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Smells like fat: A systematic scoping review on the contribution of olfaction to fat perception in humans and rodents

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ABSTRACT

Understanding how dietary fat is perceived by the senses is crucial in developing public health strategies aimed at curbing excessive fat intakes. Olfaction is one of several sensory modalities contributing to fat perception in foods, yet the nature and extent of its involvement is relatively unclear.

A systematic scoping literature review was conducted to identify and summarise relevant evidence on the contribution of olfaction to dietary fat perception in humans and rodents and highlight relevant knowledge gaps. The review was carried out in accordance with the PRISMA methodology, using combinations of olfaction-, fat- and perception-related search terms. Following searches in Scopus, Web of Science and PubMed databases, 42 articles were ultimately included.

Overall, findings are consistent with the notion that olfaction plays a role in the perception of dietary fat in rodents and humans. Rodents can perceive dietary fat via olfactory cues, and this ability may affect their preference for fat-containing feed. Humans can detect, discriminate, and identify fat and its constituents solely by olfaction, even when embedded within a complex food matrix. Food fat content can modulate the perception of various fat- and non-fat olfactory qualities, depending on the food matrix and odorant physio-chemical properties. On the other hand, the presence of fat-related odours can modify the perception of olfactory and non-olfactory sensory qualities (e.g., mouthfeel). Several knowledge gaps were identified, namely, the role of fat-related odours in eating behaviour, the nature of chemical signals underlying olfactory fat perception and factors governing sensitivity to fat-related odours.

1. Introduction

Consumption of dietary fat is exceeding recommended daily intake requirements in many Western countries, including the Netherlands (van Rossum et al., 2020), in some accounting for up to 46% of the total daily energy intake (Eilander et al., 2015). Due to its high energy density and low effect on satiation, especially in obese individuals, (Blundell et al., 1993) fat is considered a major contributor to energy overconsumption and consequential development of obesity and related comorbidities (Blundell & Macdiarmid, 1997; Bray et al., 2004; Golay & Bobbioni, 1997). Fat overconsumption is further exacerbated by its flavour, texture, and aroma-enhancing properties, all of which considerably contribute towards the pleasurable experience of eating (Drewnowski, 1997a, 1997b; Drewnowski & Almiron-Roig, 2009). The interaction of these factors has recently been illustrated by Teo et al. (2022) who found that foods associated with fat-related flavours

contributed most to higher energy intakes, independent of weight status.

Multiple sensory systems contribute to dietary fat perception (Drewnowski & Almiron-Roig, 2009; Guichard et al., 2018). Fat is known to impart a range of mouthfeel sensations, such as thickness, creaminess, mouthcoating and smoothness (Drewnowski, 1992; Mela, 1988; Schiffman et al., 1998), while the presence of free fatty acids can be detected in the oral cavity via taste receptors located on the human tongue (Chale-Rush et al., 2007; Keast & Costanzo, 2015; Mattes, 2009; Pepino et al., 2012; Running et al., 2015; Stewart et al., 2010). In addition to mouthfeel and taste cues, the involvement of olfactory cues in fat perception has also been established. Flavour release studies identified various volatile compounds, belonging to different chemical classes as being associated with fat-related sensations (Guichard, 2002; Guichard et al., 2018). When released from foods or beverages, these volatiles bind to receptors located throughout the olfactory epithelium in the nasal cavity, which ultimately results in odour perception (Delime

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et al., 2016). Orthonasal odours originate from the external environment and enter the nasal cavity via the nostrils. They are thought to be related to food source detection and the induction of appetite during the anticipatory phase of eating. Retronasal odours, on the other hand, enter the nasal cavity from the mouth during food consumption. They mainly contribute to flavour perception and may influence intake and satiation (Boesveldt & de Graaf, 2017; Bojanowski & Hummel, 2012; Delime et al., 2016; Goldberg et al., 2018). The two olfaction routes can yield distinct perceptions, even when odour intensities are matched (Sun & Halpern, 2005). In comparison to mouthfeel and taste, however, the involvement of olfaction in dietary fat perception seems to be relatively underexplored and much remains unclear about the nature and extent of its contribution.

Given the societal relevance of understanding sensory fat perception, and the lack of systematic literature reviews on this topic in academic literature, the current scoping review aimed at (1) systematically identifying and summarizing relevant evidence on the contribution of olfaction to dietary fat perception in humans and rodents, and (2) highlighting relevant knowledge gaps. The rationale behind focusing on broader literature, also involving rodents, was to gain insight from mechanistic studies, which might not be feasible or ethical to conduct in human subjects.

2. Methods

Due to the broad nature of its aims, the current work is considered a systematic scoping review. It was conducted in accordance with the Preferred Reporting Items for Systematic Reviews and Meta Analyses (PRISMA) methodology (Moher et al., 2009).

2.1. Search strategy

Three academic electronic databases (Scopus, PubMed and Web of Science) were searched for original articles published in English, without any publication date restrictions. Search strings included olfaction- (e.g. volatiles, orthonasal, aroma, odour) and fat-related words (e.g. fat, lipid, fatty acid, butter), combined with perception-related words or strings (e.g. flavour, discrimination, identification, chemosensory). Search strings for all three databases contained exclusion commands (excluding words such as cat, dog, insect, larvae from the search), to avoid articles beyond the scope of this review (e.g. insect studies). Detailed search strategies used in each database can be found in [Supplementary Material A](#). Due to search algorithm differences, a specific search string was applied to each of the databases. It must be noted that the word “preference” in combination with fat-related words was excluded from the search string applied in the PubMed database. This was done to increase specificity, as inclusion of this combination mainly yielded articles deemed beyond the scope of this review. Early search results were evaluated to determine the relevance of obtained articles, and search term modifications were made prior to the formal search procedure. Reference lists of included articles were not searched for articles not captured by the searches. Manual searching was also not undertaken.

2.2. Article inclusion

Articles met eligibility criteria if they reported an investigation of olfactory exposure (ortho- or retronasal) to fat and its constituents, in isolation or via foods (real or model), beverages or emulsions in human or rodent subjects, utilising sensory evaluation. Sensory evaluation was defined as a scientific approach utilising a measure of perception, discrimination, identification, preference, acceptance and/or detection thresholds. Articles concerning the addition of fat-related aromas/flavourings to foods were included as well if their addition impacted relevant sensory attributes. Exclusion criteria involved fat perception not being the topic of research; lack of olfactory exposure to suitable fat

sources (i.e. either no exposure to fat; or exposure to fat in combination with potentially confounding odour/flavour sources); lack of reporting relevant outcomes resulting from olfactory exposure; articles focusing on volatile compounds without relevant sensory evaluation measures; reviews, meta-analyses, books, or book chapters; articles lacking an abstract; full-text unavailability; non-English publications; and non-peer reviewed publications.

2.3. Article selection

Literature searches were performed up to April 2021 by three authors: PM, MS and FG. All identified items were exported to the reference software EndNote™ X9 (Clarivate Analytics) where they were organized, deduplicated and screened following the PRISMA guidelines (Moher et al., 2009). Title and corresponding abstract screening were carried out by FG. Screening reliability was determined by calculating the Cohen’s Kappa coefficient, after PM and FG screened a random sample of 116 titles and corresponding abstracts from the retrieved items (sample size was determined in accordance with the Cohen’s Kappa methodology). The interrater reliability score amounted to 0.90, which indicated a strong agreement (McHugh, 2012; Sim & Wright, 2005). Remaining potentially eligible items then underwent full-text screening, carried out by PM and MS. Any discordances regarding the ultimate inclusion of articles in the review were discussed by the reviewers until reaching a consensus. A list of citations excluded during the full-text screening process can be found in Table S1, [Supplementary Material B](#).

2.4. Review outcomes and data synthesis

Data from articles meeting all inclusion criteria were extracted. Extracted data included outcomes of interest relevant to our research question, study population characteristics (along with relevant population specifics, if applicable), stimuli (types used along with the applied manipulation, if applicable), route of olfactory exposure (orthonasal or retronasal), and relevant findings. Data were then evaluated and interpreted by all authors, tabulated per study, and listed by author name in an ascending alphabetical order. Rodent studies were distinguished from human ones and reported in a separate table. A narrative synthesis was ultimately conducted, meta-analysis was not performed due to the indirect nature of most of the identified work and lack of relevant and comparable data.

2.5. Risk of bias assessment

To assess the quality of included studies, two authors (MP and MS) independently reviewed and evaluated each article in accordance with the Cochrane Association Risk of Bias methodology (Higgins et al., 2011). Any discrepancies in risk of bias scores were discussed to reach agreements. Due to the nature of this review’s topic, specific risk assessment domains were generated per study subject type. Risk evaluation domains for rodent studies included random group generation, researcher blinding, incomplete outcome reporting and selective reporting. Human studies were evaluated on stimulus randomisation; isolation of olfaction from potentially confounding effects of taste, mouthfeel, and trigeminal sensations; participant blinding to sample identities; incomplete outcome reporting; and selective reporting. For each domain, the risk of bias was rated as “low risk”, “some concern”, “high risk” or “risk unclear”, based on information reported in the included articles.

3. Findings

An overview of the search process and its results can be seen in the PRISMA flowchart in [Fig. 1](#). Database searches resulted in the identification of 2596 items from all sources, with 1703 of them remaining after

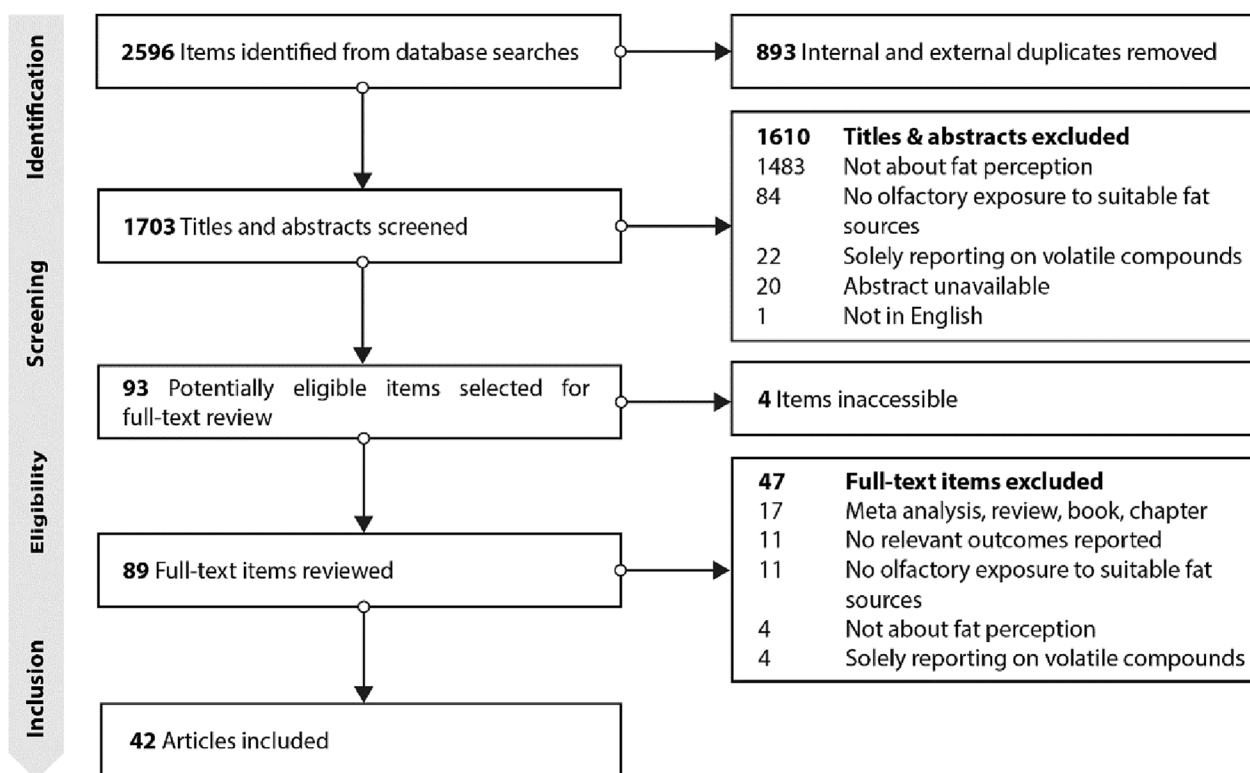


Fig. 1. Preferred Reporting Items for Systematic Reviews and Meta-Analyses flow diagram of the literature search to identify olfactory fat perception studies.

deduplication. After title and abstract screening, 93 items remained and were assessed against our eligibility criteria. In total, 51 items were excluded: 4 were not about fat perception, 11 lacked olfactory exposure to suitable fat sources, 11 did not report relevant outcomes resulting from olfactory exposure, 4 focused on volatile chemical compounds without relevant sensory evaluation measures, 17 were either *meta*-analyses, reviews, books, or book chapters, and 4 were inaccessible. Full-text assessment ultimately resulted in 42 articles being included in the current review.

