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Pleasure from Food

Hoogeveen, Heleen Rianne

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SUMMARY AND GENERAL DISCUSSION

8.1 AIM

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). An important non-physiological determinant of dietary intake is the pleasure we experience in response to visual or oral presentation of food products (Blundell & Rogers, 1991; Hetherington, 1998; Schilp, Wijnhoven, Deeg, & Visser, 2011). The aim of this thesis was to unravel the neuronal mechanisms underlying this experience of pleasantness in healthy young and older adults; that is, in individuals that reported no functional decline or disease. Whereas previous studies mainly reported manipulations of product characteristics and subsequent behavioral responses, we especially focused on several person characteristics that can affect neuronal mechanisms related to the experience of pleasantness in response to food. Here, we define person characteristics as the characteristics that uniquely define an individual, such as physiology and memories. This definition, however, does not include physical product characteristics that are not dependent on the individual, such as the concentration of tastes of the food product.

To investigate Pleasure from Food, we studied differences in taste processing between young (mean age 23 years old) and older (mean age 66 years old) adults in relation to behavioral expressions of pleasantness using functional Magnetic Resonance Imaging (fMRI) and electroencephalography (EEG). More specifically, we showed that different aspects of whole saliva (**Chapter 2**) and manipulations of taste quality and concentration (**Chapter 3**) affect neuronal responses during taste processing. Furthermore, we reported on the functional specialization of the insula (**Chapter 4**) and communication between brain networks involved in sensory and emotional processing (**Chapter 5)** of different qualities and concentrations of tastes. In addition to our investigation of pleasantness using fMRI, we investigated brain activity in response to visual food cues using EEG. We identified the neuronal representation of subtle differences in food pleasantness (**Chapter 6**) and

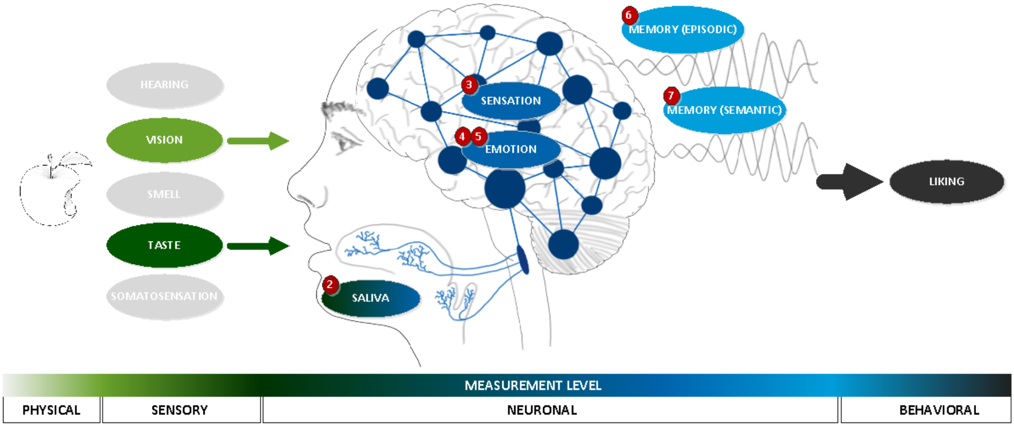

Figure 1. Mechanisms underlying food pleasantness were investigated using a combination of physical, sensory, neural, and behavioral measures. We identified how person characteristics such as saliva (Chapter 2), sensation (Chapter 3), and emotion (Chapter 4 and 5) affect taste processing and how eating experiences that are stored in memory affect the subsequent perception of visual food cues (Chapter 6 and 7).

the differential strength of sensory and non-sensory food associations stored in memory (**Chapter 7**) (Figure 1). Novel insights resulting from this investigation will be summarized and discussed below.

8.2 SUMMARY OF MAIN FINDINGS

An important question in the current research is how taste information perceived in the mouth is processed into an evaluation of pleasantness in the brain, and how this process is affected by aging. We focused on taste processing, as older adults rank the taste of food as significantly more important than other factors in food intake (Krondl et al., 1982). It was widely assumed that aging was related to changes in the sensation of taste intensity of food, which in turn was assumed to affected food pleasantness (Kremer et al., 2007b). Following the current lack of data supporting this assumption (Kozlowska et al., 2003; Rolls, 1999), we hypothesized that age-related changes in taste sensitivity may be overlooked by the use of behavioral methods (see Introduction). Consequently, we performed an fMRI study to investigate the neuronal mechanisms underlying taste processing and the behavioral expression of pleasantness in response to increasing concentrations of sweet, sour, salty, and bitter tastes.

