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Pleasure from Food

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GENERAL INTRODUCTION

1.1 GENERAL INTRODUCTION

At this moment, older adults (65+ years) constitute around 8% of the world's population and this proportion is expected to increase to approximately 16% by the year 2050 (United Nations, 2010). This demographic shift brings forth a new set of challenges aiming to delay and limit the loss of health during the process of aging. There is increasing awareness that dietary intake is an important factor in age-related pathologies and quality of life in older adults (Amarantos, Martinez, & Dwyer, 2001; Briefel et al., 1995; Dato, Bellizzi, Rose, & Passarino, 2016; Fischer & Johnson, 1990; Han, Li, & Zheng, 2009; Thomas, 2001). By modifying dietary intake, in an effort to achieve adequate intake, one might foster healthy aging. However, dietary intake across the human lifespan is regulated by a complex interplay between physiological and non-physiological factors that is not easy to disentangle (de Boer, Ter Horst, & Lorist, 2013). An important non-physiological determinant of dietary intake is the pleasure we experience from consuming food (Appleton, McGill, Neville, & Woodside, 2010; Best, 2012; Blundell & Rogers, 1991; Hetherington, 1998; Leslie, 2011). Naturally, individuals eat more of the foods they like and less of the foods they dislike (de Graaf et al., 2005). An individual may have awareness of which foods they like and dislike, while remaining unaware of the processes that underlie the experience of pleasantness (Finlayson, King, & Blundell, 2008). The aim of this thesis was to unravel the neuronal mechanisms underlying food pleasantness in healthy young and older adults; that is, in individuals that reported no functional decline or disease.

1.2 SENSORY AND CONSUMER SCIENCE – FOCUS ON PRODUCT AND PERSON CHARACTERISTICS

One way of assessing food pleasantness is to manipulate the sensory characteristics of a food product and measure the effect of this manipulation on subsequent behavioral expressions of pleasantness. The most commonly used question to measure pleasantness is “How much do you like this food?” after tasting a small sample of a food stimulus (Sørensen, Møller, Flint, Martens, & Raben, 2003). Participants are typically instructed to answer this question on Likert (fixed point) or Visual Analogue (continuous) scales. Manipulations of sensory characteristics, such as increasing the concentrations of tastes, are thought to increase food pleasantness in older adults, as is evident by older adults with sensory losses showing higher liking ratings compared to young adults for higher concentrations of tastes and stronger tasting food products (e.g., custard desserts and tomato drinks) (Griep et al., 2000; Koskinen, Kälviäinen, & Tuorila, 2003; Kremer, Bult, Mojet, & Kroeze, 2007*a*; Murphy & Withee, 1986; Schiffman & Warwick, 1993). Following this, it was widely assumed that aging was related to changes in the sensation of taste and smell intensity of food, which in turn affected food pleasantness.

The sensation of food by the human senses (i.e., smell, taste, somatosensation, sight, and hearing; see Figure 1) is studied in sensory science with the purpose of understanding how sensory signals affect the experience of pleasantness in response to food. Such studies primarily focused on chemosensation, which encompasses taste and smell sensations originating from the mouth. Methodologies applied to investigate chemosensation include behavioral ratings of intensity perception (e.g., “How intense do you perceive this food on a scale from 1-9?”) and psychophysical tests,

