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Review

Intrinsic and extrinsic factors affecting axillary odor variation. A comprehensive review

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ABSTRACT

Humans produce odorous secretions from multiple body sites according to the microbiomic profile of each area and the types of secretory glands present. Because the axilla is an active, odor-producing region that mediates social communication via the sense of smell, this article focuses on the biological mechanisms underlying the creation of axillary odor, as well as the intrinsic and extrinsic factors likely to impact the odor and determine individual differences. The list of intrinsic factors discussed includes sex, age, ethnicity, emotions, and personality, and extrinsic factors include dietary choices, diseases, climate, and hygienic habits. In addition, we also draw attention to gaps in our understanding of each factor, including, for example, topical areas such as the effect of climate on body odor variation. Fundamental challenges and emerging research opportunities are further outlined in the discussion. Finally, we suggest guidelines and best practices based on the factors reviewed herein for preparatory protocols of sweat collection, data analysis, and interpretation.

1. Introduction

Current smell perception research has conclusively discarded the 19th-century myth [113] that the sense of olfaction fulfills only a marginal role in the human experience. It is now accepted that olfaction has evolved to enable an individual to assess environmental hazards and thereby guide and regulate eating behaviors [154,182]. The sense of smell also serves a third, social communication function of enabling individuals to transmit and detect information via body odor [29,182]. Interestingly, body odor may cater to two of the three functions of olfaction: the transmission of socially relevant information as mentioned, but, due to its propensity of being perceived as unpleasant, also signifying the presence of a bodily fluid potentially holding pathogens, thus eliciting disgust-mediated avoidance behavior [195].

Examples of the social communication function of olfaction rooted in the survival and reproduction of the species are mate selection and inbreeding avoidance. Sex, age, ethnicity, health status, as well as emotional states, and personality traits, are information that can be communicated through volatile compounds in body odors. Even though the mechanisms involved in producing and perceiving body odor information are not yet fully understood [45,149,151], first insights into the established and inferred biochemistry of the production and release of sulfur compounds have been presented [123], as well as an initial understanding of the chemical "black box" of chemosignaling linked to emotions [174].

Studies investigating the perceptual mechanisms of chemosignaling are conducted under well-controlled laboratory conditions. Donors of sweat samples are usually instructed to adhere to a preparatory protocol. Such protocols aim to isolate as much as possible the target odor, by eliminating for a certain number of days one or more possible causes of noise or interference (e.g., avoid eating certain foods or using scented grooming products). Even though these kinds of control protocols help simplify the understanding of the cause-effect problem under investigation, they still pose some issues. Firstly, they partly remove the complexity of the background odors that usually accompany the odor of interest, impairing the ecological validity and broader context of the results [28,52]. Secondly, removing potential sources of variation stands in the way of a comprehensive understanding of how exactly these

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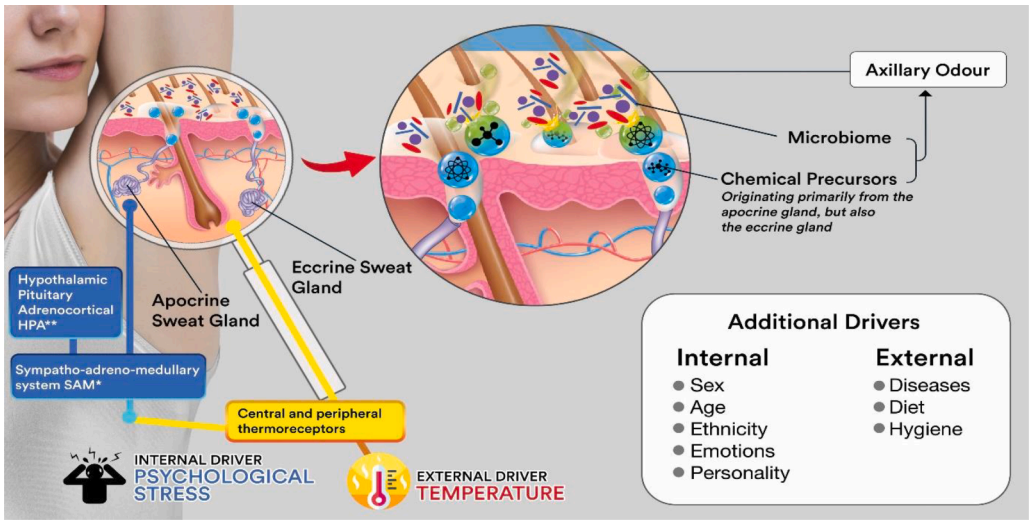

