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1 **Physiological mechanisms explaining human differences in fat perception**  
2 **and liking in food spreads-a review.**

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9

10 **Abstract**

11 *Background*

12 Fat perception and liking are the subjects of growing interest from industries and the scientific  
13 community to reduce the fat content in food products while maintaining consumers' liking.

14 *Scope and Approach*

15 In this review, the different physiological parameters involved in fat perception and fat liking  
16 for food emulsions are explored, focusing on spreads. A deeper analysis of the physiological  
17 mechanisms occurring during the melting and inversion phases, followed by bolus formation,  
18 mouth coating and oral clearance, allows an examination of the links between food  
19 composition, food structure, oral physiological parameters, fat perception and liking.

20 *Key Findings and Conclusions*

21 Fat perception is a multimodal sensation involving olfactory, gustatory and tactile cues. The  
22 main sensory descriptors associated with fat liking are creaminess, spreadability and aroma  
23 perception. During the melting and inversion phases, oral volume, saliva flow and tongue-  
24 palate compression contribute to the heat transfer and cooling effect, leading to the first  
25 sensory perception. Global acceptability is also driven by the mouthfeel sensation perceived

26 after swallowing. Mouthfeel is a consequence of the bolus formation, mouth coating and oral  
27 clearance processes that are dependent on both emulsion composition and oral physiological  
28 parameters (saliva flow, saliva composition, fungiform papillae). Understanding the  
29 physiological mechanisms controlling fat perception can lead to a better understanding of the  
30 consumer's preference and liking for food emulsions.

31

### 32 **Key words**

33 Fat perception; liking; melting; food bolus; oral physiology; food emulsions.

34

### 35 **Highlights**

36 Fat is multimodal perception involving olfaction, taste and tactile modalities

37 Fat liking is related to creaminess, spreadability, fluidness, flavour and colour

38 Melting is the first step in the mouth leading to cooling sensation and liking

39 Bolus formation is driven by food composition, structure modulated by oral physiology

40 Saliva flow and composition, oral volume and tongue palate compression are important

41

### 42 **Introduction**

43 Most developed and developing countries are confronted with a rising rate of  
44 nutrition-related pathologies, especially obesity, cardiovascular diseases, and diabetes, which  
45 are related to unbalanced diets with an excess consumption of fat, salt and sugars. A  
46 significant reduction of these food ingredients will contribute both to saving lives and  
47 reducing healthcare costs and is the subject of growing interest from both industries and the  
48 scientific community.

49 Despite numerous studies relating consumer liking with product formulation,  
50 differences in consumer perception need to be explored in more detail. One hypothesis is that

51 individual oral physiology could better explain differences in fat perception and liking than  
52 only food composition and structure. Moreover, fat perception is considered a multimodal  
53 sensation in itself that involves smell, taste and texture perception (Mattes, 2009; Schiffman,  
54 Graham, Sattely-Miller, & Warwick, 1998). As an example, fat perception in cottage cheeses  
55 was found to be driven by a creamy aroma and greasy film (Martin, et al., 2016). Thus, a need  
56 exists to consider the different sensory modalities of fat perception.

57 The aim of this review was first to present the different modalities involved in fat perception  
58 and liking when consuming spreads and related food products and then to explore the oral  
59 physiological parameters that could be involved in the different oral modalities and analyse  
60 the previously examined links between food composition and structure, oral physiological  
61 parameters, fat perception and liking.

62

## 63 **1. The different sensory modalities of fat perception**

64

### 65 *1.1. Main sensory descriptors involved in fat perception and liking in food emulsions*

66 Consumer liking for fat products seems to be driven by textural sensory descriptors  
67 (spreadability, meltability, fluidness, and creaminess), flavour and colour. For water-in-oil  
68 (W/O) food spreads, appearance can be characterized by colour, gloss and transparency. Even  
69 if appearance will not be further investigated in the present review, it has to be mentioned that  
70 these sensory attributes can modify consumers' global perception and liking of products.  
71 Many studies, but not all, have shown that changing the hue and/or intensity of the colour  
72 added to a food or beverage can influence the perceived identity and/or intensity of the  
73 flavour (Spence, 2015; Spence et al 2010). Translucency or transparency can affect the overall  
74 appearance and can influence liking of foods. Studies conducted on low fat-cheese have  
75 shown that liking of low-fat cheese was negatively influenced when the cheese appearance

76 was too translucent or too white (Wadhvani, 2012). Krause et al. mentioned that butter liking  
77 (evaluated on white bread) was associated with its desirable flavour and colour intensity and  
78 was viewed by most consumers (focus group with a questionnaire) as a tasty and natural  
79 product (Krause, Lopetcharat, & Drake, 2007). In this study, the majority of the consumers  
80 tested preferred a light-yellow colour for butter, while margarine was described as having a  
81 distinctive deeper yellow colour. An evaluation of spread (butter, margarine and two other  
82 spreads) liking consumed during a complete meal was conducted by Michicich (Michicich,  
83 Vickers, Martini, & Labat, 1999); their research found that butter was the most preferred  
84 spread, margarine was the least preferred, and the similarity between the other spreads and  
85 butter was mainly driven by flavour and not by texture. Because spreads are mainly consumed  
86 on bread, Coic et al. (Coic, Groeneschild, & Tournier, 2014) validated that the testing of  
87 spreads on bread rather than alone in a spoon was more suitable to study differences in aroma  
88 perception and, more specifically, intensity and aftertaste. s Other parameters, such as  
89 adhesiveness to spoon, meltability, flouriness and graininess, are negatively correlated to  
90 spread liking, as was observed for peanut spreads evaluated on bread (Yeh, Resurreccion,  
91 Phillips, & Hung, 2002). In another study conducted on different fat products, including  
92 spreads, the most important descriptors for the overall liking of spreads on bread were found  
93 to be “melting”, “water release”, “oil mass transport” and “lubrication”, while an analysis of  
94 consumer segment preference for mayonnaise confirmed that sensory fattiness of the spread  
95 on the bread system was influenced by additional factors than the fat level only (van den  
96 Oever, 2006). In this study, “salty taste”, “saliva” and “creamy mouthfeel” were positively  
97 associated with spread on bread liking, whereas chew force and stickiness were negatively  
98 associated.

99 The examples presented above indicate that fat perception during consumption  
100 involves different sensory modalities: olfactive, gustative, tactile and visual. Before exploring

101 the physiological mechanisms involved in the oral perception of fat, the following sections  
102 will present the different components of oral fat perception (excluding visual) together with  
103 the multimodal interactions between fat perception and other oral sensory modalities.