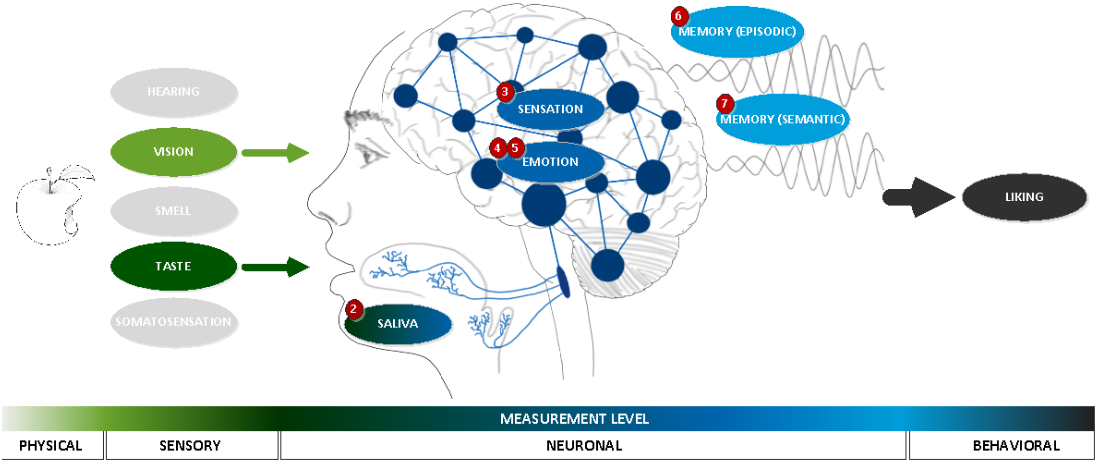

Figure 1. Mechanisms underlying food pleasantness can be investigated using a combination of physical, sensory, neuronal, and behavioral measures. Liking ratings are the final behavioral outcome of the interaction between physical product characteristics and person characteristics like saliva secretion (Chapter 2), sensation (Chapter 3), emotion (Chapter 4 and 5), and memory (Chapter 6 and 7). These neuronal mechanisms underlying pleasantness were investigated in this thesis using functional Magnetic Resonance Imaging (fMRI) and electroencephalography (EEG).

such as detection, identification, and discrimination tests (Garber, Hyatt, & Starr, 2003; Jauregui-Lobera & Bolaños Rois, 2011; Methven, Jiménez-Pranteda, & Lawlor, 2016; Sørensen, Møller, Flint, Martens, & Raben, 2003). For example, “Taste Strips”, filter paper strips impregnated with four basic taste qualities in four different concentrations, are used as a quick psychophysical test to assess taste sensitivity (Landis et al., 2009). In this test, participants are asked to place a strip on their tongue and to identify the taste from a list of five qualities (i.e., sweet, sour, salty, bitter, or neutral). Each taste quality is tested using four different concentrations. The number of correctly reported taste qualities corresponds to an overall ‘taste score’ as a measure of taste sensitivity. Based on these and related studies, using intensity rating scales and psychophysical tests, it was concluded that taste sensitivity among older adults is lower compared to young adults and that this sensitivity further decreases with advancing age (Methven, Allen, Withers, & Gosney, 2012; Mojet, Christ-Hazelhof, & Heidema, 2001; Mojet, Heidema, & Christ-Hazelhof, 2003; Murphy, 1993; Murphy et al., 2002; Ng et al., 2004). The sense of smell is described to decrease even more than the sense of taste (Stevens, Bartoshuk, & Cain, 1984). Given that product characteristics remain constant, the age-related changes in both taste and smell sensitivity are due to changes in the person perceiving food-related information. These perceptual changes are assumed to affect pleasantness; however, data supporting this assumption are currently lacking (Kozlowska et al., 2003; Kremer et al., 2007b; Mattes, 2002; Rolls, 1999).

1.3

PLEASANTNESS: A PERSON’S PERCEPTION

The distinction between sensation and perception, that takes place within a person, complicates our understanding of the relation between sensation and pleasantness. Pleasantness is the subjective perception of a person whose sense organs have been stimulated. This subjective perception tells us something about the chemosensory stimulus (i.e., taste or smell of a food product), but goes beyond the stimulus and its characteristics. For example, molecules of caffeine in coffee stimulate bitter taste receptors cells (TRCs) and we therefore experience a bitter taste. The interaction between a food product and a person's perception is crucial to induce pleasantness. Whereas humans are born with an aversion for the bitter taste, the liking of bitter tasting coffee can be developed through learning mechanisms without changing the bitter sensation on the tongue (Yeomans, 2009). A positively experienced effect of caffeine in coffee may lead to increased pleasantness for the bitter taste of coffee. Thus, pleasantness requires people to combine information from the senses with previous experiences stored in memory (Figure 1).