Fig. 1. The drivers of axillary sweat and odor production. Thermoregulatory sweating by the eccrine sweat glands is primarily activated by an increase in body temperature induced by an increase in metabolic and/or movement energy and/or ambient temperature. Psychological stress activates the sympatho-adreno-medullary system and activates sweat production by the apocrine glands. The sweat, especially that of the apocrine gland, contains odorless chemical precursors that are transformed by the skin surface axillary microbiome into the compounds that comprise axillary odor. The inset box shows the additional internal and external drivers that impact odor production by the axilla, as discussed in the paper.

factors affect body odor (see [68]). Furthermore, information on such factors often fails to be collected: for example, Kippenberger et al. [89] highlighted contradicting results when comparing two studies investigating the changes in volatile compounds of body odors in relation to age [54,72]. As the two studies were conducted with Japanese [72] and Caucasian [54] participants, Gallagher et al. [54] speculated that the different volatile compounds identified could be ascribed to a cultural factor, related to the diet of the participants. However, since Haze et al. [72] did not provide data about the dietary habits of their donors, the possible explanation for the difference remains hypothetical.

In this paper, we aim to provide a comprehensive review of the intrinsic and extrinsic factors known to influence the valence, sensory profile, and chemical composition of individuals' odor signatures. 'Intrinsic' here broadly encompasses the innate, genetic factors like sex and ethnicity, and both stable and transient traits, like age, emotions, and personality. 'Extrinsic' factors, instead, refer to outside sources of variation, like diet, diseases, climate, and hygiene habits. We further direct the reader to a previous review by Havlíček, Fialová, and Roberts [68] about inter- and intraindividual body odor variation due to personality factors, sexual orientation, hormones, diet, and diseases. The focus here is on axillary sweat because it is regarded as the "dominant note among the odors originating in various body regions" [100]. Axillary sweat was also shown to contain more volatile compounds than saliva or urine [131], thus representing the most suitable source to reflect individual body odor variations. However, body odor is not solely emitted by the axillae. Other body areas, such as hands [50,166,199], scalp [45], feet [15], mouth [37], lactating breast [75,138,159], and anogenital region, and types of bodily substances other than sweat, namely tears [56], breath [108], vaginal secretions [36], amniotic fluid [157], breast milk and areolar secretions [39,125], are also responsible for body odors. For a more detailed overview of odor-emitting body sites, we redirect the reader to Schaal and Porter [158].

Hereafter, we will refer to social olfactory communication as 'chemosignaling', while acknowledging the ongoing discussion about the difference between the words 'signal' and 'cue', based on the evolutionary biological function of signals [151,175]. Although the chemosignaling function of body odor deserves highlighting here, we do not take the position that all body odor variations serve a social signaling function. Some variations in body odor such as following from dietary choices may be consciously detectable but could be regarded as an epiphenomenon of metabolic processes that would not be considered chemosignals in their own right. Alternatively, body odors demonstrated to have different emotional effects on the receiver, that correspond to the emotions experienced by the senders ostensibly carrying sociochemical signals, may not be perceived as different by those receivers [3,19,27,30,139,209].

The discussion of the intrinsic and extrinsic factors is preceded by an overview of the biochemical mechanism of axillary odor production, focusing on the role of the sweat glands and the microbiome of the axillary area. Said mechanism is summarized in Fig. 1.

An overview of all the intrinsic and extrinsic factors reviewed here, together with the corresponding VOCs and hedonic qualities identified in the studies, can be found in the appendix (Table A).

2. The biochemical mechanism of axillary odor production

2.1. Human sweat glands

Human skin contains a variety of secretory appendages including the apocrine and eccrine sweat glands, and the sebaceous gland. Apocrine glands are located in the axillae, ear canal, areolae, and anogenital regions and their key function is unclear, although they have been suggested to be evolutionary vestiges of pheromone-producing scent glands [110,120]. Human apocrine glands secrete a turbid (milky) sweat [6,110,201]. The eccrine gland is broadly distributed across most of the skin and is primarily responsible for thermoregulation via the discharge of a clear, salt-containing sweat directly onto the skin surface [24,156,201]. The sebaceous gland is also widely distributed, correlating to that of the hair follicle, and its secretion of an oily, waxy substance helps protect the skin and maintain its condition [79,188]. Like the apocrine gland, it discharges its secretion directly into the hair follicular space.