3.1. Rodent studies

A summary of studies investigating olfactory fat perception in rodents is presented in Table 1.

Six studies employed rodent subjects, namely mice (Boone et al., 2021; Kinney & Antill, 1996; Lee et al., 2015; Takeda et al., 2001; Xavier et al., 2016) or rats (Ramirez, 1993). In all cases wild-type controls were compared to either anosmiated (Boone et al., 2021; Kinney & Antill, 1996; Lee et al., 2015; Ramirez, 1993; Takeda et al., 2001) or CD36 receptor-deficient specimens (Xavier et al., 2016). All rodent studies utilised preference paradigms in which animals were exposed to olfactory stimuli either via food varying in fat content (Boone et al., 2021; Kinney & Antill, 1996; Ramirez, 1993), scented paper (Xavier et al., 2016), sucrose-based solutions (Lee et al., 2015), or corn oil and linoleic acid (Takeda et al., 2001).

To summarize, rodents' preferences for fat-related odorants diminished when rodents were anosmiated (Kinney & Antill, 1996; Ramirez, 1993; Takeda et al., 2001) or lacked olfactory CD36 receptors (Xavier et al., 2016). Once their sense of smell was restored, preference for fat returned (Kinney & Antill, 1996). Moreover, following anosmiation, rodents lost their preference for aversion-inducing lipids (Lee et al., 2015). Anosmiation, however, did not lead to a complete preference diminishment for fat in all cases. Despite anosmiation, Boone et al. (2021) observed no preference alterations towards a high-fat diet, Ramirez (1993) observed only a decrease in preference towards fat-

containing mixtures, while Takeda et al. (2001) observed a preference decrease only for corn oil containing higher fat levels.

3.2. Human studies

A summary of studies investigating olfactory fat perception in humans is presented in Table 2.

Of the 36 studies employing human subjects, 8 presented olfactory stimuli orthonasally (Boesveldt & Lundstrom, 2014; Chen & Eaton, 2012; Dadali & Elmaci, 2019; Fernandez et al., 2000; Glumac & Chen, 2020; Kindleysides et al., 2017; Running et al., 2017; Rychlik et al., 2006), 15 retronasally (Arancibia et al., 2015; Brauss et al., 1999; Chukir et al., 2013; Ebba et al., 2012; Frank et al., 2015; González-Tomás et al., 2007; Jarvis et al., 2014; Kallas & Halpern, 2011; Kindleysides et al., 2017; Le Calvé et al., 2015; Mela, 1988; Miettinen et al., 2004; Roberts, Pollien, Antille, et al., 2003; Schoumacker et al., 2017; Yackinous & Guinard, 2000; Zhou et al., 2016) and 13 through a combination of both olfaction routes (Bolton & Halpern, 2010; Bult et al., 2007; Chale-Rush et al., 2007; de Wijk et al., 2003; Frøst et al., 2001; Han et al., 2019; Hyvönen et al., 2003; Lorenzo et al., 2015; Miettinen et al., 2003; Parat-Wilhelms et al., 2005; Running et al., 2017; Syarifuddin et al., 2016; Ventanas et al., 2010; Weenen et al., 2005). Utilised sensory methodology included perceptual ratings (Boesveldt & Lundstrom, 2014; Bult et al., 2007; Chen & Eaton, 2012; Dadali & Elmaci, 2019; de Wijk et al., 2003; Ebba et al., 2012; Fernandez et al., 2000; Frank et al., 2015; Frøst et al., 2001; Han et al., 2019; Hyvönen et al., 2003; Jarvis et al., 2014; Lorenzo et al., 2015; Mela, 1988; Miettinen et al., 2004; Miettinen et al., 2003; Parat-Wilhelms et al., 2005; Roberts, Pollien, Antille, et al., 2003; Rychlik et al., 2006; Syarifuddin et al., 2016; Ventanas et al., 2010; Weenen et al., 2005; Yackinous & Guinard, 2000; Zhou et al., 2016); discrimination testing (Boesveldt & Lundstrom, 2014; Bolton & Halpern, 2010; González-Tomás et al., 2007; Kallas & Halpern, 2011; Le Calvé et al., 2015); detection (Chale-Rush et al., 2007; Schoumacker et al., 2017), difference (Le Calvé et al., 2015; Schoumacker et al., 2017) and rejection (Running et al., 2017) threshold testing; pairwise ranking

Table 1
Summary of studies investigating olfactory fat perception in rodents.

Study	Outcome(s) of interest	Subjects	Stimuli	Relevant Findings	Interpretation
Boone et al. (2021)	Changes in feeding patterns in response to varying access to different diets (standard or standard in combination with high fat).	A total of 96–120 (exact numbers per experiment n.s.) mixed-sex adult mice, either anosmiated via complete bilateral bulbectomy or sham-operated.	Standard diet (14% energy from fat) and high fat diet (60% energy from fat).	All mice, regardless of treatment (anosmiated or sham-operated) exhibited a preference for the high-fat diet.	Olfactory information is not relevant for the formation of high-fat food preferences.
Kinney and Antill (1996)	Intake of food mixtures during a 2-h preference test.	36 male albino mice: 12 underwent bilateral olfactory nerve section, 12 underwent sham surgery (control), 12 untreated mice (control).	Corn oil-based high fat (3.42 kcal/g) and mineral oil-based low-fat (2.61 kcal/g) food mixes.	Pre-treatment, all mice preferred the high-fat food mixture; post-treatment, anosmic mice showed no preference for the high-fat mixture, preference for the high-fat mixture increased in the control groups. Preference for the high-fat mixture returned to anosmic mice after olfactory nerve recovery.	Olfactory information is relevant for the formation of high-fat food preferences.
Lee et al. (2015)	Intake following two-bottle choice tests	8 – 12 week old mice (number and sex n.s.): Sham-operated (control) or anosmiated via olfactory nerve transection.	0.15 M sucrose solutions with 7.5 μ M KODiA-PC lipids (test) and without (control)	In contrast to normosmic controls, anosmiated mice exhibited preference for the solution containing the aversive KODiA-PC lipid.	Olfaction is involved in the perception of lipids in mice.
Ramirez (1993)	Preference scores following two-bottle preference tests.	20 female rats: 12 anosmiated via bulbectomy, 8 underwent sham surgery (control).	Carbohydrate- and fat-containing mixtures. Fat-containing mixtures included 0.5% corn oil, 1% corn oil, 0.5% triolein and 1% triolein.	Preference scores for fat-containing mixtures were lower in bulbectomized rats than in sham operated ones. Bulbectomized rats still exhibited preferences for fat-containing mixtures.	Preference for fat is mediated by olfactory and non-olfactory cues.
Takeda et al. (2001)	Voluntary intake of corn oil or linoleic acid; Place preference.	28 male mice: either sham-treated or anosmiated (via ZnSO ₄ -induced olfactory blockade).	Corn oil (1, 3, 5 and 10%), linoleic acid and water.	Pre-treatment, mice preferred corn oil over the vehicle at all concentrations; post-treatment, sham-treated mice preferred corn oil over the vehicle at all concentrations, anosmiated mice preferred corn oil only at higher ones (5% and 10%), Place preference induced by corn oil was observed in both treatment conditions.	Multiple sensory modalities are involved in the perception of oil, olfactory stimuli might act as a signal for oil at low concentrations.
Xavier et al. (2016)	Innate preference for scented filter paper inferred from Investigation time.	10 mice: 6 with CD36 receptor deficiency, 4 wild type (control).	Deodorized filter paper scented with PBS (control), amyl acetate (1 mM), or a lipid concentrate.	Contrary to wild type mice (control), CD36-deficient ones showed no preference for the lipid concentrate-scented filter paper.	Receptor CD36 is involved in the perception of fat-related odorants.

(Arancibia et al., 2015); time-intensity methods (Brauss et al., 1999; Hyvönen et al., 2003; Miettinen et al., 2004; Miettinen et al., 2003; Ventanas et al., 2010); and identification testing (Chukir et al., 2013; Glumac & Chen, 2020). In addition to sensory methods, aroma volatile release or volatile compound composition analyses (Arancibia et al., 2015; Brauss et al., 1999; Dadalı & Elmacı, 2019; Frank et al., 2015; González-Tomás et al., 2007; Miettinen et al., 2004; Miettinen et al., 2003; Roberts, Pollien, Antille, et al., 2003; Ventanas et al., 2010) and dietary intake assessments (Boesveldt & Lundstrom, 2014; Kindleysides et al., 2017) were carried out. Fatty acids were exclusively used as olfactory stimuli in six studies (Bolton & Halpern, 2010; Chale-Rush et al., 2007; Chukir et al., 2013; Ebba et al., 2012; Kallas & Halpern, 2011; Kindleysides et al., 2017), with subjects being exposed to either stearic, linoleic and oleic acid (Bolton & Halpern, 2010; Chale-Rush et al., 2007; Chukir et al., 2013; Kallas & Halpern, 2011); taste strips containing varying levels of linoleic acid (Ebba et al., 2012); or oleic acid (Kindleysides et al., 2017). Food matrices served as olfactory stimuli in 31 human studies (Arancibia et al., 2015; Boesveldt & Lundstrom, 2014; Brauss et al., 1999; Bult et al., 2007; Chen & Eaton, 2012; Dadalı & Elmacı, 2019; de Wijk et al., 2003; Fernandez et al., 2000; Frank et al., 2015; Frøst et al., 2001; Glumac & Chen, 2020; González-Tomás et al., 2007; Han et al., 2019; Hyvönen et al., 2003; Jarvis et al., 2014; Le Calvé et al., 2015; Lorenzo et al., 2015; Mela, 1988; Miettinen et al., 2004; Miettinen et al., 2003; Parat-Wilhelms et al., 2005; Roberts, Pollien,

Antille, et al., 2003; Running et al., 2017; Rychlik et al., 2006; Schoumacker et al., 2017; Syarifuddin et al., 2016; Ventanas et al., 2010; Weenen et al., 2005; Yackinous & Guinard, 2000; Zhou et al., 2016). The vast majority of food matrices were dairy product-based (Arancibia et al., 2015; Boesveldt & Lundstrom, 2014; Brauss et al., 1999; Bult et al., 2007; Chen & Eaton, 2012; de Wijk et al., 2003; Frøst et al., 2001; González-Tomás et al., 2007; Han et al., 2019; Hyvönen et al., 2003; Jarvis et al., 2014; Le Calvé et al., 2015; Mela, 1988; Miettinen et al., 2004; Miettinen et al., 2003; Parat-Wilhelms et al., 2005; Roberts, Pollien, Antille, et al., 2003; Rychlik et al., 2006; Schoumacker et al., 2017; Syarifuddin et al., 2016; Weenen et al., 2005; Yackinous & Guinard, 2000; Zhou et al., 2016), others included meat products (Fernandez et al., 2000; Lorenzo et al., 2015; Ventanas et al., 2010) margarine (Dadalı & Elmacı, 2019), oil and lard (Glumac & Chen, 2020), chocolate (Running et al., 2017) and agar gels (Frank et al., 2015). Most studies utilising foods added flavour/aroma volatiles to the matrices (Arancibia et al., 2015; Brauss et al., 1999; Bult et al., 2007; Frank et al., 2015; Frøst et al., 2001; González-Tomás et al., 2007; Han et al., 2019; Hyvönen et al., 2003; Le Calvé et al., 2015; Miettinen et al., 2004; Miettinen et al., 2003; Roberts, Pollien, Antille, et al., 2003; Syarifuddin et al., 2016; Ventanas et al., 2010; Yackinous & Guinard, 2000), while some added free fatty acids (Chen & Eaton, 2012; Running et al., 2017; Rychlik et al., 2006).

Studies on the human ability to smell fatty acids found that 18-

Table 2
Summary of studies investigating olfactory fat perception in human subjects.