104

### 105 *1.2. The olfactory modality of fat perception*

106 Many volatile compounds have been described with a fatty odour note (Leffingwell,  
107 2013). These compounds belong to different chemical classes, esters, aldehydes, ketones,  
108 lactones and alcohols, and present different molecular weight and hydrophobicity values.  
109 However, within each chemical class, short-chain compounds convey mostly fruity or green  
110 notes, and the fatty odour character increases only as the number of carbon atoms rises, as it is  
111 the case for octanal, delta nonalactone, methyl decanoate (Jelen & Gracka, 2017). Moreover,  
112 diacetyl (2,3-butanedione) and acetoin (3-hydroxy-2-butanone), which are the main aroma  
113 compounds present in a creamy aroma, are not described with fatty odours but only with  
114 butter and creamy odours (Thomsen, et al., 2012). The direct relationship between the  
115 presence of such an odorant compound in a food product and fat perception of the product is  
116 thus not easily established. For example, Charles et al. (Charles, Rosselin, Sauvageot, Beck,  
117 & Guichard, 2000) found no direct relationship between the presence of diacetyl, a compound  
118 with a butter odour, and perception of a buttery aroma. They explained this discrepancy by the  
119 perception of an odour note being due to a mixture of different volatile compounds. An  
120 alternative explanation is that odour perception cannot be directly linked to the concentration  
121 of the odorant molecules in food. Odorants are volatile molecules present in the air phase at  
122 room and consumption temperature and have to reach the olfactory receptors to be perceived.  
123 However, their release from the food matrix into the air phase highly depends on their  
124 interaction with non-volatile compounds present in the food matrix (Guichard, 2002). In the  
125 present review, we only present interactions between odorants and fat. Because most aroma

126 compounds are more soluble in fat than in water, due to their hydrophobic properties,  
127 modifications of the nature and concentration of fat in a food product will hence modify the  
128 release of aroma compounds into the air phase and thus their accessibility to the olfactory  
129 receptors. However, these differences in release behaviour of aroma compounds according to  
130 the nature of fat highly depend on the physico-chemical properties of aroma compounds. The  
131 most hydrophobic compounds that are more soluble in fat than in water, such as esters,  
132 ketones or lactones are less released from spreads with a higher fat content. Their release in  
133 the air phase also depends on the nature of the fat. For example, ethyl hexanoate was released  
134 more from an oil-in-water (O/W) emulsion realised with partially hydrogenated palm kernel  
135 oil than in emulsions made with anhydrous milk fat, whereas the opposite was found for a less  
136 hydrophobic compound, diacetyl (Guichard, Fabre, & Relkin, 2008). These differences were  
137 explained by differences in the polarity of the fats. The most hydrophobic compound, ethyl  
138 hexanoate, is more soluble in the more hydrophobic (less polar) fat, which is anhydrous milk  
139 fat and thus less released in the air phase. The most polar aroma compound, diacetyl, is more  
140 soluble in the more polar fat, which is partially hydrogenated palm kernel oil. The differences  
141 in the observed aroma release induced differences in sensory perception, and emulsions  
142 realised with partially hydrogenated palm kernel oil were perceived as fruitier due to the  
143 higher release of ethyl hexanoate. Moreover, the melting point of fat influenced the volatility  
144 of aroma compounds because aroma compounds can only be solubilized in liquid fat.  
145 Working on fats differing in their melting points, Roudnitzky et al. showed that ethyl  
146 hexanoate, hydrophobic aroma compounds, was better released at a temperature of 15°C from  
147 anhydrous milk fat with the highest melting point (41°C), due to the presence of solid fat  
148 (Roudnitzky, Irl, Roudaut, & Guichard, 2003).



149 Thus, different odorant compounds are responsible for the olfactive fat modality, but  
150 the amount and nature of the fat can modify their release in the air phase and thus their  
151 perception.

152

### 153 1.3. *The taste modality of fat perception*

154 Fat taste has been principally investigated through the detection of free fatty acids  
155 (FFAs) rather than dietary fat and has been the subject of different reviews (Heinze, Preissl,  
156 Fritsche, & Frank, 2015; Running & Mattes, 2016; Tucker, et al., 2017). Dietary fats are  
157 clearly detected in the oral cavity by tactile and retronasal olfactory cues. If there is a  
158 gustatory component contributing to the liking of fat as well, free fatty acids are the most  
159 likely effective stimuli. When measuring the thresholds of different FFAs based on the C18  
160 carbon chain, differing only in their saturation level (stearic, oleic and linoleic), it was shown  
161 that, by removing the olfactive modality (orthonasal and retronasal cues), the FFAs could still  
162 be perceived through the taste modality (Chale-Rush, Burgess, & Mattes, 2007). This finding  
163 suggests that FFAs are perceived through gustatory, olfactory and somatosensory cues. In  
164 regard to oral physiological parameters and, particularly, saliva, salivary lipolysis has been  
165 positively correlated with the FFA threshold in humans (Mounayar, Septier, Chabanet, Feron,  
166 & Neyraud, 2013; Poette, et al., 2014) and negatively correlated with liking (Neyraud, Palicki,  
167 Schwartz, Nicklaus, & Feron, 2012). Moreover, the oral inhibition of lipolysis by orlistat  
168 showed a decrease in the threshold for triolein in obese subjects (Pepino, Love-Gregory,  
169 Klein, & Abumrad, 2012). Regarding the enzymes involved in lipolytic activity, the literature  
170 is quite scarce. Contrary to what was observed in rats with lingual lipase, no such specific  
171 salivary lipases were found in humans, suggesting a mechanism different to what occurs in  
172 rodents. Indeed, the expression of other lipases in minor salivary glands [von Ebner's gland  
173 (VEG)] was recently demonstrated (Voigt, et al., 2014) in human tongue tissue. However, the

174 degree of lipid hydrolysis occurring with food in the human oral cavity has yet to be  
175 determined. Moreover, non-esterified fatty acids (NEFAs) are naturally present at low  
176 concentrations in high-fat foods, with the amount of NEFAs increasing further during oral  
177 processing such as eating (Mattes, 2009). More recently, Neyraud et al. (Neyraud, et al.,  
178 2017) examined fifty-four subjects and found a significantly positive correlation between  
179 lipolytic activity and FFA concentration, suggesting that lipolytic activity modulates the basal  
180 free fatty acid pattern in saliva. However, how the amount of FFA produced through salivary  
181 lipolysis or naturally present in the food might affect fat perception remains unresolved.  
182 Free fatty acids are responsible for the tactile modality, which is modulated by salivary  
183 lipolytic activity.

