this chapter is currently under review for publication in the journal Perception. A copy of the submitted manuscript can be found here: https://doi.org/10.31219/osf.io/smzd3

5.1 Abstract

Most familiar odours are complex mixtures of volatile molecules, which the olfactory system synthesizes into a perceptual whole. However, odours are rarely encountered in isolation and thus the brain must also separate distinct odour objects from complex backgrounds. While in vision individual differences in scene analysis have been widely reported, to date, little attention has been paid to the cognitive processes underlying this olfactory ability. The aim of the present study was to determine whether local processing performance in visual tasks predicts participants' ability to identify component odours in multicomponent mixtures. 59 participants (F=39), aged 16-55, completed two visual perception tasks, (Navon and Block Design) and an odour-mixture task designed to test participants' ability to identify multi-component odour objects in binary/ternary mixtures. Performance on the Block Design Task was not significantly associated with odour mixture task performance. However, on the Navon, faster overall reaction times and lower accuracy on global incongruent trials, suggestive of greater local interference, was significantly predictive of binary odour mixture performance. These results provide initial insight into the cognitive processes required for olfactory scene analysis.

5.2 Introduction

Olfactory perception plays a significant role in human behaviour, contributing, for example, to flavour quality and supporting avoidance of potential dangers, such as smoke from a fire, or consumption of rotten foods (Boesveldt & Parma, 2021). Whilst olfactory research focusses largely on perception of mono-molecular odourants (Luckett et al. 2021; Thomas-Danguin et al. 2014; Livermore & Laing, 1998), real-world odours, such as the aroma of roasted coffee (Grosch, 2001) or red wine (Aznar et al. 2001), are complex mixtures of dozens, or even hundreds of different mono-molecules which the olfactory system synthesises into perceptual wholes, known as odour objects (Thomas-Danguin et al. 2014; Gottfried 2010; Yeshurun & Sobel 2010).

In olfactory processing, perception of an odour mixture is not simply an average of its components but results from interactions between odourants influenced by their individual quality and intensity (Laing et al.1984). For example, odour blending can occur, where a composite scent has a quality that is distinct from its individual components (Le Berre et al. 2010; Atanasova et al.2005; Laing & Willcox, 1983), while odour masking occurs when a dominant or stronger odour suppresses the perception of a weaker odour (Stevenson et al. 2007; Kay et al. 2005; Laing & Glemarec, 1992), and odour synergy describes a phenomena where the perceived quality of one odourant is enhanced by the presence of another (Thomas-Danguin et al. 2014; Miyazawa et al. 2008). As such, humans have difficulty identifying individual odours contained within the simplest of mixtures; performance declines rapidly with mixtures of more than 3 components (Le Berre et al. 2007; Laing & Francis 1989) even in those with extensive training and experience (Livermore & Laing 1996). This may reflect the notion that it is physiologically impossible for humans to process information from more than 4 odourants simultaneously (Laing & Francis 1989) as competitive mechanisms result in an inhibition of olfactory receptors (Jinks and Laing 1999) meaning odourants lose their typical character and instead, new combinatorial sensations are produced (Laing, 1994; Jinks & Laing 2001).

Humans' inability to perceive the constitutive complexity of an odour object forms the basis of the prevailing belief that olfaction is a configural sense, in which mixtures of odourants are perceived as a unified *(global)* whole (Rokni et al. 2014). While configural processing may play a crucial role in odour-object recognition, analytical *(local)* processing is required to segregate an odour of interest from a complex odourous background (Thomas-Danguin, 2014). This process relies on the brain's ability to extract fine-grained information about the structure

and olfactory profiles of different odours (Stevenson & Attuquayefio, 2013) and is influenced by temporal dynamics as well as cognitive processes such as memory, attention and, emotion (Carlson et al. 2018).

Like olfactory scenes, visual scenes comprise global structures (e.g. a forest) made up of local parts (e.g. trees) (Gerlach & Poirel, 2018). While perception of global order involves a visual processing style attending to large regions of the visual field, perception of local order requires processing restricted to smaller, component structures that can be processed in isolation (Neufeld et al. 2019; Gerlach & Poirel, 2018; Van Der Hallen et al. 2014). For instance, when completing a wordsearch puzzle, individuals will adopt a local processing style in order to focus on the individual letters within the grid, rather than the grid as a whole. Typically, a significant global processing bias is seen in the general population, known as the *"global precedence effect"* where, for example, people are faster to identify global than local features of hierarchical visual stimuli (Navon, 1977). However, this global bias isn't universally observed and both state and trait factors have been shown to influence processing of visual objects and scenes (Gasper & Clore 2002; de Groot et al.2015; Neufeld et al. 2019). For example, changes in affective state can influence processing style, with negative affect associated with enhanced local (Gasper & Clore, 2002; Gasper, 2004; Fredrickson & Branigan, 2005) and positive affect with enhanced global processing (de Groot et al.2015). Additionally, a stable bias for local visual processing has frequently been observed in autistic individuals and those with a higher level of autistic traits (Neufeld et al. 2019; Happé & Booth, 2008; Koldewyn et al. 2013).

The distinction between processing of global and local features of a scene is consistent across sensory modalities (Bouvet, 2011) and it has been argued that common perceptual and psychological mechanisms underpin them (Ivry & Roberston 1998; Bouvet et al.2011). Global processing biases have been observed in audition too (Bouvet, 2011; Ouimet et al. 2012; Schiavetto et al. 1999) with, for example, faster identification of differences in pitch pattern when they were reflected in the global melody rather than the local, triplet structure (Ouimet et al.2012). Similarly, global/local processing biases have been identified in the tactile domain, with faster recognition of large configurations than small details (Heller & Clyburn, 1993; Puspitawati et al. 2014). Direct evidence that domain general processes underpin these effects comes from a study reporting a correlation between individual global-local processing styles in visual and auditory tasks (Bouvet et al. 2011). Additionally, neuropsychological studies of patients indicate damage to the left or right hemisphere is associated with impairment in the

identification of global or local forms respectively. A dissociation which is observed in both visual (Lamb et al. 1990) and auditory tasks (Pertez et al. 1990), indicative of overlapping neural mechanisms across modalities. Furthermore, cross-modal carry-over effects have been reported with the processing style in one sensory domain induced by instruction to attend to either the local or global features of stimuli presented in another domain (Mirams et al. 2016; Lewis, 2009). For example, instruction to focus on the local features of vibro-tactile stimuli result in reduced global precedence during subsequent performance of a NAVON task (Mirams et al. 2016). Meanwhile, participants' ability to accurately identify a previously tasted wine from among three options, a task which primarily relies on comparison of their aromas, declined following completion of a NAVON task where attention was focused on local in comparison to global detail (Lewis, 2009). This finding was interpreted as reflecting a shift from configural processing of the wine's aroma at encoding to analytical processing at the recognition phase which impaired task performance.

Consistent with reports in visual and auditory tasks, autistic children, and adults with high levels of autistic traits, have been reported to show superior ability at detecting odour objects within a complex mixture (Walker et al. 2020), indicative of superior local processing. However, it is unclear whether the perceptual processes required to dissembed odour objects from complex odour backgrounds are domain general and overlap with more widely used tasks of visual perception. Thus, the aim of the current study was to obtain further insight into the cognitive processes underlying olfactory scene analysis by determining whether ability to identify odour objects against a complex background is predicted by a visual perceptual style. Factor analyses have determined that different visual measures of local-global processing tap slightly differing constructs (Milne & Szczerbinski, 2009). Therefore, for the purposes of this study, the Block Design and NAVON task were included as measures disembedding and global bias respectively (Milne & Szczerbinski, 2009). It is hypothesised that individuals who display superior local level processing on visual tasks will be better at identifying multicomponent odour objects in both binary and ternary mixtures. Further, consistent with previous literature (Shah & Frith 1993; Plaisted et al.1999; Walker et al. 2020), it is expected that higher levels of self-reported autistic traits will be associated with superior local processing in both visual and olfactory tasks.

5.3. Materials and methods

5.3.1 Participants

Fifty-nine participants (39 Female*)* aged 16-55 years (M=26.07, SD=8.48) took part in the study. They were recruited from the student population at Liverpool John Moores University. Additionally, the Psychology Research Participant Panel was used to recruit participants from the wider public. Individuals were excluded from participating if they had a cold, respiratory infection, or any known olfactory dysfunction. The experimental protocol was approved by the Ethics Committee at Liverpool John Moores University (18/NSP/049). Participants received a £10 shopping voucher to thank them for their time.

Power analysis conducted using G-power version 3.1.9.7 (Faul et al.2007) showed that a sample size of 59 is sufficient to detect a medium effect size (Cohen's 1988 criteria), with an alpha of 0.05 and power = 0.75 using bivariate correlation analysis to test a one tailed hypothesis.

5.3.2 Materials

5.3.2.1 Odour stimuli

Six food-related odours were used: blackcurrant, chocolate cake, cola bottles, marzipan, orange, and strawberry. Five of the odours were fragrances blended by a professional perfumer and varied in complexity from 3 to 32 components. These five fragrances were originally created for a project which aimed to support deaf and blind children to make food and drink choices (Murdoch et al. 2014) and were also used in a previously published study (Walker et al. 2020) from this laboratory. The other odour (orange) was an essential oil. All fragrances were diluted to 10% in ethanol. For testing, fragrances were pipetted onto individual quarters of filter paper (GE Healthcare Whatman, 55 mm diameter, Fisher Scientific), placed at the bottom of an Amber glass jar *(*Azpack, 120 mL, Fisher Scientific*).* The dose presented varied between 150 and 200 µL *(*2–4 drops from a Pasteur pipette*):* chocolate cake (150 µL), cola bottles (150 µL), marzipan (150 µL), orange (150 µL), strawberry (150 µL), and blackcurrant (200 µL). These doses were in-line with previously published research (Walker et al. 2020), established to produce perceptually iso-intense stimuli.

5.3.3 Measures

5.3.3.1 Navon Task (Navon, 1977)

A timed letter identification task in which large letters constructed from a number of smaller letters are presented (Figure 5.1*)* - the global (large) and the local (small) letters were either Congruent (e.g. global S, local Ss or global H, local Hs) or Incongruent (e.g. global H, local Ss or global S, local Hs). During a given block, participants were instructed to respond to either the large *(*global trials*)* or small letters (local trials*)* while ignoring the other type.

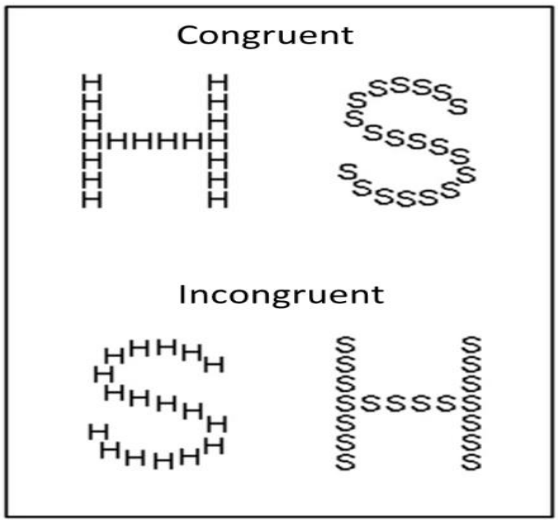

Figure 5.1: *Illustrating the 4 stimulus types from the Navon task. Trials are equally split into global (identify the large letter) and local (identify the small letter) trials, with equal presentations of Congruent and Incongruent stimuli.*

Participants were informed that they would be presented with a series of large letters composed of small letters and on successive blocks the task would instruct them to identify either the large or small letter presented. Participants completed 8 blocks of 16 trials (eight S and eight H stimuli). Half were Incongruent, such that small and large letters differed, the other half were Congruent, in which the large letter was made up of smaller versions of the same letter. As shown in Figure 5.2, each trial started with a fixation cross, presented in the centre of the screen for 500ms, followed by a stimulus screen presented for 40ms, and then a mask screen, which remained on the screen until participants made a response using the S or H keys on a keyboard. Following their response there was a 300ms intertrial interval. Visual perception depends on the integration of local elements of a visual scene into a global frame, with two indices being widely measured; the Global Precedence Effect, which reflects faster processing

of Global compared with Local trials, and the Global Interference Effect which reflects greater interference of global information on local trials.

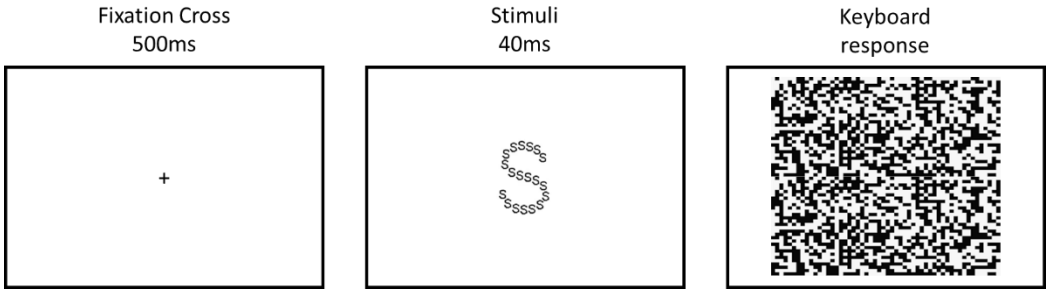

Figure 5.2: *An example trial from the Navon task, in which participants are presented with a fixation cross, a stimuli screen and a mask screen.*

5.3.3.2 Block Design Task (Kohs, 1920)

A subtest from the Wechsler Adult Intelligence Scale-Third Edition (WAIS-III) or Wechsler Adult Intelligence Scale-Revised (WAIS-R), is a cognitive assessment tool often used to measure spatial intelligence and local attentional abilities. This task requires the replication of presented red and white designs using three-dimensional coloured blocks. Participants are presented with a set of identical cubes, each of which has two red, two white and two diagonally striped faces (Figure 5.3*).* There are 9 block designs to complete in the test. On each trial, participants are presented with an image of a 2D design, which they are asked to replicate using the cubes. The number of cubes required to recreate the design increases incrementally as trials progress, from either 4 or 9. Participants are given 60 seconds to complete each of the designs 1-4, which use four blocks, and 120 seconds for designs 5-9, which use nine blocks. Task performance is measured by the number of correctly completed trials.

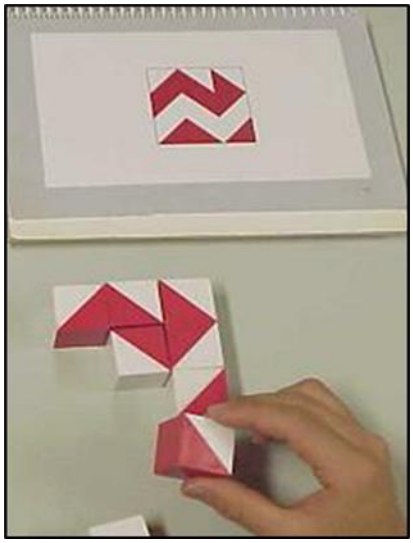

Figure 5.3: *Illustration of the Block Design task, in which individuals are required to replicate 2D patterns using 3D blocks***.**

5.3.3.3 Odour Task:

5.3.3.3.1 Odour Identification

Participants were asked to identify each of the 8 individual odours. Stimuli were presented in one of two orders, as shown in Table 5.1, and were split across participants *(Order 1: n=29, Order 2: n=30)*. The aim of the identification task was to establish that participants could reliably identify all the stimuli individually. On each trial, the participant was asked to smell the contents of the jar and using the corresponding card, select which of 4 pictures best represented the odour presented (*Figure 5.4a*). If a participant gave an incorrect answer, they were informed of the correct answer. All participants completed this part of the task twice to ensure that they were able to accurately identify all the individual stimuli on the second attempt.

Table 5.1: *Shows the contents of each jar during the identification phase. Participants were presented with jars containing single odours, in one of the orders shown.*

Jar Number	Identification Order 1	Identification Order 2
1	Strawberry	Chocolate
2	Orange	Cola Bottle
3	Marzipan	Blackcurrant
4	Blackcurrant	Marzipan
5	Cola Bottle	Orange
6	Chocolate	Strawberry

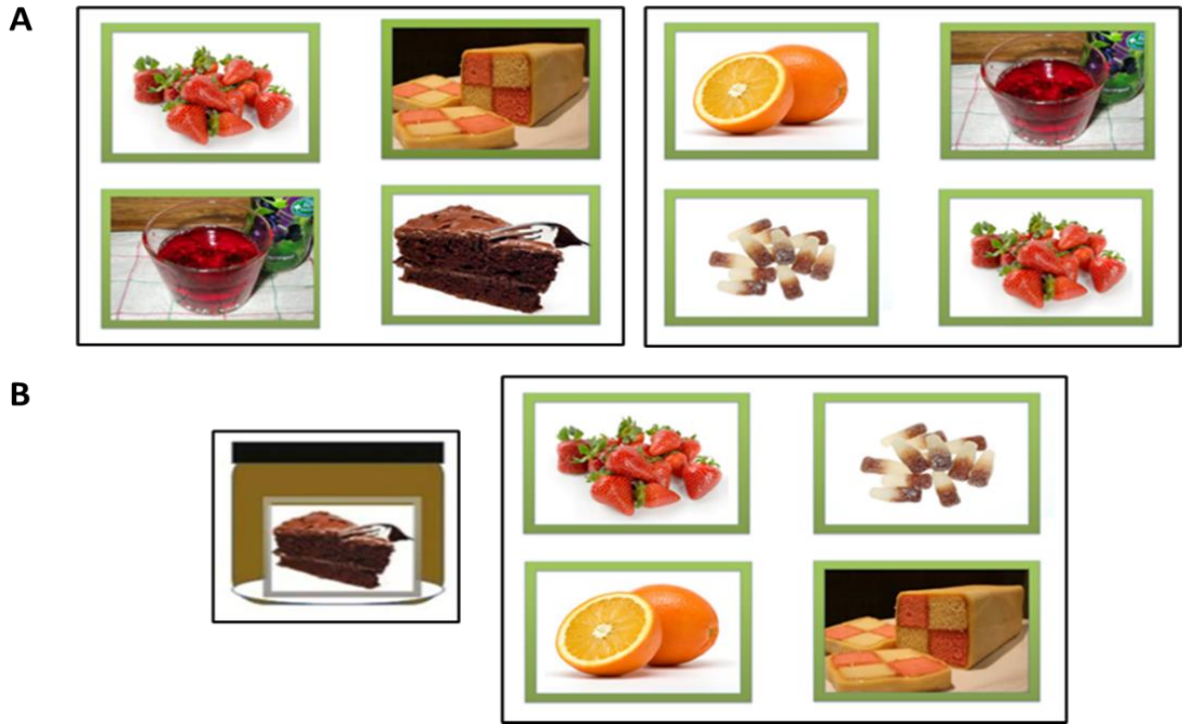

Figure 5.4: *(A) Shows 2 example cards that were used to represent the 6 food odours. (B) Depicts an exemplar Binary mixture trial. Here, participants were told that there was chocolate cake in the jar and had to identify which one of the 4 options presented was also "hidden" in there.*

5.3.3.3.2 Binary and Ternary mixtures task:

For both the Binary and Ternary mixture trials, participants were asked to identify component odours within a mixture. In both phases, trials were completed in one of four orders – the two orders shown in Table 5.2, which were both also presented in reverse order.

5.3.3.3.2.1 Binary mixture trials

Participants were presented with a jar containing two pieces of fragrance-impregnated filter paper. Upon presentation to the participant, the experimenter indicated one of the odours present in the jar (see mixture components in Table 5.2) and asked the participant to identify which one of 4 pictures represented the '*hidden'* (target) odour (see targets in Table 5.2). For example, they were told the jar contains chocolate cake and they must identify that the smell of strawberry is also present from 4 options *(*Figure 5.4b*).*

5.3.3.3.2.2 Ternary mixtures trials

Participants were presented with a jar containing three pieces of fragrance-impregnated filter paper. Upon presentation to the participant, the experimenter indicated 2 of the odours present in the jar and participants were asked to identify which one of 4 pictures represented another odour also "hidden" there. For example, they were told the jar contains Blackcurrant and Strawberries and they had to identify that the smell of Marzipan was also present from 4 options *(*Figure 5.4b*).*

On all trials, the 4 response options were a subset of the 6 test fragrances. Every trial had its own corresponding response card. All participants used the same response card for each given trial and the incorrect options were a random selection of the possible alternatives *(*Figure 5.4a*).* Each image appeared across the whole set of response cards an approximately equal number of times.

Table 5.2: *Stimuli within each phase were presented in one of four orders. Presentation 1 and Presentation 3 are shown. Whereas presentation 2 is the reverse order of presentation 1. And Presentation 4 is the reverse order of presentation 3. Target refers to the odour that participants were required to identify for the successful completion of each trial. Mixture components are the additional odours participants were made aware of in a given trial.*

	Jar	Mixture Components		Target
Presentation 1&2 (2=reverse order)	**Binary Mixtures**			
	7	Marzipan		**Blackcurrant**
	8	Chocolate		**Strawberry**
	9	Orange		**Chocolate**
	10	Strawberry		**Cola Bottles**
	11	Cola Bottles		**Orange**
	12	Blackcurrant		**Marzipan**
	Ternary Mixtures			
	13	Blackcurrant	Strawberry	**Marzipan**
	14	Marzipan	Chocolate	**Cola Bottles**
	15	Orange	Strawberry	**Blackcurrant**
	16	Cola Bottles	Chocolate	**Orange**
	17	Orange	Marzipan	**Strawberry**
	18	Cola Bottles	Blackcurrant	**Chocolate**
Presentation 3&4 (4=reverse order)	**Binary Mixtures**			
	7	Marzipan		**Blackcurrant**
	8	Orange		**Cola Bottles**
	9	Cola Bottles		**Strawberry**
	10	Chocolate		**Orange**
	11	Strawberry		**Chocolate**
	12	Blackcurrant		**Marzipan**
	Ternary Mixtures			
	13	Cola Bottle	Chocolate	**Blackcurrant**
	14	Strawberry	Orange	**Marzipan**
	15	Orange	Chocolate	**Cola Bottle**
	16	Blackcurrant	Strawberry	**Orange**
	17	Cola Bottle	Marzipan	**Chocolate**
	18	Marzipan	Blackcurrant	**Strawberry**

5.3.3.3.2 The Autism Spectrum Quotient (AQ) (Baron-Cohen et al. 2001):

Consists of 50 questions and measures autistic traits in the general population. Participants are asked to indicate how much each statement applies to them on a 4-point scale with descriptors: *"Definitely agree," "Slightly Agree," "Slightly Disagree,"* and *"Definitely Disagree."* For half the questions, an *"Agree"* or *"Slightly Agree"* response indicates characteristics similar to those on the autistic spectrum and are scored as one, whereas *"Disagree"* or *"Slightly Disagree"* responses are scored as zero. 50% of questions are reverse scored. Scores on the scale can range from 0-50 with a typical population scoring 17 on average (Ruzich et al. 2024) and over 80% of individuals diagnosed with Autism scoring over 26 (Woodbury-Smith et al. 2005).

5.3.4 Procedure

Testing took place on a one-to-one basis in a quiet room. Upon entering the laboratory, participants were asked to place their personal belongings, including their mobile phone, to one side. They were then provided with a paper version of the participant information sheet and instructed to read it carefully. Once the participant was happy with the instructions, they were asked to sign a consent form. Participants first completed the Navon task which took approximately 10 minutes; they were instructed to sit comfortably in front of the computer screen and to follow the instructions on the screen which would start the task. Upon completion, participants were moved to another table in the same room where they completed the Block Design Task. Participants were then moved to another room to complete the Odour Identification Task – during this task, jars were presented individually. On each trial, the lid was unscrewed and held away from the participant for approximately 5 seconds while the experimenter gave them instructions; the jar was then placed under the participant's nose around 5 cm away. Participants were instructed to smell the contents of the jar and asked to indicate which of the 4 pictures presented best represented the odour they smelled in the jar. For the mixtures task, participants were told 1 *(Binary mixtures)* or 2 *(Ternary mixtures)* of the odours in the jar and asked to identify which of the 4 images presented best represented the other odour that was present. To avoid olfactory fatigue, there was a 30s interval between trials and a 2-min break between each phase of testing. Participants were then asked to complete the AQ questionnaire on a laptop before being thanked for their time and debriefed. At that point, participants were given the opportunity to ask any questions.

5.3.5 Data analysis Plan

Data were analysed using SPSS (IBM – version 26**).** Kolmogorov–Smirnov tests were used to determine whether data were normally distributed. Levene's test examined variances across conditions and Mauchly's tests of sphericity were inspected and where appropriate, Greenhouse Geisser corrections to degrees of freedom are reported.

5.3.5.1 Olfactory Data

Prior to the main analysis, accuracy scores for each of the single odours used on the initial identification trials was analysed using a mixed ANOVA. Binomial logistic regression was also used to ensure odours used were equally identifiable during the identification task, prior to analysing the responses for both the Binary and Ternary trials. Nature of errors made on the

identification task were also considered, in order to understand whether there was any pattern of confusion between odours.

A Mixed ANOVA was conducted to identify whether participants displayed superior performance on the identification trials or mixture trials, as well as ensuring that order of mixture presentation, within the Binary and Ternary phases was not an issue. Logistic regression was used to ensure that the target odours used in the mixture trials were equally identifiable.

5.3.5.2 Visual Data

For the Navon task, data were removed on Accuracy trials if they were deemed to be anticipatory responses *(<200ms)*. In order to capture genuine cognitive responses while reducing the influence of extreme outliers, responses above 1500ms were also removed (Gupta et al. 2021). Reaction times for incorrect responses were excluded, which represented 9.8% of the total trials: 3.64% for Congruent-Global, 5.58% for Congruent-Local, 12.59% for Incongruent-Global, and 17.39% for Incongruent-Local. Following the removal of incorrect, anticipatory and long responses, scores for each trial type (Congruency/Level) were compared using separate within-subject ANOVAs.

Two indexes, which reflect different aspects of visual processing, were derived on a participant-by-participant basis from Navon task data (Gerlach & Poirel, 2018; Navon, 1977). The first index, termed Global Precedence Effect, measures the processing advantage for global-level information over local-level information. It is calculated by subtracting the mean reaction time (RT) for Global trials from the mean RT for Local trials. Positive values on this index indicate faster processing of global-level compared to local-level information, suggesting a global precedence effect.

The second index, termed Global-Local Interference Effect, measures the extent to which incongruent local-level information interferes with the processing of global-level information. It is calculated by subtracting the mean RT for Congruent trials from the mean RT for Incongruent trials. Positive values on this index indicate greater interference, reflecting a slower RT for incongruent trials compared to congruent trials.

Performance on the Block Design Task is assessed by the number of correctly completed trials, with each trial weighted based on the time taken to complete it. We scored participants

according to their age groups, utilising the WAIS-III norms, which are structured in increments of 2 years for ages 16 to 19, 5 years for ages 20 to 34, 10 years for ages 35 to 64, and 5 years for ages 65 to 89. Higher scores indicate better performance.

5.3.5.3 Olfactory and Visual Task Associations

Bivariate correlation and partial correlation analyses were conducted to determine whether there were any associations between visual and olfactory task performance. To address the risk of an inflated Type I error, Bonferroni correction for multiple comparisons was applied (Lee & Lee, 2018), which adjusts the significance threshold by dividing the alpha level by the total number of comparisons.

Regression modelling was used to follow up significant associations. For all regressions, linearity was assessed by partial regression plots and a plot of studentised residuals against the predicted values. There was independence of residuals, as assessed by a Durbin-Watson statistic. There was homoscedasticity, as assessed by visual inspection of a plot of standardised residuals versus unstandardised predicted values. There was no evidence of multicollinearity, as assessed by tolerance values greater than 0.1. There were no standardised deleted residuals greater than ±3 standard deviations and values for Cook's distance above 1. The assumption of normality was met, as assessed by Q-Q Plots.

5.3.5.4 Autism Quotient

Scores for the Autism Quotient Questionnaire were primarily examined to ensure the sample contained a good range of scores for a typical population (Ruzich et al. 2015). The distribution of scores for the Autism Quotient Questionnaire ranged from 6.00-45.00, with a mean score of 20.20 (SD=8.57).