Study	Outcome(s) of interest	Study Population Characteristics	Exposure	Stimuli	Relevant Findings	Interpretation
<i>STUDIES ON OLFATORY PERCEPTION OF FAT IN ISOLATION</i>						
Bolton and Halpern (2010)	Discrimination ability between fatty acids and blanks.	Untrained: - EXP 1 (ortho- and retronasal session): n = 30 (13F); 26.6 ± 9.3 y - EXP 2 (retronasal and oral-cavity-only session): n = 30 (16F); 26.0 ± 4.0 y	Orthonasal, Retronasal (I)	Linoleic and oleic acids compared to mineral oil (control); Undiluted stearic acid compared to NaCl (control).	All fatty acids were discriminated from control, ortho- and retronasally: Orthonasally, 87% of subjects discriminated linoleic acid from blanks and 83% discriminated oleic and stearic acids; Retronasally, 93% discriminated linoleic acid from control, 57% discriminated oleic acid and 83% discriminated stearic acid. Discrimination ability did not differ between the routes for linoleic and stearic acids, it was lower for oleic acid in the retronasal condition.	Humans can ortho- and retronasally distinguish fatty acids from non-fatty acid-containing controls.
Chale-Rush et al. (2007)	Orthonasal, retronasal and multimodal detection thresholds of different fatty acids.	Untrained; 6-n-Propylthiouracil tasters; n = 22 (7F); 21.2 ± 0.6 y; BMI 23.6 ± 0.4; body fat 18.3 ± 1.3 %	Orthonasal, Retronasal (I, C)	Linoleic, oxidised linoleic, oleic, and stearic acids varying in concentration.	Retronasal detection thresholds were higher than those of other exposure routes for all fatty acids. Detection thresholds for linoleic acid were lowest for orthonasal olfaction compared to other exposure routes. For oxidised linoleic and oleic acids, orthonasal thresholds did not differ from those of multimodal exposure but were lower than those of taste. Stearic acid detection thresholds did not differ between orthonasal, taste and multimodal exposure. No correlations between the different thresholds were observed.	Humans can smell 18-carbon fatty acids. Olfaction contributes independently to the perception of fatty acids. Retronasal olfaction is less sensitive to the presence of fatty acids than other chemosensory systems.
Chukir et al. (2013)	Linguistic identification derived from Check-All-That-Apply methodology following retronasal inhalation.	Untrained; n = 36 (24F); 18 – 71 y (median 21 y)	Retronasal (I)	Fatty acids: linoleic, oleic, and stearic; non-fatty acid stimuli (controls): geraniol and phenylethyl alcohol.	Fatty acid-containing samples received identifications that consistently differed from those ascribed to controls. Stearic acid was identified differently from linoleic and oleic acids by approximately one-third of assessors. Linoleic and oleic acids mostly received the same, partly food-related identifications: - Linoleic acid identifications included: new plastic, rubbery, sunflower, peanut oil, olive oil and oily; - Oleic acid identifications included: new plastic, rubbery, sunflower, peanut oil, margarine, olive oil and oily; - Stearic acid identifications included:	18-carbon fatty acids can be identified retronasally. Linoleic and oleic fatty acids may contribute to flavour perception.

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Table 2 (continued)

Study	Outcome(s) of interest	Study Population Characteristics	Exposure	Stimuli	Relevant Findings	Interpretation
					new plastic, rubbery, sunflower, and oily - the proportion of rubbery for stearic acid was about twice that for linoleic and oleic acids. Identifications of the three fatty acids were consistently different from those of non-fatty acid stimuli.	
Ebba et al. (2012)	Perceptual ratings of fat-related taste quality intensities.	Untrained; n = 88 (51F); 18 – 74 y (mean 25.1 y)	Retronasal (C)	Taste strips containing mineral oil (control), linoleic acid in amounts of 1.1, 1.3, 1.5, and 1.7 µmol.	The perceived taste intensity of linoleic acid decreased by 40% when retronasal olfaction was eliminated via nose clips.	Olfaction is involved in the perception of fatty acids and can enhance fat-related taste qualities.
Kallas and Halpern (2011)	Discrimination ability between fatty acids.	Untrained; n = 40 (30F); 18–36 y	Retronasal (I)	Linoleic (40.5%), oleic (40.0%) and stearic acids, all at suprathreshold levels; Linoleic acid (0.005% – subthreshold level concentration) compared to mineral oil (control).	Vapor phase stearic acids were discriminated from vapor-phase linoleic or oleic fatty acids: 70% of subjects discriminated between stearic and linoleic acids; 65% discriminated between stearic and oleic acids. Oleic and linoleic fatty acids were discriminated by 38% of subjects. No discrimination occurred in “negative control” trials.	Humans can discriminate 18-carbon fatty acids using solely retronasal olfaction.
Kindleysides et al. (2017)	Fatty acid olfactory detection thresholds. Dietary intake of key food groups.	Untrained; n = 50F; 18 – 45 y (median 26 y); median BMI 24 (31 normal-weight, 11 overweight, 8 obese)	Orthonasal	Oleic acid (combined with mineral oil), varying in concentration (6, 12, 24, 48, 95, 190, and 380 mM).	Olfactory detection curves increased with higher concentration of oleic acid. Oleic acid taste and olfactory detection abilities were positively correlated. Oleic acid olfactory sensitivity was not related to body composition. Dietary intakes of nuts, nut spreads, and seeds were positively correlated with high olfactory sensitivity to oleic acid.	Oleic fatty acid can be detected orthonasally. While olfactory sensitivity to oleic fatty acid is independent of body composition, it is related to the habitual consumption of fat-containing foods and gustatory sensitivity to oleic acid.
STUDIES ON OLFACTORY PERCEPTION OF FAT EMBEDDED WITHIN FOOD MATRICES						
Arancibia et al. (2015)	Relative intensities of lemon and milk flavours assessed via pairwise ranking. Aroma release parameters following nose-space sampling.	- Sensory session: trained; n = 28 (16F); 23 – 55 y - Aroma release session: n = 8	Retronasal (C)	Lemon-flavoured (added linalool and <i>cis</i> -3-hexen-1-ol) dairy desserts with added thickeners and varying in fat content: 0.14% and 3.5% fat.	Lemon flavour intensity was higher in dairy desserts with a lower fat content, while milk flavour intensity was higher in desserts with a higher fat content. Linalool release was lower in desserts with a higher fat content.	Fat content influences <i>in vivo</i> release of certain flavour compounds, which affects their perception.
Boesveldt and Lundstrom (2014)	Orthonasal discrimination ability between fat levels in dairy milk. Perceptual ratings of intensity, pleasantness. Habitual fat intake.	- EXP 1: untrained; n = 30 (16F), 27.3 ± 4.2 y, BMI 23.1 ± 3.1 - EXP 2: untrained; n = 18 (12F), 22.1 ± 1.2 y, BMI 22.7 ± 3.1 - EXP 3: Normal-weight – untrained; n = 30 (15F), 25.0 ± 3.7 y, BMI 22.5 ± 1.8; Overweight – untrained; n	Orthonasal	Manipulated milk samples varying in fat content (skimmed, semi-skimmed, whole):	Skimmed milk samples were discriminated from whole milk ones in all experiments. In EXP 1 and EXP 2, skimmed milk was not discriminated from whole milk; in EXP 3 skimmed milk was not discriminated from semi-skimmed milk. There was no difference between	Humans can smell differences between dairy milks differing in fat level, using solely orthonasal olfaction. This ability seems independent from habitual dairy fat consumption and BMI.

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Table 2 (continued)

Study	Outcome(s) of interest	Study Population Characteristics	Exposure	Stimuli	Relevant Findings	Interpretation
		= 30 (18F), 30.6 ± 7.2 y, BMI 35.6 ± 8.4			normal-weight and overweight subjects discrimination performance. In EXP 1 and EXP 2, perceived intensity increased with increasing fat content, while pleasantness decreased. In EXP 2, perceived pleasantness did not differ between the samples. In EXP 3, perceived intensity, but not pleasantness was lower in the overweight group. Discrimination ability was not correlated to BMI or habitual dairy fat consumption parameters in any of the experiments.	
Brauss et al. (1999)	Time-intensity parameters related to the perception of flavourings (2-hexenyl acetate, anethole and terpinolene) Aroma release parameters following nosespace sampling.	Trained; n = 10	Retronasal (C)	Flavoured yogurts varying in fat content (0.2, 3.5 and 10%).	Flavour compound volatility and perceived flavour intensities decreased with increasing fat content.	Fat content diminishes the volatility of certain flavour compounds, which affects their perception.
Bult et al. (2007)	Perceptual ratings of overall flavour intensity, thickness, and creaminess (taken whilst milk-like foods were present in the mouth and a cream odour was presented retro- or orthonasally).	Untrained; n = 11 (3F); 41 ± 11 y	Orthonasal, Retronasal (I, C)	Fresh skim milk (0.075% fat content) with an added cream aroma.	The odour stimulus increased intensities of thickness and creaminess, but only when the odour was presented retronasally. This was most pronounced when odours coincided with swallowing.	Fat-related retronasal odours can enhance fat-related mouthfeel sensations via cross-modal interactions.
Chen and Eaton (2012)	Perceptual ratings of creaminess following orthonasal, taste, taste and mouthfeel, and multimodal exposure.	Untrained; dairy-consumers, familiar with creamy foods; n = 16 (14F); 21–25 y	Orthonasal	Fresh single cream (19.1% fat), evaporated milk (9.0% fat), corn starch solution and corn starch solution with added oleic and stearic fatty acids (0.1%).	Orthonasal creaminess ratings were higher for fat-containing samples than non-fat ones. Despite having a higher fat content, single cream was rated as being less creamy than evaporated milk. The presence of fatty acids had no influence on creaminess aroma ratings.	Olfaction is involved in the perception of creaminess. Fat content influences the intensity of creamy odour. Oleic and stearic fatty acids do not elicit a creamy aroma.
Dadali and Elmacı (2019)	Perceptual ratings of butter, creamy, cheesy, animal-like, margarine and oxidised aroma. Relative amounts of volatiles in the headspace following fat and emulsifier content manipulation.	Trained; n = 10 (8F); 23–54 y	Orthonasal	Model margarines varying in fat content (60, 70 and 80%).	The release of 2,3-butanedione and butanoic acid was higher in model margarines with 70% and 80% fat content. The release of 2-heptanone, 2-nonanone, 2-undecanone, hexanoic acid, and delta-decalactone was higher in margarines with a lower fat ratio. Fattier margarines were rated higher in terms of butter and cheese aroma. Cream aroma was rated as	Fat content influences the volatility of certain flavour compounds, which affects their perception.

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Table 2 (continued)

Study	Outcome(s) of interest	Study Population Characteristics	Exposure	Stimuli	Relevant Findings	Interpretation
					being more intense in lower-fat margarines.	
Fernandez et al. (2000)	Perceptual ratings of smell intensity.	Trained; n = 12	Orthonasal	Cooked ham slices varying in fat content ($\leq 2\%$; 2–3%; 3–4%; $>4\%$).	Smell intensity of cured ham (pork) was not affected by fat content.	Fat content alterations do not necessarily modify smell intensity.
Frank et al. (2015)	Perceptual ratings of blue cheese flavour and overall flavour intensities. Aroma release parameters following headspace sampling.	Trained; n = 10	Retronasal (C)	Agar gels varying in fat content (0%, 10%) and aromatised with blue cheese-related volatiles.	Fat-containing agar gels were rated as more intense in terms of blue cheese flavour. Fat content had differential effects on the release of several volatiles, depending on their solubility and lipophilicity.	Fat content influences the volatility of certain flavour compounds, which affected their perception.
Frøst et al. (2001)	Perceptual ratings of creamy aroma, cream flavour, and total fattiness (meta descriptor).	Trained; n = 7	Orthonasal, Retronasal (C)	Commercially available dairy milk varying in fat content (0.1, 1.3 and 3.5%) with added cream aroma (0 or 0.75 g/L), thickener (0 or 1 g/L) and whitener (0 or 1 g/L).	With increasing fat content, Intensities of creamy odour and flavour increased, while boiled milk odour decreased. The magnitude of perceived difference in fattiness was much larger between 0.1 and 1.3% fat samples than between 1.3 and 3.5% ones. Samples with added cream aroma scored higher in terms of total fattiness. Total fattiness was highly positively correlated with creamy odour and flavour.	The addition of fat-related odours to milk enhanced the perception of milk fat content.
Glumac and Chen (2020)	Proportion of correct answers to the question: "Is this perceived as oil/fat?", posed following exposure via various sensory modalities.	Untrained; n = 30 (15F); 27.3 \pm 2.0 y; BMI 18.5–25.9	Orthonasal	Commercial rapeseed oil, commercial lard, plant-sourced oleic acid, food grade silicone oil, food-grade glycerol, and food-grade xanthan gum solution.	Using only orthonasal cues, subjects correctly identified rapeseed oil, lard and oleic acid as oil/fat-containing, while silicon, glycerol and xanthan gum solution were correctly identified as non-oil/fat. Aroma seemed to be the most informative sensory modality for oil/fat recognition, followed by tactile and taste sensations.	Humans can identify fat-containing food samples using solely orthonasal cues. For fat recognition, orthonasal olfactory cues are more informative than tactile and taste-related ones.
González-Tomás et al. (2007)	Relative intensity of strawberry flavour assessed via pairwise comparison. Aroma release parameters following nose-space sampling.	- Aroma release: n = 10 - Sensory evaluation: Trained; n = 39	Retronasal (C)	Model, strawberry-flavoured custards varying in fat content (0.14% and 3.5%), starch and emulsifier concentrations.	Fat content influenced strawberry flavour intensity and release: - Strawberry flavour of 0.14% fat samples was more intense than that of 3.5% ones. - Volatile release was higher in 0.14% milk fat samples than in 3.5% ones.	Increases in fat content may diminish the volatility of certain flavour compounds, in turn modulating their perceived intensity.
Han et al. (2019)	Perceptual ratings of cheese creaminess, butter note, overall flavour and cheese texture pleasantness following consumption of cheese cubes in the presence of either orthonasal or retronasal butter odour delivered at	Untrained; n = 20 (8F); 25–29 y	Orthonasal, Retronasal (C)	Butter odour at two concentrations: low (just above the detection threshold) and high (well above the detection threshold); Gouda cheese varying in fat content (20, 30 and 40%).	Creaminess, butter note intensity and texture pleasantness were enhanced by the addition of a butter odour – effects were more pronounced when a low odour concentration was presented and varied with the timing of odour	Fat content affects the olfactory perception of creaminess. Fat-related odours can enhance the perception of cheese-related attributes via cross-modal interactions. These enhancements are