184

#### 185 1.4. The tactile modality of fat perception

186 The presence of fat in food is often associated with textural descriptors such as meltability,  
187 spreadability and greasy film (Di Monaco, et al., 2008; Martin, et al., 2016). It is worth  
188 mentioning that the relationship between fat liking and meltability is highly dependent on the  
189 type of product, as observed in the following examples. Margarines and table spreads of  
190 varying fat content (20~80%) were ranked according to perceived meltability (Borwankar,  
191 Frye, Blaurock, & Sasevich, 1992). The perceived meltability was not simply governed by the  
192 melting of fat but also by the rheology of the product. The cooling sensation accompanying  
193 melting was only perceived in the case of butter and other high-fat spread products. In the  
194 case of low-fat products, the cooling was imperceptible; thus, melting perception was related  
195 to the flowability. The cooling sensation has been long speculated as being one key  
196 characteristic that could differentiate between butter and margarine. A recent manuscript  
197 measured the differences in the cooling perception of spreads of different fat content and  
198 structure (Galindo-Cuspinera, Valença de Sousa, & Knoop, 2017). The results confirmed that

199 high-fat spreads, particularly butter, which contains a higher number of shorter chain fatty  
200 acids that melt at body temperature, convey a stronger cooling effect than low-fat margarines.  
201 The rheology of these products is mainly governed by the phase volume fraction and droplet  
202 size. However, in the case of mixtures of different fat, it seems challenging to predict the  
203 texture perception of a mixture of fats from that of the fat itself. The physicochemical  
204 properties of a mixture of anhydrous milk fat and palm oil showed a non-linearity of hardness  
205 as a function of their respective ratios in the mixture, which was explained by changes in the  
206 polymorphic forms of fat attributed to different triacylglyceride intersolubilities (Danthine,  
207 2012). Another parameter that seems to impact fat perception and liking is the particle size as  
208 observed for milk chocolate. The presence of large particles when using bound milk fat  
209 instead of free milk fat induced the perception of a “sandy mouthfeel”, which decreased the  
210 overall liking (Bolenz, Thiessenhusen, & Schape, 2003). Fat perception is also influenced by  
211 product viscosity. Schoumacker et al. (Schoumacker, et al., 2017) noticed that subjects could  
212 better discriminate cottage cheeses with different fat content at 15°C than at 7°C, which was  
213 explained by differences in viscosity only present at the temperature of 15°C.

214 The tactile modality of fat perception is a key driver of fat liking and depends on fat  
215 properties, product rheology and in-mouth process.

216

### 217 1.5. Sensory interactions between fat and other oral sensory modalities

218 Fat perception varies according to food composition but is also modified by other sensory  
219 modalities, due to the functional integration of information transmitted by the different  
220 chemical senses (Thomas-Danguin, 2009). Next, we will review the different types of oral  
221 sensory interactions involving fat perception. As only few examples could be found in the  
222 field of food spreads, some relevant examples of sensory interactions will be taken from other  
223 fatty food products.

224

## 225 1.5.1. Sensory interactions between fat and other tastes

226 Binary taste-taste interactions have been studied in model systems between two of the five  
227 taste qualities (sweet, salty, sour, bitter and umami) in model systems. These taste-taste  
228 interactions vary according to the different taste qualities of the components and their  
229 concentration (subthreshold or suprathreshold) (Keast & Breslin, 2002). Very few studies  
230 report evidence for perceptual interactions between saltiness or sweetness and fat perception,  
231 while the impact of the fat content on salt release and saltiness perception has been shown in  
232 many studies. The main reason is probably that fat perception is complex and probably a  
233 multimodal sensation in itself. However, sodium chloride has a major impact on food  
234 structure, which then impacts both aroma release and texture perception, including fat  
235 perception.

236 The sensory interactions between saltiness and fatty perception have not been assessed in  
237 spreads, however some relevant effects have been found in dairy products. Working on model  
238 cheeses with different lipid/protein ratios and two-salt contents, Boisard et al. (Boisard, et al.,  
239 2014) found that model cheeses with added salt were perceived to be significantly more fatty  
240 regardless of the lipid/protein ratio. These cheeses were also less sticky, less elastic and less  
241 compact. However, there was no evidence regarding the saltiness-fattiness sensory  
242 interactions. The authors concluded that these model cheeses also contained larger fat  
243 globules (Boisard, et al., 2013), which could induce a higher mouth-coating responsible for fat  
244 perception and will also delay the transfer of aroma compounds with fatty notes and their  
245 release after swallowing, which could increase fatty aroma perception.

246 Sensory interaction between sweetness and fatty perception has been studied in different food  
247 products, showing that oral sensations generated by sugar and fat in familiar sugar/fat  
248 mixtures can influence the overall pleasantness of the food. However, the sensory interactions

249 between sweetness and fat can vary according to the food product. It was observed that sugar  
250 may potentiate the oral perception of fat in liquid dairy products, by raising the stimulus  
251 viscosity and, thus, creaminess, whereas it masked oral perception in cakes (Drewnowski,  
252 1993). Different results were observed by other authors. Working on biscuits, Biguzzi et al.  
253 (Biguzzi, Schlich, & Lange, 2014) found that a reduction in the sugar content had no effect on  
254 fat perception, whereas a reduction in the fat content sometimes induced a lower sweetness  
255 perception. No significant effect of the addition of sugar in milk or yogurt was noticed on fat  
256 perception (Le Calve, et al., 2015). In addition to the products being different in the above  
257 studies, it must be mentioned that sensory preferences for sugar and fat in model dairy  
258 products showed considerable inter-individual variability. The following example shows  
259 differences in sensory preferences for fat and sugar according to the body weight status.  
260 Obese women gave highest pleasantness ratings to stimuli containing 34% fat and 4% sugar,  
261 while normal-weight women preferred stimuli with 20% fat and 9% sugar (Drewnowski,  
262 Brunzell, Sande, Iverius, & Greenwood, 1985). Because the fat and sugar contents of food are  
263 predictive of the energy content, they activate common neural pathways for the reinforcement  
264 of behaviour. This activation leads to increased motivation to obtain high-fat/high-sugar foods  
265 and may reinforce energy intake and weight gain.

266 Concerning the sensory interactions with bitterness, Hayes and Duffy (Hayes & Duffy, 2007,  
267 2008) investigated the influence of the taste phenotype (PROP (6-n-propylthiouracil)  
268 bitterness) on the sweet and creamy sensations from sugar/fat milk-based mixtures (skim  
269 milk, whole milk and heavy cream). They found that fat and sweet liking depended on the  
270 subjects' PROP bitter sensitivity. The taster phenotype affects the degree of enhancement or  
271 suppression of sweetness and creaminess in liquid fat/sugar mixtures. For example, people  
272 who were more PROP sensitive rated creaminess higher than those who were less PROP  
273 sensitive, but only regarding heavy cream across all sucrose levels. As the fat level increased,

274 the positive PROP-sweet relationship decreased (Hayes & Duffy, 2007). Considering liking, it  
275 was observed that the fat and sugar levels for hedonic optima varied according to PROP  
276 sensitivity and/or the number of fungiform papillae. Women with many papillae exhibited  
277 optimal liking near 5% fat and 12% sucrose with a high effect of fat content, whereas women  
278 with a low number of papillae were less sensitive to the fat content. Thus, individuals with a  
279 low number of papillae may be less able to use oral sensory cues to identify high-fat foods,  
280 and we can hypothesize that they would be better in accepting low-fat foods than individuals  
281 with a high number of papillae who might detect differences in products faster. In that study,  
282 PROP bitterness better explained variations in creaminess than the number of fungiform  
283 papillae. The authors justified this observation because creaminess was not merely a tactile  
284 event and there was also an odorant component (Hayes & Duffy, 2007). This finding confirms  
285 that the olfactive component is important for global fat perception.