Correlation analysis was also conducted in order to determine whether scaled AQ score was associated with performance on the Odour Mixture Task (Binary and Ternary), the Navon task (trial types and indices) and the Block Design task.

5.4 Results

5.4.1 Navon

Both Reaction Times and Accuracy were analysed using within-subjects ANOVAs, with Level (Global vs. Local) and Congruency (Congruent vs. Incongruent) as factors. As shown in Figure 5.5A, for Reaction Times, there was a significant main effect of Congruency (F (1,53) = 145.90, $p < 0.001$ $\eta_p^2 = 0.73$), with faster responses to congruent than incongruent stimuli. There was also a significant main effect of Level (F (1,53) = 7.98, $p < 0.01$ $\eta_p^2 = 0.13$), with faster global compared with local identity judgements. There was no interaction between Level and Congruency (F (1,53) = 1.46, p=.23, $\eta_p^2 = 0.03$). However, for Accuracy (Figure 5.5B), whilst there was a significant main effect of Congruency (F (1,53) = 72.69, $p < 0.001$ $\eta_p^2 = 0.58$), with superior performance on Congruent compared with Incongruent trials, there was no main effect of Level (F(1,53) = 1.12, , $p < .30$ $\eta_p^2 = 0.21$), responses did not differ significantly between Global and Local trials. There was no interaction between Level and Congruency (F (1,53) = 1.26, p=.27, $\eta_p^2 = 0.03$).

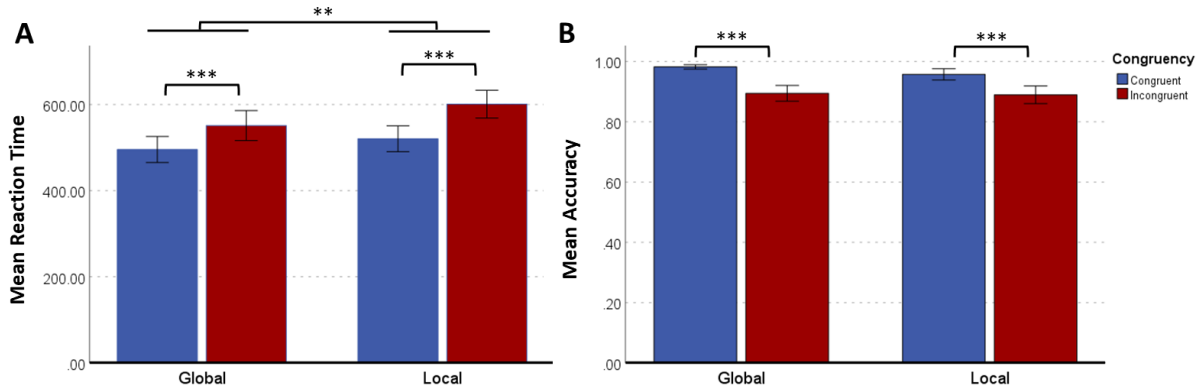

Figure 5.5: *A: Mean Reaction Time and B: Mean Accuracy, for each trial type. Blue bars represent Congruent Trials and Red bars represent Incongruent Trials. (**denotes sig <.01, ***denotes sig <.001). Error bars display 95% CI.*

5.4.1.1 Navon Indexes

The mean score on the Global-Local Interference index (M= .078, SD= .06) indicates that accuracy was greater when participants were required to identify the Global information compared to the Local information, as such Global information interfered with reporting of Local information.

The mean score on the Global-Local Precedence index (M= -37.35, SD= 67.34) indicates that reaction times were generally faster when participants were asked to identify the Global information compared to the Local information.

5.4.2 Block Design Task

Raw scores on the Block Design Task ranged from 2.00-56.00, with a mean of 30.35 (SD=14.35). Using Weschler norms, scaled scores ranged from 1.00 to 14.00, with a mean of 7.85 (SD=3.14), with participants successfully completing an average of 6.3 trials, and 30.5% of participants successfully completing all 9 trials.

5.4.3 Odour Task

The proportion of correct answers given in the identification phase, as well as in binary and ternary mixtures phases, was calculated on a participant-by-participant basis, with mean overall scores calculated for each trial type.

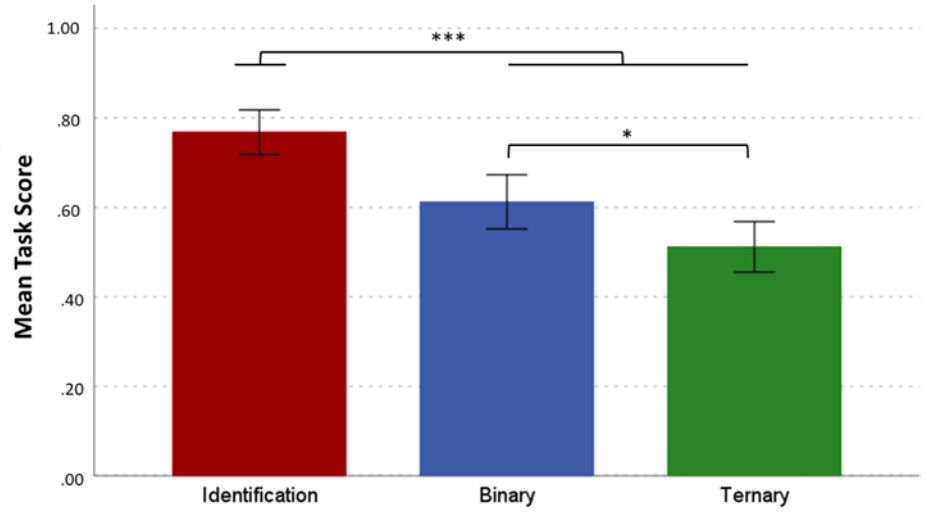

Figure 5.6: *displays the mean scores for each trial type (Identification, Binary, Ternary). (*denotes sig <.05, ***denotes sig <.001). Error bars display 95% CI.*

As multiple odour sets were used, it was important to confirm that performance did not differ between odour sets. A mixed ANOVA with Odour Set and Trial Type as factors, confirmed that there was a significant effect of Trial type, F (2, 110) = 23.80, p<.001, η_p^2=.30. As shown in Figure 3.2, performance on the Identification trials was significantly better than on the Binary Trials (p<.001) and Ternary Trials (p<.001). Performance on Binary trials was significantly better than on Ternary trials (p=.02). There was no effect of Odour set on accuracy

F (3, 55) = .75, p=.53, η_p^2=.04, that is, the order in which odours were presented for each trial type, did not influence identification accuracy. There was no interaction between Odour Set and Trial Type F (6, 110) = 2.00, p=.07, η_p^2=.10.

5.4.4 Correlations

5.4.4.1 AQ Correlations

It was of interest as to whether the AQ was significantly associated with any of the visual or olfactory tasks. For the Visual tasks, AQ was not significantly associated with the Block Design task, (r =.17, p = .11). Similarly, there was no association between AQ and Navon Precedence (r = -.08, p = .29), or Interference (r = -.12, p = *.19*). For the olfactory tasks, AQ was not significantly associated with Odour Identification (r = -.06, p =.34), Binary (r = .09, p =.26), or Ternary (r = -.06, p = .32) trials. Due to the non-significant findings in relation to AQ, this was not used in any further analysis.

5.4.4.2 Visual and Olfactory Tasks

5.4.4.2.1 Block Design Task

Performance on the Block Design Task was not significantly associated with performance on the initial Identification trials (r = .20, p = .06), the Binary trials (r = .06, p = .34), or the Ternary trials (r = .04, p = *.39*).

5.4.4.2.2 Navon

Contrary to the study hypotheses, the two standard indices of NAVON performance were not associated with Binary (Precedence r = .05, p =.36, Interference r = .01, p = .46) or Ternary (Precedence r = .09, p =.25, Interference r = .01, p = .47) mixture task performance.

Since the NAVON indices were not associated with odour mixture performance, further analyses were undertaken to explore whether a relationship emerged when considering Reaction Time and Accuracy across the four NAVON trial types (Congruent Global, Congruent Local, Incongruent Global, Incongruent Local).

5.4.4.2 Exploratory Analysis of relationship between NAVON and Odour Mixture Performance

We considered whether, irrespective of the classic NAVON indices, there was an association between speed of performance on congruent and incongruent trials and performance on the odour mixture task. As congruent global and local trials are measuring responses to exactly the same stimuli these were collapsed together to create a single congruent response factor.

It was found that superior identification on the Binary trials was significantly, moderately negatively associated with Navon Reaction Time for Congruent trials (r = -.40, p <.001) (Fig 5.7A), Incongruent Global trials (r = -.38, p = .003) (Fig 5.7B), and Incongruent Local (r = -.29, p = .016) (Fig 5.7C). Thus, revealing that participants who performed better in the binary odour mixtures task processed visual stimuli more quickly during all trial types on the Navon task.

There was no association between performance ternary odour mixture trials with Navon Reaction Time, for any trial type: Congruent trials (r = -.20, p = .07), Incongruent Global (r = -.11, p = .22), Incongruent Local (r = -.15, p = .14). This implies that faster processing speed is not an advantage to performance on the more complex mixture trials.

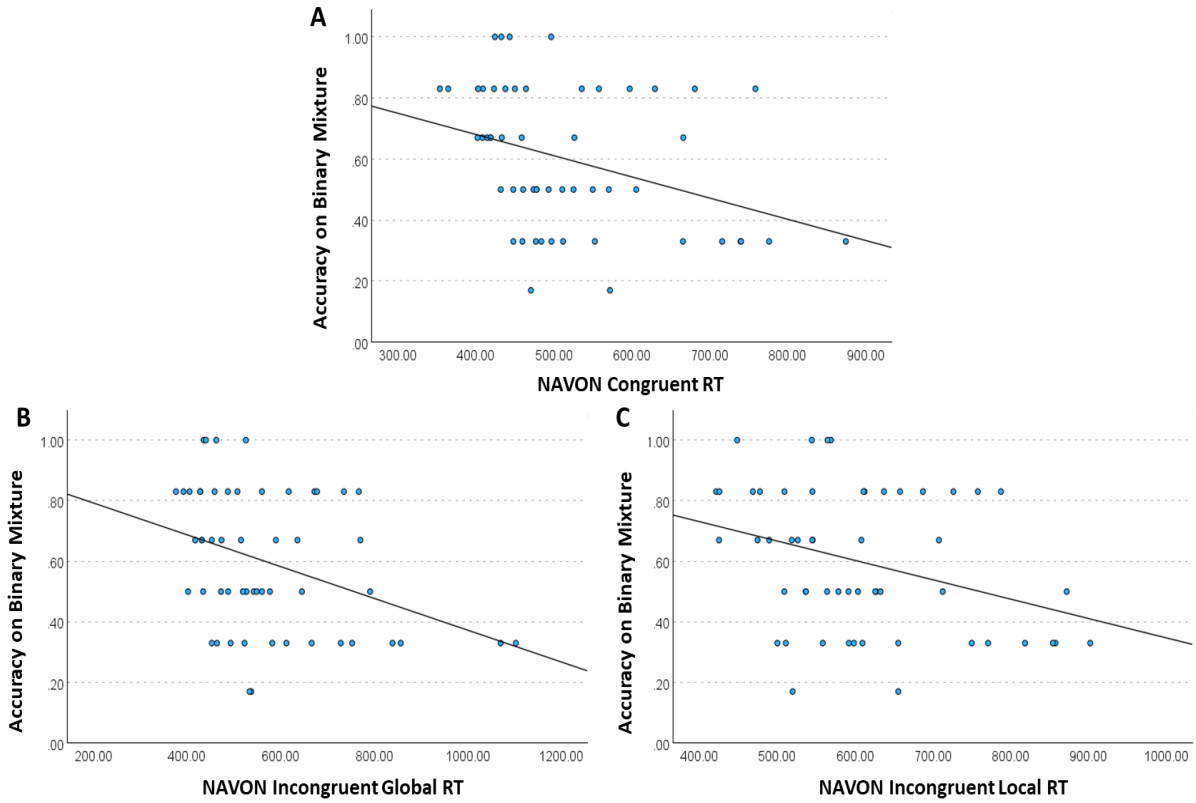

Figure 5.7: *Scatterplots depicting the relationship between odour identification performance in the binary mixture task and reaction time on the Navon trials. (A) Congruent trials, (B) Incongruent global, (C) Incongruent local. In each graph, a negative correlation is observed, indicating that faster reaction times are associated with superior performance in identifying odours from binary mixtures. The trend lines represent the linear regression fit for each dataset.*

Due to Reaction time for all trial types, being significantly associated with Binary mixture performance, three linear regression analyses were conducted in order to ascertain the amount of variance in odour mixture performance each trial type accounted for. Reaction Time on Congruent trials accounted for 10.4% of the variance in Binary mixture performance F (1, 52) = 7.16, p =.01 (Table 5.3A). Reaction Time on Incongruent Local trials accounted for 9.3% of the variance in Binary mixture performance F (1, 52) = 6.41, p =.01 (Table 5.3B). With Reaction Time on Incongruent Global trials accounting for 11.3% of the variance in Binary mixture performance F (1, 52) = 7.75, p =.007 (Table 5.3C). Thus, processing speed on the NAVON is a significant predictor of odour mixture performance.

Table 5.3: *Three separate Regression models using 'Enter' method; for Reaction Time trials predicting performance on Binary Mixture Trials. Model A depicts Congruent trials (C RT), Model B depicts Incongruent Local trials (IL RT), and Model C depicts Incongruent Global trials (IG RT). ΔR^2= Adjusted R^2, R^2= R-Squared, β = Standardised Regression coefficient, B= Unstandardised Coefficient Beta, SE B = Standard Error of the Unstandardised Coefficient. Sig levels: * = p<.02 ** = p<.01.*

	Model	ΔR^2	R^2	β	B	SE B
A	C RT	.104*	.121	-.348	-.001	.000
B	IL RT	.093*	.110	-.331	-.001	.000
C	IG RT	.113**	.130	-.360	-.001	.000

5.5 Discussion

Whilst performance on the odour mixtures task was not associated with either success on the block design task or classic indices of local processing advantage on the Navon, post-hoc exploratory analysis of reaction time and accuracy on the Navon task did indicate that there is some overlap in the domain general cognitive processes required for performance of the odour mixture and visual task. The strongest association was between general reaction time on the Navon and accuracy on the binary mixtures task, indicating processing speed confers some advantage when analysing relatively simple olfactory scenes. It is noteworthy that this association was only apparent on binary mixture trials as Navon reaction time did not predict performance on the more complex ternary mixtures, perhaps reflecting the fact successful performance of this more complex task requires additional or different cognitive strategies (Walker et al. 2020).

Additionally, although there was no association between traditional indices of local/global processing style and mixture performance, there was a negative association between performance on the binary odour mixtures trials and accuracy on global incongruent trails, suggestive of the fact participants who experienced more local interference on global trials were better at segmenting odour objects within the olfactory scene. This provides some support for the hypothesis that aspects of perceptual scene analysis are domain general. Again, this effect was only apparent with performance on the simple binary and not more complex ternary mixtures. The fact that reaction time and accuracy on incongruent local trails accounted for separable, significant, portions in the variance on binary mixture task performance confirms they are metrics of separate cognitive processes (Mulder & van Maanen, 2013).

Processing speed interacts in a critical way with other higher-order cognitive functions (Motes et al. 2018; Wong et al. 2021), such as selective attention (Jehu et al. 2014; Prinzmetal et al. 2005; Vaportzis et al. 2013). That is, faster processing speed has been associated with the ability to selectively attend to information in a more localised manner, meaning individuals can efficiently focus on specific details, elements, or features within a task or stimulus. In such cases, those with faster processing speed may excel in tasks that require a narrowed, localised attentional focus (Jehu et al. 2015; Prinzmetal et al. 2005; Vaportzis et al. 2013). This interplay between cognitive processes would support the current findings in which individuals who displayed faster processing speed and an increase in local interference, also exhibited superior performance in segmenting odour objects in Binary mixtures.

It is proposed that humans have difficulty identifying odours in mixtures of more than three components (Laing & Francis 1989; Le Berre et al. 2007), possibly due to the notion that in more complex mixtures, perceptual blending may occur. In these cases, the individual odourants may lose their distinctiveness and instead give rise to new odour sensations (Jinks & Laing, 2001; Laing, 1994; Olsson, 1998). As such, the current study opted for the use of both binary and ternary mixtures. As expected, and in-line with previous literature (Walker et al. 2020), individuals performed significantly better when identifying component odours on Binary compared to Ternary trials. Whilst perceptual blending is reported to be in mixtures of more than three components, the current study found this complexity effect for mixtures of three components. This difference in findings may be due to the fact that previous research investigating odour mixture segmentation opts for the use of mono-molecular odourants (i.e., they were based on single odourants as stimuli) (Jinks & Laing 1999; Laing & Francis, 1989; Laing & Glemarec, 1992; Livermore & Laing, 1998; Luckett et al. 2021; Thomas-Danguin et al. 2014), the current study opted for the use of real-world relevant odour stimuli, which are themselves, multi-molecular blends. In addition, the odours used may have had similar or complementary mono-molecular characteristics. When two odours share chemical similarities or have overlapping scent profiles, they have a higher chance of merging together to create a unified odour (Tromelin et al. 2020).

In contrast to previous research, in which individuals with a clinical diagnosis of Autism, or those self-reporting high levels of Autistic traits, have displayed a bias for local processing of visual stimuli on the Navon Task (Happe & Booth, 2008; Neufeld et al. 2019; Simmons et al. 2009) and the Block Design Task (Shah & Frith, 1993; Stewart et al. 2009) and Odour Mixtures task (Walker et al. 2020), the current study failed to find any association between AQ score and performance on these tasks. Whilst much of the past research focusses on Local and Global processing styles in Autistic individuals (Caron et al. 2006; Happé & Booth, 2008; Lebreton et al. 2021; Neufeld, et al. 2020), it is important to note that preference for local processing has been observed in the general population, especially when considering state and trait factors such as negative moods (Fredrickson & Branigan, 2005; Gasper, 2004; Noguchi & Tomoike 2016), superior observational drawing (Chamberlain et al. 2013; Drake & Winner, 2011), familiarity of a stimulus (Kaeppler & Mueller, 2013), increased anxiety (Becker & Plessow et al. 2017; Shilton et al. 2019) and higher levels of autistic traits (Neufeld et al. 2019; Happé & Booth, 2008). This unexpected finding may be due to the idea that a local processing bias is believed to be associated with symptom severity (Van Eylen et al. 2018), in that the bias

for local processing is reliably seen in those with a clinical diagnosis of Autism (Behrmann et al. 2006; Mottron & Belleville, 1993; Plaisted et al. 1999; Rinehart et al. 2000), rather than those with self-report high level autistic traits, such as those in the current study and other studies in which null results were reported (Hayward et al. 2012; Mottron et al. 2003). This would explain the findings of Walker et al. (2020), who found that local processing of odour mixtures was greater for clinically diagnosed autistic individuals compared to self-report of autistic traits. In addition, the distribution of AQ scores in the current study was skewed higher (Mean=20.20) than that in other studies who have also measured Autistic traits in the general population (Tan et al. 2023; Fusar-Poli et al. 2020). A systematic review of 73 published papers, found that the mean AQ score in a typical sample drawn from a non-clinical population is approximately 17 (Ruzich et al. 2024).

There are some limitations in the present study, which warrant further investigation. For example, using only six odours in the mixture trials, raises questions the consistency of the results if other odours were used. In addition, whilst the order of presentation of odour mixtures was considered, all possible combinations of stimuli from the odour set were not. This raises uncertainties regarding the identifiability of target odours in alternative mixture combinations (Jinks & Laing, 1999; Laing & Francis, 1989; Laing & Glemarec, 1992; Livermore & Laing, 1998). Future research may consider extending not only the number of odour stimuli used, but also the mixture combinations, in order to ensure comprehensive investigation of the olfactory processing mechanisms involved in identifying component odours in a mixture. The lack of association between visual processing and autistic traits which is widely reported in the literature (Happé & Booth, 2008; Neufeld et al. 2019; Simmons et al. 2009), may have been due to the skewed AQ score reported in the current population. Subsequent investigations may look to compare individuals clinically diagnosed with autism with those self-reporting minimal autistic traits.

In conclusion, the results reported here provide the first evidence that processing speed confers some advantage when analysing relatively simple olfactory scenes, supporting the notion that those with faster processing display a narrowed, localised attentional focus (Jehu et al. 2015; Prinzmetal et al. 2005; Vaportzis et al. 2013). In addition, there is partial evidence that a local processing bias in the visual domain provides an advantage in identifying odours in complex mixtures, though this was only evident with simple binary and not the more complex ternary mixtures. This may support the idea that cognitive processes underlying sensory perception are not strictly tied to a single sensory modality but instead, may generalise

across different sensory modalities. Thus, suggesting that broader cognitive mechanism at play, as opposed to domain-specific processes isolated to each sensory system. However, further research is warranted, in order to fully understand the mechanisms underlying local and global olfactory processing styles.

Chapter 6: Is taster status predictive of implicit liking of bitter, astringent and chemesthetic compounds

6.1. Abstract

Food choice and food intake are guided by both multisensory and metabolic processes. Genetic taster status (GTS) is an inherited relative sensitivity to taste stimulation, assessed via density of the fungiform papillae and/or perceptual sensitivity to the bitter compound 6-n-Propylthiouracil (PROP). However, the effects of GTS on food preferences goes beyond just bitter gustatory tastants. For example, significant relationships have been reported between GTS and responses to somatosensory (trigeminal), chemesthetic and astringent stimuli. To capture these varied sensory experiences, hedonic responses to oral stimuli are typically measured using subjective rating scales. The aim of this study was to determine whether facial Electromyography (EMG), and Electrocardiography (ECG), established implicit measures of affect, can predict individual differences in dis/liking of bitter tasting, chemesthetic, and astringent compounds. Participants were pre-screened for GTS. Then, trial by trial, facial EMG and ECG responses to threshold and super-threshold concentrations of caffeine (bitter), menthol (*chemesthetic*) and alum (*astringent*) were measured. It was found that super-tasters perceived all three stimuli to be more intense than non-tasters, with EMG, but not HR, reliably differentiating between the two groups, specifically at supra-threshold concentrations.

6.2. Introduction

Food choice is largely influenced by flavour, with the extent to which a particular food is liked being an important driver of both short and long-term food consumption. Flavour perception is a complex multisensory process that involves integration of gustatory, olfactory, chemosensory, somatosensory and visual information (Spence, 2015). Flavour perception generally determines food choice, with foods that are high in sugar and fat having a high reward value (Drewnowski, 1997), however, different individuals can have very different taste experiences when consuming the same food (Ly & Drewnowski, 2001; Melis & Barbarossa, 2017; Tepper & Nurse, 1997). These differences in food preferences can be due to various factors including sensory responses to a food's taste, smell and texture (Bartoshuk, 1991), which are determined in part by Genetic Taster Status (GTS), an inherited relative sensitivity to taste stimulation (Bartoshuk, 2000; Dietsch et al. 2019), assessed via density of the fungiform papillae on the tongue and/or perceptual sensitivity to the bitter compound 6-n-Propylthiouracil (PROP) (Bartoshuk, 1991; Smutzer et al. 2013). There are three categories of GTS, non-tasters, medium-tasters, and super-tasters (Bartoshuk, 1991), in which non-tasters are unable to detect the bitter sensation of 6-n-propylthiouracil (PROP) and have 16 times fewer taste buds on the tongue, super-tasters have a high density of taste buds on the tongue and perceive the bitter sensation PROP as extremely intense and aversive, whilst medium-tasters can detect the bitter sensation but perceive it as less intense than 'super-tasters' (Catanzaro et al. 2013).

An increase in the number of fungiform papillae on the tongue is not only associated with increased sensitivity to bitter tastants, but also with enhanced sensitivity to trigeminally mediated, chemesthetic, thermal and tactile sensations (Essick et al. 2003; Lanier et al. 2005; Tepper and Nurse, 1997, Yackinous & Guinard, 2001). For example, lingual sensitivity to a number of chemical irritants including capsaicin has been repeatedly associated with PROP taster status (Bartoshuk et al. 1993; Prescott et al. 2004; Prescott & Swain-Campbell, 2000). Capsaicin is a ligand for the heat activated TRP receptor (TRPV1), thus indicating that PROP sensitivity is associated with trigeminal chemoreception. However, the overall association between PROP taste sensitivity and lingual irritation is not very strong and is possibly sensitive to the specific concentrations, methods or stimuli utilised (Green et al. 2005). Indeed, several studies have reported a significant positive relationship between perceptions of PROP bitterness and chemesthetic sensations (Prescott & Swain-Campbell, 2000). Orosensory

thermal trigeminal afferent neurons respond to cool, warm, and nociceptive hot temperatures (Leijon et al. 2019). Capsaicin reduces the thermal threshold of activation of warm trigeminal thermoreceptors and orosensory nociceptors, while menthol elicits a cool sensation by increasing the threshold temperature for activation of cold receptors (McKemy, 2007). However, while some studies report super-tasters experience greater oral burn from capsaicin (Green, 2003; Spinelli et al. 2018; Tepper & Nurse, 1997), differences between taster groups are not always evident (Manrique & Zald, 2006). To date, there has been little interest in the impact of taster status on the oral perception of menthol, a TRPM8 ligand (Cliff & Green, 1996), with one study reporting that some individuals perceived significant levels of bitterness when menthol was applied to various areas of the tongue (Green, 2003). Thus, increased knowledge of how GTS affects responses to chemesthetic stimulation would be beneficial in developing an understanding of the relationship between GTS and food choices.

Additionally, lingual tactile sensitivity increases (tactile thresholds decreased) as fungiform papillae density increases (Bangcuyo & Simons, 2017) and PROP taster status has been observed to influence lingual texture perception (Drewnowski et al. 1998; Nasser et al. 2001; Tepper & Nurse, 1997). Evidence from psychophysical studies indicates that taster status predicts lingual tactile acuity, with supertasters showing the lowest tactile perception thresholds in comparison to both medium and non-tasters (Essick et al. 2003). This heightened oral tactile sensitivity in supertasters is hypothesised to be a consequence of the co-innervation of fungiform papillae by mechanosensitive trigeminal nerves (Bajec & Pickering, 2008; Prutkin et al. 2000). Astringency is a tactile sensation perceived as oral dryness and puckering (Gawel, 1998), often elicited by foods that contain high concentrations of polyphenol and tannins, as found in tea and red wine (Schobel et al. 2014). One study reported that supertasters perceived increased astringency from red wine (Pickering & Robert, 2006) but another study reported that taster status had no impact of the perception of red wine astringency (Ishikawa & Noble, 1995). Thus, further work is required to understand the relationship between GTS and responses to astringent stimuli.

In summary, supertasters reliably report more intense reactions to taste compounds than the other taster groups (Dietsch et al. 2014; Ko et al. 2000; Nagy et al. 2014; Pelletier & Steele, 2014) and, in general, display more negative responses to foods with sensory qualities such as bitter and sweet tastes, pungency, astringency and fattiness. Such differences in oral perception are predicted to influence eating behaviours (Tepper, 2008), however, while some studies

report links between taster status and food preference, several studies have found no correlation between taster status and food preference (Dinehart et al. 2006; Jerzsa-Latta et al. 1990; Yackinous & Guinard, 2006). Though personality traits, cultural background and food attitudes can all affect food choices (Tepper et al. 2009), inconsistent findings may also, in part, be due to the methods used to measure hedonic ratings. To date, the majority of research studies have relied on subjective measures to understand food perception, liking and choice (Cordonnier & Delwiche, 2008; Lim, 2011; Meiselman & Cardella, 2003). However, subjective ratings do not always provide an accurate measure of participant's true affective state as they can be influenced by demand characteristics and social desirability, whereas implicit psychophysiological techniques allow investigation of hedonic reactions that are not open to conscious introspection (Bell et al. 2018; Hebert et al. 2008).

