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

Matjaž Pirc¹,* , Shuo Mu¹ , Gino Frissen , Markus Stieger , Sanne Boesveldt

Division of Human Nutrition and Health, Wageningen University and Research, Wageningen, the Netherlands

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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 over-consumption 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

* Corresponding author.
E-mail address: matjaz.pirc@wur.nl (M. Pirc).
¹ These authors contributed equally to the work.

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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, chemo-sensory). 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, de-duplicated 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
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; Ryhlick 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; Gonzalez-Tomas et al., 2007; Jervis 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; Frost 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; Frost et al., 2001; Han et al., 2019; Hyvönen et al., 2003; Jervis 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; Ryhlick 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; Gonzalez-Tomas 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
varying levels of linoleic acid (Ebba et al., 2012); or oleic acid (Kin Chukir et al., 2013; Kallas Kindleysides et al., 2017), with subjects being exposed to either stearic, 2007; Chukir et al., 2013; Ebba et al., 2012; Kallas factory stimuli in six studies (Bolton Hyvönen et al., 2015; Lorenzo et al., 2015; Mela, 1988; Miettinen et al., 2004; Miettinen et al., 2003; Parat-Wilhelms et al., 2005; Roberts, Pollien, Antill 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., 2010; Yackinous & Guirard, 2000; Zhou et al., 2016). The vast majority of food matrices were dairy product-based (Arancibia et al., 2015; Boesveldt & Lundstrom, 2014; Braun et al., 1999; Bult et al., 2007; Chen & Eaton, 2012; de Wijk et al., 2003; Frost et al., 2001; González-Tomás et al., 2007; Han et al., 2019; Hyvönen et al., 2003; Jervis et al., 2014; Le Calvén et al., 2015; Mela, 1988; Miettinen et al., 2003; Parat-Wilhelms et al., 2005; Roberts, Pollien, Antill et al., 2003; Syarifuddin et al., 2016; Ventanas et al., 2010; Yackinous & Guirard, 2000), while some added margarine (Dadalı & Elmacı, 2019), oil and lard (Glumac & Chen, 2020), chocolate (Running et al., 2017) and agar gels (Franck et al., 2015). Most studies utilising foods added flavour/aroma volatiles to the matrices (Arancibia et al., 2015; Boesveldt & Lundstrom, 2014; Braun et al., 1999; Bult et al., 2007; Chen & Eaton, 2012; Dadalı & Elmacı, 2019; de Wijk et al., 2003; Fernandez et al., 2000; Franck et al., 2015; Frost et al., 2001; Glumac & Chen, 2020; González-Tomás et al., 2007; Han et al., 2019; Hyvönen et al., 2003; Jervis 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., 2010; Yackinous & Guirard, 2000; Zhou et al., 2016). The vast majority of food matrices were dairy product-based (Arancibia et al., 2015; Boesveldt & Lundstrom, 2014; Braun et al., 1999; Bult et al., 2007; Chen & Eaton, 2012; de Wijk et al., 2003; Frost et al., 2001; González-Tomás et al., 2007; Han et al., 2019; Hyvönen et al., 2003; Jervis et al., 2014; Le Calvé et al., 2015; Mela, 1988; Miettinen et al., 2003; Parat-Wilhelms et al., 2005; Roberts, Pollien, Antill et al., 2003; Syarifuddin et al., 2016; Ventanas et al., 2010; Yackinous & Guirard, 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.

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<td><strong>STUDIES ON OLFACTORY PERCEPTION OF FAT IN ISOLATION</strong></td>
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</table>
 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-Pr-pyliouracil 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. | 18-carbon fatty acids can be identified retronasally.  
 Linoleic and oleic fatty acids may contribute to flavour perception.                                                                                                                                                                                                                                                                                                                                                               |
Table 2 (continued)