2.1.1. The role of secretory glands in odor production

In humans, the creation of body-site odor originates from the skin microbiome transforming odorless skin secretions into odorous compounds [86–88].

Different body sites exhibit different odor characteristics, with the latter driven by the type of secretory glands present and the unique micro-environmental conditions and microbiomic profile of each area, e.g. axilla, foot, or scalp skin [65,83,133,181]. In terms of their contribution to odor intensity and unpleasantness, contributions by glandular type may be ranked in the following order: apocrine, eccrine, and sebaceous gland [85].

The apocrine gland produces a secretion comprised primarily of lipids and steroids and a lower proportion of proteins [44]. The secretory process is via the 'apocrine method' in which the apical portion of the apocrine secretory cell forms vesicles (or aposomes) containing the above-mentioned components [8,44,57]. The process is slow and intermittent, but human apocrine sweat has been observed to possess a fluidic component that contributes to the production of a 'milky'

end-product [6]. However, the precise mechanism underlying the apocrine secretory process is poorly understood, although it is known to be activated initially by the elevation of androgens during adolescence [79]. An immunocytochemical study using axillary skin tissue sections [104] demonstrated that apocrine gland secretory coil cells express β2- and β3-adrenoceptors, but not α1- and β1-adrenoceptors or muscarinic m3 receptors, and P2Y1 and P2Y2 purinoceptors on the apical membrane and in the cytoplasm. The former and the latter may be involved in regulating apocrine secretory events, with the possibility that odor-associated, adrenaline-driven 'emotional sweating' events could involve apocrine gland β2/β3-adrenoceptors. P2Y1, P2Y2, and P2Y4 purinoceptors were also detected on the myoepithelial cells, where it has been suggested that they contribute to myoepithelial contraction thereby aiding apocrine fluid secretion [104].

The most compelling evidence for the importance of apocrine sweat gland secretions in driving axillary odor comes from observations regarding the membrane transporter protein ABCC11 (ATP-binding cassette transporter sub-family C member 11 [65,109,192]. The ABCC11 gene is present in the human genome as two alleles, differing by one single nucleotide polymorphism (SNP). A SNP at position 538 on the ABCC11 gene encodes for either glycine or arginine in the protein product resulting in the genotypes of GG, GA (both dominant), and AA (recessive [109]). The former two genotypes are associated with high axillary odor (characteristic of Caucasian and African-descent ethnicities) and the AA genotype with no or significantly lower axillary/body odor (characteristic of Asian, especially East Asian ethnicities [65]). These differences in odor are correlated with changes in axillary skin metabolites and bacterial genera [65], but the mechanism by which ABCC11 genotypes affect the secretory processes and molecular physiology of the apocrine gland itself is unknown. However, these observations do confirm the central role of apocrine glands in generating axilla-specific body site odor. Furthermore, the disease of bromhidrosis or osmidrosis (excessive axillary and body malodor), which is associated with GG and GA genotypes, can only be treated by surgical interventions such as liposuction, or cosmetically via high efficacy ('clinical strength') antiperspirants or botulinum toxin injection [97, 132,167,184,204]. This emphasizes the need to further understand the molecular physiology underlying apocrine gland function.

The production of sweat by eccrine glands (the 'merocrine method') is well understood. Early studies from the 1950s and 60 s identified acetylcholine as the primary stimulatory agonist (although adrenaline is also important), and Sato and colleagues [156] determined that the process was driven by a rise in intracellular Ca^{2+} concentration resulting in the movement of salt (Cl^- and Na^+) across the secretory coil cell epithelium. As well as salt, eccrine sweat also contains various antimicrobial proteins (AMPs, e.g. psoriasin, lactoferrin, dermcidin), which are secreted from the dark cells in the secretory coil and are likely to impact the community profile of the skin surface microbiome [118,160,161, 202]. However, it is unclear whether they affect the odor profile of a skin site, and their role may be primarily to maintain a healthy skin microbiome.

The main component in eccrine sweat that induces malodor is the amino acid leucine. Leucine secreted in the sweat can be converted to isovaleric acid by *Staphylococcus* species on the skin [7,111]. This results in a sweaty, 'locker room' smell, and is the only type of malodor reported by East Asian individuals, especially after exercise [123]. Isovaleric acidemia (IVA) is the disease form of this process and is a rare inherited disorder, specifically an inborn error of leucine catabolism, caused by mutations in the isovaleryl-CoA dehydrogenase (IVD) gene, which results in the accumulation of derivatives of isovaleryl-CoA including isovaleric acid [164]. A specific characteristic of IVA is the distinctive odor of sweaty feet which results from the excess secretion of these derivatives onto the skin surface leading to high levels of isovaleric acid.