Affective responses to environmental stimuli can be described in terms of arousal i.e., how much a stimulus activates the sympathetic and parasympathetic branches of the autonomic nervous system, and valence, whether a stimulus is perceived as positive or negative, with resulting cardiac responses differing depending on both the valence and the magnitude of an affective cue (Bradley et al. 2001). Thus, while brief exposure to a stimulus which is perceived as unpleasant results in a rapid and sustained heart-rate deceleration, positively perceived stimuli are associated with a slower, initial deceleration, which varies in magnitude depending on intensity, and is followed by a brief cardiac acceleration (Bradley et al. 2001). Facial EMG is a well-established implicit measure of affective response to sensory stimuli, independent of subjective judgement (Sato et al. 2020). Activity of the corrugator supercilli muscle, related to brow lowering, and the zygomatic major muscle, related to lip corner pulling, are commonly used to measure dynamic affective responses to positive and negative hedonic stimuli (Larsen et al. 2003; Sato et al. 2020; Sato et al. 2008), with increased corrugator activity and increased zygomaticus activity indicative of heightened negative and positive affect respectively. While several studies have used either EMG or ECG to differentiate hedonic responses to oral stimuli (Bradley et al. 2001; Cannon et al. 2017; Hu et al. 1999; Horio, 2003), other research suggests that, although these measures can reflect physiological reactions to pleasant and unpleasant stimuli, they are not direct indicators of hedonic response. This is due to the notion that they can also be influenced by factors such as cognitive effort, attention, and other psychological states (de Morree & Marcora, 2010; Porges & Raskin, 1969). To our knowledge, no research has yet used both EMG and ECG to examine the relationship between GTS and the hedonic liking of oral stimuli. Combining both measures could provide a more comprehensive

understanding of the physiological responses involved, as EMG captures facial muscle activity related to emotional valence, while ECG provides insights into autonomic regulation, potentially offering a clearer picture of the complex physiological processes underlying hedonic experiences.

Thus, the aims of the proposed study are to investigate whether PROP Taster Status is predictive of subjective liking of threshold and suprathreshold concentrations of bitter, astringent and chemesthetic compounds, and determine whether facial Electromyography (EMG), and Electrocardiography (ECG), established implicit measures of affect, can predict individual differences in dis/liking of these stimuli. It is hypothesised that supertasters will show heightened sensitivity, and thus heightened negative affective responses, to all compounds.

6.3 Pilot Testing

Participants were recruited from the staff and student population at LJMU and were different from those involved in the main experiment. The aim of the pilot was to identify the threshold and moderate suprathreshold concentrations of the taste stimuli to be used in the main experiment. Twenty-two participants were recruited, ten rated an initial set of stimuli and twelve sampled a second set of serial dilutions.

6.3.1 Oral Stimuli

Based on a review of the published literature, two sets of serial dilutions of Caffeine, Aluminium Sulphate, and Menthol were prepared using 200ml of distilled water. Initial concentrations are shown in Table 6.1, The first set for each stimulus (Set A) was prepared in logarithmic-steps with a base of 10 and the second set (Set B) used were prepared in half logarithmic-steps with a base of 5. This approach allowed for a thorough evaluation of a wide range of concentrations.

Table 6.1: *Concentrations are presented in millimolar (mM) units. The concentrations in the first (Set A) and second (Set B) pilot test are shown. Each set are serial dilutions, one set uses a logarithmic base of 5, while the other set uses a logarithmic base of 10.*

	Log step	Caffeine (mM)	Alum (mM)	Menthol (mM)
Set A	**0.0**	2.176	2.000	3.126
	-1.0	0.217	0.200	0.312
	-2.0	0.0217	0.02	0.0312
	-3.0	0.0021	0.002	0.0031
	-4.0	0.0002	0.0002	0.0003
Set B	**0.0**	2.176	2.000	3.126
	-0.5	0.435	0.4	0.625
	-1.5	0.087	0.08	0.125
	-2.0	0.017	0.016	0.025
	-2.5	0.003	0.0032	0.005

Caffeine: Five solutions of Caffeine (C8H10N4O2) were used to generate a bitter sensation (Ly & Drewnowski, 2001; Gardener & Carpenter, 2019; Webb et al. 2015; Keast & Roper, 2007). To prepare these solutions, caffeine was dissolved in 100ml of distilled water on a magnetic mixing plate.

Potassium Alum: Five solutions of aluminium potassium sulphate ([AIK(SO4)2.12H20] – Alum) were used to generate an astringent sensation. To prepare these solutions, alum was dissolved in 100ml distilled water on a magnetic mixing plate.

Menthol: Five solutions of Menthol (C10H20O) were used to generate a trigeminal sensation. As it is only water-soluble at very low concentration, menthol crystals were first dissolved in 5ml of food grade ethanol and then added to 95ml of distilled water. The solution was mixed and heated on a mixing plate until all the crystals are dissolved.

All solutions were stored in a fridge in sealed glass bottles and brought to room temperature before testing. Unused stock solutions were discarded within 7 days (Bajec & Pickering, 2008).

6.3.2 Measures

Participants provided two subjective ratings for each solution they sampled using a Labelled Magnitude Scales (LMS) (Green et al. 1993) for Intensity and Labelled Affective Magnitude scale (LAM) (Schutz & Cardello, 2001) for Liking. Scales were presented electronically, programmed in PsychoPy. Participants responded with a mouse click on the scale.

Participants were instructed that, in making their judgements of *'intensity'*, they should rate the stimuli relative to other tastes that they have experienced in everyday life. Thus, *'strongest imaginable'* refers to the most intense sensation of taste that they can ever imagine experiencing. This includes such varied sensations as those produced by a fresh lemon, a piece of celery, or spicy mustard. When rating *liking*, participants were instructed that, in making their judgements, they should rate the stimuli relative to other tastes that they have experienced

in everyday life. For both scales, participants were made aware that they could click anywhere on the scale – and that they were not restricted to the anchor points.

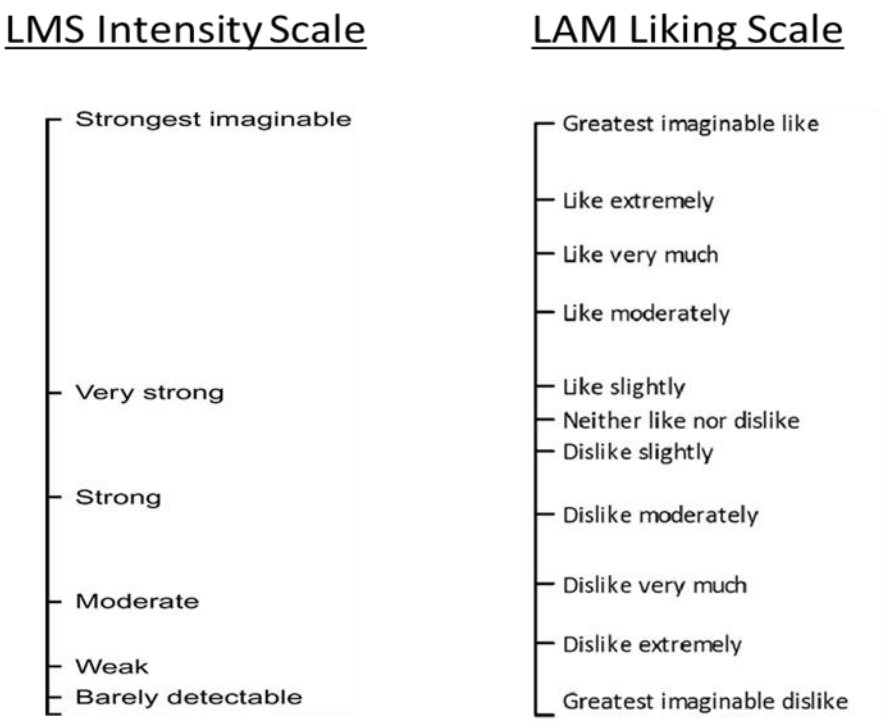

Figure 6.1: *LMS Intensity and LAM Liking scales participants were presented with when instructed to rate each solution.*

6.3.3. Procedure

Upon entering the laboratory, participants were seated in front of a computer screen and provided with verbal instructions on the procedure of the task. All instructions were also presented to participants on a computer screen using PsychoPy software *(v2024 1.1),* this was done in order to reduce direct contact with the researcher and to reduce audience effects.

Participants were first presented with an instructions screen informing them that they would complete 3 blocks, each consisting of 5 trials in a randomised order, and that after tasting each solution, they were required to rate it for Intensity and Liking, prior to rinsing with water. Following the instruction screen, participants were presented with an image of a numbered cup, instructing them to locate the cup and hold it in the ready position, just below the chin, then an 'Empty' screen instructed participants to empty the full contents of the cup into their mouth, without swallowing, whilst simultaneously pressing the space key. This was followed by a five second Swill screen and then a Spit screen, which required participants to spit the solution back

into the cup and dispose of it into a large container which was located to the participant's right-hand side. They were then presented with the '*Intensity'* and '*Liking'* rating scales (Figure 6.1), along with full instructions on how to use the scales. Scales were presented one at a time on separate screens. All participants were able to complete 3 practice trials prior to starting the pilot testing, in order to allow them to familiarise themselves with each of the scales.

6.4 Pilot Results

6.4.1. Caffeine

As can be seen in Table 6.2, there was in general a steady decrease in Intensity ratings with each dilution and, as Intensity decreased Liking increased. Though there was some variability between participants.

Table 6.2: *Mean (+SD) Intensity and Liking ratings for each of the Caffeine concentrations, at both Log and Half-Log steps.*

Set	Dilution Number	mM	Intensity Mean(+SD)	Liking Mean(+SD)
Set A	1	2.176	46.04(+22.73)	-52.81(+19.19)
	2	0.217	10.68(+10.84)	-20.30(+20.26)
	3	0.0217	3.36(+2.59)	-3.33(+4.06)
	4	0.0021	3.84(+5.40)	-6.37(+13.20)
	5	0.0002	2.81(+3.11)	-3.04(+4.42)
Set B	1	2.176	49.08(+23.39)	-60.99(+25.45)
	2	0.435	34.34(+26.03)	-44.94(+29.74)
	3	0.087	11.64(+11.26)	-9.40(+21.06)
	4	0.017	9.21(+9.94)	-9.75(+21.56)
	5	0.003	9.49(+14.67)	-6.28(+23.05)

As can be seen in Figure 6.2, ratings for the strongest solution (2.176 mM) were quite variable for both Set A (15.06-81.85) and Set B (17.90-93.83). An independent samples t-test determined that these ratings were not significantly different from each other ($t(20) = -.31$, $p = .76$). Ratings for the weakest solution in the Set A (0.12-8.52) and Set B (0.49-53.58) dilutions were also not significantly different ($t(20) = -1.41$, $p = .18$).

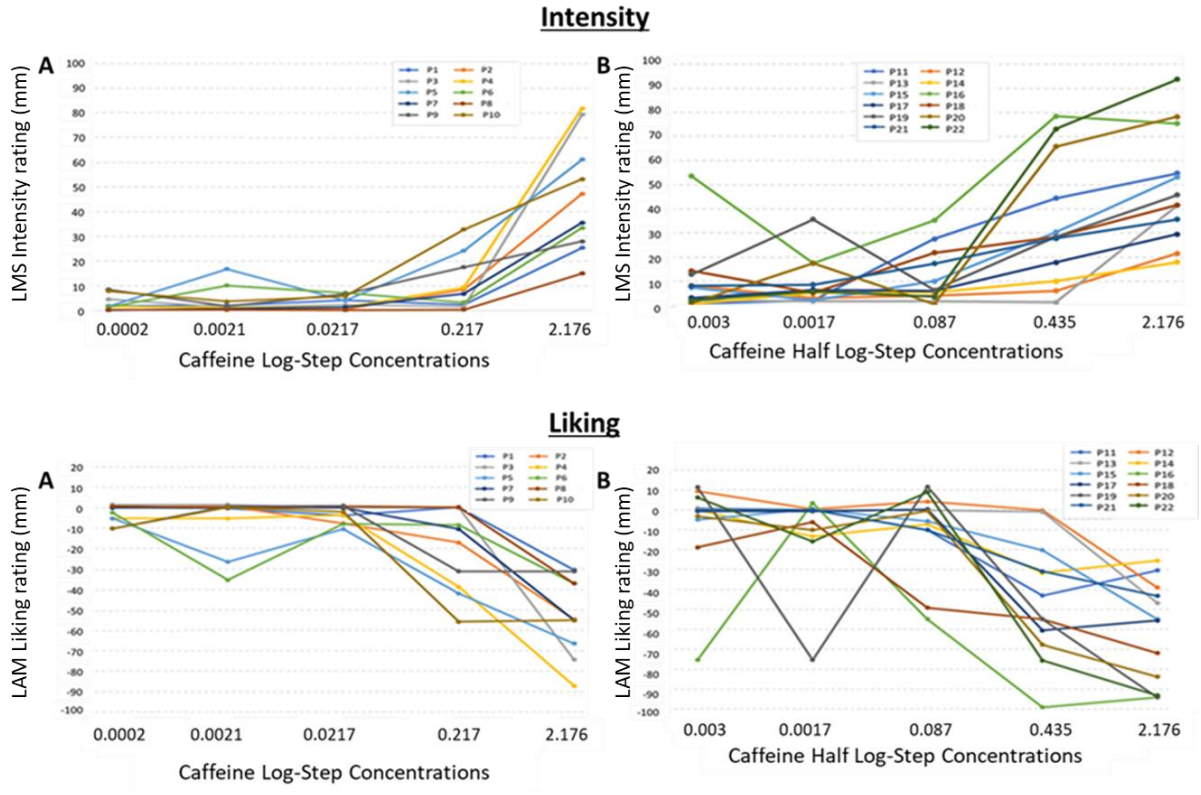

Figure 6.2: *Individual Intensity and Liking ratings for each of the Caffeine solutions during the Pilot testing.* ***Graph A*** *(top-left) depicts the Intensity ratings for the Log-Step concentrations.* ***Graph B*** *(top-right) depicts Intensity ratings for the Half-Log Step concentrations.* ***Graph C*** *(bottom-left) depicts the Liking ratings for the Log-Step concentrations.* ***Graph D*** *(bottom-right) depicts Liking ratings for the Half-Log Step concentrations.*

It was therefore decided that due to the strongest solution (2.176) having a mean overall intensity rating of 47.70 (SD = 22.60), this concentration would be used for the Suprathreshold stimuli in the main testing sessions. As intensity ratings for the weakest dilution in the Set A (0.0002) were much more consistent than Set B, thus, this was used for the Threshold solution in the main testing sessions.

6.4.2. Aluminium Sulphate

As can be seen in Table 6.3, in general, Intensity ratings decreased and Liking ratings increased as the solutions became weaker, though there was some variability between particpants.

Table 6.3: *Mean (+SD) Intensity and Liking ratings for each of the Aluminum Sulphate concentrations, at both Log and Half-Log steps*

Set	Dilution Number	mM	Intensity Mean(+SD)	Liking Mean(+SD)
Set A	1	2.0	43.15(+25.99)	-43.65(+27.78)
	2	0.2	13.80(+11.39)	-7.90(+20.54)
	3	0.02	3.97(+4.12)	-8.15(+32.83)
	4	0.002	3.09(+2.34)	5.18(+11.43)
	5	0.0002	3.16(+3.19)	-0.89(+3.30)
Set B	1	2.0	28.61(+12.64)	-24.88(+33.53)
	2	0.4	17.95(+9.13)	-3.62(+23.01)
	3	0.08	9.22(+7.17)	-11.65(+16.91)
	4	0.016	6.47(+7.38)	1.07(+15.82)
	5	0.0032	2.93(+2.08)	2.57(+11.31)

As can be seen in Figure 6.3, ratings for the strongest solution (2.0) were much more variable for Set A (10.49-84.44), compared to Set B (13.95-59.51), an independent samples t-test determined that these ratings were not significantly different from each other ($t(20) = 1.72$, $p = .10$). Ratings for the weakest solution in Set A (0.25-9.14) and Set B (1.23-6.42) dilutions were also not significantly different ($t(20) = .20$, $p = .84$).

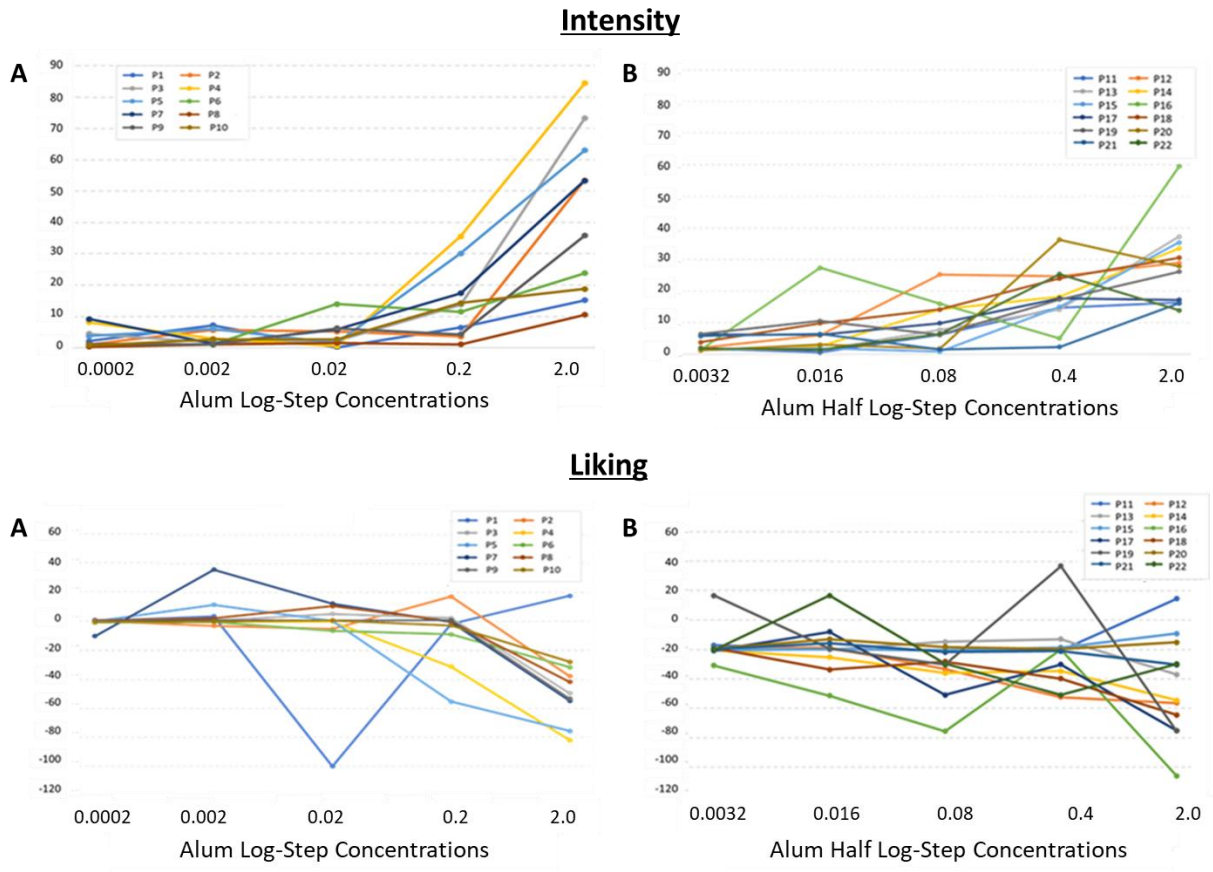

Figure 6.3: *Individual Intensity and Liking ratings for each of the Aluminum Suplhate solutions. Graph A (top-left) depicts the Intensity ratings for the Log-Step concentrations. Graph B (top-right)t depicts Intensity ratings for the Half-Log Step concentrations. Graph C (bottom-left) depicts the Liking ratings for the Log-Step concentrations. Graph D (bottom-right) depicts Liking ratings for the Half-Log Step concentrations.*

The strongest concentration (2.0), with a mean overall intensity rating of 35.12 (SD=20.69), was selected for use as the Suprathreshold stimuli in the main testing sessions. As the weakest concentration (0.0002) in Set A (M=3.16, SD=-0.89) was not considered very intense though was still perceptible, and did not differ significantly from the weakest solution in the Set B (M=2.93, SD=2.57), this was chosen for the Threshold solution in the main testing sessions.

6.4.3. Menthol

As can be seen in Table 6.4, whilst there was a steady decrease in Intensity ratings with each dilution of solution for both Sets, however the liking ratings did not follow the same linear pattern as Aluminum Sulphate or Caffeine.

Table 6.4: *Mean (+SD) Intensity and Liking ratings for each of the Menthol concentrations, at both Log and Half-Log steps*

Set	Dilution Number	mM	Intensity Mean(+SD)	Liking Mean(+SD)
Set A	1	3.126	39.05(+11.95)	4.22(+33.69)
	2	0.312	29.31(+13.95)	-0.89(+29.96)
	3	0.0312	16.85(+12.60)	5.31(+18.10)
	4	0.0031	16.43(+8.39)	0.59(+17.92)
	5	0.0003	10.58(+11.22)	8.64(+15.68)
Set B	1	3.126	59.29(+19.31)	10.534(+43.88)
	2	0.625	45.69(+24.07)	-15.97(+35.97)
	3	0.125	46.76(+18.69)	-26.48(+34.23)
	4	0.025	46.31(+21.04)	-21.21(+38.08)
	5	0.005	24.92(+14.69)	9.73(+22.31)

As can be seen in Figure 6.4, intensity ratings for the strongest solution (3.126mM) were quite variable for both Set A (17.41-55.68), and Set B (24.69-98.89). An independent samples t-test determined that mean ratings were significantly different between Set A and Set B ($t(20) = -2.88$, $p < .01$). Ratings for the weakest solution (concn) in the Set A (0.12-8.52) and Set B (0.49-53.58) dilutions were also significantly different ($t(20) = -2.53$, $p < .05$).

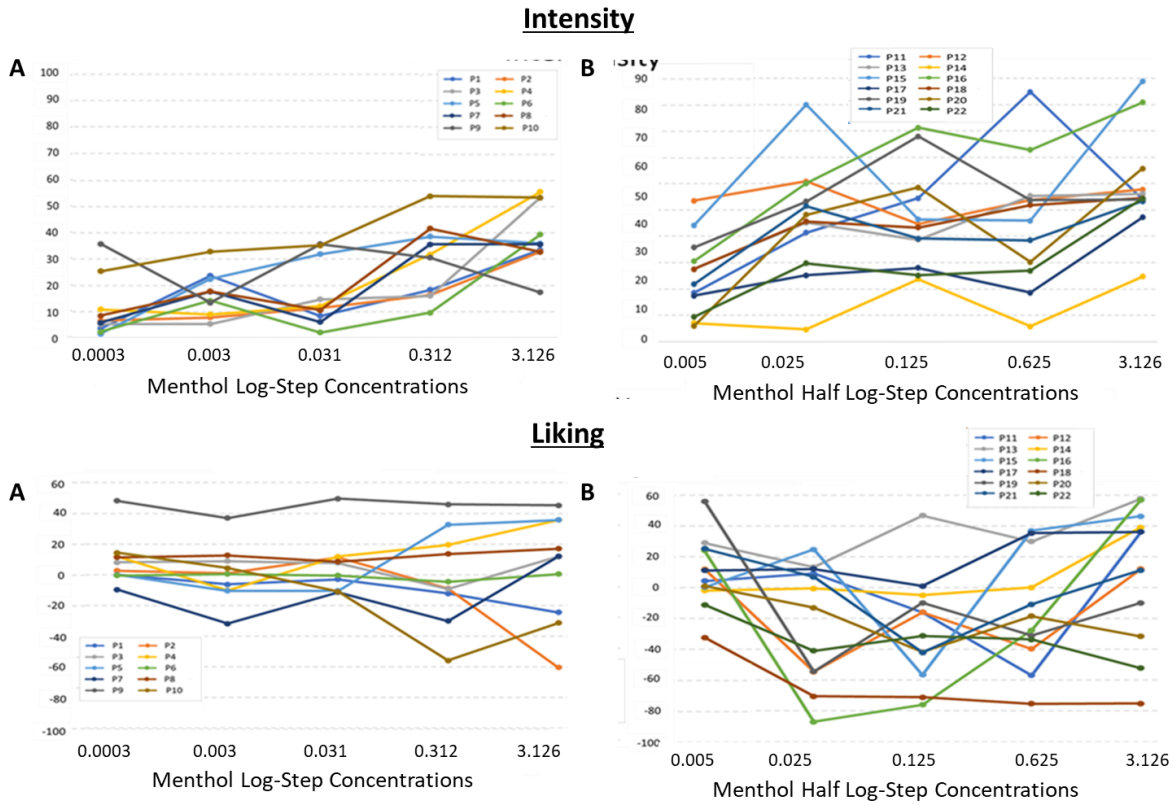

Figure 6.4: *Individual Intensity and Liking ratings for each of the Menthol solutions. Graph A (top-left) depicts the Intensity ratings for the Log-Step concentrations. Graph B (top-right) depicts Intensity ratings for the Half-Log Step concentrations. Graph C (bottom-left) depicts the Liking ratings for the Log-Step concentrations. Graph D (bottom-right) depicts Liking ratings for the Half-Log Step concentrations.*

Due to the inconsistency in Intensity and Liking ratings across both Sets, further pilot testing was conducted in which ten further concentrations were presented to ten different participtants.

6.3.4. Menthol (Set C)

The third set of Menthol solutions (Set C) started with a concentration of 3.126mM and were diluted in 200ml of distilled water using logarithmic-steps. As shown in Table 6.5, Intensity ratings were now less variable for a given concentration

Table 6.5: *Mean (+SD) Intensity and Liking ratings for each of the Menthol concentrations.*

Dilution Number	**mM**	**Intensity Mean(+SD)**	**Liking Mean(+SD)**
1	3.126	47.93(+19.83)	0.02 (+44.95)
2	0.312	35.46(+16.23)	-10.30(+34.57)
3	0.0312	10.38(+10.19)	12.45(+32.15)
4	0.003126	10.59(+9.28)	19.58(+34.18)
5	0.0003126	10.14(+8.53)	12.52(+35.75)
6	0.00003126	4.05(+4.63)	10.37(+31.90)
7	0.000003126	12.47(+13.57)	9.46(+35.52)
8	0.0000003126	10.00(+7.99)	14.00(+30.89)
9	0.00000003126	4.57(+5.09)	-0.69(+47.02)
10	0.000000003126	5.56(+8.94)	10.84(+28.83)

As can be seen in Figure 6.5, Intensity ratings for both the strongest (19.14-73.70) and weakest (0.00 – 30.25) solutions were quite variable. Due to Intensity ratings for the highest concentration (3.126) being rated similarly to Set A and Set B, this dilution was chosen for the Supra-Threshold solution to be used in the main testing sessions. Whilst the ratings for the weakest concentration in the current set (0.000000003126) had a Mean of 10.84, as shown in Figure 4, this was largely due to the rating of 30.25 from participant 9, ratings from all other participants were below 6.55. As such, this concentration was chosen for the Threshold level stimuli in the main testing session.

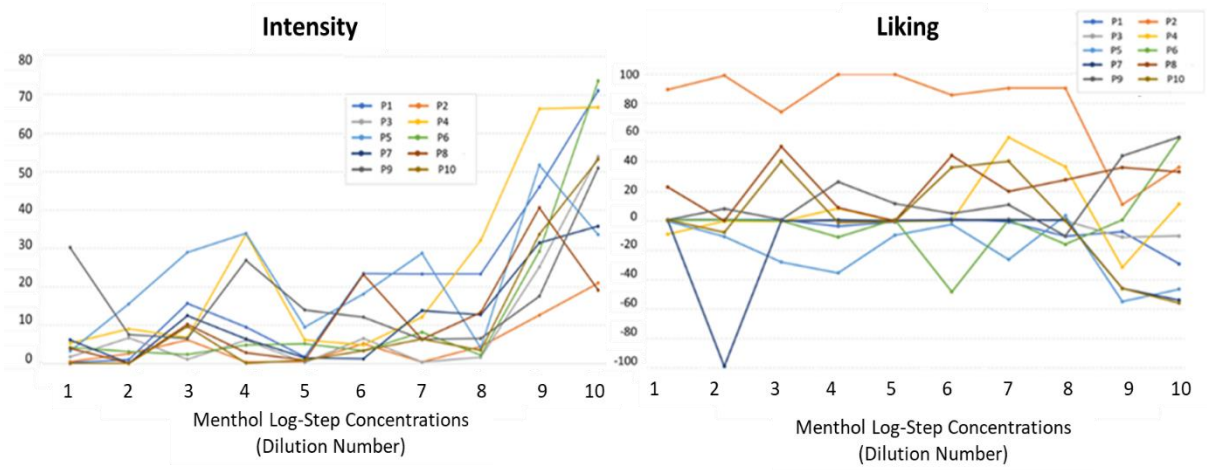

Figure 6.5: *Individual Intensity and Liking ratings for each of the Menthol solutions. Graph A (left) depicts the Intensity ratings and Graph B (right) depicts Liking ratings.*

6.5. Taster Status Screening

6.5.1. Participants

One hundred and four females aged 18-45 (M=27.21, SD=7.53) were recruited for screening via the LJMU Psychology Research Participant Panel, a list of potential participants who have agreed to be contacted for upcoming research. Additionally, recruitment emails were circulated to LJMU staff and students, and posters were placed around campus, as well as advertisements on social media sites such as Facebook and Twitter.