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<td>Ebba et al. (2012)</td>
<td>Perceptual ratings of fat-related taste quality intensities</td>
<td>Untrained; n = 88 (51F); 18 – 74 y (mean 25.1 y)</td>
<td>Orthonasal (C)</td>
<td>Taste strips containing mineral oil (control), linoleic acid in amounts of 1.1, 1.3, 1.5, and 1.7 μmol.</td>
<td>The perceived taste intensity of linoleic acid decreased by 40% when retronasal olfaction was eliminated via nose clips.</td>
<td>Olfaction is involved in the perception of fatty acids and can enhance fat-related taste qualities.</td>
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<td>Kallas and Halpern (2011)</td>
<td>Discrimination ability between fatty acids.</td>
<td>Untrained; n = 40 (30F); 18 – 36 y</td>
<td>Retronasal (I)</td>
<td>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).</td>
<td>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.</td>
<td>Humans can discriminate 18-carbon fatty acids using solely retronasal olfaction.</td>
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<td>Kindleysides et al. (2017)</td>
<td>Fatty acid olfactory detection thresholds.</td>
<td>Untrained; n = 50F; 18 – 45 y (median 26 y); median BMI 23.1 (31 normal-weight, 11 overweight, 8 obese)</td>
<td>Retronasal</td>
<td>Oleic acid (combined with mineral oil), varying in concentration (6, 12, 24, 48, 95, 190, and 380 mM).</td>
<td>Olfactory detection curves increased with higher concentration of oleic acid.</td>
<td>Oleic fatty acid can be detected orthonasally.</td>
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<td>Dietary intake of key food groups.</td>
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<td>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.</td>
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<td>Arancibia et al. (2015)</td>
<td>Relative intensities of lemon and milk flavours assessed via pairwise ranking. Aroma release parameters following nose-space sampling.</td>
<td>Sensory session: trained; n = 28 (16F); 23 – 55 y Aroma release session: n = 8</td>
<td>Retronasal (C)</td>
<td>Lemon-flavoured (added linalool and cis-3-hexen-1-ol) dairy desserts with added thickeners and varying in fat content: 0.14% and 3.5% fat.</td>
<td>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.</td>
<td>Fat content influences in vivo release of certain flavour compounds, which affects their perception.</td>
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<td>Boesveldt and Lundstron (2014)</td>
<td>Orthonasal discrimination ability between fat levels in dairy milk. Perceptual ratings of intensity, pleasantness. Habitual fat intake.</td>
<td>EXP 1: untrained; n = 30 (16F), 27.9 ± 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</td>
<td>Orthonasal</td>
<td>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</td>
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<td>Humans can smell differences between dairy milks differing in fat level, using solely orthonasal olfaction.</td>
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<td>This ability seems independent from habitual dairy fat consumption and BMI.</td>
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<td>Brauss et al. (1999)</td>
<td>Time-intensity parameters related to the perception of flavourings (2-hexenyl acetate, anethole and terpinolene)</td>
<td>Trained; n = 10</td>
<td>Retronasal (C)</td>
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<td>Flavour compound volatility and perceived flavour intensities decreased with increasing fat content.</td>
<td>Fat content diminishes the volatility of certain flavour compounds, which affects their perception.</td>
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<td>Bult et al. (2007)</td>
<td>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).</td>
<td>Untrained; n = 11 (3F); 41 ± 11 y</td>
<td>Orthonasal, Retronasal (I, C)</td>
<td>Fresh skim milk (0.075% fat content) with an added cream aroma.</td>
<td>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.</td>
<td>Fat-related retronasal odours can enhance fat-related mouthfeel sensations via cross-modal interactions.</td>
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<td>Chen and Eaton (2012)</td>
<td>Perceptual ratings of creaminess following orthonasal, taste, taste and mouthfeel, and multimodal exposure.</td>
<td>Untrained; dairy-consumers, familiar with creamy foods; n = 16 (14F); 21–25 y</td>
<td>Orthonasal</td>
<td>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%).</td>
<td>Orthonasal creaminess ratings were higher for fat-containing samples than non-fat ones.</td>
<td>Olfaction is involved in the perception of creaminess.</td>
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<td>Dadalı and Elmacı (2019)</td>
<td>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.</td>
<td>Trained; n = 10 (8F); 23–54 y</td>
<td>Orthonasal</td>
<td>Model margarines varying in fat content (60, 70 and 80%).</td>