A growing number of consumer science studies recently focused on characteristics of the person that contribute to the experience of pleasantness during eating, in addition to taste and smell sensitivity. For example, the role of emotions underlying pleasantness is increasingly acknowledged. Emotions can be defined as short-term, affective responses to the appraisal of particular stimuli (Matthews & Deary, 1998). It is important to recognize that the stimulation of sense organs by tastes, varying in quality and concentration, which are specific product characteristics, do not inherently elicit emotions; rather, emotions seem mainly dependent on the person's context and experience (Booth, 1994). Questionnaires were developed to assess which emotions people associate with food products or mealtimes (King & Meiselman, 2010). Older adults vary in the emotions that they associate with their mealtimes, due to long and divergent experiences with and memories of these occasions (den Uijl, Jager, de Graaf, Waddell, & Kremer, 2014).

It can be argued that positive and negative emotions evoked by food products are important modulators of the experience of food pleasantness, and may thereby affect dietary intake (Dalenberg, Gutjar, et al., 2014; Garber, Hyatt, & Starr, 2003; Gutjar et al., 2015; Jauregui-Lobera & Bolaños Rois, 2011). It has been suggested that especially as people grow older, emotions evoked by experience play an increasing role in decision making (Peters, Diefenbach, Hess, & Västfjäll, 2008; Roalf, Pruis, Stevens, & Janowsky, 2011). In particular, negative emotions, like sadness, decrease dietary intake in older adults (Chapman & Nelson, 1994; Marcus & Berry, 2009; Pamuk et al., 1992). We hypothesize that the increasing role of emotions may partly explain the absence of a direct relation between age-related changes in taste and smell sensitivity and pleasantness.

1.4 FROM BEHAVIORAL TO NEUROIMAGING RESEARCH

The focus on behavioral measures indexing sensitivity and pleasantness may limit our understanding of age-related changes in food pleasantness. Behavioral measures, such as taste discrimination thresholds, liking ratings, and emotion questionnaires, are based on verbal, overt behavior that taps into deliberate and controlled processes. With respect to aging, it was proposed that aging induced a switch from automatic to more controlled processing (Staub, Doignon-Camus, Marques-Carneiro, Bacon, & Bonnefond, 2015). For example, older adults might enhance attention to sensory input, in order to compensate for a decline in automatic detection of changes in the molecular composition of tastes (Alain, McDonald, Ostroff, & Schneider, 2004; Madden, Whiting, Spaniol, & Bucur, 2005). This implies that differences in discrimination thresholds between young and older adults may result from changes in input processing by the sensory organs, as well as attention (Weiffenbach, Baum, & Burghauser, 1982). In addition, with respect to the experience of pleasantness, older adults might regulate negative towards more positive emotions during food perception, compared to young adults (Carstensen, Pasupathi, Mayr, & Nesselroade, 2000; Labouvie-Vief, 2003; Onoda, Ishihara, & Yamaguchi, 2012; Tsai, Levenson, & Carstensen, 2000). Therefore, we hypothesize that behavioral measurements of age-related differences in the experience of pleasantness with liking ratings and emotion questionnaires are confounded by differences in emotion processing.

Although people may be aware of the pleasure they experience while eating, it cannot be claimed that the automatic processes that underlie the experience of food pleasantness necessarily become explicit. Due to the limitations of behavioral measures being a reflection of overt behavior, automatic processes have been largely overlooked.

In this thesis, we extend the above-described behavioral findings on the relation between sensation and pleasantness using two neuroimaging techniques (Figure 1). First, we investigated the underlying neuronal mechanisms elicited by the sensation of food in the mouth, which resulted in the behavioral expression of pleasantness by means of overt behavior reflected in liking ratings in young and older adults. In these studies we focused on the sensation of taste, since the mechanisms underlying the processing of taste information are least understood, with respect to aging. Taste processing involves deep brain structures (Doherty, Rolls, Francis, Bowtell, & Glone, 2001), posing functional magnetic resonance imaging (fMRI) as a useful method, due to its high spatial resolution (see paragraph 1.5). Furthermore, we investigated how previous eating experiences, stored in memory, affect the brain's response to pictures of food in young adults. We used the high temporal resolution of electroencephalography (EEG; see paragraph 1.5) to examine possible transfer of previous findings regarding memory towards the food domain.