Inclusion criteria required participants to be female, aged 18 to 50 years old and a non-smoker. In addition, due for need to use a small amount in one of the test solutions, participants had to be able to consume alcohol. Participants were excluded if they had been diagnosed with any neurological disorder that may affect the perception of oral sensations or touch, suffer from any food allergies and/or intolerances, had any impairment to the sense of taste or smell, or were currently suffering from a cold or respiratory infection. In addition, participants could not have undergone any form of nasal surgery or any invasive heart surgery. They were excluded if they suffered from any cardiovascular disease or had a diagnosis of Heart Arrhythmia (irregular heartbeat). Participants recruited for the taster status screening session received a £5 shopping voucher.

6.5.2. Stimuli Preparation

Following a detailed methodology (Zhao et al. 2003) outlined in Chapter 2.4, a 50mmol/l of 6-n-Propylthiouracil (PROP) solution were prepared by dissolving the PROP powder (170.23g/mol) in rapidly boiling water on a stirring hotplate until the solution was clear. Filter paper disks (15mm in diameter, Whatman, Qualitative filter paper Grade 1, Sigma) were strung onto cotton threads with a sterilised sewing needle. Plastic drinking straw segments (~0.5cm) were used as spacers to separate papers for impregnation. The disks and separators were soaked in the PROP solution for 30 seconds and then removed, excess solution lightly shaken off, and placed on an aluminium foil covered tray and oven-dried for 1h at 121^{o}C. Additionally, filter papers soaked in a 1M (58.44g/L) solution of sodium chloride (NaCl; salt) for 30 sec were prepared using the same method. Once dry, filter papers were removed from the thread and stored individually in sealed Glassine Envelopes (Lindner, 45x60mm, Germany) in a cool dry cupboard until use.

6.5.3. Procedure

Prior to attending the laboratory, participants were asked not to eat or drink anything, apart from water, for at least 3hrs before testing. Upon entering the laboratory, participants were asked to place all personal belongings, including their mobile phone, to one side – this was to ensure there were no distractions throughout the task. They were then provided a paper version of the participant information sheet and instructed to read it carefully. Once the participant was happy with the instructions, they were asked to sign a consent form.

To assess taster status, participants were asked to unwrap the NaCl impregnated filter paper and place it close to the tip of the tongue while ensuring the whole filter paper is on the tongue. They were instructed to soak the paper in saliva and leave it on their tongue for a timed period of 10 seconds. After 10 seconds they were asked to remove the paper and swallow any saliva while waiting a further 10 seconds before rating the intensity of the perceived taste on the same LMS scale as used during Pilot Testing (Cannon et al. 2017; Green et al. 1993), however, for screening, participants were provided a printed copy of the scale. After rinsing until any taste from the NaCl had disappeared, the same procedure was then used for the PROP impregnated filter paper.

Ratings of the bitter PROP paper were compared against previously published LMS taster status cut offs *(Table 6.6)*, measured in millimetres from the base of the scale; range 0–165 (Green et al. 1993).

Table 6.6: *Cut off values for each taster category, on an LMS scale ranging 0-165. Super-Tasters (rating > 100); Medium-Tasters (ratings 20–100); and Non-Tasters (ratings < 20).*

Taster Status	***Range(mm)***
Non-Taster	< 20
Medium-Taster	20-100
Super-Taster	> 100

NaCl scores were only used for participants whose PROP intensity rating fell on the cut-off between the taster groups to establish which side of the taster division they belong (Dastan et al. 2015). In such cases, if the NaCl ratings were higher than the PROP ratings, the individual was classified as a Non-Taster. If the PROP ratings were higher than the NaCl ratings, the individual was classified as a supertaster. If the ratings of the two compounds were similar, the individual was classified as a medium taster. As shown in Figure 6.6, those classified as either Non-Tasters or Super-Tasters, were invited to take part in Phase 2 of the study. Those who were classified as Medium-Tasters were not recruited for the psychophysiological stage of testing.

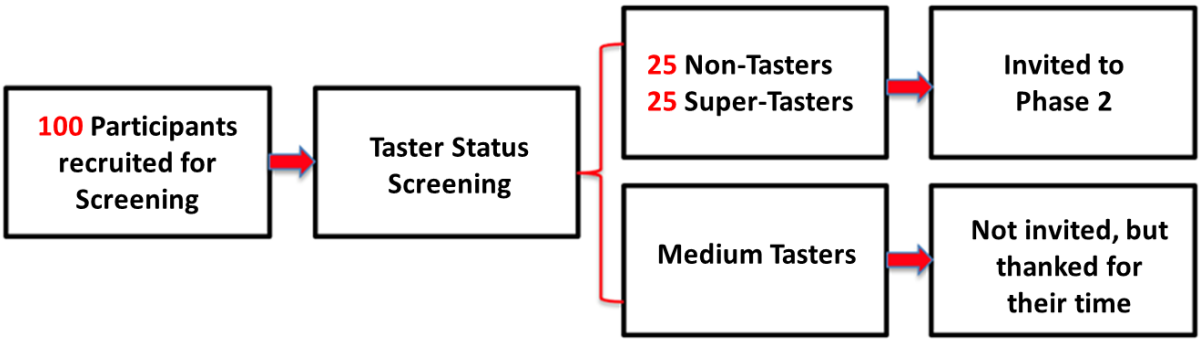

Figure 6.6: *Flowchart showing recruitment process from Phase 1 (screening session) through to the Phase 2 (the psychophysiological session)*

6.5.4. Screening Results

The number of participants within each of the three taster groups, as well as the mean sensation ratings of both PROP and NaCl are shown in Table 6.7.

Table 6.7: *Mean age and Intensity ratings of both PROP and NaCl for Super-Tasters, Medium-Tasters and Non-Tasters.*

	Non-Tasters Mean (+SD)	**Medium-Tasters** Mean (+SD)	**Super-Tasters** Mean (+SD)
N	25	52	27
Age	25.80 (+7.13)	26.73 (+7.28)	28.52 (+7.79)
PROP	7.44 (+5.65)	49.65 (+19.38)	133.33 (+17.46)
NaCl	24.56 (+21.35)	20.06 (14.13)	30.19 (+25.12)

A One-way ANOVA revealed a significant effect of Taster Status ($F(2, 101) = 398.36$, $p<.001$, $\eta p2 = .89$). Super-Tasters rated the sensation of PROP as significantly more intense than both Medium-Tasters ($p<.001$) and Non-Tasters ($p<.001$). Medium-Tasters also rated the sensation of PROP as significantly more intense than Non-Tasters ($p<.001$). There was no difference in the mean rating of NaCl ($F(2, 101) = 2.48$, $p=.09$, $\eta p2 = .05$) across the three groups ($ps>.05$). Consistent with previously reported findings that the general population contains 50% Medium Tasters, 25% Super-Tasters and 25% Non-Tasters (Bartoshuk et al. 1994), the current sample of 104 participants contained 50.00% Medium-Tasters, 24.03% Non-Tasters and 25.96% Super-Tasters.

As the current study was focused on differences between Super-Tasters and Non-Tasters, only those in the Non-Taster (n=25) and Super-Taster (n=27) groups were invited to complete the second Phase of the study.

6.6. Main Methods

6.6.1. Participants

Based on the taster groups identified during the screening phase, a total of 52 participants, consisting of 25 non-tasters aged 18-44 years (M=25.80, SD-7.13) and 27 super-tasters aged

18-45 years (M=28.52, SD=7.79) were invited to take part in the main testing session. Participants recruited for the main psychophysiological task, received a £10 shopping voucher.

6.6.1. Psychophysiological Measures

6.6.1.1. EMG

Data were collected from the Zygomaticus major and Corrugator Supercilii muscles. Following the recommendations of Fridlund & Cacioppo (1986), prior to the attachment of the 4mm surface Ag-AgCl electrodes, the skin surface was cleansed with an individually wrapped Fastaid Pre-Injection Swab (70% Isopropanol) and then lightly abraded with a small scouring pad in order to lower inter-electrode impedance (Fridlund & Cacioppo, 1986). Electrodes were attached over the muscle sites with adhesive discs, and an unshielded ground electrode placed just below the hairline in the centre of the participant's forehead. A small globule of conductive gel (SignaGel, Parker Laboratories, inc.) was then placed in each of the cleansed locations to ensure close adherence of the electrodes to the skin. Offline, the data were passed through a 20-400Hz bandpass filter and rectified (Van Boxtel, 2010).

To ensure electrodes had been placed in the correct locations, participants were asked to smile and frown to activate the ZM and CS respectively. However, to avoid any influence of demand characteristics on task performance, participants were not asked to do this until they had completed the task. Upon placement of the electrodes, a cover story was used, in which participants were informed that the electrodes were measuring activity in their frontal lobe (Pawling et al. 2017). The aim of this deception was to ensure that any recorded EMG activity was a direct implicit response to the oral stimuli, as opposed to explicit responses due to demand characteristics. In fEMG research, it is common to use a cover story in order to lead the participants' attention away from facial expressions and emotions. This ensures that their responses are unconsciously influenced by the stimuli and also aids in avoiding demand characteristics, such that, participants who are aware that their facial reactions are being measured, are more likely to exhibit exaggerated facial responses (Sato et al. 2021; Soderkvist et al. 2018; Manssuer et al. 2015).

6.6.1.2. Heart Rate

Self-adhesive, pre-gelled disposable ECG electrodes were placed on the skin just above the participant's left hip and just below their right clavicle, with a ground electrode placed below the left clavicle. The sites were cleaned with water prior to attachment. Offline the data were bandpass filtered between 0.1Hz and 30Hz and an R peak finder in the AD Instruments LabChart software used to convert the ECG trace into a heartrate trace. The performance of the R peak finder was inspected by eye for instances of missing peaks or displacements of the waveform incorrectly labelled as peaks. These were corrected manually where possible, before the calculation of the heartrate trace. Where noise or other problems with the ECG trace made it impossible to correctly locate R peaks within the analysed portion of a trial, this trial was removed from analysis. In instances where multiple trials were removed for a single participant, resulting in a missing cell, the participant was removed from the analysis.

6.6.2. Subjective Measures

Participants provided two subjective ratings for each solution they sampled *(as shown in blue in Fig 1).* On one they rated the '*intensity'* of each solution using an LMS scale, and on the other they rated the '*liking'* of each solution using a LAM scale. These scales were in line with the LMS and LAM scales used during the pilot testing (6.3.2) (Cannon et al. 2017; Green et al. 1993). Participants responded with a mouse click on the scale.

6.6.3. Oral Stimuli

Based on the findings of the Pilot Testing, the Supra-Threshold and threshold concentrations to be used during the main testing session are shown in Table 6.8. All solutions were prepared using the same methodologies described in 6.3.1.

Table 6.8: *Threshold and Supra-Threshold dilutions, for each of the stimuli (Caffeine, Aluminium Sulphate, Menthol) chosen for use in the main testing session.*

	Caffeine (mM)	**Alum (mM)**	**Menthol (mM)**
Supra-Threshold	2.176	2.000	3.126
Threshold	0.0002	0.0002	0.000000003126

6.6.4. Ratings Task

In line with the methodologies of Cannon & Grigor (2007), the main task consisted of two blocks, a tasting only block (Block 1) and a tasting/rating block (Block 2), both of which were presented on a computer running PsychoPy psychology software (*see Figure 6.7 for flow diagram*). Participants provided two subjective ratings for each solution using the same methodologies described in 6.3.2.

In the tasting only block, each trial started with a screen displaying a fixation cross, which instructed participants to press the space bar in order to start the trial. The following screen instructed participants to locate a numbered cup *(example shown in Figure 6.7).* Order of presentation was randomly assigned within blocks. Participants were instructed to pick up and hold the sample cup in the 'ready position', whilst preparing to empty the liquid into their mouth. This started a 5 second timer, during which the participant had the cup held level with their mouth and no more than 30cm away from their lips, in preparation for the emptying phase. The emptying phase screen then instructed the participant to empty the solution into their mouth and to simultaneously click a mouse button. Immediately following the mouse click, the swirling phase screen instructed participants to swirl the liquid in their mouth for 5 seconds. Participants were then instructed to spit out the solution and simultaneously click the mouse button. After spitting, the 'think screen' instructed participants to think about the taste of the liquid for 10 seconds. Participants then rinsed their mouth with water (*until any aftertaste has disappeared*) and were then required to take a 5 second break before commencing to the next trial. The 'tasting and rating' block was identical to the 'tasting' only block, however, after participants had been presented with the thinking screen, they were then presented with the '*intensity'* and '*liking'* rating scales, one at a time on separate screens, before rinsing the mouth (*shown in blue in Fig 6.7*).

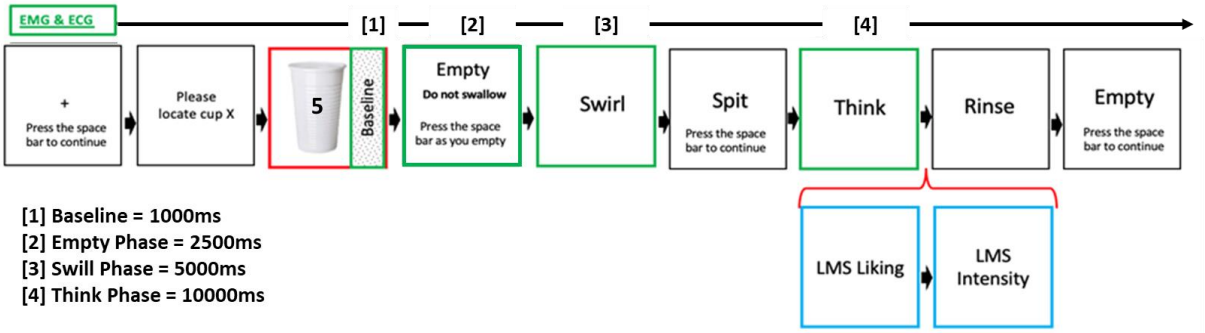

Figure 6.7: *Flow diagram showing order to procedure for both the Tasting and the Tasting/Rating blocks. During the Tasting Block, facial EMG and HR activity were recorded for the Baseline (1000ms), Empty (2500ms), Swill (5000ms) and Think (10000ms) Phases (as shown in green boxes). During the Tasting and Rating block, facial EMG and HR activity were recorded at the same phases as the Tasting block, with LMS and LAM ratings also being completed following the Think Phase, but before the Rinse Phase (as shown in blue boxes).*

During both the tasting and tasting/rating blocks, two concentrations *(threshold and suprathreshold)* of each test solution was presented twice in a randomised order, as well as one water control. To familiarise participants with the procedure, prior to starting each block, they completed three practice trials with samples of water. As shown in Table 6.9, participants completed 3 trials during each practice block, 15 trials during the 'tasting' block and 15 trials during the 'tasting and rating' block.

Table 6.9: *Total number of trials for the practice blocks (2x3) the tasting block (15) and the tasting/rating blocks (15).*

		Super-Threshold	**Threshold**	**Water**	**Block Total**
Practice				3	**3**
Tasting	Alum	2	2	1	**15**
	Caffeine	2	2	1	
	Menthol	2	2	1	
Practice				3	**3**
Tasting & Rating	Alum	2	2	1	**15**
	Caffeine	2	2	1	
	Menthol	2	2	1	

It was initially anticipated that participants would be presented with the stimuli in a randomised order, with six different orders being embedded into the task set-up. This was to account for any carry-over effects of each solution, However, a technical fault with the software resulted in Order A being the most frequent presentation (73% participants), with detail of each order shown in Table 6.10. As a result, order of presentation was not used in any of the analysis. This bug did not affect the randomisation of presentation of solution concentrations for any of the stimuli.

Table 6.10: *Six different orders of presentation that were embedded into the PsychoPy Task, with the total number of participants who received each order.*

Presentation	**Order**			**Total**
A	Alum	Caffeine	Menthol	38
B	Menthol	Alum	Caffeine	2
C	Caffeine	Menthol	Alum	1
D	Caffeine	Alum	Menthol	1
E	Alum	Menthol	Caffeine	1
F	Menthol	Caffeine	Alum	10

6.6.5. Procedure

Prior to attending the laboratories, participants were asked not to eat or drink anything, apart from water, for at least 3hrs before testing. Upon entering the laboratory, participants were asked to place all personal belongings, including their mobile phone, to one side – this was to ensure there were no distractions throughout the task. Once seated in front of the monitor running the task, the researcher attached the EMG and ECG electrodes, using the procedure described in 6.6.1.1 and ensured the participant was seated comfortably.

To familiarise participants with the procedure, prior to starting each block, they completed three practice trials with samples of water. Once attachment of electrodes was confirmed, the participant proceeded with the task. During the three practice trials, the researcher was present in order to ensure the participant did not face any difficulties. After completing the practice trials, the researcher stood behind a screen, out of sight of the participant. Once the participant had completed Block one, the researcher returned and observed completion of the practice trials for Block two, before returning behind the screen.

Upon completion of the task, all electrodes were removed, and the participant was fully debriefed and provided the opportunity to ask any questions.

6.7. Data Analysis Plan

On a participant-by-participant basis, custom macros applied in LabChart were used to extract the mean level of EMG activity and mean heartrate for the Baseline, Empty, Swill and Think periods of each trial. These data were exported to SPSS for artefact rejection and data analysis. Subjective ratings were collected using PsychoPy, via a custom script that identifies the location of mouse click responses on the LMS and outputs them as a numerical value between 0 and 100 for Intensity and between -100 and 100 Liking. These data were exported to SPSS for analysis.

All data were analysed using SPSS (IBM version 29**).** Shapiro-Wilk tests were used to determine whether data were normally distributed. Levene's test examined homogeneity of variances across conditions and Mauchly's tests of sphericity were inspected and where appropriate, Greenhouse Geisser corrections to degrees of freedom were applied. To address the risk of an inflated Type I error, Bonferroni correction for multiple comparisons was applied.

6.7.1.EMG data

The EMG data for both muscle sites were processed with custom scripts in LabChart. A pre-trial baseline level of muscle activity was calculated for every trial, so that muscle activity elicited by the taste stimuli could be expressed as a change from baseline. Baselines were achieved by calculating, on a trial-by-trial basis, the mean level of muscle activity during the 1000ms prior to the emptying phase (when the participant sat, awaiting instructions for the next trial). Any baseline trials containing muscle activity scores that exceeded three standard deviations from the mean of that participant's baseline scores were removed. For trials where an artefactual baseline period was removed, the baseline was represented by the grand mean of that participant's activity across all rest periods that did not contain artefacts. For each trial, the 2500ms Emptying phase, 5000ms Swill phase and 10,000ms Think phase were then expressed as a change score from that trial's baseline, in which baseline activity was subtracted from each phase activity for the related trial, so that positive values represent an increase in muscle activity and negative values represent a decrease. Any trials containing changes in muscle

activity that exceeded three standard deviations from the mean change in activity from the sample population were removed. This resulted in the removal of an average of 15% (6% Alum, 4.5% Caffeine, 4% Menthol) of trials for zygomaticus data, and 17.5% (5% Alum, 5.5% Caffeine, 7% Menthol) for corrugator data across all participants. Furthermore, complete corrugator data for one participant was excluded due to data acquisition errors, resulting in inadequate signal clarity in LabChart.

EMG data for each of the Taste Stimuli *(Alum, Menthol, Caffeine)* at two muscle sites (*Zygomaticus, Corrugator)* were analysed separately. Each analysis was a 2 *(Taster-Status: Non-Tasters, Super-Tasters)* x 3 *(Phase: Empty, Swill, Think)* x 2 *(Block: Tasting, Tasting & Rating)* x 2 *(Concentration: Threshold, Suprathreshold)* Repeated Measures Analysis of Variance. Any significant interactions identified were followed up using Bonferroni corrected t-tests or simple main effects analysis.

6.7.2. Heart rate data

A baseline level of heart rate was calculated for every trial, so that variation elicited by the taste stimuli could be expressed as a change from baseline. Baselines were achieved by calculating on a trial-by-trial basis, the mean of the two Inter-Beat Intervals (IBIs) immediately prior to the Emptying phase. Any baseline trials containing heart rate scores that exceeded three standard deviations from the mean of all that participant's baseline scores were removed. Removed baseline periods were represented by the grand mean of that participant's activity across all rest periods that did not contain artefacts. For each trial, the 2500ms Emptying phase, 5000ms Swill phase and 10,000ms Think phase were then expressed as a change score from that trial's baseline, in which baseline activity was subtracted from each phase for the related trial, meaning that a negative value represents heart rate acceleration, and a positive value represents heart rate deceleration. Any trials containing change scores that exceeded three standard deviations from the mean of all scores, across the sample population, were removed. This resulted in the removal of an average of 12.5% of trails (2.5% Alum, 6% Caffeine, 4% Menthol) across all participants. In addition, complete heart rate data was removed for three participants, due to a poor-quality ECG.

Responses were analysed for each of the Taste Stimuli *(Alum, Menthol, Caffeine)* separately. Each analysis was a 2 *(Taster-Status: Non-Tasters, Super-Tasters) x 2 (Block: Block 1 = Tasting, Block 2 = Tasting & Rating) x 2 (Phase: Empty, Swill, Think) x 2 (Concentration: Threshold, Suprathreshold)* Repeated Measures Analysis of Variance. Any significant interactions identified were followed up using Bonferroni corrected t-tests or simple main effects analysis.

6.7.3. Subjective ratings

The LMS ratings were downloaded to Excel (v2308) in order to identify any missing values or outliers. Data was then transferred to SPSS for analysis. Ratings of each of the Taste Solutions *(Caffeine, Alum, Menthol)* on two rating scales *(Intensity, Liking)* were analysed using an ANOVA, with Taster Status *(Non-Tasters, Super-Tasters)* as the between participant factor, and Concentration *(Threshold, Suprathreshold)* as the within participant factor.

For Intensity, ratings were made using a 0-100mm scale with the following anchor-points: *No sensation = 0.0, Barely Detectable = 1.4, Weak = 6.1, Moderate = 17.2, Strong = 35.4, Very Strong = 53.3, Strongest Imaginable = 100.0*. Ratings were then transformed in SPSS to a 0-165mm scale by multiplying the raw ratings by 1.65. Location of anchor points were also recalculated using the same calculation *(No sensation = 0.0, Barely Detectable = 2.3, Weak = 10.1, Moderate = 28.4, Strong = 58.4, Very Strong = 88.0, Strongest Imaginable = 165.0.*

For Liking, ratings were made on PsychoPy using a 200mm (-100mm-100mm) scale with the following anchor-points: *Greatest Imaginable Dislike = -100.0 , Dislike Extremely = -75.1, Dislike Very Much = -55.5, Dislike Moderately = -31.9, Dislike Slightly = -10.6, Neither-Like-nor-Dislike = 0 0, Like Slightly = 11.2, Like Moderately = 36.2, Like Very Much = 56.1, Like Extremely = 74.2, Greatest Imaginable Like = 100.0.*

6.8. Results

6.8.1. Subjective Ratings

Mixed ANOVAs were conducted separately for subjective ratings of Intensity and Liking of each of the stimuli., Each ANOVA included the Concentration (Supra-Threshold, Threshold) as the within participant factor, and Taster Status (Super-Tasters, Non-Tasters) as the between participant factor.

6.8.1.1. Intensity

Table 6.11 shows the Mean Intensity ratings for each of the Stimuli, at both Supra-Threshold and Threshold Concentrations, with higher ratings indicating greater perceived Intensity.

***Table 6.11**: Mean (+SD) Non-Taster and Super-Taster Intensity ratings for Caffeine, Alum, and Menthol at both Supra-Threshold (ST) and Threshold (T) levels.*

	Concentration	Non-Tasters	Super-Tasters
Caffeine	ST	64.16 (45.28)	100.69 (54.72)
	T	19.83 (27.58)	37.34 (43.39)
Alum	ST	68.75 (46.64)	97.64 (52.48)
	T	21.37 (38.00)	29.21 (36.24)
Menthol	ST	56.91 (40.31)	96.68 (32.40)
	T	32.02 (28.54)	40.52 (30.66)

For Caffeine, there was a significant main effect of Taster Status ($F (1, 50) = 19.16$, $p<.001$, $\eta p2 = .28$), with Super-Tasters rating Caffeine as higher in Intensity than Non-Tasters. There was also a significant main effect of Concentration ($F (1, 50) = 25.99$, $p<.001$, $\eta p2 = .34$), in that Supra-Threshold levels were rated higher in Intensity than Threshold levels. There was no interaction between Taster-Status and Concentration ($F (1, 50) = .81$, $p=.37$, $\eta p2 = .02$).

For Alum, there was a significant main effect of Taster Status ($F (1, 50) = 7.71$, $p<.01$, $\eta p2 = .13$), with Super-Tasters rating Alum as higher in Intensity than Non-Tasters. There was also a significant main effect of Concentration ($F (1, 50) = 32.05$, $p<.001$, $\eta p2 = .39$), in that

Supra-Threshold levels were rated higher in Intensity than Threshold levels. There was no interaction between Taster-Status and Concentration (F (1, 50) = 1.06, p=.31, $\eta p2$ = .02).

For Menthol, there was a significant main effect of Taster Status (F (1, 50) = 6.37, p<.05, $\eta p2$ = .11), with Super-Tasters rating Alum as higher in Intensity than Non-Tasters. There was also a significant main effect of Concentration (F (1, 50) = 52.19, p<.001, $\eta p2$ = .51), in that Supra-Threshold levels were rated higher in Intensity than Threshold levels. There was no interaction between Taster-Status and Concentration (F (1, 50) = 1.17, p=.28, $\eta p2$ = .02).

As shown in Figure 6.8, for all three stimuli, the Super-tasters' ratings were significantly higher than the Non-Tasters.

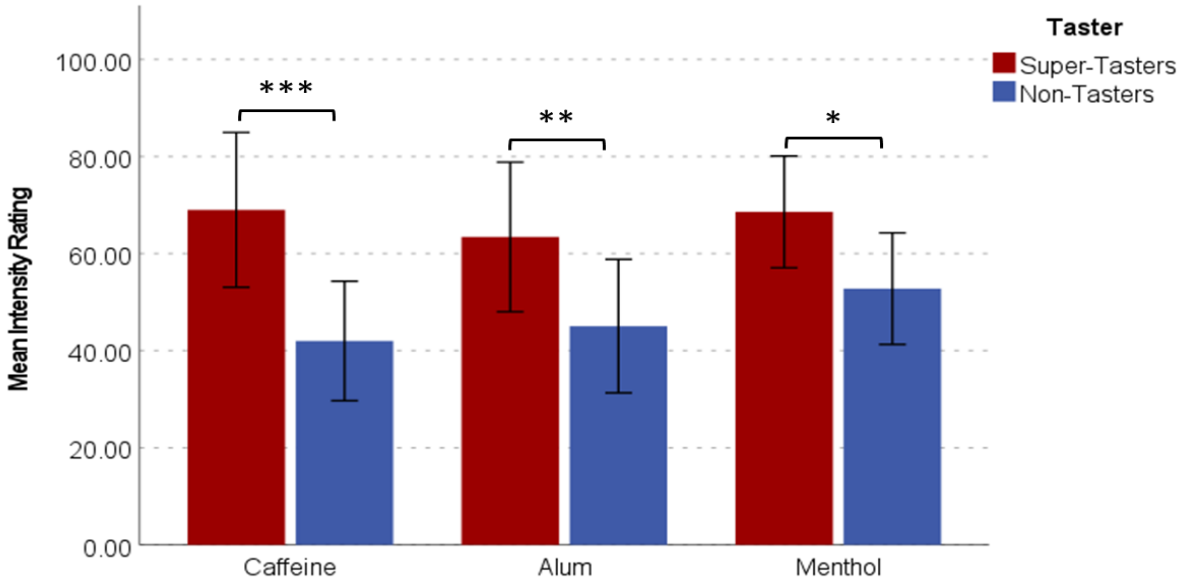

Figure 6.8: *Mean Super-Taster and Non-Taster Intensity ratings for Caffeine, Alum, and Menthol, using an LMS scale of 0-165 (* denotes sig<.05, ** denotes sig<.01, *** denotes sig<.001). Error bars display 95% CI.*

To determine whether the selected concentrations of the three test stimuli were perceptually iso-intense, two additional ANOVAs were conducted to compare each group's ratings of the at threshold and supra-threshold concentrations.