Saliva is important for the transport of tastants to taste receptor cells (de Wijk et al., 2004; Ferry et al., 2006; Vissink et al., 1996). The secretion rate and composition of saliva differs across individuals (Neyraud, Palicki, Schwartz, Nicklaus, & Feron, 2012) and functions as an important factor in influencing taste perception (Bonnans & Noble, 1995; Ferry et al., 2006). Therefore, we hypothesized that saliva is an important person characteristic of interest in how a taste is processed in the brain (Bonnans & Noble, 1995; Christensen, Brand, & Malamud, 1987). Indeed, in **Chapter 2** we demonstrated a novel association between salivary secretion and taste processing. More specifically, we showed that individual baseline levels of amylase concentration of whole saliva affect the responses of brain areas involved in taste processing. Additionally, we observed that increased mucin concentrations (as a proxy of viscosity) in saliva were related to increased responses in the mid-insular cortex, a brain area of which responses were previously associated to viscosity of stimuli (De Araujo & Rolls, 2004) and taste intensity (Small et al., 2003; Spetter et al., 2010). Following this, we hypothesized that viscosity of saliva is an important person characteristic involved in the perception of taste intensity. These findings are in line with suggestions that taste sensitivity is relative rather than absolute, because individuals have their own baseline secretion levels of whole saliva as a reference (de Wijk et al., 2004; Engelen et al., 2003). While aging was previously found to be related to changes in saliva secretion and composition (Dodds et al., 2005), we observed that saliva secretion and composition, as well as the association between saliva and brain areas involved in processing of taste intensity, were similar across age groups.

In **Chapter 3**, we continued this investigation of taste processing in the brain. More specifically, we focused on the role of the aging brain. This topic has received little attention so far, and as a result taste processing is less understood than odor processing, with respect to aging. Available evidence, however, demonstrates differential brain responses to stimuli of different taste qualities (Green, Jacobson, Haase, & Murphy, 2013; Jacobson, Green, & Murphy, 2010), and of different taste concentrations (Small et al., 2003). To the best of our knowledge, the mutual influence of both factors on taste processing in the aging brain is still largely unknown. We were the first to identify the effects of aging on taste processing, especially in different higher order brain areas. More specifically, we found that taste information delivered to the brain was not different between young and older adults in lower order brain areas, as illustrated by the absence of age effects in brainstem (i.e., the NTS) and thalamus (i.e., the VPM) activity. This indicates that changes in the taste buds are unlikely to underlie age-related changes in taste perception. Instead, our results in higher order brain areas indicated that multisensory integration changes with age; older adults showed less brain activation to integrate both taste and somatosensory information. Furthermore, we concluded that older adults reallocated attention in order to perceive taste. Finally, we hypothesized the importance of homeostatic mechanisms in understanding taste quality specificity in age-related differences in taste perception. Altogether, our findings led us to hypothesize that multisensory integration, attention, and homeostatic mechanisms are important person characteristics involved in age-related changes in taste processing.

In **Chapter 4** we further differentiated product characteristics (i.e., manipulations of taste quality and concentration) from person characteristics. We identified a functional specialization of the insular cortex, with respect to its representation of these product and person characteristics. More specifically, we showed that the left and right insular cortices are differentially engaged in processing the aforementioned characteristics. Representations of the presence of a taste stimulus, as well as its corresponding pleasantness, dominate in the left insular cortex, whereas taste concentration modulates responses in the right insular cortex. In this chapter, we specifically focused on how the response in the insula varied across taste qualities and concentration, and pleasantness scores and found no differences between young and older participants. Therefore, we concluded that although there are BOLD amplitude differences within the insula between age groups in response to taste (**Chapter 3**), variation of insular BOLD responses across taste qualities and concentration is similar across age.

Our observations regarding the effect of age on the neural representation of the taste pleasantness were partially in line with our behavioral results. On the one hand, we observed decreased responses in the ventral anterior insular cortex in response to sour tastes in older compared to young adults (**Chapter 3**). Based on our findings that responses in this brain area were inversely related to pleasantness (**Chapter 4**), we suggest that the effect of age in the ventral anterior insular cortex represents lower pleasantness for sour tastes in older, compared to young, adults. On the other hand, higher liking ratings for sweet and salty tastes in older adults could not be attributed to responses in the ventral anterior insular cortex.