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Table 2 (continued)

Study	Outcome(s) of interest	Study Population Characteristics	Exposure	Stimuli	Relevant Findings	Interpretation
	various points of the oral processing cycle.				presentation and cheese fat content: - Perceived creaminess increased when butter odour was presented retronasally at the start of chewing. - Perceived butter note intensity peaked when the odour was delivered retronasally during chewing in regardless of the butter odour concentration. - Perceived texture pleasantness was enhanced when butter odour was delivered orthonasally before chewing. - Perceived creaminess and butter note intensities increased with increasing fat content.	more pronounced at lower odour concentrations.
Hyvönen et al. (2003)	Time-intensity parameters related to the perception of strawberry flavour release and melting. 6 perceptual ratings, including fattiness and creaminess.	Untrained: - Time-intensity panel: n = 15 (9F); 28 y (SD n.s.) - Descriptive panel: n = 35 (23F); 31 y (SD n.s.)	Orthonasal, Retronasal (C)	Strawberry-flavoured ice cream varying in fat content (0, 5, 9, 14 and 18%), prepared using dairy and vegetable fat.	Flavour release from vegetable fat-based ice cream samples was slightly faster than from dairy fat-based ones. Intensity and sharpness of ice cream aroma and flavour were higher in fat-free ice cream samples than fat-containing ones No differences in the intensities of aroma and flavour attributes were observed in samples containing 5% of fat or more.	Fat type may influence the volatility of certain odour/flavour compounds, without affecting their perception. Fat content influences the volatility of certain odour/flavour compounds, which may affect their perception.
Jervis et al. (2014)	Perceptual creaminess ratings of sour cream in various conditions: Normal consumption (control); visual exposure only; visual exposure while stirring; stirring while blindfolded; tasting while blindfolded; tasting while blindfolded and wearing a nose clip; tasting while only wearing a nose clip.	Untrained: - Control session: n = 274 - Test sessions: n = 100–111	Retronasal (C)	12 samples representing the sensory space of commercial sour creams, with fat content ranging between 0 and 33%.	When the retronasal pathway was inhibited using a nose clip, creaminess perception was different from control (where all sensory modalities were used) – perceived creaminess decreased in most cases. Inhibition of retronasal olfaction had the greatest impact on creaminess perception compared to other modalities.	Retronasal olfaction is involved in the perception of creaminess.
Le Calvé et al. (2015)	Discrimination ability and fat difference thresholds between various food matrices varying in fat.	Trained; n = 35–50	Retronasal (C)	Different food matrices varying in fat, sugar and flavouring content: White sauces containing 7.5–32.5% fat; dairy milks containing 0–3.8% fat; yogurts containing 0–3.5% fat.	White Sauces: The addition of olfactory cues during tasting of flavoured and unflavoured samples could modulate discrimination ability, depending on the reference fat content and the direction of comparison. Milk: Fat content discrimination was possible only when olfactory and/or vision cues were involved. In sucrose-enriched	Retronasal fat discrimination ability depends on product type and reference fat content. Retronasal olfaction, along with other sensory systems, is involved in food fat content discrimination.

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Study	Outcome(s) of interest	Study Population Characteristics	Exposure	Stimuli	Relevant Findings	Interpretation
					<p>samples, the involvement of olfaction reduced discrimination ability. The addition of flavours had no effect on fat discrimination.</p> <p>Yoghurt: Fat discrimination was not possible in the absence of olfactory and/or visual cues. The same results were observed in sucrose-enriched samples. In samples with added flavour and/or fruit preparation fat discrimination was possible, but the ability was reduced.</p>	
Lorenzo et al. (2015)	Perceptual ratings of flavour intensity and black pepper odour.	Trained; n = 10	Orthonasal, Retronasal (C)	Sausages varying in fat content: 10, 20 and 30%.	Whereas fat content had no effect on flavour intensity, perceived black pepper odour intensity decreased with increasing fat content.	Increases in fat content may diminish the volatility of certain odour/flavour compounds, in turn modulating their perceived intensity.
Mela (1988)	Perceptual ratings of fat content and creaminess.	Untrained: - EXP 1: n = 20 (12F); 27 y (SD n.s.) - EXP 2: n = 20 (12F); 23 y (SD n.s.)	Retronasal (C)	Commercially available skim milk (0.5%), whole milk (3.3%), light cream (11.6%), a mixture of light and heavy cream (24%) and heavy cream (36%).	Elimination of olfactory cues had no effect on fat content perception in both experiments.	Fat perception is not driven by olfactory cues. Inhibiting olfactory cues might influence hedonic perception.
Miettinen et al. (2003)	<p>Perceptual intensity ratings of diacetyl and linalool aromas.</p> <p>Time-intensity parameters related to the perception of diacetyl and linalool aromas.</p> <p>Aroma release parameters following headspace sampling.</p>	Trained; n = 12; 28 y (SD n.s.)	Orthonasal, Retronasal (C)	Commercial non-fat milk with added rapeseed oil at levels of 0%, 1%, 5%, and 10% (v/v) and flavoured with either diacetyl or linalool.	<p>With increasing fat content, linalool was retained in the matrix, while the release of diacetyl was not affected.</p> <p>The addition of 1% of fat to the matrix sufficed to reduce the headspace linalool concentration and orthonasal, but not retronasal, intensity.</p> <p>The perception of linalool aroma in the sample containing most fat lasted a shorter time than in samples containing less fat.</p>	Increases in fat content may diminish the volatility of certain odour/flavour compounds, in turn modulating their perception.
Miettinen et al. (2004)	<p>Perceptual ratings of first impression and after taste-related attribute intensities (free choice profiling).</p> <p>Time-intensity parameters related to the perception of strawberry and linalool flavour.</p> <p>Aroma release parameters following nosespace sampling.</p>	Trained; n = 12 (9F); 29.5 y (SD n.s.)	Retronasal (C)	Strawberry-linalool-flavoured milks varying in fat content: 0%, 0.5%, and 5%.	<p>With increasing fat content, the maximum perceived intensity of linalool reduced, while the maximum perceived intensity of strawberry flavour increased.</p> <p>Linalool was retained in the matrix as fat content increased.</p> <p>Strawberry aroma of the fattiest sample lingered the longest, but no temporal differences were found in the release of linalool.</p>	Increases in fat content may diminish the volatility of certain flavour compounds, in turn modulating their perception.
Parat-Wilhelms et al. (2005)	Perceptual ratings of coffee-related odour and taste/retronasal odour attributes: buttery, milky, creamy, sour,	Trained; n = 15	Orthonasal, Retronasal (C)	Coffee beverages with or without added milk, varying in fat content (0, 3.5 and 7.0%).	An increase in the amount of fat in the milk samples (from 3.5% to 7.0%) led to a decrease in the perceived intensity of coffee-related	Increases in fat content may diminish the perception of certain flavours.

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Study	Outcome(s) of interest	Study Population Characteristics	Exposure	Stimuli	Relevant Findings	Interpretation
	caramel, aromatic, roasted, coffee, butter, burnt.				descriptors. No differences in the milk-related descriptors were found between the two milk samples.	
Roberts, Pollien, Antille, et al. (2003)	Flavour compound intensities Aroma release parameters following headspace and nospace sampling.	Trained; n = 5	Retronasal (C)	Food matrices varying in fat content with added aroma compounds: Water, skim (0.033% fat), semi-skim (2.7% fat) and whole milk (3.8% fat) containing either beta-damascenone, hexanal, ethyl butyrate, benzaldehyde and 2,3-butanedione.	Fat content influenced perceived intensities of the different compounds in all conditions. Volatility and Intensities of the most lipophilic compounds (beta-damascenone, hexanal and ethyl butyrate) decreased with increasing fat content.	Increases in fat content may diminish the volatility of certain flavour compounds, in turn reducing their perceived intensity.
Running et al. (2017)	Orthonasal (linoleic, oleic) and flavour (stearic) rejection thresholds.	Untrained: - Linoleic acid test: n = 75 (49F); 31.1 y (SD n.s.) - Oleic acid test: n = 69 (48F); 34.3 y (SD n.s.) - Stearic acid test: n = 80 (21F); 32.1 y (SD n.s.)	Orthonasal	Dark chocolate containing different concentrations (0.04–2.5%; w/w) of free fatty acids: linoleic, oleic, stearic.	Chocolate containing the polyunsaturated fatty acid (linoleic) was rejected at lower concentrations than the one containing monounsaturated fatty acid (oleic) in both orthonasal and taste conditions. Stearic acid-containing chocolate was not rejected at any concentration.	The addition of fatty acids to a food matrix may unfavourably alter its odour-related qualities. The degree of fatty acid unsaturation influences rejection following orthonasal exposure (the more unsaturated, at lower concentrations it gets rejected). Saturated fatty acids do not seem to contribute to flavour preference.
Rychlik et al. (2006)	Perceptual ratings of sour, cheese-like and yoghurt-like odour intensities.	Trained; n = 8	Orthonasal	Yogurt (3.5% fat) without (control) or with added short-chain fatty acids: acetic, butanoic, hexanoic, octanoic, dodecanoic.	The addition of free fatty acids to fresh yogurt diminished yogurt-like odour intensity, while enhancing intensities of off-flavour-related cheese-like and sour odours.	The addition of fatty acids to a food matrix may unfavourably alter its odour-related qualities.
Schoumacker et al. (2017)	Fat content detection and difference thresholds.	Untrained; n = 40 (18F); 25–76 y (mean 55 y); BMI 18.1–36.7 (mean 24.2 kg/m ²)	Retronasal (C)	Cottage cheese mixtures containing 1, 2, 3, 4, 5, 6, 7, 7.8, 9, 10 and 11% fat.	Eliminating olfaction using nose clips resulted in higher detection and difference thresholds.	Retronasal olfaction contributes to the perception of fat in food.
Syarifuddin et al. (2016)	Perceptual ratings of several odour, taste and texture attribute intensities, including perceived fat content.	Untrained; n = 31 (21F); 10–61 y	Orthonasal, Retronasal (C)	Model cheeses varying in fat content (20%, 40%), added aroma (none, sardine, butter), salt (0.5%, 1.5%) and pH at renneting (5.0, 6.2).	Perceptual ratings of fat content texture increased after the addition of a butter aroma. Fat content had no effect on overall odour intensity, regardless of the added aroma.	The addition of fat-related odours can enhance the perception of fat-related texture sensations.
Ventanas et al. (2010)	Perceptual ratings of mushroom and cocoa odour and flavour. Time-intensity parameters related to the perception of mushroom flavour. Aroma release parameters following headspace sampling.	Trained; n = 8 (5F); 25–59 y	Orthonasal, Retronasal (C)	Mushroom and cocoa-flavoured cooked bologna sausages varying in NaCl and fat content (from 4.4 to 22.5% fat).	With increasing fat content, mushroom odour intensity decreased, while that of cocoa odour increased. With increasing fat content, mushroom and cocoa flavour intensities decreased. Duration of mushroom flavour perception decreased with increasing fat content. Fat content influenced the volatility of mushroom but	Increases in fat content may diminish the volatility of certain odour/flavour compounds, in turn modulating their perception.