<td>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-nonenone, 2-decane-one, hexanoic acid, and delta-decalactone was higher in margarines with a lower fat ratio.</td>
<td>Fat content influences the volatility of certain flavour compounds, which affects their perception.</td>
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<td>Fernandez et al. (2000)</td>
<td>Perceptual ratings of smell intensity.</td>
<td>Trained; n = 12</td>
<td>Orthonasal</td>
<td>Cooked ham slices varying in fat content (&lt;2%; 2-3%; 3.4%; &gt;4%).</td>
<td>Smell intensity of cured ham (pork) was not affected by fat content.</td>
<td>Fat content alterations do not necessarily modify smell intensity.</td>
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<td>Frank et al. (2015)</td>
<td>Perceptual ratings of blue cheese flavour and overall flavour intensities.</td>
<td>Trained; n = 10</td>
<td>Retronasal (C)</td>
<td>Agar gels varying in fat content (0%, 10%) and aromatized with blue cheese-related volatiles.</td>
<td>Fat-containing agar gels were rated as more intense in terms of blue cheese flavour.</td>
<td>Fat content had differential effects on the release of several volatiles, depending on their solubility and lipophilicity.</td>
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<td>Frost et al. (2001)</td>
<td>Perceptual ratings of creamy aroma, cream flavour, and total fattiness (meta descriptor).</td>
<td>Trained; n = 7</td>
<td>Orthonasal, Retronasal (C)</td>
<td>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).</td>
<td>With increasing fat content, intensities of creamy odour and flavour increased, while boiled milk odour decreased.</td>
<td>The addition of fat-containing odours to milk enhanced the perception of milk fat content.</td>
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<td>Glumac and Chen (2020)</td>
<td>Proportion of correct answers to the question: ‘Is this perceived as oil/fat?’, posed following exposure via various sensory modalities.</td>
<td>Untrained; n = 30 (15F); 27.3 ± 2.0 y; BMI 18.5–25.9</td>
<td>Orthonasal</td>
<td>Commercial rapeseed oil, commercial lard, plant-sourced oleic acid, food grade silicone oil, food-grade glycerol, and food-grade xanthan gum solution.</td>
<td>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.</td>
<td>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.</td>
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<td>González-Tomás et al. (2007)</td>
<td>Relative intensity of strawberry flavour assessed via pairwise comparison.</td>
<td>Aroma release: n = 10</td>
<td>Retronasal (C)</td>
<td>Model, strawberry-flavoured custards varying in fat content (0.14% and 3.5%), starch and emulsifier concentrations.</td>
<td>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.</td>
<td>Increases in fat content may diminish the volatility of certain flavour compounds, in turn modulating their perceived intensity.</td>
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</table>
| 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 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 | (continued on next page)
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<td>Lorenzo et al. (2015)</td>
<td>Perceptual ratings of flavour intensity and black pepper odour.</td>
<td>Trained; n = 10</td>
<td>Orthonasal, Retronasal (C)</td>
<td>Sausages varying in fat content: 10, 20 and 30%.</td>
<td>Whereas fat content had no effect on flavour intensity, perceived black pepper odour intensity decreased with increasing fat content.</td>
<td>Increases in fat content may diminish the volatility of certain odour/flavour compounds, in turn modulating their perceived intensity.</td>
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<td>Mela (1988)</td>
<td>Perceptual ratings of fat content and creaminess.</td>
<td>Untrained: n = 20 (12F); 27 y (SD n.s.)</td>
<td>Retronasal (C)</td>
<td>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%).</td>
<td>Elimination of olfactory cues had no effect on fat content perception in both experiments.</td>
<td>Fat perception is not driven by olfactory cues. Inhibiting olfactory cues might influence hedonic perception.</td>
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<tr>
<td>Miettinen et al. (2003)</td>
<td>Perceptual intensity ratings of diacetyl and linalool aromas.</td>
<td>Trained; n = 12; 28 y (SD n.s.)</td>
<td>Orthonasal, Retronasal (C)</td>
<td>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.</td>
<td>With increasing fat content, linalool was retained in the matrix, while the release of diacetyl was not affected.</td>
<td>Increases in fat content may diminish the volatility of certain odour/flavour compounds, in turn modulating their perception.</td>
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<td>Miettinen et al. (2004)</td>
<td>Perceptual ratings of first impression and after taste-related attribute intensities (free choice profiling).</td>
<td>Trained; n = 12 (9F); 29.5 y (SD n.s.)</td>
<td>Retronasal (C)</td>