1.5

METHODS TO STUDY THE NEURAL MECHANISMS OF FOOD PLEASANTNESS.

Magnetic resonance imaging (mri)

MRI is a non-invasive imaging technique, primarily used to produce high quality images of the structure of tissue inside of the body. The MRI technique is based on the magnetic properties of hydrogen molecules. These molecules have an axis of rotation and a magnetic moment (i.e., they behave like a compass needle), which aligns when placed in a static magnetic field. However, alignment is not perfect, resulting in a precessional movement (i.e., the axis of rotation sweeps out a cone). When a radiofrequency (RF) pulse is applied, the precessional movement of the hydrogen molecules is tilted. When the RF pulse is turned off, the precession remains. In other words, after a RF pulse is applied, there is a rotating magnetic field which can be picked up by a receiver in the MRI device. The signal intensity measured by the MRI device differs, depending on tissue density in the brain, which forms the basis for constructing a structural image of the brain (Ward, 2010).

If one is interested in changes of brain responses over time, functional magnetic resonance imaging can be used (fMRI). The signal measured with fMRI is based on the magnetic properties of hemoglobin, a protein that binds oxygen in the blood. Hemoglobin may disturb the local magnetic field, causing an alteration of the signal from hydrogen molecules as described above. It is known that blood that has released its oxygen (deoxygenated hemoglobin) causes a larger distortion of the magnetic field than blood that is carrying its oxygen (oxygenated hemoglobin). Changes in the relative concentration of deoxygenated hemoglobin give rise to the blood oxygenation level dependent (BOLD) effect, which increases when brain areas become more active and need more oxygen. BOLD responses are measured across multiple functional images of the brain during task performance. The time scale of the BOLD response is much slower than the time scale of neuronal activity, leaving fMRI with a low temporal resolution (~ 2s). In this thesis, we used fMRI to measure BOLD responses during tasting as an indirect measure of neuronal activity related to taste processing (Goebel, 2007; Heeger & Ress, 2002) (**Chapter 2, 3, 4, and 5**).

Each functional image has a high spatial resolution, because it consists of small three-dimensional cubes called voxels (~ 3 x 3 x 3mm). Classical fMRI analysis involves running a linear regression model per voxel, including the measured BOLD response for that voxel over time as a dependent variable. This way, voxels of which the BOLD response is modulated by a particular stimulus or task, can be identified. Furthermore, stimulus- or task-related BOLD responses can be compared between experimental groups (e.g., young and older adults).

In order to spatially localize the signals in the brain, functional images can be overlaid on a structural image. In this thesis, we focused on investigating age-related changes in BOLD responses in grey matter brain tissue. In general, loss of grey matter in frontal brain areas is one of the most consistent findings in the aging brain (Fjell et al., 2009; Raz et al., 1997), followed by reduced grey matter in the caudate nucleus, hippocampus, temporal and parietal cortices, and minimal age-related grey matter changes in the occipital lobes (Raz & Rodrigue, 2006; Raz et al., 2005). Overall, the findings of age-related changes in grey matter are highly variable across individuals and brain functions (MacDonald, Nyberg, & Bäckman, 2006; Vaidya, Paradiso, Boles Ponto, McCormick, & Robinson, 2007). In this thesis, we have taken possible age-related differences in grey matter into account when investigating age-related changes in taste processing, by overlaying functional images of the brain on a group specific structural image instead of using the Montreal Neurological Institute (MNI) structural image composed of 152 young brains (Ashburner, 2007) (**Chapter 2, 3, 4, and 5**).