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Study	Outcome(s) of interest	Study Population Characteristics	Exposure	Stimuli	Relevant Findings	Interpretation
					not cocoa flavour-related volatiles.	
Weenen et al. (2005)	Perceptual ratings of 60 odour, taste/flavour, mouthfeel, and aftertaste-related attributes.	Trained; n = n.s.	Orthonasal, Retronasal (C)	10 commercially available vanilla custards (fat content between < 0.5 and 3.5%); Mayonnaises (fat content between 0 and 80%); Warm sauces (mainly starch-based).	The use of nose clips decreased the perception of creamy and fatty mouthfeel in vanilla custards.	Retronasal, cues contribute to the perception of fat-related mouthfeel sensations.
de Wijk et al. (2003)	Perceptual ratings of 66 descriptive attributes, including 6 odour and 11 flavour-related sensations.	Trained; n = 9 (7F) (22–49 y)	Orthonasal, Retronasal (C)	16 vanilla-flavoured model custards varying in fat content (0 and 4.5%), carrageenan and starch.	Compared to 0% fat custard samples, 4.5% fat ones were rated as more intense in terms of vanilla, caramel and milk odour, and less intense in terms of synthetic odour. 4.5% custard samples were also rated as more intense in terms of vanilla, caramel, milk, cream and fat flavour and less intense in terms of chemical and sickly flavour.	Increases in fat content may alter the perception of certain odour and flavour-related sensory qualities.
Yackinous and Guinard (2000)	Perceptual ratings of fattiness, intensity and liking.	Untrained; n = 106 (66F); 19.3 ± 1.6 y; BMI 21.9 ± 2.7	Retronasal (C)	4 foods varying in fat and flavour concentration: - Butter-flavoured mashed potatoes: (0.5% fat + 0.08% flavour; 15% fat + 3.75% flavour); - Dairy-flavoured vanilla pudding (4% fat + 0.05% flavour; 28% fat + 1.75% flavour); - Sour cream and onion-flavoured potato chips (1% fat + 0.05% flavour; 5% fat + 1.00% flavour); - White chocolate-flavoured chocolate drink (5.29% fat + 4.50% flavour; 15.87% fat + 7.00% flavour).	The use of nose clips reduced the perception of fattiness across all investigated foods. A product-specific effect of flavour concentration on fattiness ratings was observed: The addition of high levels of fatty-type flavours enhanced the perception of fattiness in mashed potatoes and potato chips.	Olfaction contributes to the perception of fat in food. Adding fat-related flavours to foods can enhance the perception of their fattiness.
Zhou et al. (2016)	Perceptual ratings of fattiness intensity following exposure to mixtures differing in fat content via various combinations of sensory modalities (taste, taste + odour, taste + mouthfeel, all modalities).	- EXP 1: n = 46 (21F); 19–53 y; BMI 16.5–43.5 - EXP 2: n = 51 (35F); 18–55 y; BMI 17.0–39.3	Retronasal (C)	- EXP 1: Five mixtures differing in fat content (0, 7.5, 10, 15 and 20%) produced from non-fat skimmed milk, single cream (19.1% fat) and double cream (50.5% fat). - EXP 2: Two more mixtures differing in fat content were added (2.5 and 5.5%).	Perceived fattiness intensity rated from taste + odour (without nose clips) was higher than that from just taste (with nose clips) or all modalities. Perceived fattiness intensity rated from all modalities was higher than just from taste + mouthfeel.	Retronasal olfaction contributes to the perception of fat.

carbon fatty acids, namely linoleic, oleic and stearic, can be detected orthonasally (Chale-Rush et al., 2007; Kindleysides et al., 2017) and retronasally (Chale-Rush et al., 2007), with retronasal detection thresholds being higher than orthonasal ones (Chale-Rush et al., 2007). Linoleic, oleic and stearic acids can also be discriminated from blanks ortho- and retronasally, with discrimination ability for oleic acid being lower for retronasal olfaction (Bolton & Halpern, 2010); discriminated from each other retronasally (Kallas & Halpern, 2011); and retronasally identified from blanks and each other, with their chemical structure (i. e., the number of double bonds) influencing identification (Chukir et al., 2013). Upon removing retronasal cues, the detection of linoleic acid on taste strips diminishes (Ebba et al., 2012). The addition of oleic and

stearic acids to a corn starch solution had no effect on perception of creaminess odour (Chen & Eaton, 2012), whereas adding short chain fatty acids, namely acetic, butanoic and hexanoic acid, to yogurt decreased yogurt-like odour intensity while simultaneously increasing intensities of off-flavours (Rychlik et al., 2006). Chocolate containing linoleic fatty acids was rejected at lower concentrations than chocolate containing oleic acid, whereas stearic acid had no effect on rejection thresholds (Running et al., 2017).

Studies investigating olfactory fat perception ability in food matrices show that humans can orthonasally distinguish rapeseed oil, lard and oleic acid from non-fat controls (Glumac & Chen, 2020) and discriminate fat content of dairy milks (Boesveldt & Lundstrom, 2014).

Moreover, the presence of retronasal cues can impact the ability to discriminate fat content in white sauces, milk, and yogurt, with the impact depending on the reference fat content, direction of comparison, and other factors such as added ingredients and the presence of sensory cues from other modalities (Le Calvé et al., 2015). The presence of retronasal cues enhances the perception of fattiness in dairy-based mixtures, while their elimination increases fat content detection and difference thresholds in cottage cheese (Schoumacker et al., 2017), decreases the perception of creamy and fatty mouthfeel in vanilla custard and affects the perception of creaminess in sour cream (Jervis et al., 2014). In contrast, one study reported that elimination of retronasal cues does not affect fat content and creaminess perception in commercially available dairy products (Mela, 1988).

Fat content was reported to have differential effects on the release of flavour volatiles (Arancibia et al., 2015; Brauss et al., 1999; Dadali & Elmáci, 2019; Frank et al., 2015; González-Tomás et al., 2007; Hyvönen et al., 2003; Lorenzo et al., 2015; Miettinen et al., 2004; Miettinen et al., 2003; Roberts, Pollien, Antille, et al., 2003; Ventanas et al., 2010) and influenced the perception of various odours in diverse food matrices. Increases in fat content were found to decrease lemon flavour intensity, while increasing that of milk flavour in dairy desserts (Arancibia et al., 2015); increase overall odour intensity in dairy milk (Boesveldt & Lundstrom, 2014); decrease flavour intensities of 2-hexenyl acetate; anethole and terpinolene in yogurt (Brauss et al., 1999); increase creamy odour intensity in fresh cream and evaporated milk, with the increase being larger in evaporated milk, despite having a lower fat content than fresh cream (Chen & Eaton, 2012); increase butter and cheese odour in margarine, while decreasing that of cream (Dadali & Elmáci, 2019); increase blue cheese flavour in flavoured agar gel (Frank et al., 2015); decrease boiled odour in milk, while increasing creamy odour, flavour intensities and fattiness – a descriptor which was highly positively correlated with creamy aroma and flavour, and increased more in low-fat samples than in high-fat ones (Frøst et al., 2001); decrease strawberry flavour intensity in strawberry custard (González-Tomás et al., 2007); increase creaminess and butter note intensities in Gouda cheese (Han et al., 2019); decrease overall odour and flavour intensity and sharpness in strawberry ice cream (Hyvönen et al., 2003); decrease black pepper odour intensity in dry-ripened sausages (Lorenzo et al., 2015); decrease the odour intensity of linalool in dairy milk (Miettinen et al., 2003); increase linalool odour intensity in strawberry-flavoured milk while decreasing strawberry flavour intensity (Miettinen et al., 2004); decrease intensities of various coffee-related (e.g. roasty, coffee, burnt), but not milk-related (e.g. milky, butter, creamy) flavour qualities (Parat-Wilhelms et al., 2005); decrease flavour intensities of beta-damascenone, hexanal and ethyl butyrate in flavoured dairy milk (Roberts, Pollien, Antille, et al., 2003); decrease mushroom odour intensity, while increasing that of cocoa odour in mushroom and cocoa-flavoured bologna sausages (Ventanas et al., 2010); increase intensities of vanilla, caramel, milk odour and flavour, as well as cream and fat flavour in vanilla custards, while decreasing synthetic odour and chemical and sickly flavour (de Wijk et al., 2003). Fat content was not found to affect cured ham odour intensity in cooked ham (Fernandez et al., 2000) and overall odour intensity in cheese (Syarifuddin et al., 2016).

Five studies investigated the perceptual consequences of adding fat-related odours to foods. In dairy milk, the addition of a cream aroma led to an increase in perceived fattiness (Frøst et al., 2001), creaminess and thickness (Bult et al., 2007); butter aroma added to cheese enhanced perceived creaminess and texture pleasantness (Han et al., 2019) and fat content texture (Syarifuddin et al., 2016), while it enhanced fattiness when added to mashed potatoes (Yackinous & Guinard, 2000); fattiness was also enhanced after adding cream and onion aroma to potato chips (Yackinous & Guinard, 2000); the addition of a butter odour enhanced texture pleasantness in cheese (Han et al., 2019).

EXP, experiment; **n.s.**, not specified; **n**, sample size (**F**, female); **y**, years of age (mean \pm SD/range); **BMI**, body mass index, expressed in

kg/m² as mean \pm SD or range); **I**, isolated from taste and mouthfeel (e.g. inhalation); **C**, combined with taste and mouthfeel (e.g. during ingestion);

3.3. Risk of bias assessment

Risk of bias evaluations of included rodent studies are presented in Figures S1 and S2 in Supplementary Material C. No information reported in rodent studies indicated a high bias risk or concerns in any of the evaluated domains. Overall, there was a considerable amount of unclear risk of bias due to lack of explicit reporting, particularly not stating whether the researchers were blinded to treatments.

Risk of bias evaluations of included human studies are presented in Figures S3 and S4 in Supplementary Material C. In human studies, there was a moderate amount of unclear risk of bias due to lack of explicit reporting on stimulus presentation orders and participant blinding. Moreover, incomplete outcome reporting (i.e. attrition bias) could not be assessed in several studies due to lack of clarity regarding the inclusion of all participants in the final outcome reports. Not isolating olfaction from effects of potentially confounding sensory modalities, namely taste, mouthfeel and trigeminal sensations was identified as a common source of high bias risk or concerns. Most of the “some concerns” judgements in this domain were given when mouthfeel and taste effects were clearly eliminated, but potential involvement of the trigeminal system could not be ruled out completely, or when orthonasal exposure was combined with non-isolated retronasal exposure.

4. Discussion

This systematic scoping review aimed at (1) identifying and summarizing relevant evidence on the contribution of olfaction to dietary fat perception and (2) highlighting relevant knowledge gaps. It yields consistent evidence supporting the notion that olfaction is involved in the perception of dietary fat in rodents and humans. Olfaction alone is sufficient for detecting fat and its components (i.e. fatty acids), whether they are present on their own or as part of a complex food matrix. Food fat content plays a considerable role in modulating the perception of various fat- and non-fat-related olfactory qualities, depending on the food matrix and odorant properties. Furthermore, the perception of fat in food can be influenced by the addition of fat-related odours, which may enhance olfactory, as well as non-olfactory fat-related attributes, such as mouthfeel.

Albeit limited, evidence from rodent studies supports the involvement of olfaction in fat perception. With the exception of Boone et al. (2021), all studies demonstrated that olfactory cues contribute to the formation of preferences towards fat-related odorants (Kinney & Antille, 1996; Lee et al., 2015; Ramirez, 1993; Takeda et al., 2001; Xavier et al., 2016). Anosmia having no effect on preference in the case of Boone et al. (2021), and preference partially diminishing following anosmia in the case of Ramirez (1993) and Takeda et al. (2001), suggests that preference for fat in rodents is mediated by olfactory, as well as non-olfactory cues. Moreover, anosmia eliminating preference only for low-fat stimuli, as shown by Takeda et al. (2001), points towards olfaction in rodents acting as a signalling mechanism for fat at lower concentrations. Lastly, as suggested by (Xavier et al., 2016), receptor CD36 seems to play a role in detecting fat-related stimuli in rodents.

Findings of human studies utilising free fatty acids as olfactory stimuli are aligned in suggesting that humans possess the ability of perceiving fatty acids via the olfactory system (Bolton & Halpern, 2010; Chale-Rush et al., 2007; Chukir et al., 2013; Ebba et al., 2012; Kallas & Halpern, 2011; Kindleysides et al., 2017; Running et al., 2017; Rychlik et al., 2006). The interpretation of some findings, however, requires caution. It must be acknowledged that although most studies (Bolton & Halpern, 2010; Chale-Rush et al., 2007; Chukir et al., 2013; Kallas & Halpern, 2011; Kindleysides et al., 2017), attempted to isolate olfactory inputs from potentially confounding effects of non-olfactory systems (e.

g., vision, gustation, somatosensation), only Bolton and Halpern (2010) verified the absence of trigeminal system involvement. They did so by demonstrating that the presentation of fatty acids to the oral cavity resulted in no discrimination from blanks. As the oral cavity is innervated by trigeminal but not olfactory nerve branches (Halpern, 2014), this shows that the discrimination observed by Bolton and Halpern (2010) was indeed olfaction-based and provides the most convincing evidence of 18-carbon fatty acids being effective olfactory stimuli. The involvement of olfaction in fatty acid perception is further corroborated by the fact that elimination of retronasal cues considerably decreases the perceived taste intensity of linoleic acid presented to the oral cavity (Ebba et al., 2012).