#### 287 1.5.2. Aroma-fat interactions

288 Most of the studies dealing with the sensory interactions between aroma and other modalities  
289 are focused on the impact of aroma on taste perception, and only a few of them report results  
290 on the impact of aroma on texture perception (Thomas-Danguin, 2009). The quality of the  
291 aroma-taste interaction basically depends on the capacity of two stimuli to be appropriate for  
292 the combination in a food product (congruency) (Schifferstein & Verlegh, 1996). Aroma-  
293 taste-integrated perception highly depends on learned associations, the context in which the  
294 food is consumed and the consumer's previous experience (Stevenson, Boakes, & Prescott,  
295 1998). Aroma-taste interactions have been extensively reported in model solutions and much  
296 lower in real-food samples. The impact of aroma on sweet perception has been extensively  
297 studied compared with other taste attributes, partly due to the common observation that  
298 certain odours smell "sweet". As an example, for the same sugar concentration, subjects

299 perceived whipped cream with a strawberry aroma as being sweeter than whipped cream  
300 alone (Frank & Byram, 1988). In custard desserts, it was also observed that a fruity aroma  
301 increased the sweet perception and vice versa, likely through cognitive mechanisms  
302 (Tournier, et al., 2009). Cross-modal interactions were also significantly reported for saltiness  
303 and aroma, mainly for lowering the salt content in foods while maintaining the saltiness  
304 intensity (Lawrence, et al., 2011). Only a few papers have reported on aroma-fat interactions.  
305 Syarifuddin et al. (Syarifuddin, Septier, Salles, & Thomas-Danguin, 2016) studied aroma-fat  
306 and aroma-salt interactions in model cheeses varying in fat, salt and pH levels, in which  
307 sardine (salt-related) and butter (fat-related) aromas were added. Although the butter aroma  
308 intensity in the model cheeses was lower than the sardine aroma intensity, the butter aroma  
309 was found to have greater enhancement of fat perception than sardine aroma in the different  
310 model cheeses. Sardine aroma was found to induce higher saltiness enhancement in model  
311 cheeses with a low fat level. Moreover, the variation in texture did not affect fat perception  
312 but only saltiness. Bult et al. (Bult, de Wijk, & Hummel, 2007) studied the interactions  
313 between cream aroma presented ortho- or retronasally and the oral texture (thickness and  
314 creaminess) of fresh milk with or without iota-carrageenan, using an air-dilution olfactometer.  
315 The researchers reported that the odour stimulus increased the intensities of oral texture  
316 perception, such as thickness and creaminess, but only when the odour was presented  
317 retronasally, that is, as if the odour would have originated from the liquid. In real food  
318 products, multimodal interactions involving texture, taste and aroma perception occur and  
319 affect differently fat perception and liking. The release of two aroma compounds from six  
320 model cheeses differing in fat content and firmness was followed in relation to perception  
321 (Guichard, Repoux, Qannari, Labouré, & Feron, 2017). The perception of blue cheese aroma  
322 (nonan-2-one) was not only explained by *in vivo* aroma release behaviour but also by the  
323 amount of fat remaining in the mouth, suggesting aroma-fat sensory interactions.

324 This first section highlighted that global oral fat perception involves olfactive, gustative and  
325 tactile modalities and that these different modalities of fat perception interact together and  
326 with other oral sensory modalities. The next paragraph will present the oral physiological  
327 parameters that could be involved in fat perception and liking and could explain inter-  
328 individual differences in fat perception and liking.

329

## 330 2. Food oral processing and bolus formation in relation to fat perception

331 Fat liking has been shown to be positively correlated with spreadability and fluidness and  
332 negatively with adhesiveness (Di Monaco, et al., 2008). Thus, bolus formation, structure and  
333 residence time are important factors in fat perception and liking. Most of the studies related to  
334 fat perception and liking reported great inter-individual variability, which could be mainly  
335 attributed to differences in oral physiology, saliva composition (Feron & Poette, 2013; Poette,  
336 et al., 2014) and food oral processing (Guichard, et al., 2017). This finding emphasizes the  
337 key impact of food breakdown in the mouth and bolus formation on fat perception and liking.  
338 We will first present the in-mouth food breakdown leading to the formation of a food bolus,  
339 and then we will examine the specific role of saliva, followed by the other physiological  
340 activities involved in the different steps of oral processing.

341

### 342 2.1. Food bolus structure

343 Regarding food emulsions, the role of teeth and chewing in the oral processing of the  
344 food matrix can be considered negligible. The main events that contribute to in-mouth  
345 emulsion breakdown are shear forces due to the compression of the tongue and palate, tongue  
346 movements, heat transfer (melting) and interactions with saliva. These events will lead to the  
347 destabilisation of the emulsion through flocculation and coalescence phenomena. To date,  
348 most studies on food boluses describe *ex vivo* or *in vitro* experiments under conditions



349 mimicking in-mouth processing and consider only a subset of the variables involved in the  
350 formation of the bolus. Thus, very few studies were conducted *in vivo* by describing the  
351 structure of the bolus just after spitting in humans, and most of them were performed on O/W  
352 emulsions only.

353         The first indications on food bolus structure, after the spitting of emulsions, showed  
354 that in-mouth food breakdown leads to the formation of particles (droplets) whose size is  
355 dependent on the level of emulsion thickening, the thinnest product leading to the smallest  
356 droplet size (De Bruijne, Hendrickx, Anderliesten, & De Looff, 1993). Moreover, O/W  
357 emulsions with mm-sized particles could be broken in the mouth into smaller droplets (20-30  
358  $\mu\text{m}$ ) by elongational flow (van Aken, Vingerhoeds, & de Hoog, 2007). By contrast,  
359 Dresselhuis et al. showed that the coalescence of O/W emulsions occurs in the mouth with the  
360 formation of droplets larger than 100  $\mu\text{m}$  for the lowest stabilized product (Dresselhuis,  
361 Stuart, van Aken, Schipper, & de Hoog, 2008). This coalescence phenomenon depends on the  
362 stability of the emulsion but also on the individual. The role of the stabilizer has been recently  
363 confirmed. Emulsions stabilized with Na-caseinate showed no considerable change after  
364 mixing with saliva, while the opposite trend was observed for lysozyme-stabilised emulsions,  
365 regardless of the concentration of emulsifier used (Camacho, den Hollander, van de Velde, &  
366 Stieger, 2015). However, in the mouth, emulsion coalescence depends not only on its stability  
367 but also on the solid fat content (SFC). High SFC emulsions show moderate coalescence  
368 scores, while medium SFC emulsions lead to a clear increase in the coalescence rating after  
369 oral processing (Benjamins, Vingerhoeds, Zoet, de Hoog, & van Aken, 2009). A change in  
370 the emulsion structure after oral processing will modify viscosity properties. After the oral  
371 processing of emulsions with different stabilities, droplet aggregation leads to an increase in  
372 viscosity by a factor of 2–7 for reversibly flocculated whey protein isolate (WPI)-stabilised  
373 emulsions and a much larger factor, 15–30-fold, for an irreversibly flocculated lysozyme-

374 stabilised emulsion. Such increases in viscosities are large enough to be perceived in the  
375 mouth. This observation provides indirect evidence for the sensory impact of the effect (van  
376 Aken, et al., 2007).