Electroencephalography (EEG)

In addition to the use of an indirect measure of neuronal activity, the results of direct measurement of neuronal activity are also reported in this thesis. When large populations of neurons are active together, they produce electrical potentials large enough to be measured by electrodes placed on the scalp (**Figure 1**). A change in voltage corresponding to the difference in potential between the signal at a recording electrode and the signal at a reference electrode is measured. The recorded signal is called an electroencephalogram.

Approaches used to gain insight in brain function focus on how brain responses are modulated by a particular stimulus or task. The evoked response, or event-related potential (ERP), is a tiny signal embedded in the ongoing EEG. Averaging the evoked response across stimuli reduces the background noise, leaving the ERP (Luck, 2014). A significant feature of evoked responses is that they provide a precise temporal representation (i.e., ms level) of underlying neuronal activity. The ERP consists of different positive and negative peaks, or components, elicited by a specific event (e.g., stimulus presentation or behavioral response), which are typically related to specific stages of information processing. For this reason, ERPs are especially suited to address questions about the time course of neuronal processes, whereas the fMRI BOLD responses elucidate the spatial representation of neuronal processes. This important temporal resolution of the ERPs was utilized in this thesis. We investigated how information about food pleasantness stored in memory (i.e., episodic memory: **Chapter 6**; semantic memory: **Chapter 7**) affected different stages of processing of pictures of food in young adults.

Recently, the interest of many researchers has broadened from ERPs to oscillatory changes that reflect induced neuronal activity. Whereas ERPs are defined by the amplitude of the neuronal activity, oscillatory changes are defined by the frequency of neuronal activity. Power is used as a measure of frequencies over time. There is, for example, an increased use of asymmetries of alpha power over the frontal cortex as a measure of emotional experience (Allen & Kline, 2004). The tool that is most often used to study oscillatory changes in neuronal activity is time-frequency analysis (Cohen, 1995). This technique has been used to examine oscillatory changes induced by food stimuli (**Chapter 6**).

1.6 NEURAL MECHANISMS OF FOOD PLEASANTNESS

Product characteristics

Food products are very complex stimuli with respect to the molecular composition. The sensation of food in the mouth is the result of simultaneous stimulation of at least three sensory systems: the gustatory (taste), the olfactory (odor), and the somatosensory (touch) system. Processing of information from these sensory systems involves multiple areas in the brain. In this thesis, we manipulated product characteristics affecting the gustatory system; that is, the taste quality (e.g. sweet, salty, sour, and bitter) and concentration, and examined the BOLD response in brain areas involved in taste processing. The pathway of how taste information is transmitted from our sensory taste organs towards the brain in humans is illustrated in Figure 2. Taste receptor cells (TRCs) are located on the taste buds, distributed on the tongue, palate, larynx, pharynx, and epiglottis. After stimulation, the TRCs excite nerve fibers of the facial nerve (cranial nerve VII), glossopharyngeal nerve (cranial nerve IX), and vagus nerve (cranial nerve X). These nerves converge in the solitary nucleus in the brainstem and transmit information to the ventral posteromedial nucleus of the thalamus, and ventral anterior insular cortex subsequently (Chandrashekar, Hoon, Ryba, & Zuker, 2006; Kurth, Zilles, Fox, Laird, & Eickhoff, 2010; Small, 2010; Veldhuizen, Albrecht, et al., 2011).