Clearly, sensations elicited via olfactory exposure to fat in its isolated form (i.e., fatty acids) are sufficient to evoke perception. However, since fat-related odorants are usually perceived in conjunction with a multitude of other stimuli present in a particular food matrix, the more relevant question is whether fat can be smelled when embedded within a food matrix, and if so, how does that influence perception. Various studies on the matter demonstrated that, even when dietary fat is embedded within a food matrix, olfactory cues enable or facilitate its perception. Using solely olfaction, humans are able to distinguish natural oils and oleic acid from non-fat controls (Glumac & Chen, 2020) and discriminate between fat content differences in dairy milk (Boesveldt & Lundstrom, 2014). The latter has been replicated by our own experiments as well (not included in this review as they were unpublished at the time of search), where we observed that ortho- or retronasal cues in isolation are sufficient to allow for dairy fat content discrimination (Pirc et al., 2022), and identified headspace composition differences underlying the ability (Mu et al., 2022). The involvement of olfaction in detecting food fat content differences seems to be particularly relevant in certain food products, as demonstrated by Le Calvé et al. (2015), who observed that fat content discrimination in milk and yoghurt was possible only after retronasal cues were added to those of other sensory modalities. They also showed that, despite olfaction not being crucial for discriminating fat content in white sauces, retronasal cues can modulate fat content discrimination, depending on the fat content levels being compared and added sweeteners or flavours. Similarly, elimination of retronasal cues via the use of nose clips has been reported to hinder food fat content discrimination (Schoumacker et al., 2017) and affect the perception of fat-related qualities (Jervis et al., 2014; Zhou et al., 2016). The role of olfaction in perceiving fat embedded within food is further underscored by findings that the addition of fatty acids to a food matrix unfavourably alters odour-related qualities by producing off-odours (Rychlik et al., 2006), which may lead to rejection, depending on fatty acid type (Running et al., 2017). All in all, although relatively limited, evidence suggests that olfactory cues are integral for the perception of fat in food (Jervis et al., 2014; Le Calvé et al., 2015; Schoumacker et al., 2017; Zhou et al., 2016). They not only signal its presence (Glumac & Chen, 2020; Rychlik et al., 2006), but may also provide information about its quantity (Boesveldt & Lundstrom, 2014; Mu et al., 2022; Pirc et al., 2022) or type (Running et al., 2017). These findings, in combination with those from studies on fatty acids, indicate that humans possess a functional olfaction-based system for detecting dietary fat in isolation or when part of a food matrix.

Studies investigating the effects of fat content on odour perception found that fat content impacts (i.e. accentuates or diminishes) intensities of various fat and non-fat olfaction-related qualities, in a range of diverse food matrices (Arancibia et al., 2015; Boesveldt & Lundstrom, 2014; Brauss et al., 1999; Chen & Eaton, 2012; Dadali & Elmaci, 2019; de Wijk et al., 2003; Frank et al., 2015; Frøst et al., 2001; González-Tomás et al., 2007; Han et al., 2019; Hyvönen et al., 2003; Lorenzo et al., 2015; Miettinen et al., 2004; Miettinen et al., 2003; Parat-Wilhelms et al., 2005; Ventanas et al., 2010). Some qualities, such as creaminess, seem to be positively related to fat content (Chen & Eaton, 2012; Dadali & Elmaci, 2019; Frøst et al., 2001; Han et al., 2019), yet the relationship is not always linear (Chen & Eaton, 2012; Frøst et al., 2001).

It has to be acknowledged that fat content alterations do not always modulate olfaction-related qualities, as was the case in Fernandez et al. (2000) and Syarifuddin et al. (2016). Olfaction-related quality or intensity shifts following fat content alteration, likely arise from changes in the volatility of odorous compounds contained the food matrix. Various factors, such as lipophilicity and solubility (Guichard, 2002; Guichard et al., 2018), modulate their release, which influences subsequent perception, as demonstrated by several studies included in the current review (Arancibia et al., 2015; Brauss et al., 1999; Dadali & Elmaci, 2019; Frank et al., 2015; González-Tomás et al., 2007; Hyvönen et al., 2003; Lorenzo et al., 2015; Miettinen et al., 2004; Miettinen et al., 2003; Roberts, Pollien, Antille, et al., 2003; Ventanas et al., 2010). In most instances, increases in fat content seem to accentuate the perception of fat-related flavour volatiles, while diminishing that of non-fat-related ones. There are, however, exceptions. For example, as demonstrated by Dadali & Elmaci, the release of Hexanoic acid, a fat-related odorant responsible for eliciting fatty, waxy or cheesy qualities, decreased despite an increase in fat content. Further discussion about the intricacies behind factors that influence fat-related volatile release are beyond the scope of the current review - for further information on the matter, see the review on flavour compound and food ingredient interactions and their influence on flavour perception by Guichard (2002). In summary, fat content clearly has an influence on the perception of food-related odours and/or flavours. Olfaction-related perceptual consequences of fat content alteration depend on the food matrix and physio-chemical properties of the odorants in question (Guichard et al., 2018).

Conversely, the perception of fat content-related attributes can be modified by the presence of odours associated with fat. All studies exploring perceptual effects of adding fat-related odours to foods observed an enhancement of fat-related qualities (Bult et al., 2007; Frøst et al., 2001; Han et al., 2019; Syarifuddin et al., 2016; Yackinous & Guinard, 2000). The enhancement, however, is not limited solely to olfaction-related attributes, but may also affect non-olfactory ones, such as thickness (Bult et al., 2007), fat-related mouthfeel (Syarifuddin et al., 2016), and texture pleasantness (Han et al., 2019). The enhancing effects of odours on other sensory modalities have also been demonstrated by Ebba et al. (2012), observing that the removal of retronasal cues diminished taste intensity of linoleic acid, and Weenen et al. (2005), where their absence diminished creamy and fatty mouthfeel. These findings underscore the multi- and cross-modal nature of fat perception (Guichard et al., 2018), wherein the presence of fat-related odours can enhance fat-related mouthfeel and even taste sensations. For additional information on the taste-enhancing potential of odours, see the reviews by Ai and Han (2022) and Spence (2022). For insights on fat-related odour-mouthfeel interactions, see the review by Guichard et al. (2018).

All human studies included in this review, with the exception of Mela (1988), demonstrated that olfaction is involved in the perception of fat or fat-related odours to some degree. Several even found that dietary fat can be perceived using solely olfactory cues (Boesveldt & Lundstrom, 2014; Bolton & Halpern, 2010; Chukir et al., 2013; Glumac & Chen, 2020; Kallas & Halpern, 2011; Le Calvé et al., 2015). We speculate that the low sample serving temperature (4 °C) in the study of Mela et al (11) might have reduced the volatility of fat-related odorants, thus hindering the perception of sensory differences between the fat content of their samples. Since fat perception is multi-modal, the exact contribution of olfaction to the overall flavour percept is difficult to approximate. Not only because of the inherent difficulty in disentangling olfactory inputs from non-olfactory ones, but also due to complex cross-modal interactions occurring between olfaction and other modalities, as discussed above. Nevertheless, findings of the current review clearly show that olfaction has a relevant, even independent, role to play in the perception of dietary fat in humans.

Another relevant point that requires discussion is on the differential role the two olfactory routes might play in fat perception, given that they seem to serve distinct purposes in the context of eating (Boesveldt &

de Graaf, 2017; Goldberg et al., 2018). Few studies included in the current review aimed specifically at comparing the two routes. Nevertheless, some observations can be highlighted. Although free fatty acids can be perceived by either route, retronasal olfaction seems to be less sensitive to their presence (Chale-Rush et al., 2007). The two routes, however, are relatively comparable in discriminating between specific fatty acid types (Bolton & Halpern, 2010). As demonstrated by our recent work on the topic (Pirc et al., 2022) the routes are also comparable in discriminating fat content of dairy milk. When it comes to perception of fat-related odours in the context of food, Han et al. (2019) compared the two routes and observed differential effects on perception of butter aroma delivered during consumption of cheese, depending on the route of delivery. Specifically, when delivered retronasally, butter aroma enhanced creaminess and butter note intensity, while orthonasally it enhanced texture pleasantness. In contrast, Bult et al. (2007) reported enhancements to creaminess and thickness in dairy milk following retronasal, but not orthonasal exposure to cream aroma. In summary, there seem to be differences in fat perception between the olfactory routes. However, to reach reliable conclusions, more research focussing specifically on the distinctions between the two is needed. For an overview of distinctions between ortho- and retronasal olfaction in the context of flavour perception in general, see the review by Goldberg et al. (2018).

The current work has identified several other relevant knowledge gaps that require attention in order to further our comprehension of the topic. One of the more relevant blind spots is the potential impact of olfactory fat perception on subsequent eating behaviour. Apart from six studies, whose findings on fat odour-related hedonics (Boesveldt & Lundstrom, 2014; Han et al., 2019; Jervis et al., 2014; Running et al., 2017; Syarifuddin et al., 2016; Yackinous & Guinard, 2000) merely hint at possible behavioural implications without experimentally determining them, no other study included in this review aimed at investigating the potential behavioural consequences of fat-related odours. It must be acknowledged that much is still unclear about how, and under what circumstances, food odours impact eating behaviour. Although it has been established that orthonasal food odours can induce appetite specific for the cued product during the anticipatory phase of eating, findings on their effects on food choice and intake are limited and conflicting (Boesveldt & de Graaf, 2017). The effect of retronasal exposure to food odours on eating behaviour has received even less attention. While there is some evidence of their influence on appetite (Ruijschop et al., 2008), which does not seem to translate into actual food intake (Boesveldt & de Graaf, 2017), reports on their potential role in food choice are practically non-existent, even more so when it comes to behavioural consequences of fat-related odours. Future studies should therefore aim to fill this important knowledge gap by investigating potential effects of exposure to various ambient and retronasal fat-related odours on appetite, food choice and intake. One of the key prerequisites to this approach is the elucidation of the exact nature of fat-related olfactory chemical signals. Although fatty acids seem to be effective olfactory stimuli on their own (Bolton & Halpern, 2010; Chale-Rush et al., 2007; Chukir et al., 2013; Kallas & Halpern, 2011), most fat-related odours largely originate from volatile compounds bound to dietary fats – which are known to act as volatile compound reservoirs (Carrapiso, 2007; Doyen et al., 2001; Haahr, 2000; Roberts, Pollien, & Watzke, 2003). Future research should thus aim to identify effective fat-related olfactory stimuli; extend the knowledge on headspace compositions of different fat-based food matrices, varying in fat content and type; and establish which volatiles underly specific fat-related olfactory qualities (e.g., using gas chromatography–olfactometry or proton transfer reaction-mass spectrometry). Efforts should also be focussed towards identifying fat-related olfactory receptors and elucidating their role. Examining the exact role of receptor CD36, which was suggested to be involved in the perception of fat-related odorants in rodents (Xavier et al., 2016), appears a reasonable initial step. Lastly, and similar to previous work for fat taste (Tucker et al., 2017), additional work is

required to illuminate factors governing olfactory sensitivity to fat-related odorants. Sensitivity to fat-related odours seems independent of body composition (Boesveldt & Lundstrom, 2014; Kindleysides et al., 2017; Pirc et al., 2022), and has been found to be related with gustatory sensitivity to oleic acid (Kindleysides et al., 2017). Moreover, our own findings show that olfactory fat content discrimination ability is independent of habitual consumption (Mu et al., 2022; Pirc et al., 2022). However, the evidence base is limited, which warrants further investigation. Future studies should thus aim to replicate initial findings on the topic and seek other potential influences (e.g., genetics). Lastly, expanding the knowledge on mouthfeel and taste-enhancing qualities of specific fat-related odours might also prove worthwhile, especially for commercial applications. Specifically, the addition of fat-related odours to foods as fat substitutes seems a potentially viable approach for reducing food fat content in various food products, without compromising on their appealing fat-related sensory characteristics and negatively impacting food choice and intake. Considering that fat flavour-related foods seem to contribute most to energy intakes (Teo et al., 2022), the development of such sensory optimised foods might help maintain existing dietary flavour patterns, while moderating dietary energy density, as suggested by (Teo et al., 2022) and (Forde & de Graaf, 2022). Findings on the interactions between olfaction and other sensory modalities involved in fat perception could thus prove instrumental in developing strategies aimed at curbing excess dietary fat intakes.

The current review is the first to summarize findings specific to olfactory fat perception. It yields consistent evidence supportive of olfaction's contribution to the perception of fat, yet conclusions are inherently influenced by the studies selected for inclusion. Our choices of search strings, literature eligibility criteria and their appraisal, and the decision to forgo manual literature searching and sifting through reference lists of included articles are likely to have resulted in the omission of other relevant studies. Publication bias remains a possibility as well. Furthermore, potential bias sources should be considered when interpreting reported findings, particularly those that arise from interactions between olfaction and potentially confounding sensory modalities (see Figures 3 and 5), namely taste, mouthfeel and trigeminal sensations. The risks of cross-modal interactions are, however, generally difficult to avoid, mainly due to the inherent complexity in separating retronasal olfaction from other sensations, particularly when it comes to flavour release studies. Even when olfaction is completely isolated from mouthfeel and taste, prying it apart from trigeminal sensations is virtually impossible. Since most odorants can activate the trigeminal system (Goldberg et al., 2018), we decided to take a conservative approach when scoring this domain, to raise caution when interpreting results. This resulted in multiple studies receiving “some concerns” bias risk scores. Nevertheless, we deem the methodological quality and validity of findings reported in this review as high. Especially considering that findings from the vast majority of included studies are aligned. Furthermore, the main conclusions of this review were drawn from studies where the bias risk due to potentially confounding effects of other sensory modalities was minimised. Future work on olfactory fat perception should consider employing control conditions, where possible, wherein the potential involvement of the trigeminal system can be established (as demonstrated by Bolton and Halpern (2010)).