In addition to modulations in the insular cortex as a “hedonic hotspot”, pleasantness has also been found to be related to BOLD responses in a network of brain areas (Phillips et al., 2003). Aging was found to affect connectivity in this network, in response to pleasant and unpleasant stimuli. For example, older adults showed increased communication between the right amygdala and ventral anterior cingulate cortex, possibly reflecting increased emotion regulation when individuals evaluated pleasant, unpleasant, and neutral images (St Jacques et al., 2010). Conversely, older adults showed decreased functional connectivity between the amygdala and posterior brain regions, likely reflecting decreased perceptual processing (St Jacques et al., 2010). These and other observations (Mather & Carstensen, 2005) led us to suggest that older adults recruit frontal brain areas to generate increased emotion processing in response to decreased sensory processing. Indeed, our results reported in **Chapter 5** show that age modulates the connectivity between networks of brain areas involved in emotion processing during taste perception. More specifically, the results indicate that: 1) tastes are less salient to older adults, 2) older adults rely more on emotion processing during taste perception, and 3) older adults show increased cognitive control in comparison to young adults during taste perception. We therefore believe it is important to study age-related changes in emotion and cognitive processing of taste, in addition to changes in sensory functioning, to be able to understand mechanisms underlying changes in perceived taste pleasantness in older adults. Thus **Chapters 2, 3, 4, and 5** together demonstrate several person characteristics that affect taste processing, in addition to effects of manipulation of product characteristics such as quality and concentration of tastes.

Besides the investigation of neuronal mechanisms underlying pleasantness induced by tasting, we studied how information about food pleasantness that is stored in memory affects the brain response to visual food cues in young adults (see **Chapter 6 and 7**). Based on the existing literature and our observation that pleasantness experienced in response to taste is localized in the left, but not the right, insular cortex (**Chapter 4**), it is suggested that asymmetric neural activity underlies the experience of food pleasantness (Harmon-Jones, Gable, & Peterson, 2010; Small, Zald, Jones-Gotman, et al., 1999). More recent research suggests that this asymmetric activity is especially salient in the frontal cortex. The majority of studies focus on brain responses towards pleasant and unpleasant visual stimuli, not related to food. So far, little attention has been focused on the neuronal representation of subtle differences in pleasantness perceived in response to visual food cues. The results reported in **Chapter 6** indicate that the behavioral expression of pleasantness, as reflected in a liking rating, is related to multiple processes underlying the perception of visual food cues. First, food stimuli that were evaluated higher, compared to lower, on liking were followed by smaller amplitudes between 230 and 270ms in right fronto-central brain areas. This might indicate that higher liking is related to increased automatic approach tendencies towards pictures of food, and that liking scores reflect a form of utility evaluation of the food product depicted on the pictures. Second, the observed effect of larger amplitudes between 270 and 600ms in right fronto-central-parietal brain areas in response to food stimuli that were evaluated higher, compared to lower, on liking, most likely indicates increased arousal elicited by higher liking. Third, we demonstrated larger lateralized cortical activity later in the EEG signal (1000 through 1500ms) for higher, compared to lower-liked, food products, suggesting that information from affective representations of food products is drawn upon in order to express liking. Altogether, the results of **Chapter 6** show that the use of pictures of food products combined with regression based methods enabled us to shed light on the course of the formation of food liking in the brain, that underlies subtle differences in the experience of liking between food products.

Previous eating experiences stored in memory can be partitioned into episodic and semantic memory (Tulving, 1985). Episodic memory represents our memory of autobiographical experiences, including associated emotions; whereas semantic memory is a more structured record of facts and knowledge about the external world. We most likely addressed episodic memory in **Chapter 6**, as participants were asked to rate liking in response to pictures of food product, which requires retrieval of previous eating experiences of that specific product from memory. In **Chapter 7**, we investigated semantic memory of food associations by means of an associative priming paradigm. Our results demonstrated that associations related to taste quality that are stored in memory are stronger represented than context associations, such as time of consumption and health beliefs. Altogether, the work described in this thesis shows the neuronal mechanisms of how person characteristics, such as age, saliva secretion, sensation, emotion, and memory affect the experience of pleasantness in response to tastes and visual food cues.