377 The way food is broken in the mouth impacts food bolus structure and thus tactile perception.

378

## 379 2.2. Role of saliva in food bolus formation

380 The multifunctional role of saliva as an unavoidable ingredient during the eating process has  
381 been recently reviewed, highlighting its surface coating and clustering properties, colloidal  
382 and enzymatic interactions, which may impact sensory perception (Mosca & Chen, 2017).

383 The amount of saliva incorporated contributes significantly to the change in the food bolus  
384 properties. Regarding fat emulsions and spreads, the level of moistening is both subject and  
385 product dependent. For instance, less saliva (20%) is incorporated in light and ultra-light  
386 products than in spreads and butter (26-28%). For subject effect, the amount of saliva  
387 incorporated ranges from 10% to 50% regardless of the matrix (light or fat). Regarding butter,  
388 the subjects were highly reproducible; however, for ultra-light products, an important intra-  
389 individual variability was observed (Feron, unpublished data). It is likely that these  
390 differences in oral processing have an impact on the food bolus structure with direct  
391 consequences on sensory perception and liking.

392 Saliva flow contributes mainly to the oral clearance of the mouth after food swallowing  
393 (Carpenter, 2012). The coating of food particles by the incorporation of saliva is necessary to  
394 form a bolus to be swallowed. Saliva stress in the mastication process has been estimated to  
395 be 50 Pa, and foods with a higher yield stress cannot be broken up and dispersed with the  
396 saliva flow. Thus, the resulting perceived mouthfeel will be rather grainy, sticky, or waxy  
397 than smooth (De Bruijne, et al., 1993). Such behaviour was observed in the case of nut butter  
398 (Hawthornthwaite, Ramjan, & Rosenthal, 2015; Rosenthal & Share, 2014). The authors

399 showed that the adsorption of water from the saliva gives rise to a sticky mass which coats the  
400 tongue and palate due to the presence of non-fat components within the spread (namely, dry  
401 complex carbohydrates and proteins).

402 Salivary viscosity has been estimated to be from 1 mPas to 6 mPas depending on the method  
403 of measurement (Schipper, Silletti, & Vingerhoeds, 2007). While suspected, the relationship  
404 between salivary viscosity and food bolus structure after oral processing of emulsions has not  
405 been formally demonstrated except through modelling approaches (De Bruijne, et al., 1993).  
406 However, experiments conducted *in vitro* on mayonnaises and custard with added artificial  
407 saliva containing mucin and not alpha-amylase failed to show any effect in friction properties,  
408 leading to the conclusion that no evidence was found that salivary mucins or salivary  
409 viscosity play a role in the lubrication of oral tissues (de Wijk & Prinz, 2005).

410  
411 Different saliva components might contribute to the destabilisation of O/W emulsions during  
412 the oral processing of food and are considered important in fat detection. Some salivary  
413 proteins (mucins), enzymes (amylase) and ions have been suggested as key components in in-  
414 mouth emulsion destabilisation. These components can provoke flocculation and coalescence  
415 by depletion phenomena and/or by electrostatic attraction and can hydrolyse the emulsion  
416 stabilisers (starch) located either at the surface of the oil droplets or in the continuous  
417 medium. However, these effects are related to the type and concentration of emulsifying  
418 proteins at the oil-water interfaces.

419 Vingerhoeds et al. showed flocculation phenomena after mixing W/O emulsion with real  
420 saliva (Vingerhoeds, Blijdenstein, Zoet, & van Aken, 2005). The researchers observed that  
421 these phenomena were subject and product dependent. Moreover, aggregation was observed  
422 with whole saliva but not with parotid saliva, suggesting the role of mucins as the main  
423 component in saliva responsible for the observed aggregation. This role of mucins on

424 emulsion destabilisation was described recently in numerous studies. Altogether, these studies  
425 concluded that flocculation was caused by a depletion mechanism and that  
426 adsorption/association of mucins onto the emulsion droplets was related to the type of  
427 emulsifying proteins at the oil-water interfaces and probably driven by the overall net charge  
428 at the droplet's oil-water interfaces at neutral pH (Vingerhoeds, Silletti, de Groot, Schipper, &  
429 van Aken, 2009; Silletti, Vitorino, Schipper, Amado, & Vingerhoeds, 2010; Sarkar, Goh, &  
430 Singh, 2009).

431 Alpha-amylase is the single most abundant protein in parotid saliva and a prominent  
432 component of whole-mouth saliva (Carpenter, 2012). The role of alpha-amylase can be two-  
433 fold. First, alpha-amylase can associate with an emulsion favouring droplet aggregation, thus  
434 contributing to the modification of the food bolus structure and then texture perception  
435 (Silletti, et al., 2010). Second, alpha-amylase can hydrolyse food containing starch, resulting  
436 in a loss in viscosity of the product in the mouth (van Aken, et al., 2007). This action was  
437 observed on mayonnaise during *in vitro* experiments. The consequence is a higher lubrication  
438 due to a higher release of fat from the matrix after starch digestion by alpha-amylase (de Wijk  
439 & Prinz, 2005; de Wijk, Prinz, Engelen, & Weenen, 2004). Under *in vivo* conditions,  
440 preliminary results presented in a recent review showed significantly reduced stability when  
441 starch emulsions (but not caseinate emulsions) were mixed with saliva due to the enzymatic  
442 action of alpha-amylase (Chen, 2015). The authors also conclude that this colloidal  
443 destabilisation may lead to a rough and watery sensation.

444 It has been shown that interaction between emulsion droplets and saliva was not limited to  
445 mucins or alpha-amylase but also involves other salivary proteins in the molecular mass range  
446 of 10–100 kDa such as polymeric Ig receptor and low-molecular-weight protein fractions  
447 (Silletti, et al., 2010). However, the large amount of salivary proteins associated with the  
448 droplets raises several questions regarding the nature of the interactions involved and nature

449 of the proteins. In particular, proline-rich proteins (PRPs) are the most abundant proteins in  
450 stimulated saliva. With an isoelectric point of 4 or 9/10 (depending the type of PRP), they can  
451 be either positively or negatively charged and, thus, can contribute significantly to droplet  
452 aggregation/repulsion.