For Threshold Concentrations, there was no significant effect of Taster Status (F (1, 50) = 1.98, p=.17, $\eta p2$ = .04). Nor was there significant effect of Stimulus (F (2, 100) = 3.02, p=.053, $\eta p2$ = .06), confirming that all Threshold concentrations of the three test stimuli were perceptually iso-intense. The interaction between Taster-Status and Concentration was not significant (F (2, 100) = .70, p=.50, $\eta p2$ = .01).

For Supra-Threshold Concentrations, there was a significant effect of Taster Status (F (1, 50) = 6.93, $p<.05$, $\eta p2$ = .12), with Super-Tasters rating the stimuli as more intense than Non-Tasters. The effect of Stimulus was not significant (F (2, 100) = .14, $p=.87$, $\eta p2$ = .00), confirming that Supra-Threshold concentrations of the three test stimuli were perceptually iso-intense. The interaction between Taster-Status and Concentration was not significant (F (2, 100) = .81, $p=.45$, $\eta p2$ = .02).

6.8.1.2. Liking

Table 6.12 shows the Mean Liking ratings for each of the Oral Stimuli, at both Supra-Threshold and Threshold Concentrations.

Table 6.12: *Mean (+SD) Non-Taster and Super-Taster Liking ratings for Caffeine, Alum, and Menthol at both Supra-Threshold (ST) and Threshold (T) levels.*

	Concentration	**Non-Tasters**	**Super-Tasters**
Caffeine	ST	-47.45 (+30.72)	-60.73 (+34.54)
	T	-6.29 (+25.08)	-17.04 (+35.95)
Alum	ST	-38.98 (+ 33.36)	-48.61 (+40.96)
	T	-4.36 (+33.55)	-3.59 (+27.29)
Menthol	ST	-3.61 (+31.95)	-8.80 (+35.16)
	T	8.30 (+29.31)	5.17 (+27.23)

For Caffeine, there was a significant main effect of Taster Status (F (1, 50) = 7.69, $p<.01$, $\eta p2$ = .13), with Super-Tasters rating Caffeine as lower in Liking than Non-Tasters. There was also a significant main effect of Concentration (F (1, 50) = 29.95, $p<.001$, $\eta p2$ = .38), in that Supra-Threshold levels were rated lower in Liking than Threshold levels. There was no interaction between Taster-Status and Concentration (F (1, 50) = .03, $p=.87$, $\eta p2$ = .00).

For Alum, there was no main effect of Taster Status (F (1, 50) = .54, $p=.46$, $\eta p2$ = .01), with no difference in Liking ratings between Super-Tasters and Non-Tasters. There was a significant main effect of Concentration (F (1, 50) = 29.47, $p<.001$, $\eta p2$ = .37), in that Supra-Threshold levels were rated lower in Liking than Threshold levels. There was no interaction between Taster-Status and Concentration (F (1, 50) = 1.06, $p=.31$, $\eta p2$ = .02).

For Menthol, there was no main effect of Taster Status (F (1, 50) = .33, p=.57, $\eta p2$ = .01), with no difference in Liking ratings between Super-Tasters and Non-Tasters. There was a significant main effect of Concentration (F (1, 50) = 7.73, p<.01, $\eta p2$ = .13), in that Supra-Threshold levels were rated lower in Liking than Threshold levels. There was no interaction between Taster-Status and Concentration (F (1, 50) = .05, p=.83, $\eta p2$ = .00).

As shown in Figure 6.9, whilst Liking rating differed significantly between Super-Tasters and Non-Tasters in response to Caffeine, liking ratings of Alum and Menthol did not differ according to Taster Status.

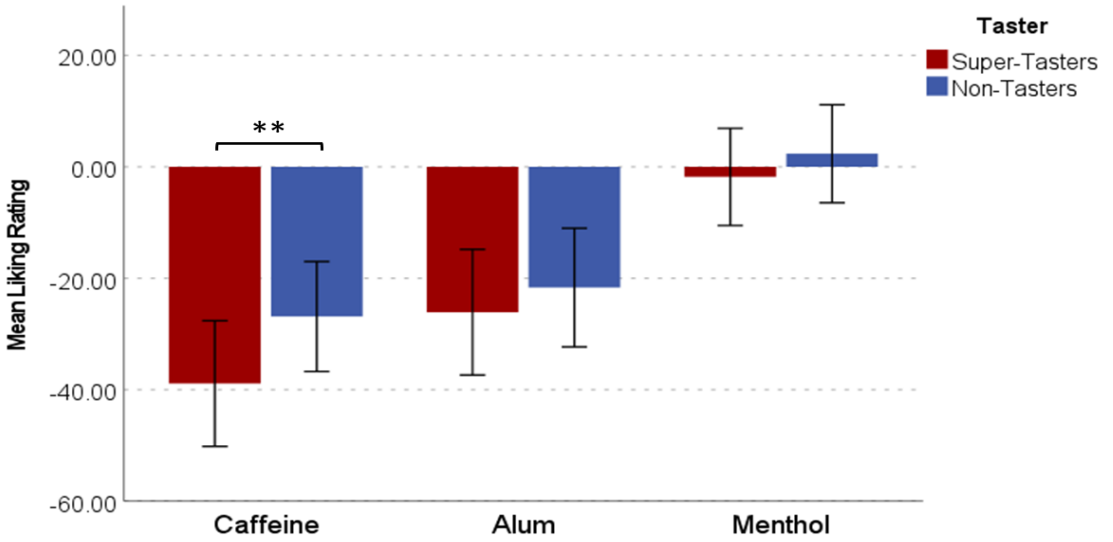

Figure 6.9: *Mean Intensity ratings for both Supra-Threshold and Threshold Solution, during each Phase. (** denotes sig<.01). Error bars display 95% CI.*

The liking ratings were further analysed for each group to determine if they differed significantly from a neutral rating (zero on the LMS scale). Single sample t-tests indicated that for Non-Tasters, the liking ratings were significantly lower than neutral for Alum (t (24) = −5.84, p<.001) and Caffeine at Suprathreshold concentrations (t(24) = −7.72, p<.001). However, Alum and Caffeine at Threshold concentrations, as well as Menthol at both Threshold and Suprathreshold concentrations, did not show significant deviations from neutral, suggesting these do not evoke strong negative reactions.

For Supertasters, liking ratings were significantly lower than neutral for Caffeine at Suprathreshold concentrations (t(26) = −9.14, p<.001) and Threshold concentrations (t(26) =

−2.46, p=.010), and for Alum at Suprathreshold concentrations (t(26) = −6.17, p<.001). Liking ratings of Menthol, at both concentrations, and Alum at Threshold concentrations did not significantly deviate from neutral, again, indicating a more neutral perception of these solutions.

6.8.2. EMG Results

6.8.2.1. Caffeine

6.8.2.1.1. Corrugator

There was a significant main effect of Taster Status (F (1, 42) = 5.60, $p<.05$, $\eta p2 = .12$), with Super-Tasters producing an overall increase in Corrugator muscle activity compared to Non-Tasters, and there was a trend towards a significant effect of Concentration (F(1, 84) = 4.04, $p=.0508$, $\eta p2 = .09$)

There was no significant effect of Block (F(1, 42) = .09, $p=.76$, $\eta p2 = .00$), however, there was a significant effect of Phase, (F(2, 84) = .16.47, $p<.001$, $\eta p2 = .28$), this reflected the fact Corrugator activity was greater in the Think Phase than the Empty and Swill Phases (ps<.001), with greater activity in the Swill Phase compared to the Empty Phase (p<.05).

There was a significant interaction between Block and Taster-Status (F (1, 42) = .4.24, $p<.05$, $\eta p2 = .09$). As can be seen in Figure 6.10, Super-Tasters produced significantly greater Corrugator activity during the first, Tasting Block compared to Non-Tasters (p<.05), while there was no difference in corrugator activity between the two groups during the second, Tasting and Rating Block (p=.64). No other interactions were significant.

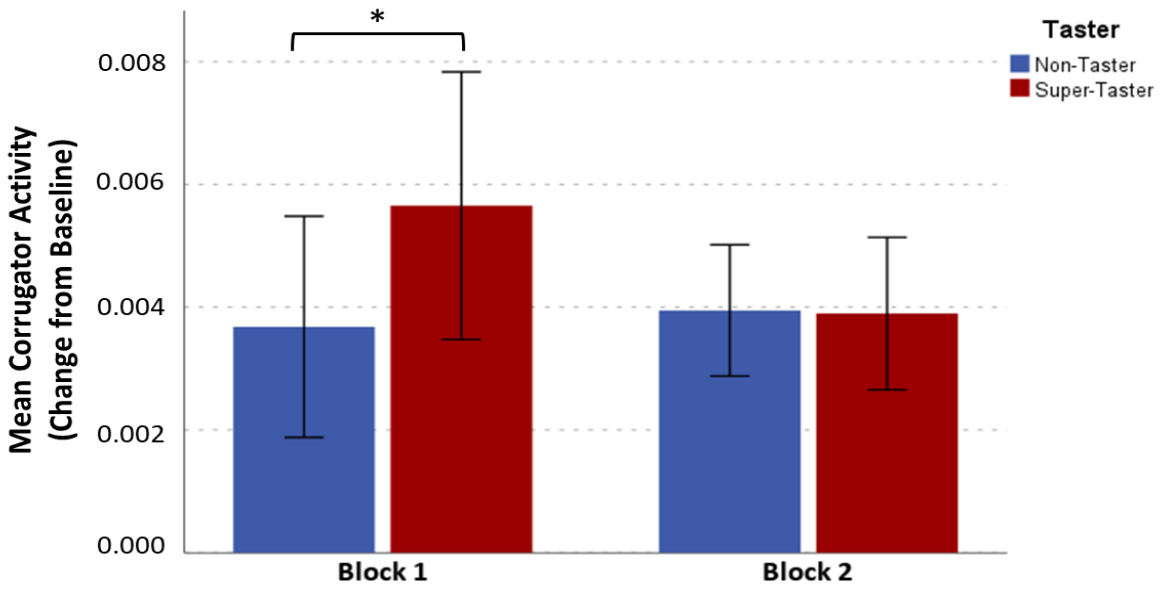

Figure 6.10: *Mean Super-Taster and Non-Taster Corrugator activity in response to Caffeine during Block 1 (The Tasting Block) and Block 2 (the Tasting and Rating Block). There was a significant interaction between Taster-Status and Block. Super-Tasters had significantly greater Corrugator activity during Block 1 (The Tasting Block) compared to Non-Tasters, there was no difference in Corrugator activity between the two groups during Block 2 (The Tasting and Rating Block). (* denotes sig<.05). Error bars display 95% CI.*

6.8.2.1.2. Zygomaticus

There was a significant main effect of Taster-Status (F (1, 43) = 4.97, $p<.05$, $\eta p2 = .10$), with Super-Tasters producing greater Zygomaticus muscle activity in response to Caffeine compared to Non-Tasters (Figure 6.11). However, there was no effect of Concentration (F (1, 43) = .69, $p=.41$, $\eta p2 = .02$). Whilst there was no significant interaction between Taster Status and Concentration (F (1, 43) = .08, $p=.78$, $\eta p2 = .00$), pairwise comparisons showed that it was only during Supra-Threshold trials that Super-Tasters produced significantly a significantly greater increase in activity compared to Non-Tasters.

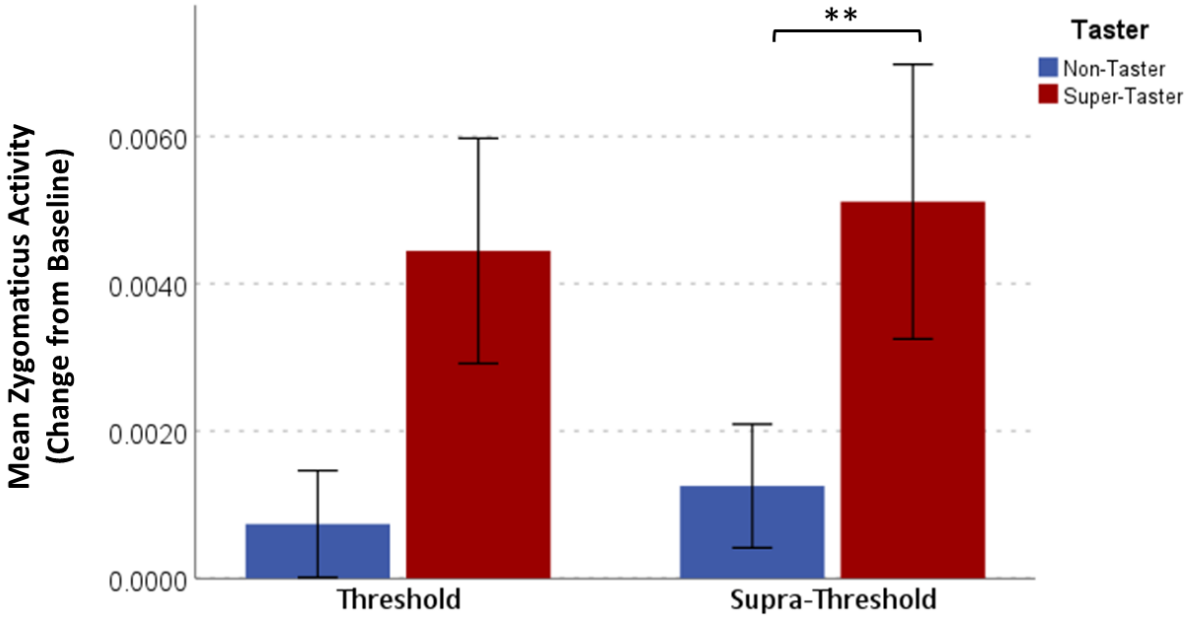

Figure 6.11: *Mean change score in Zygomaticus activity in response to Caffeine, for Super-Tasters and Non-Tasters. There was a significant effect of Taster-Status, in that Zygomaticus activity was greater for Super-Tasters compared to Non-Tasters. however, pairwise comparisons showed that this was only evident for Supra-Threshold trials. (* denotes sig<.05). Error bars display 95% CI.*

There was no significant effect of Block ($F(1, 43) = .00$, $p=.96$, $\eta p2 = .00$), however, there was a main effect of Phase, ($F(2, 86) = .9.53$, $p<.001$, $\eta p2 = .18$), with a greater increase in muscle activity during the Think Phase, compared to the Empty and Swill Phase (ps<.01). The Swill Phase did not differ significantly from the Empty Phase (p=.68) (Figure 6.12). No other interactions were significant.

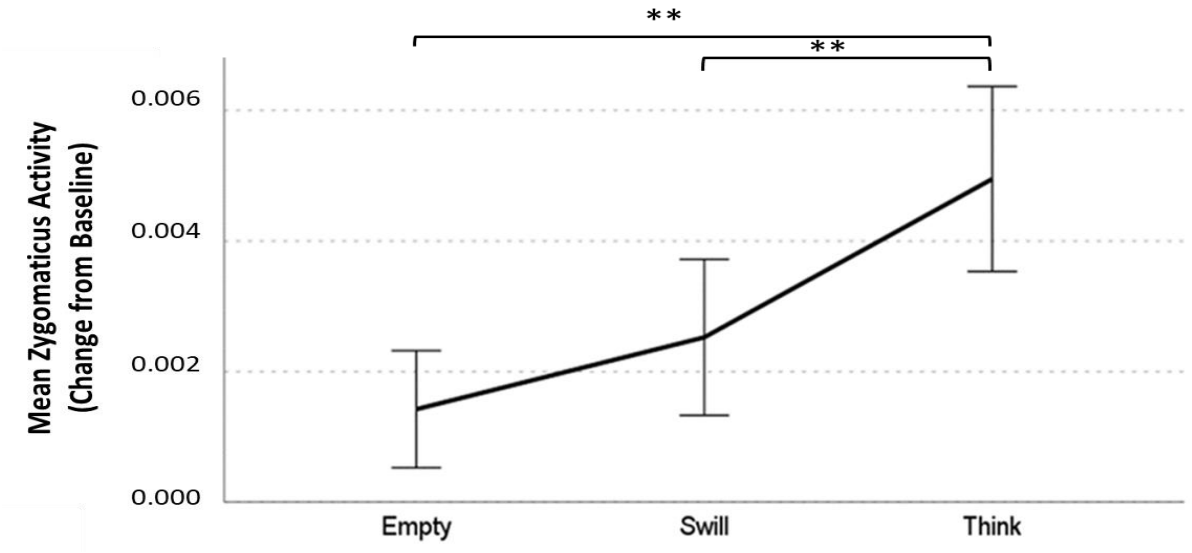

Figure 6.12: *Mean change score in Zygomaticus activity in response to Caffeine, during each Phase of the trials. There was a significant effect of Phase, in that Zygomaticus activity was greater during the Think Phase, compared to the Empty and Swill Phase. ** denotes sig<.01. Error bars display 95% CI.*

6.8.2.1.3. Heart Rate

In contrast to the study hypothesis, there was no significant effect of Taster Status (F (1, 47) = .56, p=.46, $\eta p2$ = .01) or Concentration (F(1, 47) = .55, p=.46, $\eta p2$ = .01). There was no effect of Block (F (1, 47= .22, p=.64, $\eta p2$ = .01), however, there was a significant effect of Phase, (F(2, 94) = 9.43, p<.001, $\eta p2$ = .17). As shown in Figure 6.13, there was a greater increase in the Swill Phase compared to both the Think Phase and the Empty Phase (p<.05). Heat-Rate did not change during either of the other two phases. There were no significant interactions.

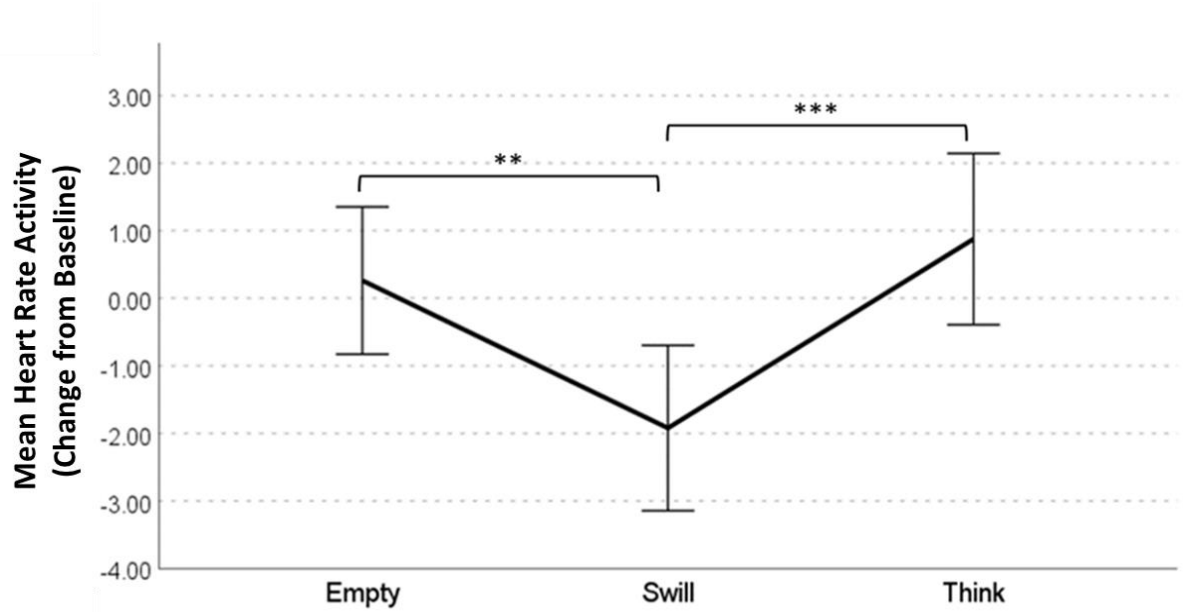

Figure 6.13: *Mean change score in Heart Rate, during each Phase of Caffeine trials. In which negative values represent heart rate acceleration, and a positive value represents heart rate deceleration. The Swill Phase produced a significant increase in Heart Rate compared to either the Empty or Think Phase. (** denotes sig<.01, *** denotes sig<.001). Error bars display 95% CI.*

6.8.2.1.4. Summary

In summary, in response to Caffeine solutions, both Corrugator and Zygomaticus activity differentiated between Super-Tasters and Non-Tasters, with Super-Tasters showing a greater increase in activity in both muscles. However, there was no difference in Heart Rate across taster groups.

6.8.2.2. Alum

6.8.2.2.1. Corrugator

There was no significant main effect of Taster-status (F (1, 41) = 2.76, p=.10, $\eta p2$ = .06), however, there was a significant main effect of Concentration, with Supra-Threshold trials producing a greater response than Threshold trials (F(1, 41) = 13.66, p<.001, $\eta p2$ = .25). There was a significant main effect of Block (F (1, 41) = 7.28, p<.05, $\eta p2$ = .15), with Block 1 (The Tasting Block) eliciting stronger responses compared to Block 2 (The Tasting and Rating Block), as well as a significant effect of Phase (F(2, 82) = 18.15, p= .001, $\eta p2$ = .03). As can

be seen in Figure 6.14, there was a significantly greater increase in Corrugator activity during the Think Phase compared to the Swill Phase (ps<.01) and the Empty Phase (p<.001). The Swill Phase additionally produced significantly more activity compared to the Empty Phase (p<.01). The interaction between Block and Phase was not significant (F (2, 82) = 1.26, *p*=.29, *ηp2* = .30).

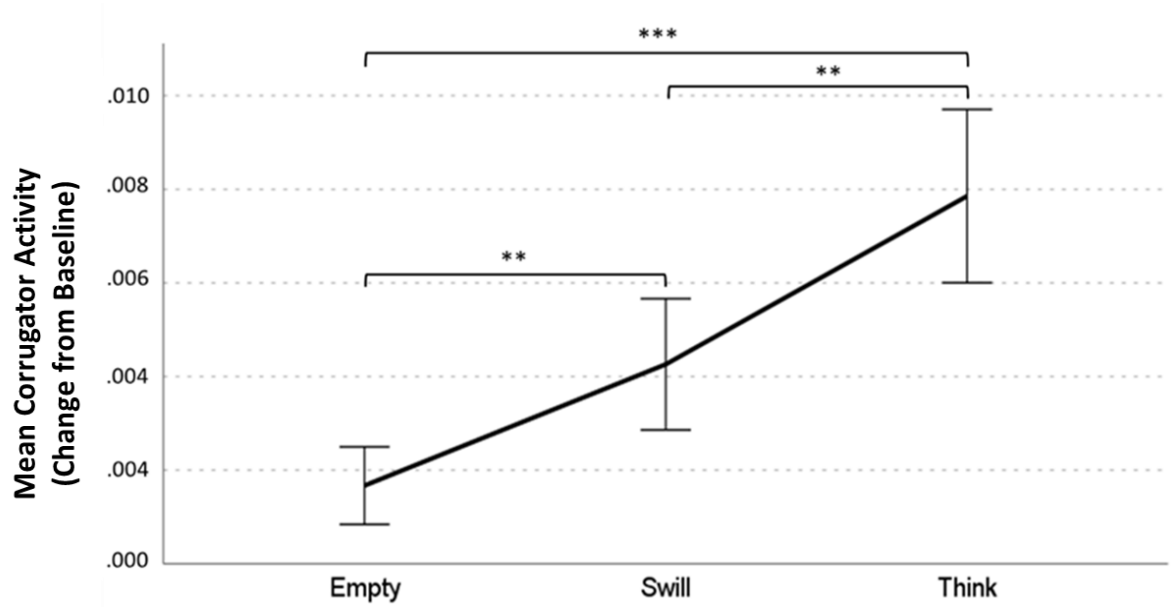

Figure 6.14: *Mean change score in Corrugator activity, during each Phase of Alum trials. There was a significant effect of Phase. The Think and Swill Phase produced a greater increase in activity compared to the Swill Phase and Empty Phase. The Swill Phase also produced a greater increase in activity compared to the Empty Phase. (** denotes sig<.01, *** denotes sig<.001). Error bars display 95% CI.*

The interaction between Phase and Concentration was also significant (F (2, 41) = 9.38, *p*<.001, *ηp2* = .19). As can be seen in Figure 6.15, Supra-Threshold Concentrations elicited greater muscle activity than Threshold Concentrations during both the Think (p<.001) and Swill (p<.01) Phases, with no difference during the Empty Period (p=.48). For Supra-Threshold Concentrations, the Think Phase elicited greater muscle activity compared to the Empty Phase (p<.001) but not the Swill Phase (p=.06) The Swill Phase elicited greater activity than the Empty Phase (p<.001). There was no difference in muscle activity across any of the Phases for Threshold Concentrations (ps>.05).

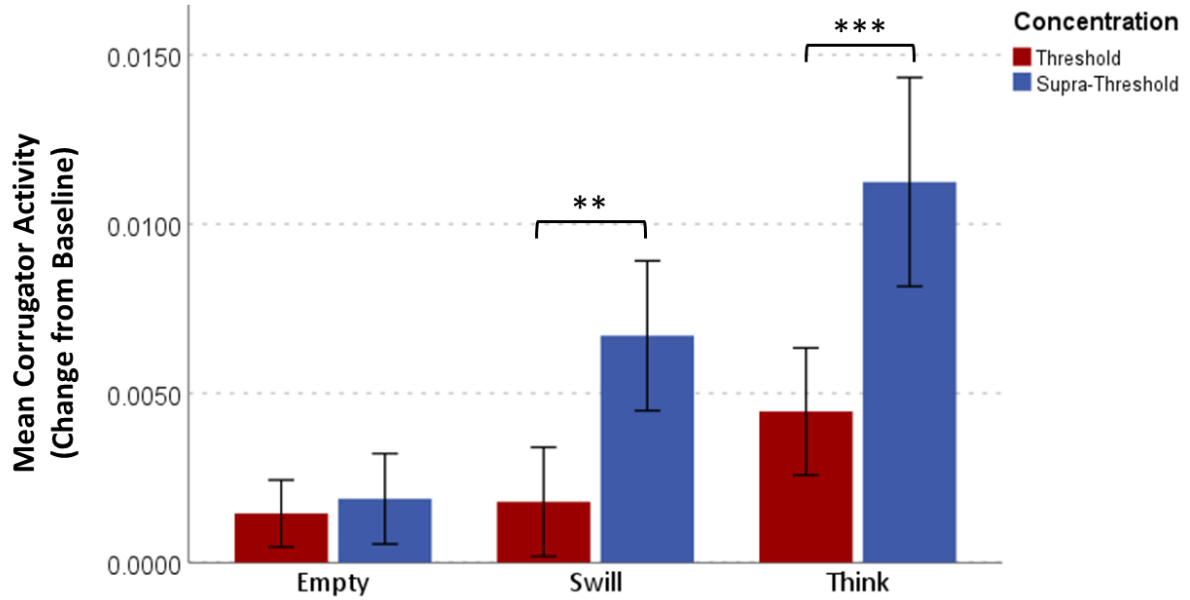

Figure 6.15: *Mean change score in Corrugator activity for both Supra-Threshold and Threshold trials, during each Phase of Alum trials. Supra-Threshold Concentrations elicited greater muscle activity than Threshold Concentrations during both the Swill) and Think Phases, with no difference during the Empty Period. (** denotes sig<.01, *** denotes sig<.001). Error bars display 95% CI.*

There was a significant three-way interaction between Block, Concentration and Taster-Status (F (1, 41) = 5.22, p<.05, $\eta p2$ = .11). As shown in Figure 6.16, for Super-Tasters, there was a significant difference in muscle activity for Supra-Threshold trials between Block 1 (The Tasting Block) and Block 2 (The Tasting and Rating Block), in that Block 1 elicited a significant higher activity compared to Block 2 (p<.05), however, there was no significant difference in muscle activity for Threshold Concentrations between Block 1 and Block 2 (p=.41). For Non-Tasters, there was no difference in muscle activity for Supra-Threshold Concentrations between Block 1 (The Tasting Block) and Block 2 (The Tasting and Rating Block) (p=.93), however, for Threshold Concentrations, Block 2 elicited a significantly smaller change in muscle activity compared to Block 1 (p<.01).