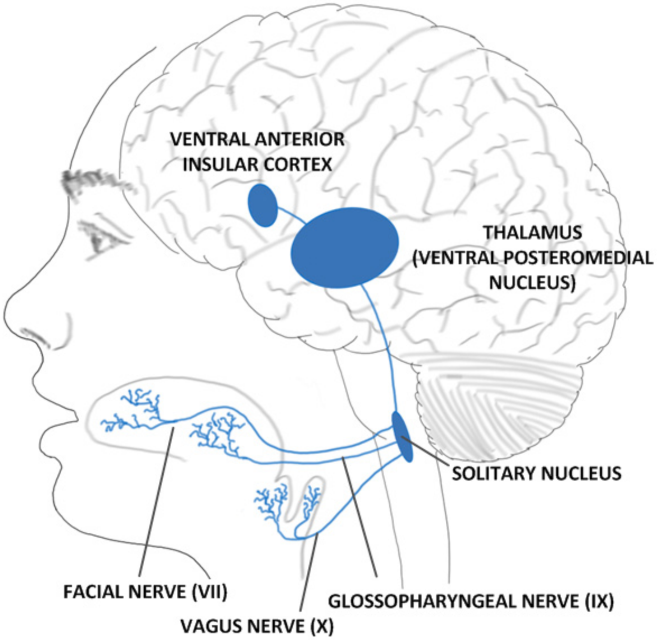

Figure 2. A sagittal illustration of the pathway of taste processing from the mouth towards the primary taste cortex in the ventral anterior insular cortex. Roman numerals indicate the numbered cranial nerves involved in taste processing.

The ventral anterior insular cortex has been referred to as the primary taste cortex since manipulations of taste quality and concentration modulated the BOLD response in this brain area (Nakamura et al., 2013; Simon, De Araujo, Gutierrez, & Nicolelis, 2006). Very few studies have investigated the effect of aging on the brain response to taste. Jacobson et al. (2010) showed that aging is accompanied by a reduced response in the thalamus during processing of sweet, sour, salty, and bitter tastes. In **Chapter 3**, we focus on extending these findings on taste processing in older adults. We examined responses in the brain during the tasting of different concentrations of the four basic tastes and related these measures to behavioral expression of pleasantness using liking ratings.

Person characteristics affect taste processing

As mentioned previously, existing knowledge of taste processing is primarily based on manipulations of product characteristics (i.e., taste quality or concentration). Our main goal was to investigate how, in addition to these product characteristics, person characteristics affect the processing of taste information in the brain, which also underlie the behavioral expression of pleasantness. Differences between individuals in the secretion, components, and properties of saliva influence the chemical processing of tastes and the transport of tastes to TRCs (de Wijk, Prinz, Engelen, & Weenen, 2004; Ferry et al., 2006; Matsuo, 2000; Vissink, Spijkervet, & Van Nieuw Amerongen, 1996; Weel et al., 2002). The aging process is associated with many physiological changes in the oral cavity, including a decrease in the secretion rate of saliva (Percival, Challacombe, & Marshi, 1994; Ship, Nolan, & Puckett, 1995; Ship, 2010). These decreased rates have been related to higher taste detection thresholds and decreased ability to discriminate between taste concentrations in both young and older adults (Christensen, Navazesh, & Brightman, 1984; de Jong, Mulder, de Graaf, & van Staveren, 1999; Zaidan, Al-Omary, & Al-Sandook, 2009). Also, age-related changes in mucin levels have been observed (Denny et al., 1991). Mucin serves as a protective layer against potential pathogens in the oral cavity. However, so far, it remains unclear how salivary secretion rates and saliva composition affect taste processing in the brain and how these factors are modulated by age (Figure 1). These factors were investigated in the study described in **Chapter 2**.

As mentioned before, pleasantness requires people to combine information from the senses with previous experiences stored in memory (Nguyen, Breakspear, Hu, & Guo, 2015). It was proposed that responses in the ventral anterior insular cortex provide the basis for all subjective feelings (Craig, 2002; Dolan, 2002; Suzuki, 2012), including (un)pleasantness perceived in response to tastes. Indeed, responses in the ventral anterior insular cortex were correlated with subjective experiences of pleasantness (Bender, Veldhuizen, Meltzer, Gitelman, & Small, 2009; Cerf-Ducastel, Haase, & Murphy, 2012; Frank et al., 2008). Responses in the mid insular cortex were influenced by manipulations of taste concentration (Small et al., 2003; Spetter, Smeets, de Graaf, & Viergever, 2010). However, it remains unclear how the different parts of the insular cortex represent information from the senses (i.e., taste quality and concentration) alongside the subjective experiences of pleasantness (Chikazoe, Lee, Kriegeskorte, & Anderson, 2014). In **Chapter 4**, we present results of how person and product characteristics affect activity patterns in the insula.