453 In addition to proteins and enzymes, saliva is also rich in positively or negatively charged ions  
454 that could play a role in emulsion destabilization during oral processing. This role has been  
455 investigated by Sarkar et al. on O/W emulsions with lactoferrin or beta-lactoglobulin as the  
456 interfacial layer (Sarkar, et al., 2009). The authors showed that lactoferrin-stabilized emulsion  
457 droplets (positively charged at the salivary pH) showed considerable aggregation in the  
458 presence of salts (anionic) due to their screening effects. This salt-induced aggregation was  
459 reduced in the presence of mucin at different concentrations. Based on this result, the authors  
460 proposed an elegant mechanism describing the equilibrium between ions and mucins and  
461 droplet aggregation for lactoferrin-stabilised emulsion. Interestingly, this mechanism was not  
462 observed for the beta-lactoglobulin-stabilised emulsion, which is negatively charged at  
463 salivary pH, suggesting a major role of anionic salts.

464 Salivary composition impacts food bolus structure which will affect tactile perception.

465

### 466 2.3. Food oral processing in relation to bolus formation and fat perception

467 This section will present the different steps of food oral processing with their associated  
468 physiological parameters and the resulting impact on fat perception.

469

#### 470 *Tongue pressure and frictional effects*

471 Upon swallowing an emulsion, the tongue is pressed against the oral palate, producing a  
472 frictional effect (Malone, Appelqvist, & Norton, 2003). The shear forces destabilize the  
473 emulsion in a product-dependent manner (oral-processing emulsions stabilised with less

474 emulsifier resulted in larger coalescence phenomena). In contrast, although emulsions with  
475 solid fat (palm oil) had a greater tendency to make larger structures than emulsions with  
476 sunflower oil during *in vitro* experiments, this phenomenon was not observed in food bolus  
477 formation, likely because of the instantaneous melting of palm oil in the mouth (Dresselhuis,  
478 de Hoog, Stuart, Vingerhoeds, & van Aken, 2008; Sarkar & Singh, 2012). Thus, the role of  
479 tribology in the field of the oral processing of food is gradually gaining importance (Sarkar &  
480 Singh, 2012). However, *in situ* measurements of the shear stress and rate are difficult to  
481 obtain; evaluation of these parameters has been attempted through sensory experiments on  
482 various products (Shama, Parkinson, & Sherman, 1973; Shama & Sherman, 1973). The  
483 authors concluded that a wide range of shear rates was involved, extending from  
484 approximately  $10 \text{ s}^{-1}$  to over  $1000 \text{ s}^{-1}$ . The operative shear rate depended on the flow  
485 characteristics of the food, being much higher for viscous foods than for fluid foods. For  
486 example, the shear rates occurring in the mouth ranged from  $5 \text{ s}^{-1}$  for products such as hard  
487 margarine to  $37 \text{ s}^{-1}$  for more fluid products such as tomato ketchup (Malone, et al., 2003). In a  
488 similar study, 3 groups of sensory attributes were identified (Kokini, Kadane, & Cussler,  
489 1977). The first group, exemplified by “thickness”, was closely associated with viscous force;  
490 the second group, characterized by “smoothness”, was associated with the frictional force  
491 caused by contact between the tongue and roof of the mouth; the third group, as suggested by  
492 “slipperiness”, was most closely associated with a combined force involving both frictional  
493 and viscous components.

494 Tongue pressure and frictional effects impact food bolus structure and fat perception  
495 differently according to food composition and structure.

496

497 *Mouth coating and oral clearance*

498 Mouth coating is the result of the action of saliva, oral movement and swallowing due to the  
499 pressure of the tongue to the soft palate.

500 Evaluating oral coating after O/W emulsion consumption is of high interest because it impacts  
501 directly on the fatty after feel perception. Using O/W emulsions, Camacho et al (Camacho,  
502 van Riel, de Graaf, van de Velde, & Stieger, 2014) concluded the following: (i) a direct  
503 positive relationship exists between the amount of lipid ingested and level of coating; (ii) a  
504 rapid oral clearance of the oral surfaces was observed after spitting; (iii) a higher coating was  
505 evident on the back of the tongue than on the front or lateral; and (iv) an important effect of  
506 the stabilizer and thickener was exerted on coating. In particular, the authors showed that  
507 emulsions with a higher thickener concentration rated higher on fattiness. This finding  
508 suggests that thickeners might create a lubricating layer on the tongue, thereby decreasing the  
509 friction and increasing fatty after-feel (Camacho, den Hollander, van de Velde, & Stieger,  
510 2015). For margarines differing on the level of fat and fat type (vegetal or mix), similar  
511 experiments were conducted using fluorescent probes (Poette, et al., 2014). Significant  
512 differences between products were observed regardless of the time of the measurement, with  
513 pure vegetal spreads coating the tongue more than the mix products. Moreover, high-fat  
514 spreads coated the tongue more than low-fat spreads, and the coating was higher at the back  
515 of the tongue than at the front and lateral parts. Finally, the oral clearance of fat was linked to  
516 salivary flow. This is an interesting result showing similar tongue coating with w/o emulsion  
517 and o/w emulsion. It is likely that the fatty after-feel after swallowing is also impacted.

518 Mouth coating and oral clearance depends on emulsion structure and impact fatty after feel  
519 sensation.

520

521 *Oral volume and oral residence time*

522 Surprisingly, the oral volume was rarely investigated in oral-processing behaviour, although it  
523 may be the dominant factor in determining the exchange surface in the oral cavity. The oral  
524 volume varies significantly among individuals with an overall mean of  $38.6 \pm 10.5 \text{ cm}^3$   
525 (Feron, Ayed, Qannari, Courcoux, Laboure, et al., 2014). Regarding O/W emulsions, the oral  
526 volume was directly and negatively correlated with fat sensitivity (Poette, et al., 2014). The  
527 influence of the oral volume on sensory perception has already been highlighted for model  
528 cheeses, showing a negative correlation between the oral volume and rate of aroma perception  
529 (Guichard, et al., 2017), which was explained by a dilution effect.

530 The oral residence time of the product in the mouth has never been directly related to sensory  
531 perception, but it depends on the product's properties. In the case of liquid or semi-liquid  
532 food, the duration of oral processing is normally short. Considering 28 semi-solid products,  
533 Chen and Lolivret showed an average oral residence time from 1.6 s for yoghurt to 7.7 s for  
534 honey (Chen & Lolivret, 2011), and Camacho et al. examined 25 subjects and found an  
535 approximate value of 8 s for the oral residence time for O/W emulsions (Camacho, Liu,  
536 Linden, Stieger, & Velde, 2015).

537 Oral volume impacts the dynamic of aroma release and the resulting olfactive modality of fat  
538 perception.

539

#### 540 *Heat transfers and melting*

541 The melting of emulsions in the mouth occurs immediately after ingestion of the product. It  
542 results from the rapid transfer of heat from the mouth oral surface to the product, leading to  
543 the perception of coolness (Galindo-Cuspinera, et al., 2017). Melting depends on the crystal  
544 structure and nature of the fat in the product. In the case of spreads, melting leads to the  
545 immediate inversion of the emulsion, from W/O to O/W. Indeed, it has been shown that if the  
546 droplet size exceeds  $30 \mu\text{m}$  in diameter, some droplets will join to form channels or 'lakes'.