Further mixed ANOVAs were conducted for each Block, in order to investigate this interaction, however, it was found that there was no interaction between Taster Status and Concentration for either Block 1 (F (1, 44) = 2.17, p<=.15, $\eta p2$ = .05) or the Block 2 (F(1, 45) = 53, p<=.47, $\eta p2$ = .01).

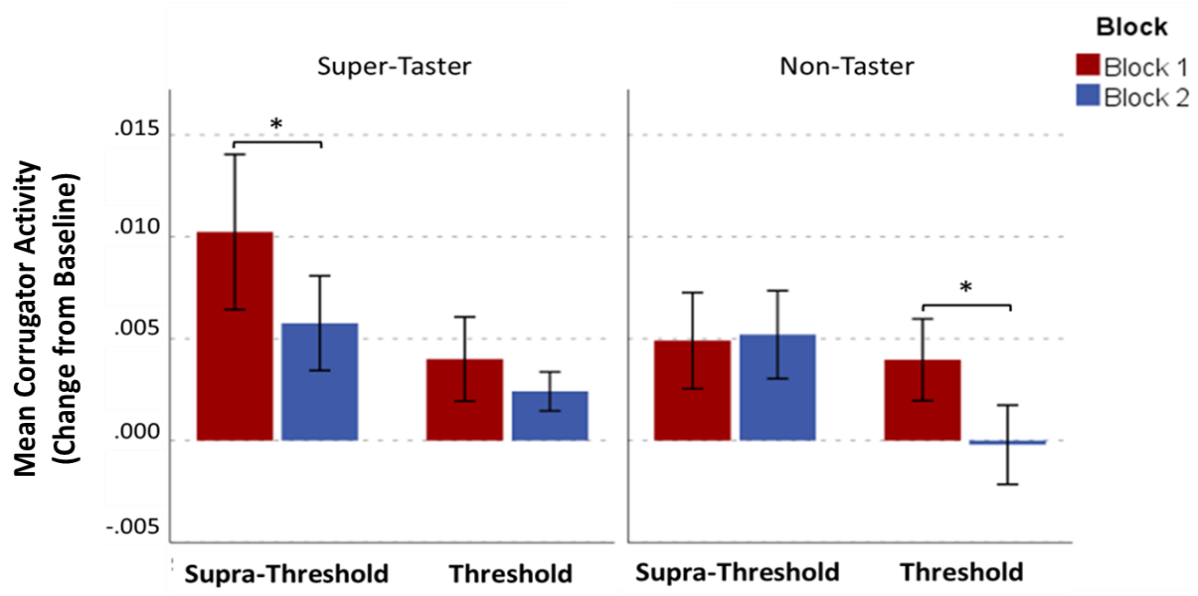

Figure 6.16: *Mean corrugator activity for Supra-Threshold and Threshold Concentrations, for both Super-Tasters and Non-Tasters. Red bars show activity during The Tasting Block and Blue bars show activity for The Tasting and Rating Block. (* denotes sig<.05). Error bars display 95% CI.*

6.8.2.2.2. Zygomaticus

There was a significant main effect of Taster-Status (F (1, 42) = 5.42, p<.05, $\eta p2$ = .11), with Super-Tasters producing a greater response in Zygomaticus muscle activity compared to Non-Tasters (Figure 6.17). However, there was no significant effect of Concentration (F (1, 42) = .15, p=.70, $\eta p2$ = .00). Whilst there was no significant interaction between Taster Status and Concentration (F (1, 42) = .63, p=.43, $\eta p2$ = .02), exploratory pairwise comparisons showed that, consistent with the other stimuli, it was only during Supra-Threshold trials that Super-Tasters produced a significantly greater increase in activity compared to Non-Tasters.

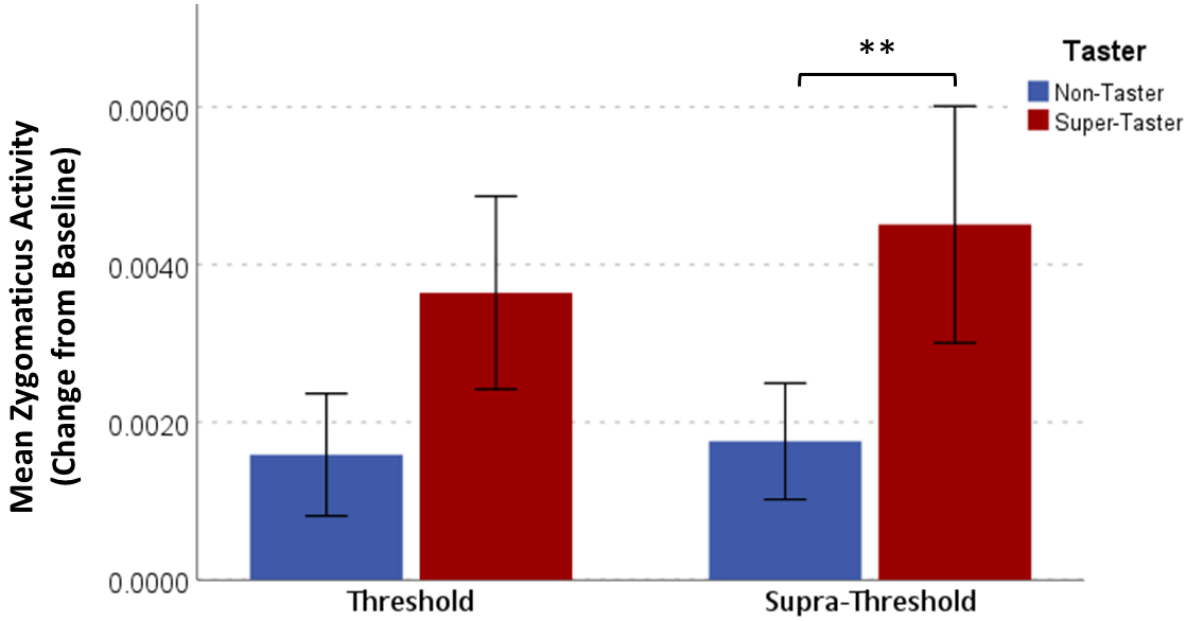

Figure 6.17: *Mean change score in Zygomaticus activity, for Super-Tasters and Non-Tasters in response to Threshold and Supra-Threshold Concentrations of Alum. There was a significant main effect of Taster-Status, in that Zygomaticus activity was greater for Super-Tasters compared to Non-Tasters, however, pairwise comparisons showed that this was only evident for Supra-Threshold trials. (** denotes sig<.01). Error bars display 95% CI.*

While there was no significant main effect of Block (F (1, 42) = 3.20, p=.08, $\eta p2$ = .07), there was a significant effect of Phase, (F (2, 84) = .13.40, p<.001, $\eta p2$ = .24). As shown in Figure 6.18, there was a greater increase in muscle activity during the Think Phase, compared to the Swill Phase (p<.05) and Empty Phase (p<.001). The Swill Phase additionally had a greater increase in activity than the Empty Phase (p<.05). No other interactions were significant.

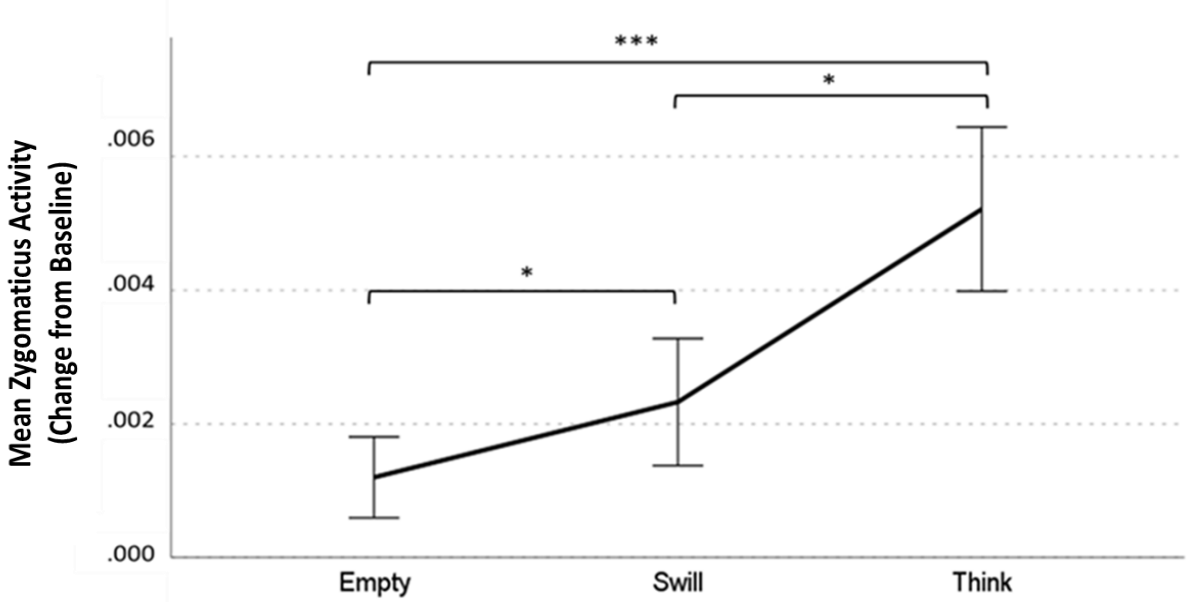

Figure 6.18: *Mean change score in Zygomaticus activity during each Phase of Alum trials. There was a significant effect of Phase. The Think and Swill Phase produced a greater increase in activity compared to the Swill Phase and Empty Phase. The Swill Phase also produced a greater increase in activity compared to the Empty Phase. (* denotes sig<.05, *** denotes sig<.001). Error bars display 95% CI.*

6.8.2.2.3. Heart Rate

In contrast to the study hypothesis, there was no significant main effect of Taster-Status (F(1. 47) = 2.18, p=.15, $\eta p2$ = .04), however, there was a significant main effect of Concentration (F (1, 47) = 4.21, p<.05, $\eta p2$ = .08), with Supra-Threshold trials producing a significant decrease in Heart Rate compared to Threshold trials (Figure 6.19).

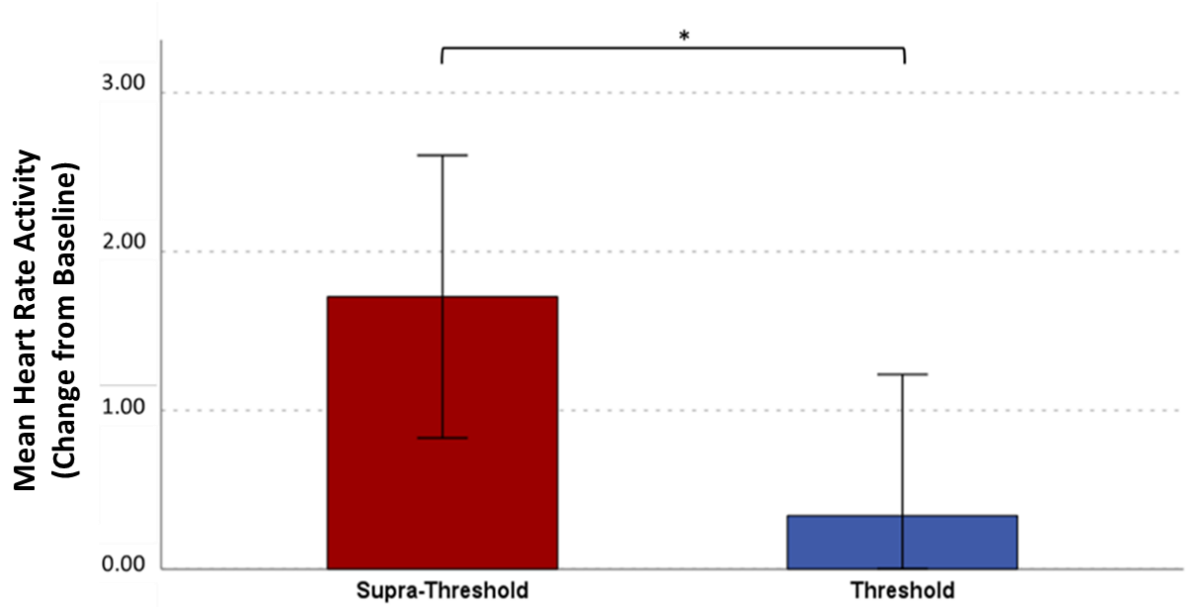

Figure 6.19: *Mean change score in Heart Rate activity during Supra-threshold and Threshold Alum trials. In which negative values represent heart rate acceleration, and positive values represent heart rate deceleration. There was a significant effect of Concentration. Supra-Threshold trials produced significantly greater increase in Heart Rate compared to Threshold trials. (* denotes sig<.05). Error bars display 95% CI.*

There was no significant effect of Block (F (1, 47= .07, p=.80, $\eta p2$ = .00), however, there was a significant effect of Phase, (F(2, 94) = 15.69, p<.001, $\eta p2$ = .25). As shown in Figure 6.20, there was a greater decrease in Heart Rate during the Think Phase, compared to the Empty (p<.01) and Swill (p<.001) Phases. The Swill Phase produced a greater increase in Heart Rate compared to the Empty Phase (p<.01).

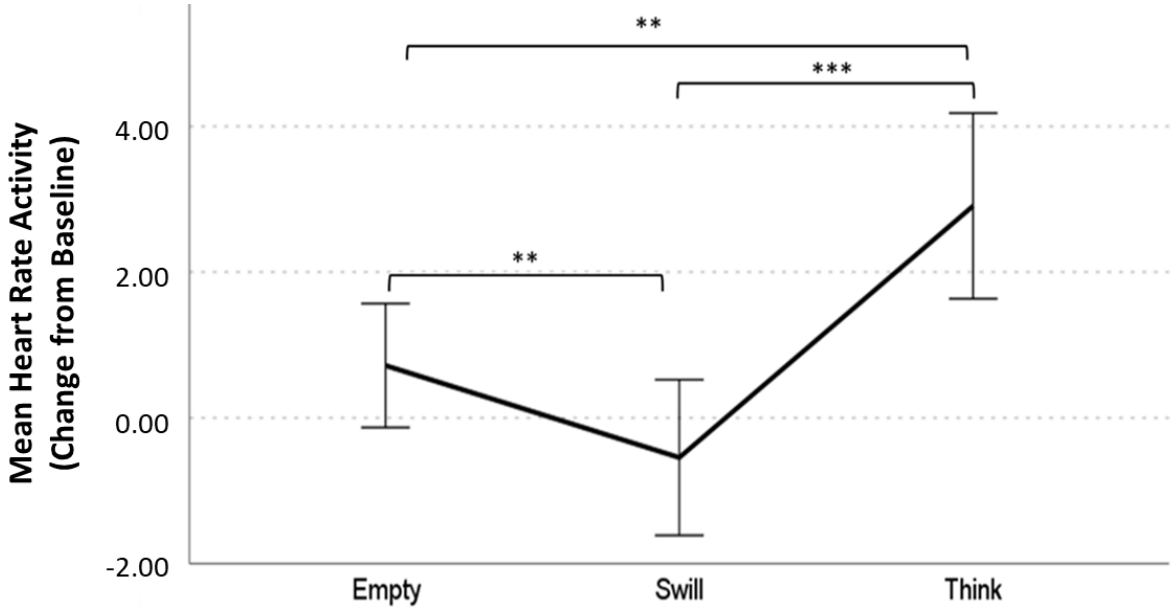

Figure 6.20: *Mean change score in Heart Rate activity across each Phase of Alum trials. In which negative value represents heart rate acceleration, and a positive value represents heart rate deceleration. There was a greater decrease in Heart Rate during the Think Phase, compared to the Empty and Swill Phases. The Swill Phase produced a greater increase in Heart Rate compared to the Empty Phase. (** denotes sig<.01, *** denotes sig<.001). Error bars display 95% CI.*

The interaction between Phase and Concentration was significant (F (2, 94) = 4.18, $p<.05$, $\eta p2 = .08$). As shown in Figure 6.21, during the Empty Phase, there was no difference in Heart Rate between Supra-Threshold and Threshold Concentrations (p=.60), however, during both the Swill and Think Phases, Supra-Threshold Concentrations elicited a greater decrease in Heart Rate compared to the Threshold Concentrations (ps<.05).

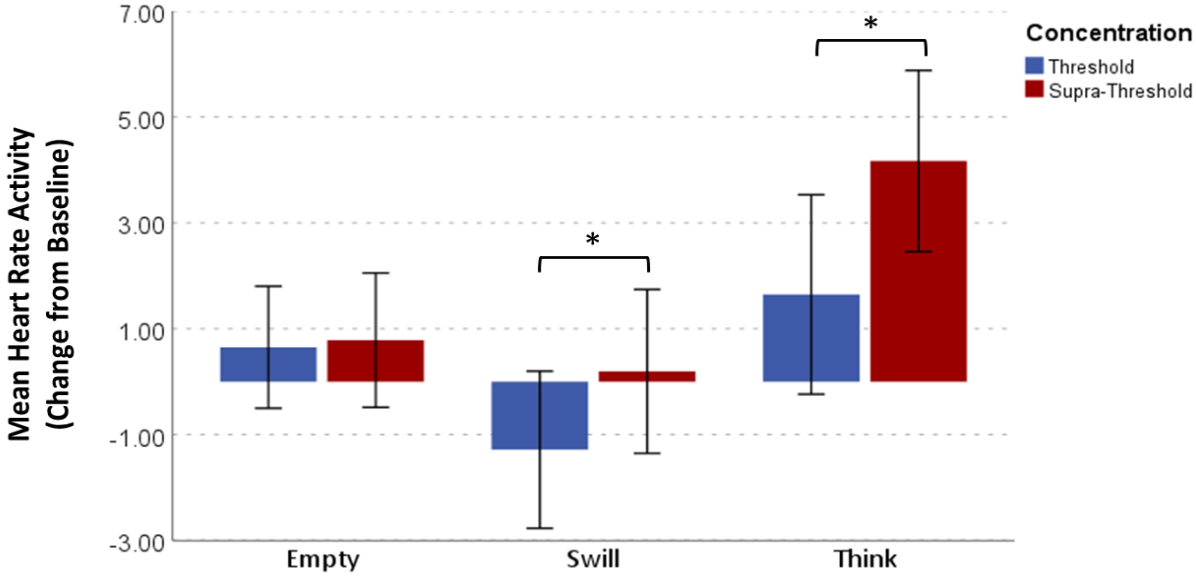

Figure 6.21: *Mean change score in Heart Rate activity between Supra-Threshold and Threshold concentrations, for each Phase of Trials. In which negative value represents heart rate acceleration, and a positive value represents heart rate deceleration. (* denotes sig<.05). Error bars display 95% CI.*

6.8.2.2.4. Alum Summary

In summary, in response to Alum solutions, only Zygomaticus activity differentiated between Super-Tasters and Non-Tasters, with Super-Tasters showing a greater increase in muscle activity. Corrugator activity and Heart Rate differentiated between Threshold and Supra-Threshold Concentrations, with greater Zygomaticus activation and heart-rate deceleration in response during Supra-Threshold trials.

6.8.2.3. Menthol

6.8.2.3.1. Corrugator

There was no significant effect of Taster-Status (F (1, 39) = .28 p=.60, $\eta p2$ = .01), however, there was a significant main effect of Concentration (F(1, 39) = 10.77, p<.01, $\eta p2$ = .22), with greater muscle activity for Supra-Threshold compared to Threshold Concentrations (Fig 6.22).

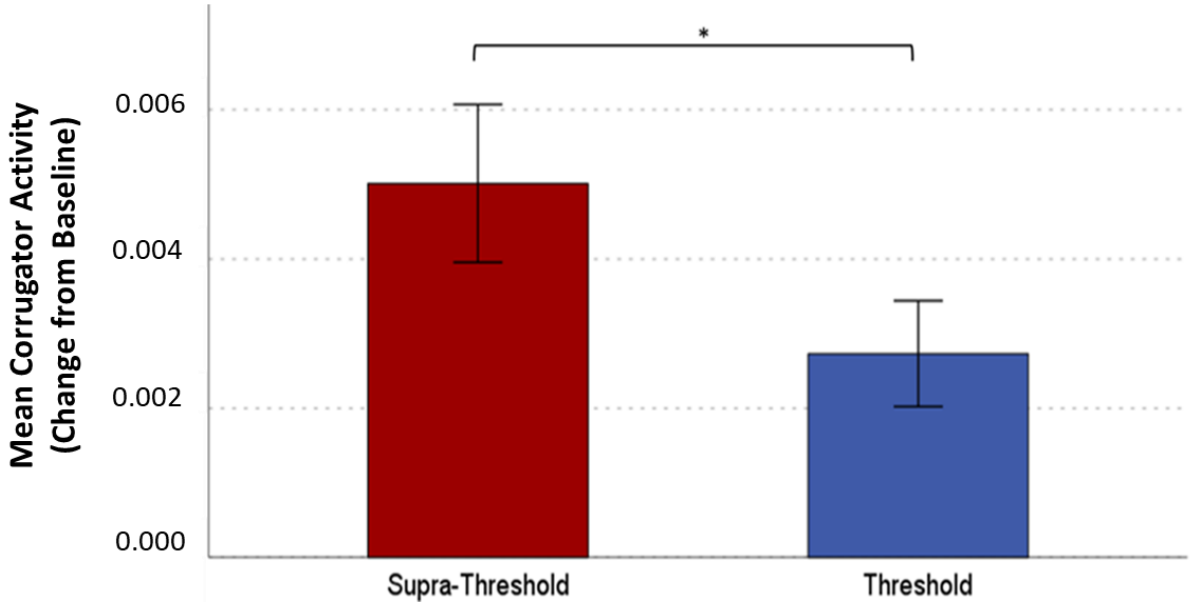

Figure 6.22: *Mean change score in Corrugator activity between Supra-Threshold and Threshold concentration of Menthol. (* denotes sig<.05). Error bars display 95% CI.*

The effect of Block was borderline significant (F (1, 39) = .4.03, *p*=.05, *ηp2* = .09). There was a significant effect of Phase, (F (2, 78) = .8.27, *p*<.001, *ηp2* = .18), as shown in Figure 6.23, muscle activity was significantly greater during the Think and Swill Phases compared to the Empty Phase (ps<.05). There was no difference between the Swill and Empty Phases (p=.53).

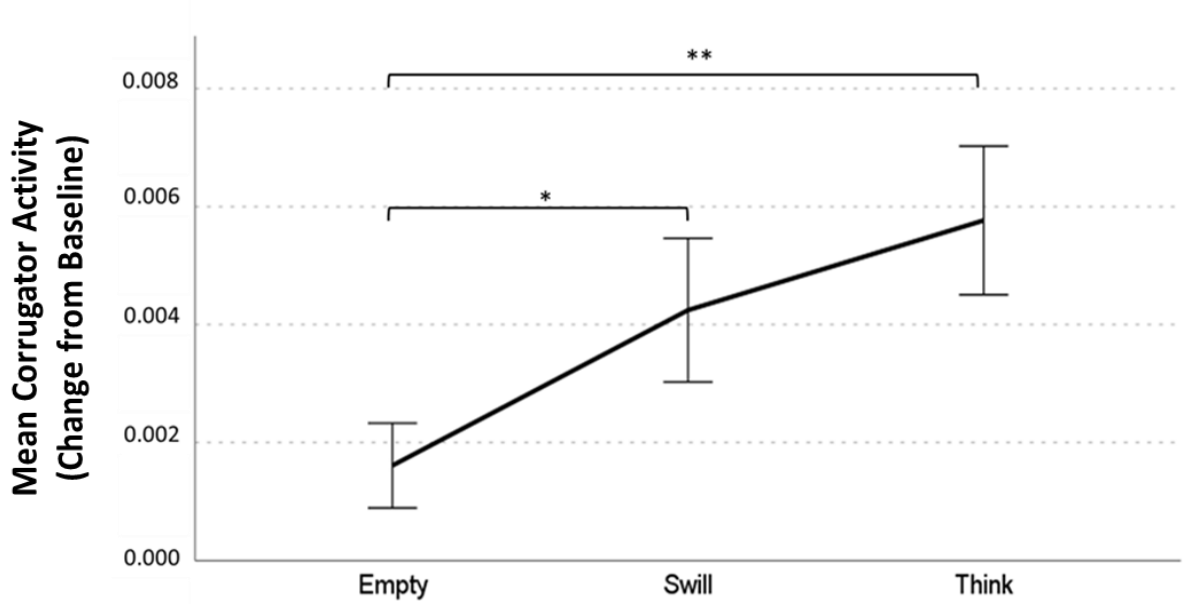

Figure 6.23*: Mean change score in Corrugator activity across each Phase of Menthol trials. There was a greater increase in muscle activity during the Think Phase, compared to the Empty and Swill Phases. There was no difference in activity between the Swill and Think Phases. (* denotes sig<.05, ** denotes sig<.01). Error bars display 95% CI.*

There was no significant interaction between Block and Phase (F (2, 78) = 2.35, *p*=.10, *ηp2* = .06). As shown in Figure 6.24, during the Empty Phase, there was no difference in Corrugator activity between Supra-Threshold and Threshold Concentrations (p=.17), however, during both the Swill (p<.001) and Think Phases (p<.05), Supra-Threshold Concentrations elicited a greater increase in muscle activity compared to the Threshold Concentrations.

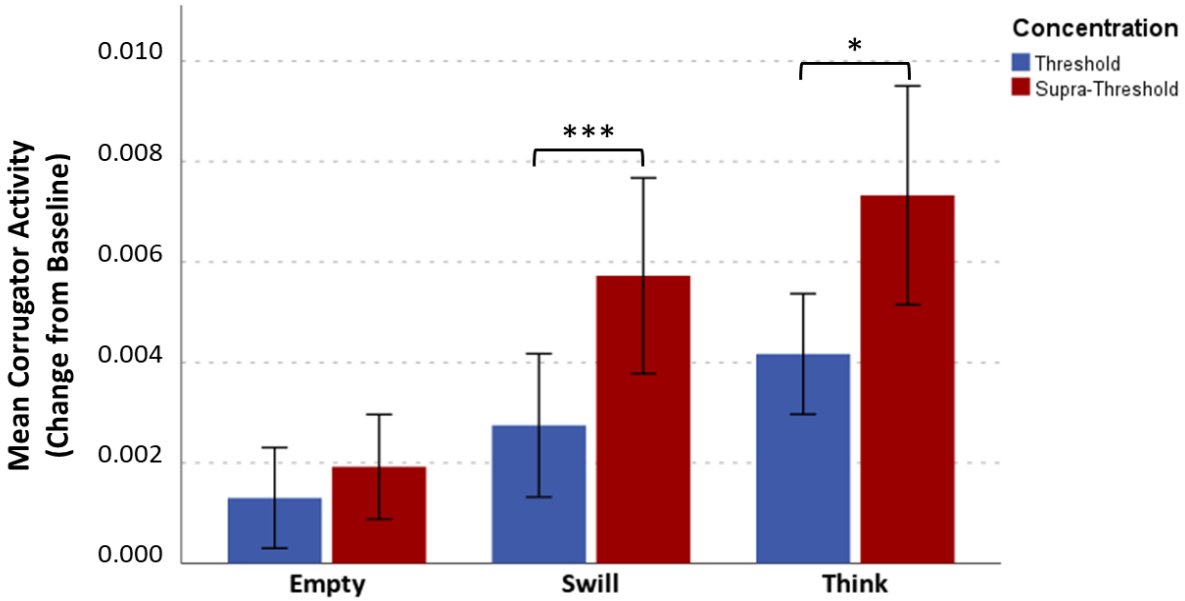

Figure 6.24: *Mean corrugator activity for both Supra-Threshold and Threshold Solution, during each Phase of Menthol trials. (* denotes sig<.05, *** denotes sig<.001).Error bars display 95% CI.*

6.8.2.3.2. Zygomaticus

There was no significant main effect of Taster Status (F (1, 45) = 3.06, *p*=.09, *ηp2* = .06) and no significant main effect of Concentration (F(1, 45) = 3.71, *p*=.06, *ηp2* = .08). However, there was a significant interaction between Taster-Status and Concentration (F (1, 45) = 6.30, *p*<.05, *ηp2* = .12) As shown in Figure 6.25, Super Tasters produced significantly greater muscle activity in response to Super Threshold, compared to Threshold trials (p<.01) There was no difference in muscle activity between Concentrations for Non-Tasters (p=.69).