In addition to modulations in the ventral anterior insular cortex, pleasantness has also been related to BOLD responses in other brain areas, namely the striatum and ventral pallidum (Grabenhorst & Rolls, 2010; Rolls, 2015; Sewards, 2004; Wang et al., 2004), cingulate cortex (Shackman et al., 2011; Vogt, 2005), orbitofrontal cortex (OFC) (Kringelbach, O'Doherty, Rolls, & Andrews, 2003), and amygdala (Kelley et al., 2005; Kirouac & Ganguly, 1995; Phillipson, 1979; Wise, 2006). These brain areas showed increased responses in older, compared to younger, adults when evaluating taste pleasantness, while decreased activation relative to the young adults was seen in brain areas involved in processing taste information (Jacobson, Green, & Murphy, 2010). Furthermore, older adults showed increased communication between brain networks involved in emotion and frontal areas when evaluating pleasant, unpleasant, and neutral images (St Jacques, Dolcos, & Cabeza, 2010). This is in line with indications that aging affects the communication between brain networks, in addition to age-related changes in responses in local brain areas (Allard & Kensinger, 2014; Antonenko & Flöel, 2014; Geerligs, Saliasi, Renken, Maurits, & Lorist, 2014; Sala-Llonch, Bartrés-Faz, & Junqué, 2015). Along with similar findings, these observations led to the suggestion that older adults recruit frontal brain areas to regulate increased compensatory emotion processing as a result of decreased sensory processing (Cabeza, Anderson, Locantore, & McIntosh, 2002; Grady et al., 1994; McCarthy, Benuskova, & Franz, 2014). Therefore, we examined the influence of age on the communication between brain networks involved in sensation and emotion during taste processing, in order to study the interaction between the representation of product characteristics (i.e., taste quality and concentration) and person characteristics (i.e., age) in the brain (**Chapter 5**).

In addition to the investigation of neuronal mechanisms underlying pleasantness induced by tasting, we studied how information about food pleasantness stored in memory affects the brain response to pictures of food in young adults (Figure 1). There is an ongoing debate on whether the same neuronal mechanism codes for pleasantness during actual consumption and sight of food (Berridge, Robinson, & Aldridge, 2010; Havermans, 2011; Small, Veldhuizen, Felsted, Mak, & McGlone, 2008). While animal research shows the separability of pleasantness experienced during consumption and while looking at food, human experiments have produced contradictory results.

Pleasant, as well as unpleasant, eating experiences are stored in memory. These memories are triggered during the sight of food, and thereby guide people to select food they previously liked and ignore foods they have previously learned to dislike (Oeusoonthornwattana & Shanks, 2010; Thoma & Williams, 2013). This effect of memory on the perception of food is reflected in the results of both fMRI and EEG studies, in which participants were exposed to visual food cues. For example, a greater BOLD response was observed in the orbitofrontal cortex (OFC) following a visual cue that signalled subsequent administration of a pleasant taste, compared to a visual cue that signalled the administration of an unpleasant taste (O'Doherty, Deichmann, Critchley, & Dolan, 2002). The OFC also showed an enhanced response during the actual administration of a pleasant taste. Furthermore, pleasantness has been related to multiple components and oscillatory changes of the EEG signal using non-food-related stimuli (Eimer & Holmes, 2007; Franken, Gootjes, & van Strien, 2009; Taake, Jaspers-Fayer, & Liotti, 2009; Williams, Palmer, Liddell, Song, & Gordon, 2006). For example, the pleasantness of faces was positively correlated with the amplitude of a neuronal activity between 400 and 700ms over the dorsal scalp (Johnston & Oliver-Rodriguez, 1997). Furthermore, higher left, relative to right, alpha (8-13Hz) power in frontal areas was associated with better discrimination between pleasant and unpleasant visual stimuli (Coan, Allen, & McKnight, 2006; Davidson, 2004; De Cesarei & Codispoti, 2011; Gable & Harmon-Jones, 2008; Kuriki, Miyamura, & Uchikawa, 2010; Zion-Golumbic, Kutas, & Bentin, 2010). Pictures of pleasant and unpleasant stimuli alone did not evoke asymmetrical alpha power, but differences between individuals modulated these asymmetrical frontal alpha power effects (Gable & Harmon-Jones, 2008). We investigated how variability of pleasantness within individuals in response to food pictures was related to EEG components and oscillatory changes (**Chapter 6**). This study illustrates how previous eating experiences may shape information processing during the sight of food products.