547 Eventually, the water phase may become continuous during oral processing (i.e., inversion of  
548 the emulsion may occur). On the other hand, if the water droplets are too small or are highly  
549 stabilized, the phase inversion in the mouth under the influence of shear and added aqueous  
550 phase (saliva) will not occur or will occur too slowly. Such spreads will have an unpleasant  
551 gummy mouth feel. The cooling sensation because of melting fat will also be absent (Keogh,  
552 2006). The melting rate and softening of margarines are directly linked to the level of  
553 crystallised fat. Therefore, products containing more crystal fat will be perceived to melt  
554 slower than products containing more liquid oil (Bot et al., 2003). Moreover, when high-  
555 melting-point (above mouth  $T^{\circ}$ ) triglycerides (HMTs) are used in margarine or butter, they act  
556 as a barrier that prevents the coalescence of droplets (Keogh, 2006). This point is particularly  
557 relevant considering the in-mouth inversion phase of W/O emulsions leading to O/W  
558 emulsions because these HMTs will behave as solid particles (likely with different shapes and  
559 sizes) floating in a liquid phase. This behaviour can lead to the perception of rough,  
560 heterogeneous and granny attributes.

561 Melting depends on fat nature and impacts the tactile modality of fat perception.

562

#### 563 2.4. Physiological parameters explaining interindividual differences in fat perception and 564 liking

565 Due to the great impact of saliva on food bolus formation, inter-individual differences in  
566 saliva composition should impact fat perception. Engelen et al. investigated how variations in  
567 salivary characteristics affect the sensory perception of semi-solid products: in this case,  
568 mayonnaise and custard dessert by eighteen subjects (Engelen, et al., 2007). The results  
569 obtained for mayonnaise showed that a high salivary protein concentration is negatively  
570 associated with low oily and sour flavours, a thick and smooth texture, followed by sticky and  
571 fatty after feels. A high mucin level increased the heterogeneity and decreased the prickling  
572 mouth feel, and a high alpha-amylase activity induced a low prickling mouth feel and creamy

573 after feel. High protein concentrations could possibly induce a decrease in the viscosity of the  
574 product (through enzymatic breakdown), hindering the formation of a fatty layer on the  
575 mucosa and leading to a low thickness sensation. The saliva composition can impact in-mouth  
576 aroma release through enzymatic reactions occurring in the mouth between salivary proteins  
577 and aroma compounds (Ployon, Morzel, & Canon, 2017) or through hydrophobic interactions  
578 as demonstrated in model systems between mucins or alpha-amylase and aroma compounds  
579 (Canon, Pagès-Helary, & Guichard, 2014; Pagès-Hélary, Andriot, Guichard, & Canon, 2014).  
580 If a decrease in aroma release has been demonstrated in the presence of salivary proteins, the  
581 direct relationship between salivary protein concentration and aroma perception has not been  
582 established yet.

583 Sensitivity to fat has also been related to the number of fungiform papillae (FP) present on the  
584 tongue with potential consequences on fat intake (Nachtsheim & Schlich, 2014). Individuals  
585 with a high FP (HFP) count were more sensitive to the fat content and tended to consume less  
586 fat than individuals with less FP (LFP) when evaluating high-fat margarine and milk. These  
587 differences in the sensitivity to fat as related to the number of FP and how they correlate to  
588 food intake were not observed for cheese or sausage. The authors suggested that FP could be  
589 involved in modulating sensory attributes specific to spreads and milk such as creaminess and  
590 melting. Interestingly, the authors showed a negative correlation between the salivary flow  
591 (SF) and number of FP. This observation suggests that individuals with a low SF may have a  
592 lower oral clearance after spread consumption, and, given the higher number of FP present,  
593 these individuals are likely more sensitive to fatty/greasy attributes (Nachtsheim & Schlich,  
594 2014).

595 Differences in saliva composition and FP induce differences in fat perception.

596

### 597 **3. Conclusion**

598 Based on the information presented, a general mechanism can be proposed for the breakdown  
599 of spreads in the mouth leading to fat perception, involving first a melting phase, followed by  
600 an inversion phase and then bolus formation and swallowing (Figure 1).

601 Insert Figure 1

602

603 The **melting phase** begins as soon as the emulsion is placed in the mouth. In the case of W/O  
604 emulsions, the emulsion is inverted, and the progress of this inversion is driven by the  
605 physico-chemical properties of the fat, particularly the fat concentration, type of fat present  
606 and crystal structure. Thus, the solid fat content is an important parameter because it drives  
607 the cooling sensory descriptor, which appears to be an important attribute for product liking.  
608 In terms of physiological variables playing a role in the melting phase, it is difficult to find  
609 supporting data in the literature. However, we can propose that the oral volume and tongue-  
610 plate compression contribute to favour heat transfer and, thus, to emulsion melting.

611 In the case of W/O emulsions, the **inversion phase** often occurs at the same time as the  
612 melting phase, and the rate of this inversion is controlled mainly by the product's physico-  
613 chemical properties, particularly the level of fat as well as emulsifiers and stabilizers. The  
614 difficulty is to find the good balance in terms of meltability and emulsion stability that would  
615 lead to a desirable mouthfeel. Having fat crystals that do not melt in the mouth will lead to a  
616 waxy feeling. Furthermore, if water droplet stability is too high, inversion does not occur, and  
617 the taste/aroma release will be affected. If the stability is too low, the inversion is too fast, and  
618 the creaminess will decrease. In addition to other physiological variables involved in the  
619 melting phase, a high salivary flow may favour moistening and, thus, inversion. At the end of  
620 this phase, we have an O/W emulsion composed of fat, water, aroma and taste compounds,  
621 food additives and also a significant amount of salivary components.

622

623 During **bolus formation**, which starts with the breakup of the emulsion in the mouth and  
624 continues after phase inversion and until swallowing, oral processing events are similar to  
625 what is observed for O/W emulsions. Food oral processing consists mainly of flocculation and  
626 coalescence phenomena, leading to a food bolus that is heterogeneous and viscous. These  
627 phenomena will directly impact sensory perception, particularly creaminess, roughness and  
628 fattiness and, thus, liking. In this phase, the role of the individual's physiology is highlighted,  
629 particularly the salivary flow (effect on oral coating), salivary viscosity (effect on droplet  
630 size) and some salivary components, such as alpha-amylase, mucins, ions (effect on droplet  
631 flocculation and coalescence) and PRP. Concerning the product, the fat level, quality, product  
632 stabilizers and thickeners are important for the emulsion breakup in this phase. However,  
633 aroma composition and, thus, aroma release during food oral processing are also important  
634 drivers of fat/spread perception and, thus, liking, as highlighted previously. Some aroma notes  
635 can contribute positively to liking (e.g., creamy and buttery), but others contribute negatively  
636 to liking (e.g., greasy notes). The dynamic of aroma release that depends on the solid fat  
637 content (the higher the solid fat content is, the slower the aroma release is) and the dynamic of  
638 the amount of product remaining in the mouth are drivers of the dynamics of perception.  
639 Controlling the release of the different aroma compounds during bolus formation and  
640 swallowing will lead to a well-balanced aroma perception, contributing positively to liking.  
641 The remanence of off-flavour aroma compounds in the mouth will contribute to an  
642 undesirable after taste and a low liking. Most importantly, the interactions among the different  
643 perceptual modalities (texture, taste, aroma, appearance and perhaps even sound) involved in  
644 fat perception must be considered for the global acceptability of fat-containing products.