8.3 GENERAL DISCUSSION AND FUTURE PERSPECTIVES

Connecting sensory science to neurobiology in the study of taste sensitivity (part I)

We examined taste perception in individuals without reported taste disturbances, as measured with "Taste Strips" (Landis et al., 2009), indicating that neither our young nor older participants had a reduced ability to detect and identify sweet, sour, salty, or bitter tastes (**Chapters part I**). This indication was further substantiated by our observation that saliva secretion rates, which were previously related to changes in taste sensitivity (Lugaz, Pillias, Boireau-Ducept, & Faurion, 2005; Zaidan, Al-Omary, & Al-Sandook, 2009), were similar across age groups (**Chapter 2**). Altogether, our behavioral and oral sensory (saliva) findings suggest that age is not necessarily associated with differences in taste sensitivity, i.e., the subjective perception of an individual whose taste buds have been stimulated by a tastant.

The subjective perception of taste tells us something about the characteristics of the perceived taste, such as its intensity, but goes beyond the stimulus and its characteristics, such as concentration. This distinction becomes especially relevant when studying taste processing on a neuronal level and investigating differences in taste sensitivity between individuals, for example, young and older adults. We did not observe differences in responses between age groups in the first relay areas of taste information in the brain (i.e., the NTS and the ventral posteromedial nucleus of the thalamus) (**Chapter 3**). These findings show that taste information entering the brain in young and older adults does not seem to differ. Furthermore, we reported that manipulations of taste concentration were related to brain responses in the mid-insular cortex (**Chapter 4**), and age did not affect this association (**Chapters 3 and 4**). Following previous findings that behavioral expressions of taste intensity modulate the response in the mid-insular cortex, in addition to modulations of concentrations (Anderson & Sobel, 2003*a*; Spetter et al., 2010), our results imply that young and older adults do not differ in how intensely they perceive taste. Since we did not explicitly investigate perception of intensity in these age groups, future studies should take this hypothesis into account.

With respect to aging, it was proposed that aging induces a switch from automatic to more controlled processing of information (Staub, Doignon-Camus, Marques-Carneiro, Bacon, & Bonnefond, 2015). For example, older adults may enhance attention to sensory input in order to compensate for a decline in automatic detection of changes in the composition of sensory input (Alain, McDonald, Ostroff, & Schneider, 2004; Madden, Whiting, Spaniol, & Bucur, 2005). We are the first to confirm the presence of this compensation mechanism in older adults, with respect to taste processing, especially in response to low concentrations of tastes. More specifically, we showed that older adults recruit attentional mechanisms (i.e., dorsal anterior insular cortex) to compensate for lower automatic responses in attentional mechanisms (i.e., medio-dorsal nucleus of the thalamus), indicating decreased salience elicited by tastes (**Chapter 3**). These observations in separate brain areas were further established by our findings of decreased connectivity within the salience network in older, compared to young, adults (**Chapter 5**). Altogether, these findings regarding the role of attention in perceiving sensory input are in agreement with resting state studies of the salience network in older adults (He et al., 2013; Onoda et al., 2012), and indicate that taste is perceived as less saliently by older adults.

When molecules touch the tongue: the role of somatosensation in taste sensitivity (part I)

Another factor that is increasingly recognized as important for taste sensitivity is oral somatosensation, which refers to perceptions, such as touch, pain, temperature, and itch, in the mouth (Haggard & de Boer, 2014). Similar to the information regarding the concentration of tastes, oral sensory information of touch from the tongue and other oral structures reaches the brainstem (i.e., the NTS) (Bradley, Smoke, Akin, & Najafi, 1992), thalamus, and anterior insular cortex (De Araujo & Rolls, 2004; Katz, Nicolelis, & Simon, 2002; Pritchard, Hamilton, Morse, & Norgren, 1986; Pritchard, Hamilton, & Norgren, 1989; Verhagen, Kadohisa, & Rolls, 2004). The anterior insular cortex is a site for processing both chemical and somatosensory characteristics of tastes, in that activations of this brain area were correlated with concentration and viscosity of stimuli placed in the mouth, respectively (**Chapter 4**; De Araujo & Rolls, 2004; Grabenhorst, Rolls, & Bilderbeck, 2008). Moreover, mucin concentration as a proxy of viscosity of saliva modulated the response in the anterior insular cortex in response to taste (**Chapter 2**). Therefore, we advocate taking the role of oral somatosensation into account when investigating taste sensitivity.

With respect to the effect of age on oral somatosensation, previous behavioral findings were inconsistent, showing both stable and decreased sensitivity in older adults (Fukunaga et al., 2005; Steele, Hill, Stokely, & Peladeau-Pigeon, 2014). We speculate that oral somatosensation is decreased in older adults, based on our neuronal findings of decreased response in the primary somatosensory area (**Chapter 3**) as well as the effect of aging on the association between mucin concentration as a proxy of viscosity and responses in the anterior insula (**Chapter 2**). This hypothesis needs further investigation, for example, by manipulating somatosensory characteristics such as fattiness, temperature, or viscosity of stimuli perceived in the mouth, and measuring brain responses and intensity in young and older adults.