<td>Strawberry-linalool-flavoured milks varying in fat content: 0%, 0.5%, and 5%.</td>
<td>With increasing fat content, the maximum perceived intensity of linalool reduced, while the maximum perceived intensity of strawberry flavour increased.</td>
<td>Increases in fat content may diminish the volatility of certain odour/flavour compounds, in turn modulating their perception.</td>
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<td>Parat-Wilhelms et al. (2005)</td>
<td>Perceptual ratings of coffee-related odour and taste/retronasal odour attributes: buttery, milky, creamy, sour.</td>
<td>Trained; n = 15</td>
<td>Orthonasal, Retronasal (C)</td>
<td>Coffee beverages with or without added milk, varying in fat content (0, 5.5 and 7.0%).</td>
<td>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 odours.</td>
<td>Increases in fat content may diminish the perception of certain flavours.</td>
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<td>Roberts, Pollien, Antille, et al. (2003)</td>
<td>Flavour compound intensities</td>
<td>Trained; n = 5</td>
<td>Retronasal (C)</td>
<td>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.</td>
<td>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.</td>
<td>Increases in fat content may diminish the volatility of certain flavour compounds, in turn reducing their perceived intensity.</td>
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<td>Running et al. (2017)</td>
<td>Orthonasal (linoleic, oleic) and flavour (stearic) rejection thresholds.</td>
<td>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.)</td>
<td>Orthonasal</td>
<td>Dark chocolate containing different concentrations (0.04–2.5% w/w) of free fatty acids: linoleic, oleic, stearic.</td>
<td>Chocolate containing the polyunsaturated fatty acid (linoleic) was rejected at lower concentrations than the one containing mono-unsaturated fatty acid (oleic) in both orthonasal and taste conditions. Stearic acid-containing chocolate was not rejected at any concentration.</td>
<td>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.</td>
</tr>
<tr>
<td>Rychlik et al. (2006)</td>
<td>Perceptual ratings of sour, cheese-like and yoghurt-like odour intensities.</td>
<td>Trained; n = 8</td>
<td>Orthonasal</td>
<td>Yogurt (3.5% fat) without (control) or with added short-chain fatty acids: acetic, butanoic, hexanoic, octanoic, decanoic and dodecanoic.</td>
<td>The addition of free fatty acids to fresh yogurt diminished yoghurt-like odour intensity, while enhancing intensities of off-flavour-related cheese-like and sour odours.</td>
<td>The addition of fatty acids to a food matrix may unfavourably alter its odour-related qualities.</td>
</tr>
<tr>
<td>Schoumacker et al. (2017)</td>
<td>Fat content detection and difference thresholds.</td>
<td>Untrained; n = 40 (18F); 25–76 y (mean 55 y); BMI 18.1–36.7 (mean 24.2 kg/m²)</td>
<td>Retronasal (C)</td>
<td>Cottage cheese mixtures containing 1, 2, 3, 4, 5, 6, 7, 8, 9, 10 and 11% fat.</td>
<td>Eliminating olfaction using nose clips resulted in higher detection and difference thresholds. Retronasal olfaction contributes to the perception of fat in food.</td>
<td>Retronasal olfaction contributes to the perception of fat in food.</td>
</tr>
<tr>
<td>Syarifuddin et al. (2016)</td>
<td>Perceptual ratings of several odour, taste and texture attribute intensities, including perceived fat content.</td>
<td>Untrained; n = 31 (21F); 10–61 y</td>
<td>Orthonasal, Retronasal (C)</td>
<td>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).</td>
<td>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.</td>
<td>The addition of fat-related odours can enhance the perception of fat-related texture sensations.</td>
</tr>
<tr>
<td>Ventanas et al. (2010)</td>
<td>Perceptual ratings of mushroom and cocoa odour and flavour.</td>
<td>Trained; n = 8 (5F); 25–59 y</td>
<td>Orthonasal, Retronasal (C)</td>
<td>Mushroom and cocoa-flavoured cooked bologna sausages varying in NaCl and fat content (from 4.4 to 22.5% fat).</td>
<td>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...</td>
<td>Increases in fat content may diminish the volatility of certain odour/flavour compounds, in turn modulating their perception.</td>
</tr>
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(continued on next page)
Linoleic, oleic and stearic acids can also be discriminated from blanks thresholds being higher than orthonasal ones (Chale-Rush et al., 2007) retronasally (Chale-Rush et al., 2007), with retronasal detection carbon fatty acids, namely linoleic, oleic and stearic, can be detected retrorinally (Chale-Rush et al., 2007), identifying 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 acetate, 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 intensities of off-flavours (Rychlik et al., 2006). Chocolate containing stearic acids to a corn starch solution had no effect on perception of fattiness in vanilla custards. 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.