Previous eating experiences stored in memory can be partitioned into episodic and semantic memory (Tulving, 1985). Episodic memory represents our memory of experiences including associated emotions, whereas semantic memory is a more structured record of facts and knowledge about the external world. In addition to the selection of liked food products, people select food products that match the eating context and their health beliefs (Von Essen & Mårtensson 2014). For example, Birch, Billman, and Richards (1984) found evidence that when food is categorized as "for breakfast", it is more preferred in the morning than in the afternoon, while food categorized as "for dinner", is more preferred in afternoon than in the morning. The extent to which knowledge stored in semantic memory differentially affects food choice was addressed in **Chapter 7**.

1.7 THESIS OUTLINE

The aim of the studies described in this thesis was to identify the mechanisms underlying food pleasantness (Figure 1). Our main goal was to investigate how person characteristics influence processing of visual food and taste stimuli on a sensory, neuronal, and behavioral level, in addition to manipulations of specific product characteristics. The work on taste processing described in this thesis focused on differences between healthy young and older adults; individuals that reported no functional decline or disease.

This thesis encompasses six chapters, resulting from three empirical studies (Figure 1). The first study involved a fMRI study in which we investigated responses in the brain elicited during pleasantness evaluation of four increasing concentrations of sweet, sour, salty, and bitter tastes in young (mean age 23 years old) and older (mean age 66 years old) adults. We focused on four research questions. First, we studied the effect of different aspects of whole saliva on the neuronal processing of basic tastes and how this effect is influenced by age using analysis of covariance (Chapter 2). Second, we investigated whether young and older adults differ in their brain response associated with processing of taste quality and concentration using linear mixed-effects effect modeling (Chapter 3). Third, we focused more specifically on disentangling the representation of product characteristics related to tasting (i.e., taste quality and concentration) and person characteristics (i.e., age) in the primary taste cortex located in the insular cortex using data-driven factor analysis (Chapter 4). Fourth, we examined how age influences communication between brain networks involved in processing product and person characteristics. We separated brain networks using independent component analysis (Chapter 5). Subsequently, we investigated the relationship between memory processes and food pleasantness in two EEG studies. First, we assessed how differences in pleasantness within individuals modulate the EEG response to visual food cues in thirty-three young adults (Chapter 6). Previous studies mainly focused on electrophysiological responses that were averaged across pleasant and unpleasant food cues. We extended our work by investigating how components and oscillatory changes of the EEG signal were modulated by differences within persons in pleasantness using general linear modelling instead of averaging across food cues. Finally, we assessed the differential strength of food associations stored in semantic memory using an associative priming paradigm (Chapter 7). Thirty young participants were exposed to a forced-choice picture-categorization task, during which we took EEG recordings. In Chapter 8, the different findings of the studies are integrated and discussed. In addition, critical considerations are presented along with perspectives for future research.

The mechanisms that we identified, in response to sensory stimulation with tastes or pictures of food, provide a better understanding of how person characteristics affect food pleasantness. In order to strive for a healthy balanced diet that fosters healthy aging, we must start with an understanding of how age affects the experience of food pleasantness. Modifying product characteristics may not be the only effective strategy in increasing food pleasantness. Furthermore, the methodologies described in this thesis are intended to form a general model of food information processing, on which future research investigating pleasantness can build.

PART 1: Processing information from basic tastes