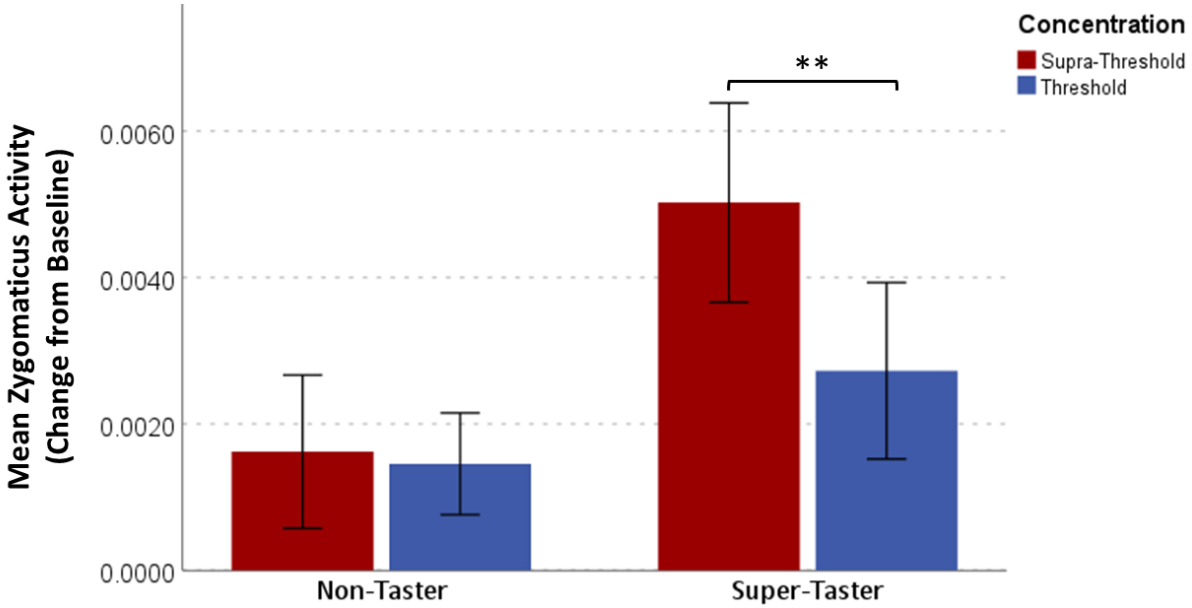

Figure 6.25: *Mean muscle activity for Super-Tasters and Non-Tasters, for both Supra-Threshold and Threshold Menthol Concentrations. Super Tasters produced significantly greater muscle activity in response to Super Threshold, compared to Threshold trials. There was no difference in muscle activity between concentrations for Non-Tasters. (** denotes sig<.01). Error bars display 95% CI.*

There was no significant main effect of Block ($F(1, 45) = .62$, $p=.43$, $\eta p2 = .01$), however, there was a significant main effect of Phase, ($F(2, 90) = .8.48$, $p<.001$, $\eta p2 = .16$), as shown in Figure 6.26, there was a greater increase in muscle activity during the Think Phase, compared to the Empty ($p<.01$) but not the Swill Phase ($p=.08$). The Swill Phase did not differ from the Empty Phase ($p=.06$).

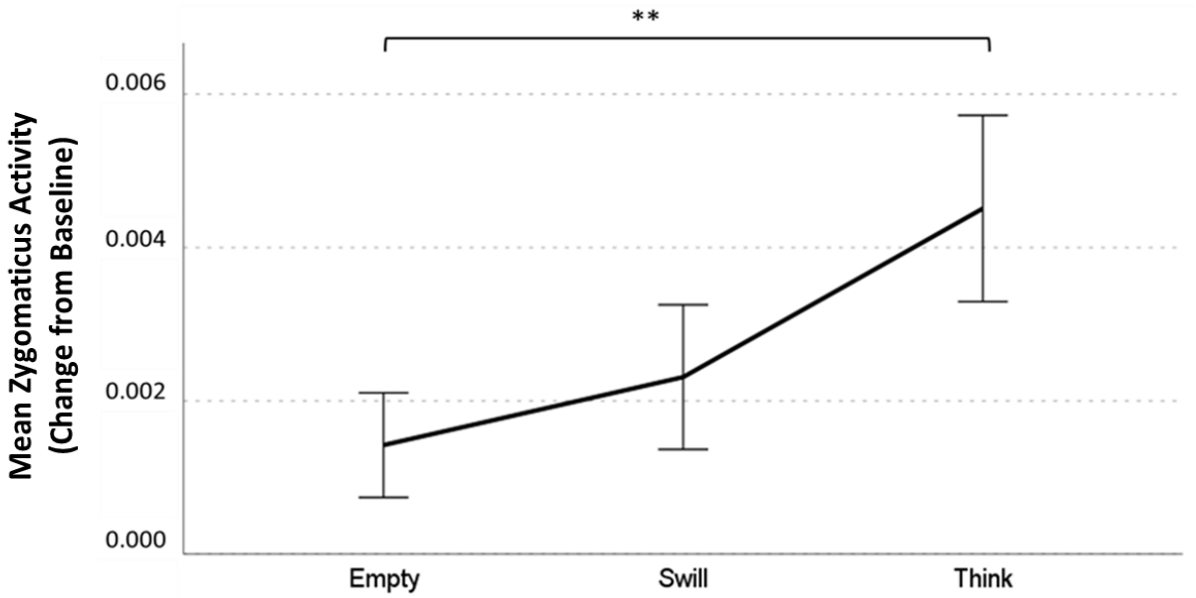

Figure 6.26: *Mean muscle activity during each Phase of Menthol trials. The Think Phase produced significantly greater muscle activity, compared to the Empty Phase but not the Swill Phase. The Swill Phase did not differ from the Empty Phase. (** denotes sig<.01). Error bars display 95% CI.*

There was a significant interaction between Phase and Taster Status (F (2, 90) = 3.32, $p<.05$, $\eta p2 = .07$). As shown in Figure 6.27, it was only during the Think Phase that Super-Tasters produced a significant increase in muscle activity compared to Non-Tasters ($p<.05$), activity did not differ between Tasters for the Empty or Swill Phases ($ps>.05$). No other interactions were significant.

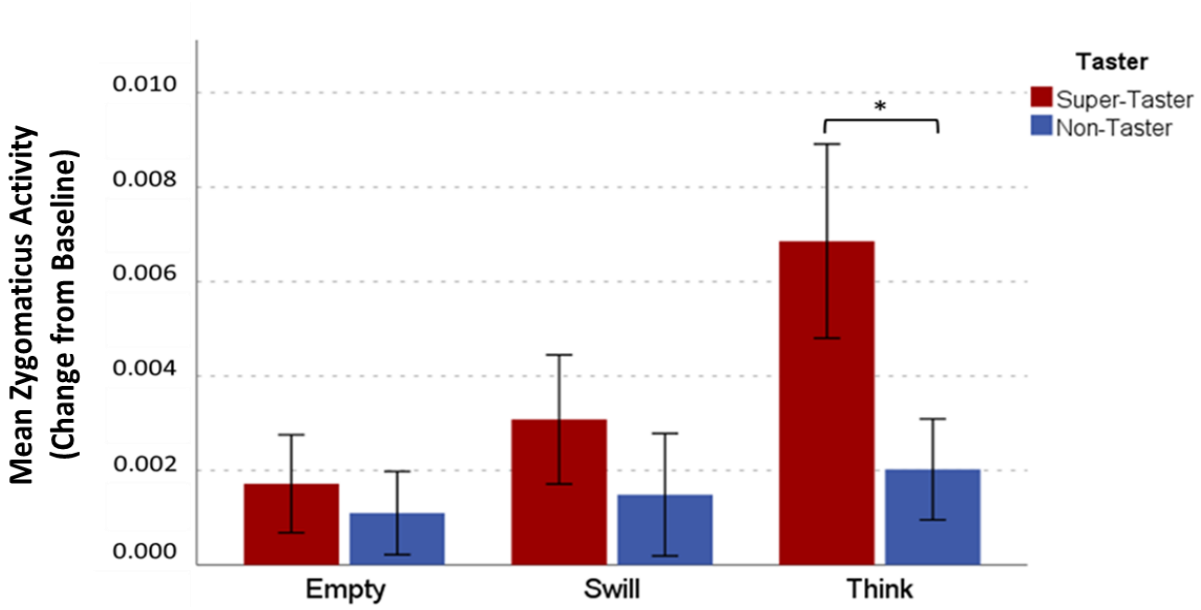

Figure 6.27: *Mean muscle activity or Super-Tasters and Non-Tasters ratings during each Phase of Menthol trials. Super-Tasters produced significantly greater muscle activity during the Think Phase compared to Non-Tasters. Muscle activity did not differ between Super-Tasters and non-Tasters for the Swill Phase or Empty Phase. (* denotes sig<.05). Error bars display 95% CI.*

6.8.2.3.3. Heart Rate

In contrast to the study hypothesis, there was no significant main effect of Taster-Status ($F(1, 45) = 1.24$, $p=.27$, $\eta p2 = .03$) or Concentration ($F(1, 45) = .33$, $p=.57$, $\eta p2 = .01$). While there was no significant effect of Block ($F(1, 45= 1.67$, $p=.20$, $\eta p2 = .03$), there was a significant main effect of Phase, ($F(2, 90) = 7.57$, $p<.001$, $\eta p2 = .14$). As shown in Figure 6.28, there was a greater increase in Heart Rate during the Swill Phase compared to the Think Phase ($p<.01$). The Swill Phase also produced a significant increase in Heart Rate compared to the Empty Phase ($p<.05$). No other interactions were significant.

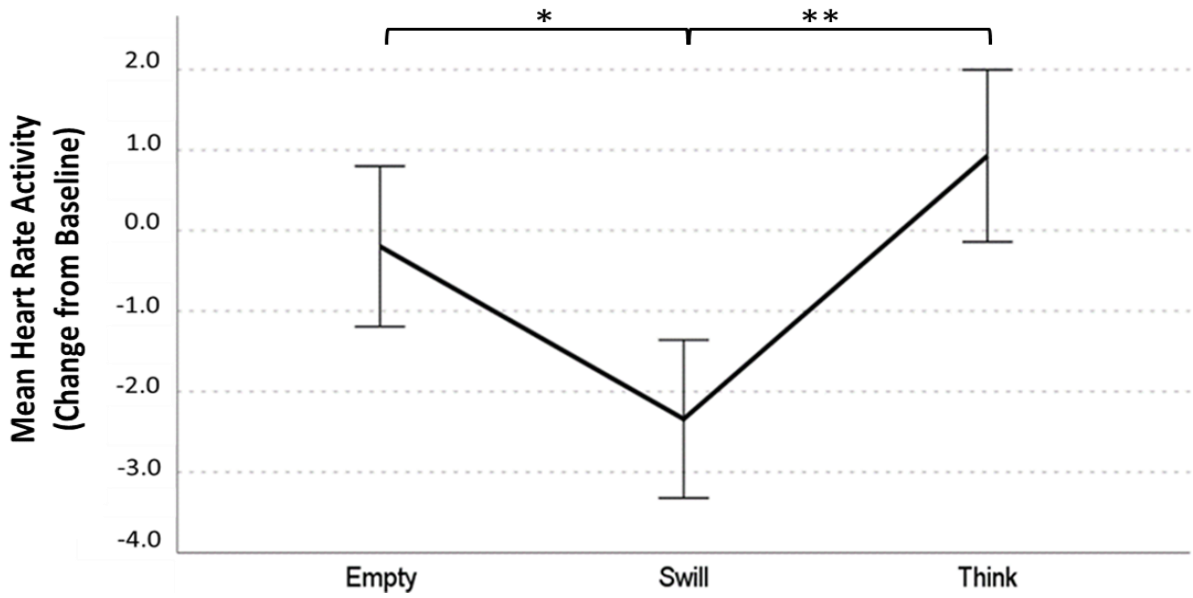

Figure 6.28: *Mean Heart Rate activity during each Phase of Menthol trials. In which negative values represent heart rate acceleration, and positive values represent heart rate deceleration. The Think phase produced significantly greater decrease in Heart Rate compared to the Swill Phase but not the Empty Phase. The Swill Phase produced a significant increase in Heart Rate compared to the Empty Phase (* denotes sig<.05, * denotes sig <.01). Error bars display 95% CI.*

6.8.2.3.4. Menthol Summary

In summary, in response to Menthol solutions, only Zygomaticus activity was able to differentiate between Super-Tasters and Non-Tasters, with Super-Tasters showing a greater increase in muscle activity, however, this was only in response to Supra-Threshold concentrations. Corrugator activity was able to differentiate between Threshold and Supra-Threshold Concentrations, with greater activation in response during Supra-Threshold trials.

6.9. Discussion

Consistent with the published literature, there were a distinct difference in the subjective perception of bitter tastes between PROP Super-Tasters and Non-Tasters (Bartoshuk et al. 1994; Delwiche et al. 2001; Dinehart et al. 2006; Lanier et al. 2005; Sandell & Breslin, 2006; Tepper et al. 2009; Zhao & Tepper, 2007). In addition, the observed differences in sensitivity to astringent and chemesthetic stimuli provide compelling evidence that super-tasters' heightened responsiveness to bitter tastes extends to other oral sensations. For intensity, Super-Taster's ratings were significantly higher than Non-Tasters for Supra-Threshold concentrations of Caffeine, Alum and Menthol. However, for liking ratings, it was only Caffeine that elicited significantly lower ratings from Super-Tasters, with no difference in taster groups for liking of Alum and Menthol (Drewnoswki et al. 1998). These finding highlights that while Super-Tasters report greater intensity in response to bitter, astringent and chemesthetic stimuli, their overall liking for these stimuli does not necessarily align with this heightened sensitivity, as caffeine was the only solution to distinguish between Super-Tasters and Non-Tasters on both Intensity and Liking scales.

To date, research reporting that Super-Tasters display heightened sensitivity to chemesthetic sensations, have primarily used irritants such as capsaicin, cinnamaldehyde, and ethyl alcohol (Bartoshuk et al. 1993; Karrer & Bartoshuk, 1991; Prescott & Swain-Campbell, 2000), however, the perception of menthol, despite its wide spread use in oral hygiene products, remains significantly understudied, and to our knowledge, this study is the first to identify and report GTS differences in sensitivity to menthol. This difference could be attributed to the notion that menthol has been reported to produce a bitter sensation when applied to various areas of the tongue, with increasing intensity, thus suggesting stimulation of bitter taste neurons (Green & Schullery, 2003; Gwartney & Heymann, 1995). Alternatively, this heightened menthol sensitivity in Super-Tasters may be attributed to the increased innervation density of TRPM8 positive nerve endings as a result of super-tasters having a greater density of fungiform papillae on their tongues (Abe et al. 2005; Bangcuyo & Simons, 2017; Bajec & Pickering, 2008; Prutkin et al. 2000). This finding is consistent with previous reports that taster status predicts lingual tactile acuity, with supertasters showing the lowest tactile perception thresholds in comparison to non-tasters (Essick et al. 2003). This heightened oral tactile sensitivity in supertasters is hypothesised to be a consequence of the co-innervation of fungiform papillae by mechanosensitive trigeminal nerves. In considering astringent sensations, whilst a wide

array of research has attempted to link GTS with astringency perception from red wine, results have been conflicting (Criado et al. 2024; Hayes & Pickering, 2012; Smith et al. 1996). Such inconsistent findings may be due to the complexity of red wine's composition, involving tannins, acids, sugars, and alcohol, which may obscure perceived astringency. Indeed, studies which isolate single compounds, such as those used in the current study, appear to offer a more controlled measure, from which distinct differences in sensitivity to astringent stimuli across GTS emerge (Bajec & Pickering, 2008).

In support of the hypothesis that EMG responses could differentiate Super-Tasters from Non-Tasters, zygomaticus muscle activity effectively differentiated the two groups in responses to bitter, astringent, and chemesthetic oral stimuli, specifically at Supra-Threshold concentrations. While EMG studies typically consider increases in zygomaticus muscle activity to be associated with response to pleasant stimuli (Beyts et al. 2017; Cannon & Grigor, 2017; Larsen et al. 2003; Sato et al. 2008; Sato et al. 2020), activity in this muscle is also reported as a result of grimacing to unpleasant stimuli (Armstrong et al. 2007; Merrill et al. 2023). The current findings align with those from other research in which zygomaticus activity in response to tasting unpleasant pickle juice were significantly larger compared to a neutral condition (water) (Hu et al. 2000). Armstrong et al. (2007) found similar results in response to four odourants *(2 pleasant and 2 unpleasant)* and four tastants *(2 pleasant and 2 unpleasant)* and reported that, whilst zygomaticus activation was pronounced for both pleasant and unpleasant stimuli, it is unable to discriminate between the two. It was suggested that in order to determine whether stimuli being perceived as pleasant or unpleasant, information is required from both zygomatic and levator labii muscles, due to the levator labii being activated by wrinkling of the nose in response to unpleasant stimuli (Armstrong et al. 2007). Given that the current study exclusively featured neutral and hedonically unpleasant stimuli, as indicated by the subjective liking ratings it would be appropriate to attribute the increase in zygomatic activity to negative affective responses, such as grimacing (Armstrong et al. 2007; Hu et al. 2000).

In contrast to the zygomaticus, enhanced corrugator activity only differentiated GTS responses to bitter Caffeine. It is noteworthy, that while intensity ratings were matched across stimuli, liking ratings varied and caffeine was the least liked. Generally, corrugator activity was more pronounced for Supra-Threshold concentrations compared to Threshold concentrations, regardless of GTS. Whilst most other research agrees with the finding that unpleasant tastes elicit greater corrugator activity, this is often in comparison to pleasant tastes in which

corrugator activity is less pronounced (Sato et al. 2008; Beyts et al. 2017; Cannon et al. 2017). The current study differed in that, to our knowledge, it is the first to distinguish between Threshold and Supra-Threshold concentrations, confirming, that in order to effectively measure facial responses to oral stimuli, intensity levels should be above detection threshold level (Green & Schullery, 2003; Armstrong et al. 2007).

There was no support for the hypothesis that HR would differentiate between Super-Tasters and Non-Tasters. Whilst increases in HR are often associated with exposure to unpleasant stimuli, such as images (Costa et al. 2022) and non-affective touch, (Sailer & Ackerley., 2019), it has been suggested that physiological measures such as HR and skin conductance, are the most effective autonomic nervous system measures for differentiating between basic taste solutions, and these differences are linked to the pleasantness of the tastes (Rousmans et al. 2000). However, the limited research using autonomic nervous system measurements in more general oral sensory evaluation has produced inconsistent results (Brouwer et al. 2017; Danner et al. 2014; de Wijk et al. 2012; de Wijk et al. 2014; Verastegui-Tena et al. 2019). For instance, increases in HR has been associated with both pleasant (Brouwer et al. 2017; de Wijk et al. 2014) and unpleasant (Horio, 2000; Rousmans et al. 2000) oral stimuli, with others reporting no change (Danner et al. 2014; Kaneko et al. 2019; de Wijk et al. 2012). As such, it may be that using HR as a measure of physiological response to oral perception, is only effective when comparing pleasant and unpleasant tastes, as opposed to differentiating between the perceived intensity of affectively neutral or mildly unpleasant oral sensations used in the current study.

Both EMG and HR showed a significant increase in activity during the Think Phase compared to other Phases, however, this did not differ between Non-Tasters and Super-Tasters. These findings are not consistent with that of a similar study by Cannon and Grigor (2007), who reported that increases in EMG from a sample of Medium-Tasters, were more pronounced during the Empty phase, compared with Swill and Think phases, with effects diminishing across phases. However, methodologies differed significantly between studies, in that, while Cannon and Grigor (2007) examined both pleasant and unpleasant stimuli, our study focused on affectively neutral and unpleasant stimuli, which may explain differences in EMG activity patterns. Additionally, our study differentiated between Super-Tasters and Non-Tasters to explore how taste sensitivity affects physiological responses, whereas Cannon and Grigor (2007) included only medium tasters, potentially influencing their findings. In addition, instructions to "think," during a task, engages cognitive faculties, focussing mental effort and

processing information deeply, which prompts heightened cognitive engagement, involving increased mental involvement, attention, and active information processing during a task (Pendleton et al. 2016). It has been suggested that physiological measures, such as EMG and HR can be used to indicate changes in mental processing, in which changes occur particularly when individuals are engaged in tasks that require them to allocate attention and mentally process information (Hess., 2014; Thayer et al. 2009; Schuurink et al. 2008). Whilst this notion has not been widely investigated in relation to oral stimulation, other areas of research have evidence that physiological measures such as HR and skin conductance can effectively indicate changes in cognitive engagement and mental processing (Dallaway et al. 2022; Mehler et al. 2009; Reimer & Mehler, 2011). However, if cognitive engagement during the Think Phase were a primary driver of increased physiological activity, we would expect more pronounced physiological effects in Block 2, the evaluation block, compared to Block 1. However, this was not observed, suggesting other factors might also be influencing the results. In addition, movement and breathing variations during each phase may impact the results, for instance, during the Empty and Swill phase, participants might exhibit more pronounced facial movements and variations in breathing patterns due to the physical act of swilling the solution around their mouth, which could lead to increased muscle activity and potentially elevated HR (Quintana & Heathers, 2014).

The current study is not without its limitations. Whilst the order of Concentrations were randomised within stimuli, due to a technical fault with the task set-up, the order of oral stimuli was not randomised across participants. Pure taste solutions, such as those used in the current study, are known to have lingering effects, in which the oral sensation persists even after rinsing with water and may alter taste perception of subsequent compounds (Delompre et al. 2019). In order to account for any oral sensation cross-over effects, future studies should ensure that either, the order of stimuli is randomised, or stimuli are tested during separate sessions. Research investigating physiological responses to oral stimuli generally consider responses to both pleasant and unpleasant stimuli, however, the current study focussed solely on affectively neutral and unpleasant stimuli. It is widely reported that perception of sweet tastes such as sucrose and saccharin, differs based on GTS. As such, it would be beneficial to understand whether the findings reported in the current study, extend to pleasant as well as unpleasant tastes. In addition, whilst the current study only included female participants, due to the notion that Super-Tasters are more prominent in the female population, it would be interesting to investigate whether physiological responses to oral stimuli differs across genders.

Research suggests that oral perception is sensitive to novelty (Verastegui-Tena et al. 2018), with oral stimuli rated as higher in intensity and lower in liking when experienced for the first time. The current study had participants rate the intensity and liking of oral sensations during the second block after all solutions had already been experienced. If the notion of novelty is true, it is possible the ratings of intensity and liking would have been much higher/lower (respectively) if taken during the Tasting Block (Block 1). However, in a similar study conducted by Cannon & Grigor (2007), it was found that facial EMG responses were greater during a second block, when subjective responses were required, thus suggesting that it was not novelty that impacted ratings, but rather the cognitive and evaluative processes involved in making subjective judgments. When participants are required to actively evaluate and rate their experiences, they engage in deeper cognitive processing, which can amplify their physiological responses. In replicating the current methods, further word should control for order of rating, in which participants rate stimuli over both blocks.

Given the results of the current study, subsequent studies could expand the range of stimuli to include more complex mixtures, such as combinations of tastants, as well as chemesthetic, thermal and tactile sensations, to provide a more comprehensive understanding of how different oral compounds interact and how these interactions are perceived by individuals with varying taste sensitivities. The use of EMG has proven to be a robust and sensitive measure of affective response to oral sensations (Armstrong et al. 2007; Beyts et al. 2017; Cannon & Grigor, 2017; Hu et al. 2000; Larsen et al. 2003; Merrill et al. 2023; Sato et al. 2008; Sato et al. 2020;), as such, future research should continue to leverage EMG to explore these more complex taste interactions, as it offers precise, real-time insights into the physiological underpinnings of taste perception. In addition, incorporating medium-tasters (Cannon & Grigor, 2017) in future studies, researchers can explore a more complete spectrum of taste sensitivity and examine whether EMG responses form a gradient across the taster groups. This could help elucidate whether the physiological measures observed are specific to the extremes of taste sensitivity or if they follow a more continuous pattern. Furthermore, investigating the role of other sensory modalities, such as olfaction and texture, in combination with taste stimuli, could offer insights into MSI in gustatory perception (Meredith et al. 1987; Stein et al. 2014). By broadening the scope of stimuli and participant groups, future research can build on the foundational findings of this study to enhance our understanding of the nuanced ways in which taste perception and sensitivity are encoded and differentiated by EMG measures.

In conclusion, the current findings demonstrate that the heightened sensitivity to bitter tastes observed in super-tasters also extends to other oral sensations, such as astringent and chemesthetic stimuli, thus, suggesting that super-tasters experience a more intense overall oral experience. Not only is this difference evident from subjective intensity ratings, but the current findings provide compelling evidence that physiological measures, particularly facial EMG, are effective in distinguishing between the sensitivities of oral sensations in super-tasters and non-tasters. Therefore, these findings highlight the utility of EMG as a robust tool for measuring implicit variations in oral sensory perception. In contrast to previous literature, HR did not distinguish between Tasters, which may be due to methodological differences, in which previous research focusses on differentiating responses to pleasant and unpleasant tastes, as opposed to between Non-Tasters and Super-Tasters.

Chapter 7: General Discussion

Grounded in the model of incentive salience, which posits that *'wanting'* and liking are distinct constructs (Berridge & Robinson, 1998), this thesis investigated the motivational, affective, and cognitive mechanisms driving oral behaviours, in determining how these shape consummatory experiences, preferences, and food-seeking behaviours. Specifically, it investigated how these sensory modalities influence health-related dietary behaviours and consumer choices, offering insights valuable to both health research and the food industry. Four studies were conducted to achieve these aims, each addressing different aspects of sensory perception and motivation. Initially, an objective measure of *'wanting'* was employed to assess whether implicit odour cues or food consumption influence incentive motivation for foods that are congruent with those cues, whilst also determining the effectiveness of an objective measure in capturing incentive wanting. The concept of liking was also examined, with particular attention to GTS, to evaluate whether physiological measures such as EMG and ECG can effectively measure whether the heightened sensitivity to bitter tastes observed in Super-Tasters extends to other oral sensations. Additionally, individual differences in olfactory perception were explored to determine if there is variability in how individuals process odours and whether this variability is associated with local versus global processing in the visual domain. This comprehensive approach aimed to deepen our understanding of the complex interplay between sensory perception and dietary behaviours, potentially informing health research and guiding the development of consumer products in the food and beverage industry. This final chapter will revisit the aims and objectives of each study, interpret the key findings, discuss their broader implications, and suggest future research directions.