Other, more minor variables which may affect the volume of eccrine sweat secreted include gland size, which can increase with exercise or decrease with age, and geographical location [22,81,187]. As a rule of thumb, individuals residing closer to the equator tend to sweat more than those located further away from it [90]. These factors could impact odor intensity, especially in the case of axillary odor.

Finally, the contribution of sebaceous gland sebum to skin odor is thought to be minor. Sebaceous gland secretion is via the 'holocrine method' in which whole secretory cells slowly break down to form the oils and waxes found in sebum [79,188]. Although long-chain fatty acids in sebum can be broken down to short-chain fatty acids such as isobutyric acid by *Corynebacterium* species on axillary skin [86], this does not lead to the formation of either isovaleric acid or apocrine-associated volatile fatty acids (VFAs) such as 3-methyl-2-hexenoic acid (3M2H; [85]).

Taken together, these studies show that apocrine sweat glands are the primary cause of axillary and body odor but sweat secretion by eccrine sweat glands also makes a significant contribution. Sebaceous glands are not strongly implicated.

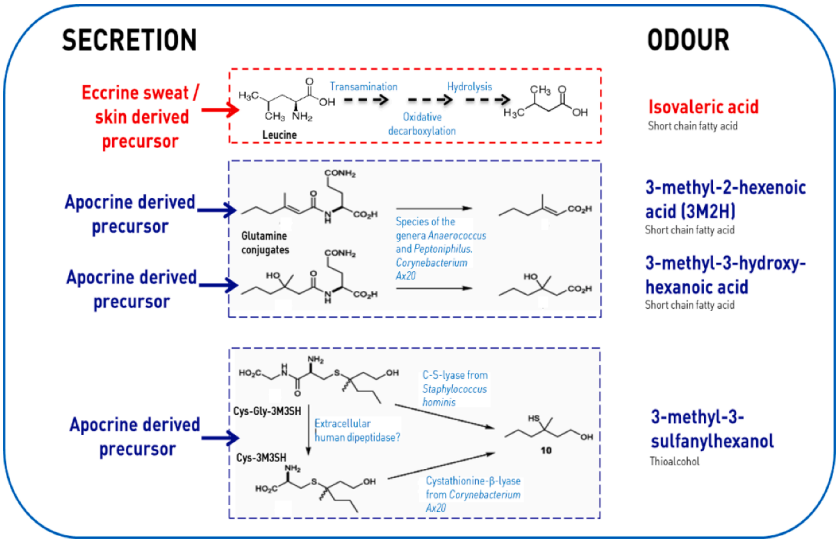

Fig. 2. The generation of axillary odor from sweat gland-derived precursor,olecules. Axillary odor is produced from leucine present in eccrine gland sweat, and from both glutamine conjugates and the peptides Cys-Gly-3M3SH and Cys-3M3SH, found in apocrine gland sweat. Leucine is converted to isovaleric acid (the 'locker room' smell), glutamine conjugates to short chain fatty acids such as 3M2H (a fruity smell), and Cys-Gly-peptides to thioalcohols (with a rancid, cheese-like smell).

2.2. Microbiome

Pioneering studies by Shelley et al. [168] first showed that odor generation on axillary skin is caused by the biotransformation of naturally secreted precursor molecules into volatile odorants by members of the commensal microbiota, also known as the skin microbiome. Since that breakthrough, extensive studies on the axillary microbiota and its relationship with underarm odor have been reported, notably by Leyden et al. [100] and Taylor et al. [186], in each case highlighting the high bacterial density in the underarm, typically averaging $\sim 10^6$ colony-forming units per cm^2 of skin (CFU/cm^2). These studies used traditional culture methods to determine the axillary microbial ecology of multiple subjects and, with modern taxonomic terminology overlayed [85], show that the microbiome consists mainly of the Gram-positive bacterial genera *Staphylococcus, Corynebacterium* and *Cutibacterium* (formerly *Propionibacterium* [165], with corynebacteria showing the strongest association with odorous sweat (Fig. 2). The past 12–15 years have witnessed a revolution in microbiology, manifested in the adoption of the culture-independent metataxonomic approach, 16S rRNA gene profiling, to probe the skin microbiome. Specifically, concerning the axillary microbiome, metataxonomic studies confirm it is dominated by members of the *Staphylococcus, Cutibacterium,* and *Corynebacterium* genera [61], although the presence of taxa not indicated by culture methods is also evident, notably Gram-positive anaerobic cocci (GPAC) of the *Anaerococcus* and *Peptoniphilus* genera [41].