5. Conclusion

Our findings support the notion that olfaction contributes to the perception of dietary fat in rodents and humans. The identified evidence base, although relatively heterogenous and limited in some areas, is consistent in showing that olfaction is involved in detecting, discriminating, and identifying fat and its constituents, when either isolated or embedded within a complex food matrix. When embedded within complex food matrices, fat content and type can modulate the perception of various fat- and non-fat related olfactory qualities, likely by influencing the volatility of odorous compounds. Furthermore, the

addition of fat-related odorants to a food matrix may modulate not only its olfactory, but also non-olfactory sensory characteristics, such as mouthfeel. This demonstrates that, although olfaction can act as an independent fat-sensing modality, it also interacts with other sensory systems. Several knowledge gaps have been identified by the current review, including the role of fat-related odours in the choice and intake of various foods; the nature of chemical signals underlying olfactory fat perception; and factors governing olfactory sensitivity to fat-related odours. Replication of included studies and examination of suggested knowledge gaps are warranted given the public health and commercial relevance of this topic. Potentially, the cross-modal nature of olfactory cues in fat perception could be exploited in product reformulation. Specifically, fat-related odorants could be used as dietary fat substitutes, to enhance palatability in various low-fat or reduced-fat food products. The current systematic scoping review is the first of its kind focussing specifically on the olfactory component of fat perception. It provides an extensive overview of the topic, which has the potential of facilitating future research and providing useful information to the food industry.

CRedit authorship contribution statement

Matjaž Pirc: Conceptualization, Methodology, Investigation, Data curation, Writing – original draft, Writing – review & editing, Project administration. **Shuo Mu:** Conceptualization, Methodology, Investigation, Data curation, Writing – review & editing, Project administration. **Gino Frissen:** Methodology, Investigation, Data curation. **Markus Stieger:** Conceptualization, Supervision, Writing – review & editing, Project administration. **Sanne Boesveldt:** Conceptualization, Supervision, Writing – review & editing, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foodqual.2023.104847>.

References

- Ai, Y., & Han, P. (2022). Neurocognitive mechanisms of odor-induced taste enhancement: A systematic review. *International Journal of Gastronomy and Food Science*, 28. <https://doi.org/10.1016/j.ijgfs.2022.100535>
- Arancibia, C., Castro, C., Jublot, L., Costell, E., & Bayarri, S. (2015). Colour, rheology, flavour release and sensory perception of dairy desserts. Influence of thickener and fat content. *LWT - Food Science and Technology*, 62(1), 408–416. <https://doi.org/10.1016/j.lwt.2014.08.024>
- Blundell, J. E., Burley, V. J., Cotton, J. R., & Lawton, C. L. (1993). Dietary fat and the control of energy intake: evaluating the effects of fat on meal size and postmeal satiety. *Am J Clin Nutr*, 57(5 Suppl), 772S-777S; discussion 777S-778S. doi:10.1093/ajcn/57.5.772S.
- Blundell, J. E., & Macdiarmid, J. I. (1997). Fat as a risk factor for overconsumption. *Journal of the American Dietetic Association*, 97(7), S63–S69. [https://doi.org/10.1016/s0002-8223\(97\)00733-5](https://doi.org/10.1016/s0002-8223(97)00733-5)
- Boesveldt, S., & de Graaf, K. (2017). The differential role of smell and taste for eating behavior. *Perception*, 46(3–4), 307–319. <https://doi.org/10.1177/0301006616685576>
- Boesveldt, S., & Lundstrom, J. N. (2014). Detecting fat content of food from a distance: Olfactory-based fat discrimination in humans. *PLoS One*, 9(1), e85977.
- Bojanowski, V., & Hummel, T. (2012). Retronasal perception of odors. *Physiology & Behavior*, 107(4), 484–487. <https://doi.org/10.1016/j.physbeh.2012.03.001>
- Bolton, B., & Halpern, B. P. (2010). Orthonasal and retronasal but not oral-cavity-only discrimination of vapor-phase fatty acids. *Chemical Senses*, 35(3), 229–238. <https://doi.org/10.1093/chemse/bjq002>
- Boone, M. H., Liang-Guallpa, J., & Krashes, M. J. (2021). Examining the role of olfaction in dietary choice. *Cell Reports*, 34(7). <https://doi.org/10.1016/j.celrep.2021.108755>
- Brauss, M. S., Linforth, R. S., Cayeux, I., Harvey, B., & Taylor, A. J. (1999). Altering the fat content affects flavor release in a model yogurt system. *Journal of Agricultural and Food Chemistry*, 47(5), 2055–2059. <https://doi.org/10.1021/jf9810719>
- Bray, G. A., Paeratakul, S., & Popkin, B. M. (2004). Dietary fat and obesity: A review of animal, clinical and epidemiological studies. *Physiology & Behavior*, 83(4), 549–555. <https://doi.org/10.1016/j.physbeh.2004.08.039>
- Bult, J. H., de Wijk, R. A., & Hummel, T. (2007). Investigations on multimodal sensory integration: Texture, taste, and ortho- and retronasal olfactory stimuli in concert. *Neuroscience Letters*, 411(1), 6–10. <https://doi.org/10.1016/j.neulet.2006.09.036>
- Carrapiso, A. I. (2007). Effect of fat content on flavour release from sausages. *Food Chemistry*, 103(2), 396–403. <https://doi.org/10.1016/j.foodchem.2006.07.037>
- Chale-Rush, A., Burgess, J. R., & Mattes, R. D. (2007). Multiple routes of chemosensitivity to free fatty acids in humans. *American Journal of Physiology. Gastrointestinal and Liver Physiology*, 292(5), G1206–G1212. <https://doi.org/10.1152/ajpgi.00471.2006>
- Chen, J., & Eaton, L. (2012). Multimodal mechanisms of food creaminess sensation. *Food & Function*, 3(12), 1265–1270. <https://doi.org/10.1039/c2fo30116d>
- Chukir, T., Darlington, R. B., & Halpern, B. P. (2013). Shared retronasal identifications of vapor-phase 18-carbon fatty acids. *Chemical Senses*, 38(4), 343–353. <https://doi.org/10.1093/chemse/bjt005>
- Dadali, C., & Elmaci, Y. (2019). Characterization of volatile release and sensory properties of model margarines by changing fat and emulsifier content. *European Journal of Lipid Science and Technology*, 121(6). <https://doi.org/10.1002/ejlt.201900003>
- de Wijk, R. A., van Gemert, L. J., Terpstra, M. E. J., & Wilkinson, C. L. (2003). Texture of semi-solids; sensory and instrumental measurements on vanilla custard desserts. *Food Quality and Preference*, 14(4), 305–317. [https://doi.org/10.1016/s0950-3293\(02\)00107-6](https://doi.org/10.1016/s0950-3293(02)00107-6)
- Delime, P., O'Mahony, K., Desforges, N., Taylor, A. J., & Hort, J. (2016). Comparing the relative sensitivity of ortho- and retronasal perception of a strawberry flavour model using omission testing. *Flavour and Fragrance Journal*, 31(5), 377–384. <https://doi.org/10.1002/ffj.3326>
- Doyen, K., Carey, M., Linforth, R. S., Marin, M., & Taylor, A. J. (2001). Volatile release from an emulsion: Headspace and in-mouth studies. *Journal of Agricultural and Food Chemistry*, 49(2), 804–810. <https://doi.org/10.1021/jf000853a>
- Drewnowski, A. (1992). Sensory properties of fats and fat replacements. *Nutrition Reviews*, 50(4 (Pt 2)), 17–20. <https://doi.org/10.1111/j.1753-4887.1992.tb01285.x>
- Drewnowski, A. (1997a). Taste preferences and food intake. *Annual Review of Nutrition*, 17, 237–253. <https://doi.org/10.1146/annurev.nutr.17.1.237>
- Drewnowski, A. (1997b). Why do we Like Fat? *Journal of the American Dietetic Association*, 97(7), S58–S62. [https://doi.org/10.1016/s0002-8223\(97\)00732-3](https://doi.org/10.1016/s0002-8223(97)00732-3)
- Drewnowski, A., & Almiron-Roig, E. (2009). Human Perceptions and Preferences for Fat-Rich Foods. In *Fat detection: taste, texture, and post ingestive effects*. Boca Raton (FL).
- Ebba, S., Abarintos, R. A., Kim, D. G., Tiyouh, M., Stull, J. C., Movalia, A., & Smutzer, G. (2012). The examination of fatty acid taste with edible strips. *Physiology & Behavior*, 106(5), 579–586. <https://doi.org/10.1016/j.physbeh.2012.04.006>
- Eilander, A., Harika, R. K., & Zock, P. L. (2015). Intake and sources of dietary fatty acids in Europe: Are current population intakes of fats aligned with dietary recommendations? *European Journal of Lipid Science and Technology*, 117(9), 1370–1377. <https://doi.org/10.1002/ejlt.201400513>
- Fernandez, X., Mouro, J., Leuret, B., Gilbert, S., & Monin, G. (2000). Influence of intramuscular fat content on lipid composition, sensory qualities and consumer acceptability of cured cooked ham. *Journal of the Science of Food and Agriculture*, 80(6), 705–710. [https://doi.org/10.1002/\(sici\)1097-0010\(20000501\)80:6<705::Aid-jsfa592>3.0.Co;2-8](https://doi.org/10.1002/(sici)1097-0010(20000501)80:6<705::Aid-jsfa592>3.0.Co;2-8)
- Forde, C. G., & de Graaf, K. (2022). Influence of sensory properties in moderating eating behaviors and food intake. *Frontiers in Nutrition*, 9, Article 841444. <https://doi.org/10.3389/fnut.2022.841444>
- Frank, D., Eyres, G. T., Piyasiri, U., Cochet-Broch, M., Delahunty, C. M., Lundin, L., & Appelqvist, I. M. (2015). Effects of agar gel strength and fat on oral breakdown, volatile release, and sensory perception using in vivo and in vitro systems. *Journal of Agricultural and Food Chemistry*, 63(41), 9093–9102. <https://doi.org/10.1021/acs.jafc.5b03441>
- Frøst, M. B., Dijksterhuis, G., & Martens, M. (2001). Sensory perception of fat in milk. *Food Quality and Preference*, 12(5–7), 327–336. [https://doi.org/10.1016/S0950-3293\(01\)00018-0](https://doi.org/10.1016/S0950-3293(01)00018-0)
- Glumac, M., & Chen, J. (2020). Contribution analysis of sensory cues to oil/fat perception. *Journal of Sensory Studies*, 35(3). <https://doi.org/10.1111/joss.12566>
- Golay, A., & Bobbioni, E. (1997). The role of dietary fat in obesity. *International Journal of Obesity and Related Metabolic Disorders: Journal of the International Association for the Study of Obesity*, 21, S2–S.
- Goldberg, E. M., Wang, K., Goldberg, J., & Aliani, M. (2018). Factors affecting the ortho- and retronasal perception of flavors: A review. *Critical Reviews in Food Science and Nutrition*, 58(6), 913–923. <https://doi.org/10.1080/10408398.2016.1231167>
- González-Tomás, L., Bayarri, S., Taylor, A. J., & Costell, E. (2007). Flavour release and perception from model dairy custards. *Food Research International*, 40(4), 520–528. <https://doi.org/10.1016/j.foodres.2006.10.002>