7.1. The impact of ambient food odours in inducing sensory-specific satiety and priming effects

Chapter 3 sought to extend previous research that primarily used subjective reports and choice tasks (Chae et al. 2023; Gaillet et al. 2013; Morquecho-Campos, 2021; Proserpio et al. 2019; Ramaekers et al. 2014; Rolls & Rolls, 1997), which are susceptible to demand characteristics and dietary habits, by employing a more objective measure of motivation. Consistent with past research (Ziauddeen et al. 2012), it was found that participants showed greater motivation towards food images compared to control images, reflecting an appropriate response to motivationally salient visual cues, with greater effort to win high calorie, indulgent,

than low calorie, non-indulgent foods. However, the study found no evidence that ambient odour exposure influenced motivation for congruent food images, or food choices, which contrasts with previous research reporting odour priming effects, where non-conscious ambient odour exposure of 10-20 minutes is reported to impact food choice, appetite ratings, and food cue reactivity (Gaillet et al. 2013; Mas et al. 2020; Proserpio et al. 2019; Ramaekers et al. 2014). Despite some recent studies suggesting priming effects with shorter exposure times (Biswas & Szocs, 2019; Chae et al. 2023), the present study's five-minute exposure did not yield changes in incentive motivation towards associated foods.

It is, therefore, uncertain, as to whether the absence of odour exposure having an effect on motivation for food rewards, may be attributed to either the use of an objective grip-force measure of incentive motivation, or the odour exposure methodologies. Challenges in controlling odour concentration may contribute to inconsistencies, as effective priming requires that odours be neither too perceptible nor undetectable (Loersch & Payne, 2011; Smeets & Dijksterhuis, 2014). While the study's pilot tests showed low detection levels unless participants actively attended to the stimuli, indicating that the intensity was appropriately controlled, it underscores the necessity for standardised guidelines for odour dispersion and quantification. As such, further research is necessary, both to validate the use of objective measures of motivation and to explore how factors such as timing, intensity, or characteristics of food odours might influence and drive food behaviours. Future studies should consider varying exposure times, rigorously controlling odour concentration, and measuring subjective hunger levels to better understand the conditions under which odour priming might occur. These inconsistent findings underscore the reproducibility issues in the odour priming literature (Cesario, 2014) and the importance of detailed methodological reporting and replication in future studies.

7.2. The effectiveness of objective measures in assessing incentive *'wanting'*

Chapter 4 aimed to build on the findings of Chapter 3. As the previous study did not show any priming or satiety effects following odour exposure, it was of interest to explore whether this was due to uncertainties around odour exposure methodologies, or a lack of sensitivity of the grip-force task. The study, therefore, intended to validate the grip-force paradigm as an effective measure of motivation and to explore its sensitivity to changes in incentive value following food consumption. It was found that the grip-force paradigm, was indeed, an effective measure of motivation, in which the magnitude of expected reward correlated with

the amount of physical effort exerted. This was evident in that, force exerted for chocolate images declined significantly following chocolate consumption, in the absence of any decline in grip exerted for orange images.

This study validated the grip-force paradigm as an effective measure of incentive motivation, which aligns with previous research, supporting the notion that using rapid spontaneous responses to gauge implicit 'wanting' for rewards (Chong et al. 2016; Koningsbruggen et al. 2012; Mathar et al. 2015; Pessiglione et al. 2006; Schmidt et al. 2010; Ziauddeen et al. 2012;), is a less biased reflection of motivation compared to self-report measures, which are more influenced by cognitive and conscious processes (Berridge, 2009). In line with the findings of Chapter 4, prior to food consumption, participants exerted more effort for food items compared to non-food items. After consuming food, a classic sensory-specific satiety effect was observed, in that, force applied to chocolate images significantly decreased following chocolate consumption, whereas no such decrease was noted for orange images. Additionally, this satiety effect was also evident for food choices, in that, food consumption led to a greater number of incongruent food choices, with participants favouring food items incongruent to what they had consumed.

These findings align with existing literature on sensory-specific satiety, which suggests that metabolic state and the sensory attributes of consumed foods interact to influence motivated behaviours (Bijleveld et al. 2010; Ziauddeen et al. 2012). The effect was not observed in the orange condition, possibly due to the lower satiety value of oranges compared to chocolate, which had a higher caloric and macronutrient density. This discrepancy is consistent with research indicating that foods high in protein, fibre, and fat tend to produce greater satiety effects than lower-calorie alternatives (Astbury et al. 2010; Bertenshaw et al. 2009). The choice of non-matched macronutrient foods, such as chocolate and oranges, reflects previous studies comparing indulgent and non-indulgent foods (Biswas & Szocs, 2019), in that, satiety effects often follow intake of high-calorie foods such as full-fat chocolate milk and desserts, corroborating the satiety effect observed with chocolate cake in this study (Pirc et al. 2019; Ziauddeen et al. 2012).

7.3. Cognitive processes underlying processing of complex odour mixtures.

Chapter 5 sought to provide insight into the cognitive processes underlying olfactory processing and to explore the domain generality of sensory perception. It was found that there

is, indeed, some overlap in the domain general cognitive processes required for performance of complex odour mixtures and visual tasks, specifically, processing speed presented some advantage olfactory scene analysis. In exploring odour mixture complexity, participants performed better with Binary mixtures compared to Ternary mixtures, which is consistent with previous literature, suggesting that more complex mixtures, involving perceptual blending of multiple components, can obscure the distinctiveness of individual odours (Laing & Francis, 1989; Le Berre et al. 2007). However, the current study's use of ecologically relevant multi-molecular blends may contribute to increased perceptual blending compared to previous research that utilised mono-molecular odourants (Tromelin et al. 2020).

Whilst there was no direct association between performance on the odour mixture task and traditional measures of local processing advantage on the Navon task or the block design task, exploratory analysis revealed some overlap in the cognitive processes required for these tasks. Specifically, faster response times on the Navon task were associated with greater accuracy on the Binary odour mixture task, suggesting that processing speed benefits the analysis of simpler olfactory scenes. An advantage that did not extend to the more complex Ternary mixtures, indicating that different or additional cognitive strategies might be needed for such tasks (Walker et al. 2020). The interaction between processing speed and higher-order cognitive functions such as selective attention is well documented (Motes et al. 2018; Wong et al. 2021), in that, faster processing speed is often associated with improved ability to focus on specific details, which aligns with our finding that individuals with faster processing speeds excelled in segmenting odour objects in simpler mixtures (Prinzmetal et al. 2005; Vaportzis et al. 2013; Jehu et al. 2015). Contrary to some previous studies, we did not find an association between autistic traits and performance on visual or olfactory tasks (Happe & Booth, 2008; Neufeld et al. 2019; Simmons et al. 2009). This may be due to the negatively skewed distribution of AQ scores in our sample or the difference in how autistic traits affect sensory processing compared to clinical diagnoses (Behrmann et al. 2006; Van Eylen et al. 2018).

Future research could expand the variety and combinations of odour stimuli to thoroughly investigate the olfactory processing mechanisms involved in identifying individual odours within a mixture. While controlled studies often focus on mono-molecular odourants (e.g. vanillin, butanol), real-world odour mixtures, such as those found in food, perfumes, or wine, feature complex, multi-molecular interactions that lead to emergent perceptual phenomena (Thomas-Danguin et al. 2014). Comparing simple molecules with more complex mixtures

could bridge this gap, enhancing our understanding of the interaction dynamics and processing styles within the olfactory system. By doing so, it would help shed light on the complexities of odour perception and the factors that affect the accuracy and sensitivity of odour detection, such as blending, masking, and synergy effects (Laing & Willcox, 1983; Stevenson et al. 2007; Miyazawa et al. 2008). This approach would also provide valuable insights into how these mechanisms may differ in clinical populations, such as individuals with autism, by examining the relationship between olfactory processing and autistic traits in clinical versus non-clinical population, thus, allowing for a more comprehensive understanding of how olfactory sensitivities influence food preferences. Additionally, exploring a broader range of odours and their combinations could reveal more nuanced insights into sensory integration and its impact on behaviour and quality of life in various populations.

7.4. Assessing the effectiveness of physiological measures in differentiating between Super-Tasters and Non-Tasters

Chapter 6 looked to determine whether facial EMG, an established measure of affective responses to sensory stimuli, can be used to differentiate between PROP Super-Tasters and Non-Tasters in their affective responses to threshold and suprathreshold bitter, astringent and chemesthetic compounds. The findings support the use of facial EMG as a reliable measure of hedonic responses to oral stimuli and highlight the influence of genetic taster status on sensory perception. The results suggest that individual differences in affective responses to oral stimuli are not limited to taste but also involve other oral sensory modalities. This underscores the importance of considering genetic and individual differences in sensory research and highlights the potential for using implicit measures to capture immediate liking and emotional reactions.

Consistent with previous literature, significant differences were observed between Super-Tasters and Non-Tasters in their subjective perception of bitter, astringent and chemesthetic compounds. Specifically, Super-Tasters rated the intensity of supra-threshold concentrations of caffeine, alum, and menthol higher than Non-Tasters, although it is noteworthy that liking ratings for alum and menthol did not differ significantly between the groups. The study is notably the first to report heightened sensitivity to menthol in Super-Tasters, which may potentially be due to a greater density of TRPM8-immunoreactive nerve fibres are rich in fungiform papillae, or menthols interaction with bitter taste receptors. EMG was effective in differentiating between Super-Tasters and Non-Tasters, particularly for supra-threshold concentrations. Zygomaticus muscle activity, typically associated with positive, but also with

negative affect via grimacing, showed increased responses to perceptually intense, affectively neutral, and unpleasant tastes in Super-Tasters. Corrugator muscle activity was more pronounced for bitter solutions, which were the most aversively rated highlighting the established relationship between corrugator activation and negative affect. Contrary to expectations, HR did not distinguish between Super-Tasters and Non-Tasters. suggesting HR is better suited to differentiating hedonic responses to clearly pleasant and unpleasant stimuli rather than the perceived intensity of oral sensations. Both EMG and HR showed increased activity during the "Think Phase," but this was consistent across taster groups, suggesting that cognitive engagement during this phase influenced physiological responses.

Future research should address several critical areas to refine and extend the findings. Expanding the scope of stimuli to include a wider array of taste profiles, such as sweet and pleasant tastes, will allow for a more comprehensive examination of how different taste sensitivities impact perception across a broader spectrum. In order to minimise the potential impact of lingering taste effects, it is essential to randomise the order of stimuli or conduct testing across separate sessions. This adjustment will help control for any cross-over effects that might alter taste perception of subsequent compounds. Additionally, future studies should include both male and female participants to investigate any potential gender differences in physiological responses. Incorporating medium-tasters alongside super-tasters and non-tasters will help determine if EMG responses form a gradient across varying levels of taste sensitivity. Lastly, integrating other sensory modalities, such as olfaction, will provide insights into MSI and its effects on gustatory perception. By addressing these areas, future studies can leverage facial EMG to offer a more nuanced understanding of the physiological mechanisms underlying taste perception.

7.5. Conclusion

Overall, the findings of this thesis indicate that reward cues can influence incentive motivation for food reward, however, whilst this is evident following food consumption, the effectiveness of odour cues remains under explored, and thus, warrants further investigation with a focus on methodological details. In addition, the way in which individuals process real-world odours can be influenced by their overall processing speed and cross-sensory skills, suggesting that those with quicker cognitive processing and strong abilities in one sensory

domain may excel in recognising and distinguishing complex smells. Lastly, facial EMG is a valuable tool for assessing individual differences in perception oral stimuli, offering an alternative to rating scales which are sensitive to demand characterises and the completion of which disrupts ongoing behaviour. This method also reveals that variations in the perception of bitterness can extend to other oral sensations, providing insight into how genetic differences influence broader sensory experiences and emotional responses.

7.6. Practical Implications

Integrating findings from this thesis into practical applications for both the food industry and oral health sectors can significantly enhance our understanding and management of sensory and dietary behaviours. Oral health is a critical yet often overlooked aspect of overall well-being, with alarming statistics highlighting that globally, poor oral hygiene contributes to significant health disparities, manifesting in high rates of dental caries, periodontal disease, and oral cancers. Nearly 3.5 billion people suffer from oral diseases (WHO, 2022). This research highlights the importance of considering individual differences in taste sensitivity and sensory perception when developing dietary recommendations and oral health interventions. Understanding how factors such as taste sensitivity impact food choices and consumption patterns can aid in creating more personalised dietary guidelines and educational materials that promote better oral hygiene and prevent oral diseases. For the food industry, insights into how sensory cues, such as taste and smell, influence food preferences and consumption can inform the development of products that better meet consumer needs and preferences. By leveraging knowledge about the distinct motivational and affective responses to various flavours and food cues, companies can design products that appeal to a broader audience or cater to specific taste sensitivities, improving customer satisfaction and engagement.

Understanding cognitive processes and individual differences in odour and taste perception, and the way in which individuals respond to various scent and flavour combinations, can allow manufacturers to develop customised oral care products (e.g. toothpaste, mouthwash) for individuals with specific sensory preferences or challenges, allowing for more positive user compliance and satisfaction rates. By optimising the sensory experience, oral health companies can create products that not only meet functional needs but also make daily routines more enjoyable, potentially increasing adherence to oral hygiene practices. Additionally, in public health contexts, insights from this research could be utilised to develop environmental cues in food establishments that either reduce unhealthy eating

behaviours or promote healthier food choices. For instance, ambient scents could be strategically used in public spaces to reduce the appeal of high-calorie foods and encourage healthier eating patterns, however, given the inconsistent findings across the priming literature, along who those in Chapter 3, more research is needed in order to refine the conditions under which odour priming occurs.

Physiological measures, such as facial EMG, can offer significant insights into taste sensitivity and its impact on oral care by capturing real-time, involuntary facial responses to different taste stimuli. This approach has highlighted important findings, particularly regarding individuals with heightened sensitivity to specific tastes such as menthol, a common ingredient in oral health products. This heightened sensitivity means that Super-Tasters might experience stronger or more discomforting reactions to menthol compared to non-Tasters, possibly resulting in avoidance of oral care routines. Understanding these nuanced responses enables the development of oral care products that are tailored to diverse taste sensitivities. For Super-Tasters, reducing the concentration of menthol or offering alternative flavourings can make oral health products more comfortable and acceptable. By incorporating these physiological insights into product formulation, manufacturers can enhance the overall user experience, particularly for those with altered taste perceptions due to genetic differences. This approach not only improves user satisfaction but also promotes better adherence to oral health routines, ensuring that oral care products are effective and enjoyable for a wider range of consumers. In health research and clinical practice, insights into taste sensitivity can inform personalised dietary recommendations and interventions. For individuals with heightened sensitivity to bitter or astringent tastes, tailored dietary advice can help manage conditions such as hypertension or diabetes, where taste preferences play a role in adherence to dietary guidelines. Additionally, exploring the interactions between taste sensitivity and other sensory modalities can lead to a more comprehensive understanding of how multisensory experiences impact dietary behaviours, ultimately contributing to more effective strategies for promoting healthy eating habits.

Measures of incentive motivation, such as the grip-force paradigm, and physiological measures such as facial EMG, also offer significant advantages for the consumer food and health industries, which typically rely on self-report methods to gather feedback on the production of new products. Traditional self-report methods are often subject to demand characteristics and disrupt on-going behaviours, potentially altering natural emotional

responses to a product. In contrast, measures of incentive motivation can provide objective insights into product desirability by assessing implicit responses to sensory cues, revealing genuine consumer preferences that are less influenced by cognitive biases and more reflective of automatic, unconscious desires. Physiological measures like facial EMG allow for the assessment of affective responses without interrupting ongoing behaviour, providing a more nuanced and accurate understanding of consumer reactions. Facial EMG continuously monitors subtle muscle activities associated with emotional expressions without requiring consumers to pause and reflect on their experience. This enables the capture of spontaneous and genuine emotional reactions in real time, as consumers engage with a product, whether eating, drinking, or using an oral care item. This non-intrusive monitoring provides a deeper and more accurate understanding of consumer reactions, capturing immediate, unconscious responses that self-reports might miss.

Overall, integrating these research findings allows oral health and food industries to innovate in ways that enhance user experience, improve adherence to oral care routines, and address individual sensory needs. By leveraging insights from sensory perception, motivational factors, cognitive processes, and physiological responses, industries can develop more effective and user-friendly oral health products, ultimately supporting better oral health and patient well-being.

7.7. Next steps

In the context of MSI, the findings from our EMG study provide important insights into the differential sensitivity of Super-Tasters and Non-Tasters to bitter tastes and other oral sensations such as astringency and chemesthetic stimuli. Our results support the hypothesis that EMG is effective in differentiating between Super-Tasters and Non-Tasters based on their sensitivity to these oral sensations.

To extend this work, future research could explore the integration of more complex oral stimuli. For example, studies could investigate how the simultaneous presentation of multiple taste, smell, and chemesthetic stimuli affects the perceptual experience and neural processing in super-tasters and non-tasters. This would involve looking at how different combinations of stimuli (e.g. sweet/bitter, menthol/astringent) are integrated and how this integration differs between individuals with varying taste sensitivities. This could build on findings that simultaneous presentation of stimuli from different modalities enhances sensory perception,

such as how simultaneous presentation of benzaldehyde with a saccharin solution significantly increased taste enhancement (Djordjevic et al. 2004; Pfeiffer et al. 2005). Moreover, incorporating the principles of MSI, such as the temporal and spatial congruence of stimuli, could provide a deeper understanding of the mechanisms underlying taste perception. For instance, studies have shown that temporal congruence significantly impacts MSI, with stronger effects observed when stimuli are presented simultaneously (Meredith et al. 1987; Stein et al. 2014). This principle was demonstrated in flavour perception studies were holding a sub-threshold concentration of saccharine in the mouth reduced detection thresholds for a sweet almond aroma (Dalton et al. 2000; Pfeiffer et al. 2005). Future work could look at examining whether the temporal binding window for taste and smell integration differs on the basis of GTS, revealing new insights into whether these groups process multisensory information differently. Additionally, using techniques like fMRI in conjunction with EMG could help identify the specific brain regions involved in the integration and oral sensitivity of complex oral stimuli. This could further elucidate the neural pathways that contribute to the enhanced or diminished sensory experiences observed in Super-Tasters and Non-Tasters. For example, previous research has shown differential activation in brain regions such as the insula/operculum, thalamus, hippocampus, amygdala, and orbitofrontal cortex based on whether an odour is perceived orthonasally or retronasally (Small et al. 2005). Understanding these neural mechanisms could inform how different sensory modalities contribute to the overall flavour experience and whether this differs in-line with oral sensitivity.

By building on the MSI framework outlined in the introduction, future studies could not only validate the current findings but also explore new dimensions of MSI in taste perception. This would enhance our understanding of how sensory modalities interact and contribute to the overall flavour experience, ultimately informing the development of more effective interventions for individuals with altered taste perception. Furthermore, the role of MSI in flavour perception could be expanded by investigating how different sensory pathways (orthonasal vs. retronasal) interact with taste and other oral sensations to influence perceptual and hedonic responses (Lim & Green, 2007; Rozin, 1982; Small & Green, 2011).

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Appendix 1: 12cm Visual Analogue Scales (VAS) for Odour Jars.

Age:……. Gender:……..

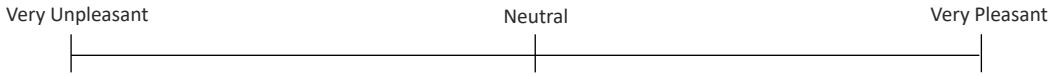
Upon smelling the contents of the jar, please state whether you are able to perceive an odour.

- ☐ Yes ***(If you answered yes, please complete the rest of this form)***
- ☐ No ***(If you answered no, you do not need to complete the rest of this form)***

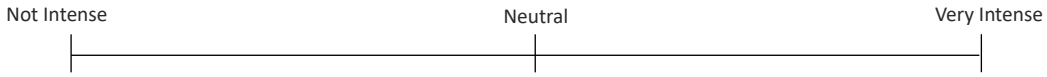
Can you identify this odour? .....

Please use the scales below to rate the pleasantness, intensity, familiarity, edibility and expected liking of the odour, whilst also trying to identify the odour.
Please note: you are able to make your ratings anywhere on the line.

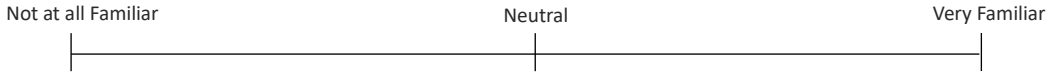
Pleasantness – How pleasant is this odour.



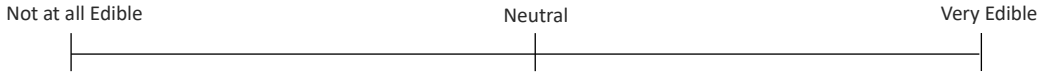
Intensity – How intense is this odour.



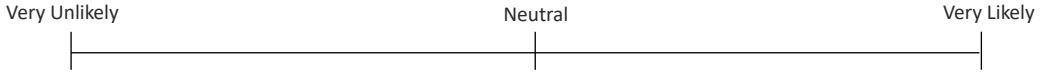
Familiarity – How familiar is this odour to you



Edibility – How likely would you be to eat the food (if applicable) associated with this odour.



Expected liking – How much do you think you would like the food associated with the odour (if applicable)



Appendix 2: 12cm Visual Analogue Scales (VAS) for Odour Rooms.

Age:……. Gender:……..

Upon entering each room, please state whether you are able to perceive an odour.

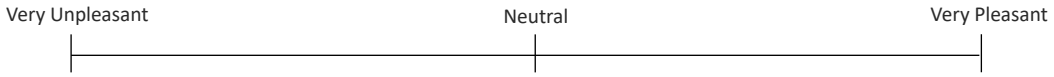
- ☐ Yes ***(If you answered yes, please complete the rest of this form)***
- ☐ No ***(If you answered no, you do not need to complete the rest of this form)***

Can you identify this odour? .....

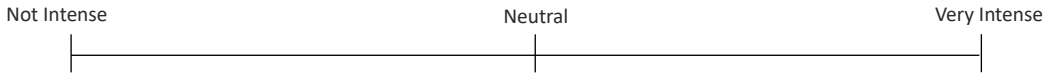
Please use the scales below to rate the pleasantness, intensity, familiarity, edibility and expected liking of the odour, whilst also trying to identify the odour.

Please note: you are able to make your ratings anywhere on the line going across the sheet.

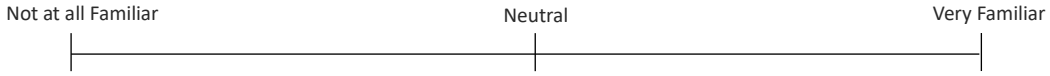
Pleasantness – How pleasant is this odour.



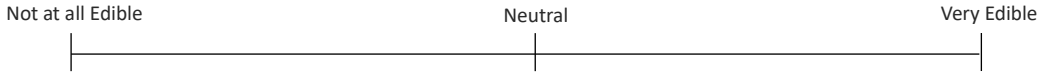
Intensity – How intense is this odour.



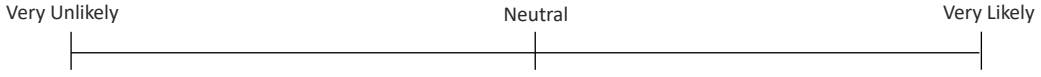
Familiarity – How familiar is this odour to you.



Edibility – How likely would you be to eat the food (if applicable) associated with this odour.



Expected liking – How much do you think you would like the food associated with the odour (if applicable).



Appendix 2: Supplementary Data from Chapter 3

Identification

On the initial identification task, participants were able to correctly identify the odours on a total of 76.8% of trials. As shown in Figure 3.2, Cola Bottles were correctly identified most frequently *(84.7%),* with Marzipan being identified least frequently (62.7%*).* All other odours had similar amount of correct response *(Blackcurrant = 76.3%, Orange = 81.4%, Chocolate = 81.4%, Strawberry = 74.6%).* A binomial logistic regression was performed to ascertain the effect of Odour on Identification Accuracy. The logistic regression model was not statistically significant, $\chi^2(5) = 9.80$, $p = .08$ and explained 4.0% (Nagelkerke R^2) of the variance in Identification, indicating all odours were equally well identifiable when presented individually.

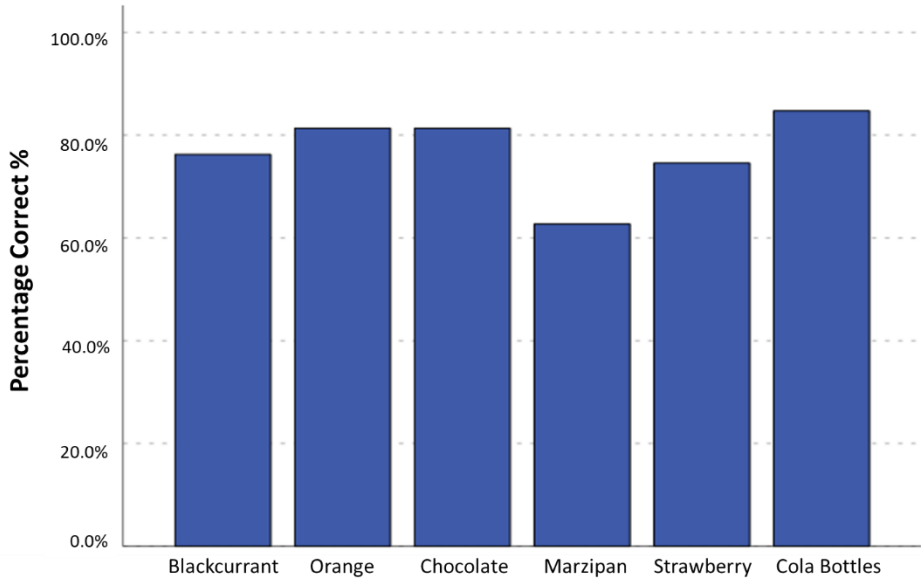


Figure 1*: Percentage of correct responses for each odour during phase one of the Identification task.*

The nature of the errors made during identification testing for each individual odour are shown in Table 3.2. The odours most often confused were Chocolate and Marzipan, with Chocolate being mistaken for Marzipan 15.25% of trials and Marzipan also being mistaken for Chocolate 15.25% of trials. During the first identification phase, participants were provided the correct answer after each trial. Identification accuracy on the second phase was 100%.

***Table 1**: Number/Percentage and nature of incorrect responses for each odour during phase one of the identification task.*

Target	Response - n(%)						
	Blackcurrant	Orange	Chocolate	Marzipan	Strawberry	Cola Bottles	Total
Blackcurrant	45 (76.27)	3 (5.08)	-	-	-	11 (18.64)	59 (100.00)
Orange	7 (11.86)	48(81.36%)	-	2 (3.39)	-	2 (3.39%)	59 (100.00)
Chocolate	2 (3.39)	-	48 (81.36)	9 (15.25)		-	59 (100.00)
Marzipan	6 (10.17)	-	9 (15.25)	37 (62.71)	2 (3.39)	5(8.47)	59 (100.00)
Strawberry	11 (18.64)	-	-	4 (6.78)	44 (74.58)	-	59 (100.00)
Cola Bottles	3 (5.08)	3 (5.08)	2 (3.39)	1 (1.69)	-	50 (84.75)	59 (100.00)

Mixtures

During the mixture trials, each participant completed six Binary and six Ternary trials, with each of the odours being presented as the target odour twice *(once for Binary and once for Ternary).* As shown in table 3.2, participants were more accurate at identifying the target odour on the Binary (M=.61, SD=.23), compared to the Ternary (M.51, SD=.22) trials. A binomial logistic regression was performed to ascertain the effect of Odour on Identification Accuracy on the Binary and Ternary trials. Logistic regression models were not statistically significant for the Binary $\chi^2(1) = .45, p = .50$, or Ternary trials $\chi^2(1) = .35, p = .55$, and explained 0.2% and 0.1% of the variance (Nagelkerke R^2) respectively. Thus, the target odours did not differ significantly in how identifiable they were in either binary or ternary mixtures.

Table 2: *Number and Percentage of correct responses for the Binary and Ternary mixture combinations. Target shows the odour the participants were required to identify.*

	Target	n(%) Correct
Binary	Blackcurrant	35(59.3)
	Strawberry	27(45.8)
	Chocolate	37(62.7)
	Cola Bottles	46(78.0)
	Orange	38(64.4)
	Marzipan	36(61.0)
	Combined Total of all Trials	**219(61.9)**
Ternary	Blackcurrant	30(50.8)
	Strawberry	24(40.7)
	Chocolate	29(49.2)
	Cola Bottles	33(55.9)
	Orange	35(59.3)
	Marzipan	28(47.5)
	Combined Total of all Trials	**179(50.6)**