The current view is that VFAs and thioalcohols (sulfanylalkanols) are the primary causal molecules of axillary odor (see Fig. 2). The involvement of short-chain ($C_4 - C_5$) VFAs has long been acknowledged, and various metabolic routes to these acids (notably isovaleric acid, as detailed above (Section 2.1.1), which drive the perception of underarm odor in *ABCC11* AA individuals, particularly in East Asia [65], have been elucidated [86,87]. In the early 1990s, it was established that a group of structurally unusual medium-chain ($C_6 - C_{10}$) acids, in particular the *trans* (*E*) isomer of 3M2H, is the main aspect of VFA-based underarm odor [207], at least in populations of European and African origin, where the *ABCC11* G-allele dominates [142,206]. Natsch et al. [121, 122] later showed that 3M2H, the structurally related 3-hydroxy-3-methylhexanoic acid (3H3MH), and a range of additional medium-chain VFAs exist in apocrine sweat as N^{α}-conjugates of L-glutamine, and are released by the corynebacterial enzyme N^{α}-acylglutamine aminoacylase. While these findings support the link between corynebacteria and odor derived from microbial ecology studies [100,186], more recent evidence has challenged this paradigm. In the context of VFA-based odor, Fujii et al. [51] described an axillary *Anaerococcus* strain capable of efficiently releasing 3H3MH from its L-glutamine N^{α}-conjugated precursor.

The importance of sulfanylalkanols, particularly 3-methyl-3-sulfanylhexan-1-ol (3M3SH), in axillary odor emerged in the mid-2000s (see Fig. 2), and it was initially believed that the direct precursors to these odorants were *S*-hydroxyalkyl-L-cysteine conjugates, converted by *Corynebacterium* carbon-sulfur (C-S) β-lyases to the corresponding thioalcohols [85]. However, it was subsequently shown that the true sulfanylalkanol precursors are *S*-hydroxyalkyl-L-cysteinylglycine conjugates present in apocrine sweat (Starkenmann et al., 2005), and the pathway by which *S*-Cys-Gly-3M3SH is taken up and metabolized by a limited range of staphylococcal species (mainly *Staphylococcus hominis*) present in the axilla has since been elucidated, resulting in the production and secretion of the pivotal thioalcohol malodorant 3M3SH [10].

The axillary microbiota is unique for each individual, and its composition is affected by all the other intrinsic and extrinsic factors reviewed in this paper [14,101].

3. Intrinsic factors

3.1. Sex

Several studies have shown that people can discriminate between donors' sex just by smelling samples of male and female odors. In one of the two pioneering studies about sex differentiation through smell [77, 153], Russell [153] found a striking 75% of correct answers. On the other hand, Hold and Schleidt [77] got only 32% of significantly correct answers, which precipitated as low as 6% when no control protocol was implemented on the use of scented body products [162], and ranged between 20 and 60% when German and Italian participants were tested against Japanese ones [163]. The difference between the results of Russell [153] and the first study of Hold and Schleidt [77] could be ascribed to their different experimental methods. Where Russell [153] tested sex differentiation using a two-alternative choice discrimination test, Hold and Schleidt [77] presented 10 t-shirts simultaneously to be categorized as belonging to males or females. However, the wide fluctuation of results reported in the following studies by Schleidt and colleagues [162,163] implied that people do not discriminate sex per se, as much as they distinguish between odor intensity and pleasantness. The results by Doty et al. [38] support this hypothesis, as they found that participants could not unequivocally identify the donors as males or females and that stronger and less pleasant odors were regarded as masculine despite the actual sex of the donor. Similar conclusions were reached by Lindqvist [105] and Mutic et al. [119]. One study found that the correct identification of the sex of people wearing perfumes was not different from chance [105]. In another study, participants rated the samples of axillary body odor from male and female donors, along a masculinity-femininity scale, plus hedonic ratings of intensity, pleasantness, and familiarity [119]. They confirmed that people cannot determine the sex of the donor from the stimuli, but they tended to show a bias toward judging all the odors as more masculine.