- Guichard, E. (2002). Interactions between flavor compounds and food ingredients and their influence on flavor perception. *Food Reviews International*, 18(1), 49–70. <https://doi.org/10.1081/fri-120003417>
- Guichard, E., Galindo-Cuspinera, V., & Feron, G. (2018). Physiological mechanisms explaining human differences in fat perception and liking in food spreads—a review. *Trends in Food Science & Technology*, 74, 46–55. <https://doi.org/10.1016/j.tifs.2018.01.010>
- Haahr, A. (2000). Flavour release of aldehydes and diacetyl in oil/water systems. *Food Chemistry*, 71(3), 355–362. [https://doi.org/10.1016/S0308-8146\(00\)00184-9](https://doi.org/10.1016/S0308-8146(00)00184-9)
- Halpern, B. P. (2014). Human trigeminal sensory responses to vapor-phase stimuli. *Chemosensory Perception*, 7(3–4), 126–139. <https://doi.org/10.1007/s12078-014-9174-3>
- Han, P., Fark, T., de Wijk, R. A., Roudnitsky, N., Iannilli, E., Seo, H. S., & Hummel, T. (2019). Modulation of sensory perception of cheese attributes intensity and texture liking via ortho- and retro-nasal odors. *Food Quality and Preference*, 73, 1–7. <https://doi.org/10.1016/j.foodqual.2018.11.019>
- Higgins, J. P., Altman, D. G., Gotzsche, P. C., Juni, P., Moher, D., Oxman, A. D., ... G. (2011). The Cochrane Collaboration's tool for assessing risk of bias in randomised trials. *BMJ*, 343, Article d5928. <https://doi.org/10.1136/bmj.d5928>
- Hyyönen, L., Linna, M., Tuorila, H., & Dijksterhuis, G. (2003). Perception of melting and flavor release of ice cream containing different types and contents of fat. *Journal of Dairy Science*, 86(4), 1130–1138. [https://doi.org/10.3168/jds.S0022-0302\(03\)73695-9](https://doi.org/10.3168/jds.S0022-0302(03)73695-9)
- Jervis, S. M., Gerard, P., Drake, S., Lopetcharat, K., & Drake, M. A. (2014). The perception of creaminess in sour cream. *Journal of Sensory Studies*, 29(4), 248–257. <https://doi.org/10.1111/joss.12098>
- Kallas, O., & Halpern, B. P. (2011). Retronasal discrimination between vapor-phase long-chain, aliphatic fatty acids. *Chemosensory Perception*, 4(1–2), 16–24. <https://doi.org/10.1007/s12078-011-9085-5>
- Keast, R. S. J., & Costanzo, A. (2015). Is fat the sixth taste primary? Evidence and implications. *Flavour*, 4(1). <https://doi.org/10.1186/2044-7248-4-5>
- Kindleysides, S., Beck, K. L., Walsh, D. C. I., Henderson, L., Jayasinghe, S. N., Golding, M., & Breier, B. H. (2017). Fat sensation: Fatty acid taste and olfaction sensitivity and the link with disinhibited eating behaviour. *Nutrients*, 9(8). <https://doi.org/10.3390/nu9080879>
- Kinney, N. E., & Antill, R. W. (1996). Role of olfaction in the formation of preference for high-fat foods in mice. *Physiology & Behavior*, 59(3), 475–478. [https://doi.org/10.1016/0031-9384\(95\)02086-1](https://doi.org/10.1016/0031-9384(95)02086-1)
- Le Calvé, B., Saint-Léger, C., Babas, R., Gelin, J. L., Parker, A., Erni, P., & Cayeux, I. (2015). Fat perception: How sensitive are we? *Journal of Texture Studies*, 46(3), 200–211. <https://doi.org/10.1111/jtxs.12120>
- Lee, S., Eguchi, A., Sakamoto, K., Matsumura, S., Tsuzuki, S., Inoue, K., ... Fushiki, T. (2015). A role of CD36 in the perception of an oxidised phospholipid species in mice. *Biomedical Research*, 36(5), 303–311. <https://doi.org/10.2220/biomedres.36.303>
- Lorenzo, J. M., Fonseca, S., Gómez, M., & Domínguez, R. (2015). Physicochemical and sensory properties of Celta dry-ripened “salchichón” as affected by fat content. *Grasas y Aceites*, 66(1). <https://doi.org/10.3989/gya.0709142>
- Mattes, R. D. (2009). Oral detection of short-, medium-, and long-chain free fatty acids in humans. *Chemical Senses*, 34(2), 145–150. <https://doi.org/10.1093/chemse/bjn072>
- McHugh, M. L. (2012). Interrater reliability: The kappa statistic. *Biochemia Medica*, 276–282. <https://doi.org/10.11613/bm.2012.031>
- Mela, D. J. (1988). Sensory assessment of fat content in fluid dairy products. *Appetite*, 10(1), 37–44. [https://doi.org/10.1016/S0195-6663\(88\)80031-x](https://doi.org/10.1016/S0195-6663(88)80031-x)
- Miettinen, S. M., Hyyönen, L., Linforth, R. S., Taylor, A. J., & Tuorila, H. (2004). Temporal aroma delivery from milk systems containing 0–5% added fat, observed by free choice profiling, time intensity, and atmospheric pressure chemical ionization-mass spectrometry techniques. *Journal of Agricultural and Food Chemistry*, 52(26), 8111–8118. <https://doi.org/10.1021/jf040218v>
- Miettinen, S. M., Hyyönen, L., & Tuorila, H. (2003). Timing of intensity perception of a polar vs nonpolar aroma compound in the presence of added vegetable fat in milk. *Journal of Agricultural and Food Chemistry*, 51(18), 5437–5443. <https://doi.org/10.1021/jf0342066>
- Moher, D., Liberati, A., Tetzlaff, J., Altman, D. G., & Group, P. (2009). Preferred reporting items for systematic reviews and meta-analyses: The PRISMA statement. *BMJ*, 339, Article b2535. <https://doi.org/10.1136/bmj.b2535>
- Mu, S., Stieger, M., & Boesveldt, S. (2022). Olfactory discrimination of fat content in milks is facilitated by differences in volatile compound composition rather than odor intensity. *Food Chemistry*, 393, Article 133357. <https://doi.org/10.1016/j.foodchem.2022.133357>
- Parat-Wilhelms, M., Denker, M., Borchering, K., Hoffmann, W., Luger, A., & Steinhart, H. (2005). Influence of defined milk products on the flavour of white coffee beverages using static headspace gas chromatography-mass spectrometry/olfactometry and sensory analysis. *European Food Research and Technology*, 221(3–4), 265–273. <https://doi.org/10.1007/s00217-005-1152-1>
- Pepino, M. Y., Love-Gregory, L., Klein, S., & Abumrad, N. A. (2012). The fatty acid translocase gene CD36 and lingual lipase influence oral sensitivity to fat in obese subjects. *Journal of Lipid Research*, 53(3), 561–566. <https://doi.org/10.1194/jlr.M021873>
- Pirc, M., Maas, P., De Graaf, K., Lee, H.-S., & Boesveldt, S. (2022). Humans possess the ability to discriminate food fat content solely based on retronasal olfaction. *Food Quality and Preference*, 96. <https://doi.org/10.1016/j.foodqual.2021.104449>
- Ramirez, I. (1993). Role of olfaction in starch and oil preference. Retrieved from *American Journal of Physiology - Regulatory Integrative and Comparative Physiology*, 265(6 34–6), R1404–R1409 <https://www.scopus.com/inward/record.uri?eid=2-s2.0-0027731470&partnerID=40&md5=fe0095d45a5914bfef436940110a4a5>
- Roberts, D. D., Pollien, P., Antille, N., Lindinger, C., & Yeretzian, C. (2003). Comparison of nose-space, headspace, and sensory intensity ratings for the evaluation of flavor absorption by fat. *Journal of Agricultural and Food Chemistry*, 51(12), 3636–3642. <https://doi.org/10.1021/jf026230+>
- Roberts, D. D., Pollien, P., & Watzke, B. (2003). Experimental and modeling studies showing the effect of lipid type and level on flavor release from milk-based liquid emulsions. *Journal of Agricultural and Food Chemistry*, 51(1), 189–195. <https://doi.org/10.1021/jf025646k>
- Ruijschop, R. M., Boelrijk, A. E., de Ru, J. A., de Graaf, C., & Westerterp-Plantenga, M. S. (2008). Effects of retro-nasal aroma release on satiation. *The British Journal of Nutrition*, 99(5), 1140–1148. <https://doi.org/10.1017/S0007114507837482>
- Running, C. A., Craig, B. A., & Mattes, R. D. (2015). Oleogustus: The unique taste of fat. *Chemical Senses*, 40(7), 507–516. <https://doi.org/10.1093/chemse/bjv036>
- Running, C. A., Hayes, J. E., & Ziegler, G. R. (2017). Degree of free fatty acid saturation influences chocolate rejection in human assessors. *Chemical Senses*, 42(2), 161–166. <https://doi.org/10.1093/chemse/bjw116>
- Rychlik, M., Sax, M., & Schieberle, P. (2006). On the role of short-chain free fatty acids for the development of a cheese-like off-note in pasteurized yoghurt. *LWT - Food Science and Technology*, 39(5), 521–527. <https://doi.org/10.1016/j.lwt.2005.03.014>
- Schiffman, S. S., Graham, B. G., Sattely-Miller, E. A., & Warwick, Z. S. (1998). Orosensory perception of dietary fat. *Current Directions in Psychological Science*, 7(5), 137–143. <https://doi.org/10.1111/1467-8721.ep10836808>
- Schoumacker, R., Martin, C., Thomas-Danguin, T., Guichard, E., Le Quééré, J. L., & Laboure, H. (2017). Fat perception in cottage cheese: The contribution of aroma and tasting temperature. *Food Quality and Preference*, 56, 241–246. <https://doi.org/10.1016/j.foodqual.2016.04.003>
- Sim, J., & Wright, C. C. (2005). The kappa statistic in reliability studies: Use, interpretation, and sample size requirements. *Physical Therapy*, 85(3), 257–268. <https://doi.org/10.1093/ptj/85.3.257>
- Spence, C. (2022). Factors affecting odour-induced taste enhancement. *Food Quality and Preference*, 96. <https://doi.org/10.1016/j.foodqual.2021.104393>
- Stewart, J. E., Feinle-Bisset, C., Golding, M., Delahunty, C., Clifton, P. M., & Keast, R. S. (2010). Oral sensitivity to fatty acids, food consumption and BMI in human subjects. *The British Journal of Nutrition*, 104(1), 145–152. <https://doi.org/10.1017/S0007114510000267>
- Sun, B. C., & Halpern, B. P. (2005). Identification of air phase retronasal and orthonasal odorant pairs. *Chemical Senses*, 30(8), 693–706. <https://doi.org/10.1093/chemse/bji062>
- Syarifuddin, A., Septier, C., Salles, C., & Thomas-Danguin, T. (2016). Reducing salt and fat while maintaining taste: An approach on a model food system. *Food Quality and Preference*, 48, 59–69. <https://doi.org/10.1016/j.foodqual.2015.08.009>
- Takeda, M., Sawano, S., Imaizumi, M., & Fushiki, T. (2001). Preference for corn oil in olfactory-blocked mice in the conditioned place preference test and the two-bottle choice test. *Life Sciences*, 69(7), 847–854. [https://doi.org/10.1016/S0024-3205\(01\)01180-8](https://doi.org/10.1016/S0024-3205(01)01180-8)
- Teo, P. S., Tso, R., van Dam, R. M., & Forde, C. G. (2022). Taste of modern diets: The impact of food processing on nutrient sensing and dietary energy intake. *The Journal of Nutrition*, 152(1), 200–210. <https://doi.org/10.1093/jn/nxab318>
- Tucker, R. M., Kaiser, K. A., Parman, M. A., George, B. J., Allison, D. B., & Mattes, R. D. (2017). Comparisons of fatty acid taste detection thresholds in people who are lean vs. overweight or obese: A systematic review and meta-analysis. *PLoS One*, 12(1), e0169583.
- van Rossum, C. T. M., Buurma-Rethans, E. J. M., Dinissen, C. S., Beukers, M. H., Brants, H. A. M., Dekkers, A. L. M., & Ocke, M. C. (2020). *The diet of the Dutch – Results of the Dutch national food consumption survey 2012–2016*. The Netherlands: Retrieved from Bilthoven.
- Ventanas, S., Puolanne, E., & Tuorila, H. (2010). Temporal changes of flavour and texture in cooked bologna type sausages as affected by fat and salt content. *Meat Science*, 85(3), 410–419. <https://doi.org/10.1016/j.meatsci.2010.02.009>
- Weenen, H., Jellema, R. H., & de Wijk, R. A. (2005). Sensory sub-attributes of creamy mouthfeel in commercial mayonnaises, custard desserts and sauces. *Food Quality and Preference*, 16(2), 163–170. <https://doi.org/10.1016/j.foodqual.2004.04.008>
- Xavier, A. M., Ludwig, R. G., Nagai, M. H., de Almeida, T. J., Watanabe, H. M., Hirata, M. Y., ... Glezer, I. (2016). CD36 is expressed in a defined subpopulation of neurons in the olfactory epithelium. *Scientific Reports*, 6, 25507. <https://doi.org/10.1038/srep25507>
- Yackinos, C., & Guinard, J. X. (2000). Flavor manipulation can enhance the impression of fat in some foods. *Journal of Food Science*, 65(5), 909–914. <https://doi.org/10.1111/j.1365-2621.2000.tb13611.x>
- Zhou, X., Shen, Y., Parker, J. K., Kennedy, O. B., & Methven, L. (2016). Relative effects of sensory modalities and importance of fatty acid sensitivity on fat perception in a real food model. *Chemosensory Perception*, 9, 105–119. <https://doi.org/10.1007/s12078-016-9211-5>