645

#### 646 4. Future trends

647 The main outcome from this review is that consumer segmentation from a physiological view  
648 should be primarily based on the melting and inversion phases for O/W emulsions because,  
649 together, they constitute the first dynamic events when the product is placed into the mouth  
650 and contribute to the emulsion breakup, leading to the first sensory sensations. Considering  
651 the previous conclusion and limited work published in this area, there is a need for a thorough  
652 investigation of the melting and inversion phases that play a crucial role in bolus formation  
653 with consequences in sensory perception and liking. In particular, the relationship between the  
654 melting phase, inversion phase, cooling perception, nature and structure of the fat phase and  
655 how they affect the emulsion breakup and oral behaviour needs to be explored through a  
656 mechanistic approach at different levels, from the molecular to the more global oral system.  
657 This investigation can allow prioritization of the different physiological oral characteristics  
658 (oral volume, oral surface exchanges) that drive this step and explain inter-individual  
659 consumer differences.

660 A secondary outcome is that mouth feel is another important sensory sensation contributing to  
661 the global liking of the product. Mouth feel is highly related to mouth coating and oral  
662 clearance. Thus, there is a need to investigate deeply the mechanisms occurring during bolus  
663 formation and how differences in physiology affect mouth coating and clearance. While  
664 several literature reports have been published on the role of saliva in perception, the relative  
665 impact of salivary proteins, fungiform papilla, salivary flow, mucosal pellicle and PROP  
666 sensitivity on fat liking has not been fully elucidated yet.

667 Third, understanding the olfactory contribution to fat perception should account for the  
668 different aroma molecules with fatty notes, their molecular interactions with fat, salivary  
669 proteins and impact of food oral processing on dynamic aroma release and dynamic sensory  
670 perception.

671 Finally, fat should be considered as a multimodal perception; thus, the relative contribution of  
672 the different modalities (olfactive, gustative and tactile) underlying to fat liking must be  
673 unravelled. Due to the growing development of cognitive neurosciences to unravel  
674 multisensory integration, the mechanisms leading to multimodal interaction could now be  
675 envisaged at the central level. Brain imaging approaches could provide better insights into our  
676 understanding of the brain processes implied in multimodal interactions and their impact on  
677 the holistic perception of flavour and subsequent liking.

678

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681

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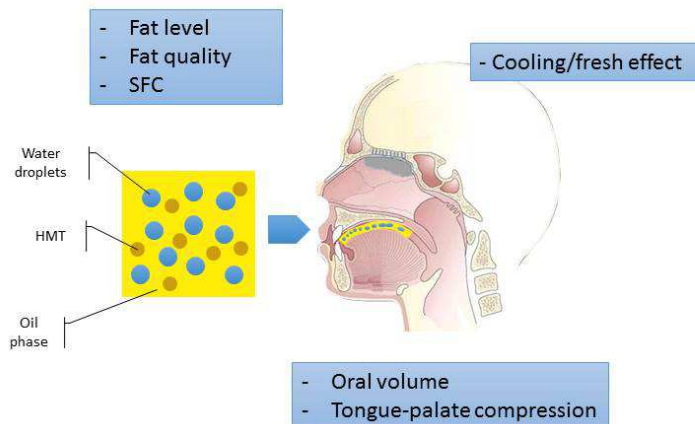
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921 Figure caption

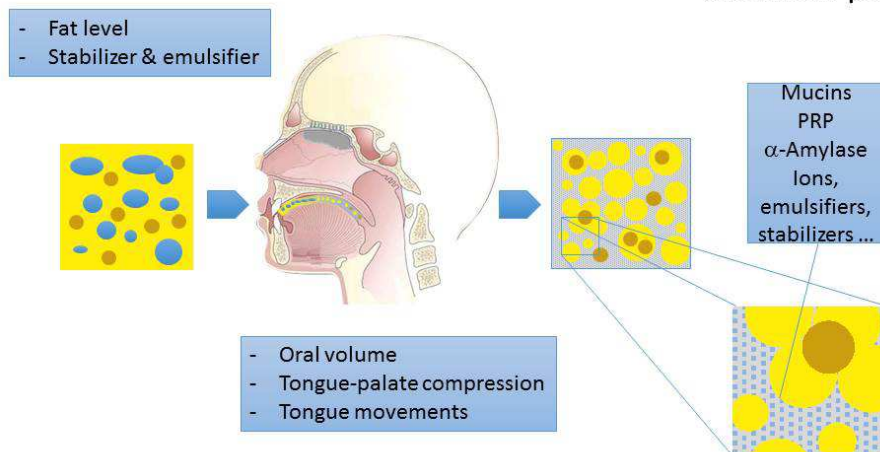
922 Figure 1: proposed mechanisms describing the different oral events occurring during  
923 consumption of spread and their putative impact on sensory attributes.

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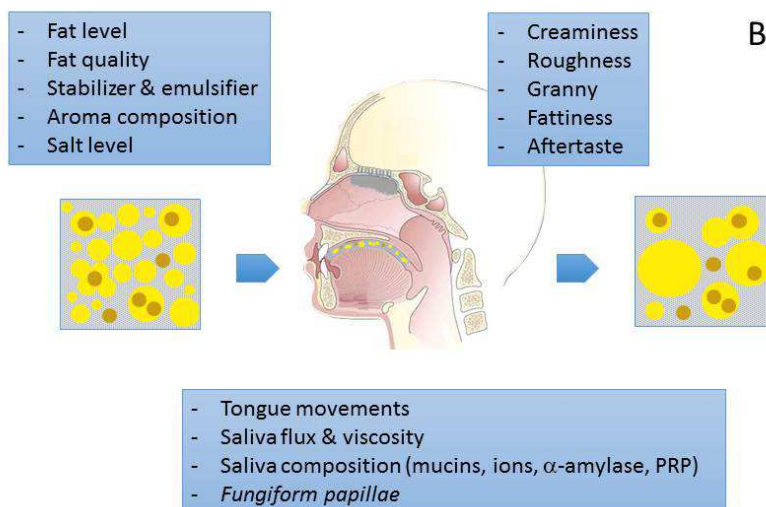
## Melting phase



## Inversion phase



## Bolus formation



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