Taste processing in older adults: more than a matter of taste intensity (part I)

Evidence on dissociable representations of taste intensity and pleasantness is accumulating. Whereas taste intensity is related to responses in the mid-insular cortex, behavioural expressions of pleasantness modulate responses in the ventral anterior insular cortex (**Chapter 4**; Anderson & Sobel, 2003b; Cerf-Ducastel, Haase, & Murphy, 2012). The ventral anterior insular cortex processes the emotional significance of sensory input (Phillips et al., 2003). We observed that the ventral anterior insular cortex showed higher responses in older adults in response to sour and salty taste stimuli, indicating increased emotional significance of these tastes in older, compared to young, adults (**Chapter 3**). In addition to enhanced responses in the ventral anterior insular cortex, we observed decreased responses in the right amygdala in response to sweet, sour, salty, and bitter tastes (**Chapter 3**). Among other functions, the right amygdala was engaged in fast processing of emotional stimuli, such as taste (see for meta-analysis and review: Costafreda, 2009; Markowitsch, 1998). We therefore believe that emotional processing of taste is affected by aging. This suggestion was further established by our observation that older adults showed increased functional connectivity between brain areas involved in affective processing, such as between the subcortical mesolimbic areas and the anterior striatum and the ventral anterior insular cortex (**Chapter 5**). We hereby extended previous observations of the effect of aging on emotion processing towards the taste domain, indicating that older adults process the emotional significance of taste in a different manner than young adults.

Besides age-related differences in the perception of different concentrations of tastes, we studied whether taste processing showed taste-quality specificity. Older adults reported lower liking ratings for sour tastes, but higher liking ratings for sweet and salty tastes compared to young adults (**Chapter 3**). Whereas the effects of age on sour and bitter perception were located in brain areas involved in homeostatic mechanisms, the current data (**Chapters part I**) did not show a clear indication of the neuronal mechanisms underlying behavioral observations regarding sweet and salty perception and age.

Food pleasantness is lateralized, irrespective of sensory modality (part I and II)

Several theories of cerebral lateralization of pleasantness processing have been postulated (Killgore & Yurgelun-Todd, 2007). For example, the right-hemisphere hypothesis suggests that the right hemisphere is dominant for affective processing of stimuli (Borod et al., 1998). In addition, the right hemisphere was especially responsive during recall of emotional autobiographical memories (Fink, 2003; Philippi et al., 2015). This constitutes a finding that corroborates the right-lateralized pleasantness results, reported in **Chapter 6**; but initially seems to contrast the left-lateralized pleasantness results that we described in **Chapter 4**. However, our results indicated that taste quality was closely related to the effect of pleasantness observed in the left ventral anterior insular cortex (see Figure 5 of **Chapter 4**), although this effect did not reach significance. This indication is in line with previous observations showing that the left ventral anterior insular cortex responds to taste when judging quality (Bender, Veldhuizen, Meltzer, Gitelman, & Small, 2009; Duerden, Arsalidou, Lee, & Taylor, 2013). The absence of an effect of taste quality in this brain area may have resulted from the fact that participants judged pleasantness instead of taste quality. Although our results can neither strongly support nor dismiss these functional interpretations, we show that the left and right hemispheres are differently involved in pleasantness processing in response to the perception of taste in the mouth (**Chapter 4**), as well as the perception of visual food cues (**Chapter 6**). Future studies should provide more insight into the functional role of lateralized findings in pleasantness processing, for which we advocate that stimulus manipulations, as well as task demands, are essential for adequate interpretation.

Future perspectives: investigating how previous eating experiences affect food choice

The methodologies described in this thesis are intended to form a general model of food information processing, on which future research investigating pleasantness perceived in response to food across the human lifespan, can build. The future aim of studies extending on the studies reported in this thesis, is to contribute to developing strategies to modify dietary intake, in an effort to achieve adequate intake, which fosters healthy aging. Before such strategies can be developed and optimized, more research is necessary to unravel how Pleasure from Food translates to food choice.