### Table 2 (continued)

<table>
<thead>
<tr>
<th>Study</th>
<th>Outcome(s) of interest</th>
<th>Study Population Characteristics</th>
<th>Exposure</th>
<th>Stimuli</th>
<th>Relevant Findings</th>
<th>Interpretation</th>
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</thead>
<tbody>
<tr>
<td>Weenen et al. (2005)</td>
<td>Perceptual ratings of 60 odour, taste/flavour, mouthfeel, and aftertaste-related attributes.</td>
<td>Trained; n = n.s. (66F); 19.3 ± 1.6 y; BMI 21.9 ± 2.7</td>
<td>Orthonasal, Retronasal (C)</td>
<td>10 commercially available vanilla custards (fat content between &lt; 0.5 and 3.5%); Mayonnaises (fat content between 0 and 80%); Warm sauces (mainly starch-based).</td>
<td>The use of nose clips decreased the perception of creamy and fatty mouthfeel in vanilla custards.</td>
<td>Retronasal cues contribute to the perception of fat-related mouthfeel sensations.</td>
</tr>
<tr>
<td>de Wijk et al. (2003)</td>
<td>Perceptual ratings of 66 descriptive attributes, including 6 odour and 11 flavour-related sensations.</td>
<td>Trained; n = 9 (7F); (22–49 y)</td>
<td>Orthonasal, Retronasal (C)</td>
<td>16 vanilla-flavoured model custards varying in fat content (0 and 4.5%), carrageenan and starch.</td>
<td>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. Increases in fat content may alter the perception of certain odour and flavour-related sensory qualities.</td>
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<tr>
<td>Yackinous and Guinard (2000)</td>
<td>Perceptual ratings of fattiness, intensity and liking.</td>
<td>Untrained; n = 106 (66F); 19.3 ± 1.6 y; BMI 21.9 ± 2.7</td>
<td>Retronasal (C)</td>
<td>4 foods varying in fat and flavour concentration: - Butter-flavoured mashed potatoes: (0.5% fat + 0.08% flavour; 15% fat + 3.75% flavour); - Dairylflavoured 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).</td>
<td>The use of nose clips reduced the perception of fattiness across all investigated foods. A product-specific effect of fattiness perception 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.</td>
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<tr>
<td>Zhou et al. (2016)</td>
<td>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).</td>
<td>- EXP 1: n = 46 (21F); 19-53 y; BMI 16.5–43.5</td>
<td>Retronasal (C)</td>
<td>- 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%).</td>
<td>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.</td>
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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 Calve 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 & Elmaci, 2019; Frank et al., 2015; Gonzalez-Tomàs et al., 2007; Hyvönén 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 intensities, 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 & Elmaci, 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 (Frost et al., 2001); decrease strawberry flavour intensity in strawberry custard (González-Tomàs 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 (Hyvönén et al., 2003); decrease black pepper odour intensity in dry-ripened sausages (Lorenzo et al., 2015); decrease the odour intensity of linseed 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-as et al., 2000) and overall odour intensity in cheese (Syrifuddin 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 increased in perceived fattiness (Frost 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 (Syrifuddin 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 ± SD/range); BMI, body mass index, expressed in kg/m2 as mean ± 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 odors (Kinney & Antill, 1996; Lee et al., 2015; Ramirez, 1993; Takeda et al., 2001; Xavier et al., 2016). Anosmiation having no effect on preference in the case of Boone et al. (2021), and preference partially diminishing following anosmiation 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, anosmiation 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; Ryckli 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 products (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; Frost 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; Frost et al., 2001; Han et al., 2019), yet the relationship is not always linear (Chen & Eaton, 2012; Frost 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; Frost et al., 2001; Han et al., 2019; Syarifuddin et al., 2016; Yackinous & Guiraud, 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 is it hindered by 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 & Lundstrom, 2014; Bolton & Halpern, 2010). It 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).
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 orthona-
sally 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 focusing 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; Syariifuddin et al., 2016; Yackinous & Guinard, 2000) merely hint at possible behavioural implications without experimentally deter-
mining them, no other study included in this review aimed at investi-
gating 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 po-

tential 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 ol-
factory chemical signals. Although fatty acids seem to be effective ol-
factory stimuli on their own (Bolton & Halpern, 2010; Chale-Rush et al., 2007; Chakir 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 (Carra-
piso, 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 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 inde-
pendent of habitual consumption (Mu et al., 2022; Pirc et al., 2022). However, the evidence base is limited, which warrants further investi-
gation. 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 compromis-
ing on their appealing fat-related sensory characteristics and nega-
tively 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 modali-
ties involved in fat perception could thus prove instrumental in de-
veloping strategies aimed at curbing excess dietary fat intakes.

The current review is the first to summarize findings specific to ol-
factory fat perception. It yields consistent evidence supportive of ol-
faction’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 in-

teractions between olfaction and potentially confounding sensory mo-
dalities (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 val-
idity 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, discrimi-
nating, 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 percep-
tion 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, and cues in fat perception could be exploited in product reformulation. Future research and providing useful information to the food industry. Specifically, fat-related odorants could be used as dietary fat substitutes, and cues in fat perception could be exploited in product reformulation. Future research and providing useful information to the food industry. Specifically, fat-related odorants could be used as dietary fat substitutes, and cues in fat perception could be exploited in product reformulation. Future research and providing useful information to the food industry. Specifically, fat-related odorants could be used as dietary fat substitutes, and cues in fat perception could be exploited in product reformulation. Future research and providing useful information to the food industry. Specifically, fat-related odorants could be used as dietary fat substitutes, and cues in fat perception could be exploited in product reformulation. Future research and providing useful information to the food industry.