It is known that food choice changes with advancing age (i.e., > 65 years of age) (van der Meij, Wijnhoven, Finlayson, Oosten, & Visser, 2015; Wurtman, Lieberman, Tsay, Nader, & Chew, 1988). More specifically, older adults (i.e., 60-75 years) consume less sweet, salty, and high-caloric foods compared to young adults (i.e., 20-30 years) (Chambers et al., 2008; Drewnowski, Renderson, Driscoll, & Rolls, 1997; Drewnowski & Shultz, 2001; Pelchat, 1997; Wurtman et al., 1988). Many attempts to understand age-related changes in food choice have focused on changes in sensation of taste and smell during actual consumption of food products, but no clear relation was observed between taste and smell sensitivity and food choice in older adults (Arganini & Sinesio, 2015; Jin et al., 2015; Kremer, Bult, Mojet, & Kroeze, 2007*a*; Rolls, 1999). This is in agreement with our observations that age-related changes in liking of basic tastes are not accompanied by changes in taste sensitivity; rather that aging primarily affects responses in brain areas involved in emotion and memory processing (**Chapters part I**). Remarkably, how emotions and memories affect the choice of food products in older adults is largely ignored.

Memories of pleasant or unpleasant eating experiences are retrieved during the sight of pleasurable food products on a later occasion and are translated either into the motivation to choose (in the case of a pleasant memory) or not choose (in the case of an unpleasant memory) that particular food product. This motivation is known as anticipatory food reward. Visual features of specific food products have been found to be a very strong cue in eliciting anticipatory food reward, and therefore may be a strong predictor of food choice (Epstein et al., 2004; Stice, Spoor, Ng, & Zald, 2009). Behavioral and neuronal observations indicate that anticipatory reward can change as people age (Dreher, Meyer-lindenberg, Kohn, & Berman, 2008; Klostermann, Braskie, Landau, O'Neil, & Jagust, 2012; Lorenz et al., 2014; Schilp, Wijnhoven, Deeg, & Visser, 2011). Although several fMRI studies have explored the link between response in reward-related brain areas to the sight of foods and actual food choice, no study has investigated the age-related differences in the neural substrates of anticipatory reward to foods so far.

Altogether, pleasantness experienced during eating and motivation to eat, induced by memories of these experiences, are the major forces in guiding food intake. Food intake follows a cyclical time course with phases related to expectation and consumption (Kringelbach, Stein, & van Hartevelt, 2012). While human food intake is complex, we are making progress in understanding the underlying mechanisms for expecting and consuming pleasant and unpleasant food stimuli (Stice et al., 2009). With respect to the cyclical time course of food intake, I advocate considering aging as an ongoing adaptive process across the lifespan, which should not necessarily be regarded as a deterioration of adequate food intake at the end of life.

Highlights:

- Aging is not necessarily associated with behavioral changes in taste sensitivity (**Chapters part I**).

- Secretion rate and composition of saliva differs across individuals and influences taste processing in the brain (**Chapter 2**).

- Individual differences in emotion, cognitive, and homeostatic mechanisms, in addition to sensation, should be taken into account to gain a better understanding of (taste-specific)effects of aging in taste perception (**Chapter 3, 4, and 5**).

- Subtle differences in food pleasantness within individuals are represented in neuronal mechanisms related to arousal (**Chapter 6**).

- Food associations stored in memory, related to taste quality, are represented more strongly than context associations such as time of consumption and health beliefs (**Chapter 7**).

Future research: Shift the focus from pleasantness to motivation in order to predict food intake.

Take home message: Neuronal mechanisms underlying sensation, emotion, and memory are the connection between physical characteristics of food products and a person's perception of pleasantness. Age-related differences in *Pleasure from Food* extend beyond taste sensation.

Box 1. Main findings and future recommendations

Conclusion

The desire to understand the neuronal mechanisms underlying changes in food pleasantness is becoming increasingly prominent in various disciplines, such as sensory and consumer science, biology, and psychology. Cognitive neuroscience that incorporates physical product manipulations and behavioral measures in neuroimaging research can provide important insights on how a person processes information from food in different brain areas across time, resulting in Pleasure from Food. It is the brain that is critically involved in this interaction between food products and individual experiences. Methodologies described in this thesis are intended to form a general model of food information processing, on which future research can build.

The effect of aging on brain function should probably be perceived as a complex interplay of changes on multiple functions, such as sensation, emotion, and memory, with varying degrees. The puzzle for cognitive neuroscientists is not so much to explain age-related decline; but rather, to understand the high level of emotional and cognitive functioning that can be maintained by older adults in order to maintain adequate dietary intake.