These studies show that people tend to rely mostly on the perceived intensity and pleasantness of the sweat odor in order to establish whether the donor is male or female. Such sex attribution is likely done by learned association [74], possibly linked to the fact that, in general, men have larger apocrine sweat glands, which positively correlates with the intensity of body odor [38]. Moreover, the attribution of masculinity to body odors was found to be related to the sex stereotype that males smell worse than females [16].

Even though the subjective ability to discriminate sex via olfaction seems to be mainly driven by learned associations, there are also some objective differences in the chemical composition of sweat between males and females. Penn et al. [131] analyzed the volatile organic compounds (VOCs) present in the axillary sweat of men and women using gas chromatography-mass spectrometry (GC–MS). They found no VOCs exclusively related to either sex, but rather a different distribution of chemical compounds that could significantly predict the sex of the donors. Single molecules are indeed not expected to characterize individual differences. Since human body odor is a complex mixture of chemical compounds, studies should look for patterns of molecules that are sufficiently distinctive for each transmitted information.

In another study, Troccaz et al. [193] isolated the precursors of the two main chemical compounds considered to be the cause of sweat malodor, namely (R)/(*S*)−3-methyl-3-sulfanylhexan-1-ol ((R)/(*S*)-MSH) and (R)/(*S*)−3-hydroxy-3-methylhexanoic acid ((R)/(*S*)−3H3MH). They found that females secreted the sulfur precursor in higher amounts than males, leading to higher instances of producing tropical fruit or onion-like odors (typical of (R)/(*S*)-MSH), rather than cheese-like, rancid odors (typical of (R)/(*S*)−3H3MH).

3.1.1. Hormones

The most likely explanation for such variations in axillary secretions between sex is due to genetic and hormonal factors. The effect of steroid hormones on body odor has received particular attention due to their

role in mate attraction and reproductive processes.

For example, the axillary odor of women has been shown to change according to the different phases of the menstrual cycle. While testing the relationship between the attractiveness of body odor and the amount of body fluctuating asymmetry in both men and women, a study found that men did not perceive the odor of women in their fertile phase as more attractive than that of women in the luteal phase of their menstrual cycle [190]. They, therefore, suggested that attractiveness perception is unrelated to the fertility phase of a woman.

Singh and Bronstad [172] challenged this conclusion and ascribed it to a limitation of the between-subjects design employed by Thornhill and Gangestad [190]. To account for this potential confound, they opted for a within-subject design by collecting t-shirts worn by the same women in both the follicular and the luteal phases. They found that the body odors collected during the follicular phase were judged by men as significantly more pleasant and sexier compared to the luteal phase. However, during the rating experiment, the authors informed the receivers that one sample in the pair of t-shirts (coming from the follicular and the luteal phases of each donor) belonged to an attractive woman and the other to an unattractive one. Such information might have introduced a priming effect that led receivers to successfully discriminate between the two samples of the pair.

A study extending on the results of Singh and Bronstad [172], tested whether men can detect the chemosignal of ovulation also when comparing different women in different phases of their cycle [95]. To answer this question, they conducted a between-subjects experiment similar to Thornhill and Gangestad [190], collecting the body odor of women in different cycle phases as well as of women taking oral contraceptives. They confirmed that men prefer the body odor of women in their fertile phase. They also found that this relationship was no longer significant when judging the odor of women using contraceptives, indicating the role of hormones in the variation of body odor.

Havlíček et al. [67] evaluated the attractiveness of female body odor during all the different phases of the menstrual cycle, including menstruation. Using a within-subject design, male receivers rated the intensity, pleasantness, attractiveness, and femininity of cotton pads used to sample axillary sweat during the menstrual, follicular, and luteal phases. The results showed that pleasantness and attractiveness were highest in the follicular phase and lowest during menstruation.

Gildersleeve et al. [59] addressed the potential limitation of previous studies which relied solely on self-reported recall of the last menstruation, by measuring the actual presence of the luteinizing hormone in the female donors to establish objectively in which phase of their cycle they were. They found that male receivers not only judged the axillary sweat collected during the follicular phase as more pleasant, but receivers were also able to discriminate between samples of high vs. low fertility. A later study showed that the attractiveness of women's body odor as judged by male receivers could be predicted by the women's levels of estradiol and progesterone [106]. Higher levels of estradiol and lower levels of progesterone, corresponding to peak fertility, predicted higher attractiveness.

These results taken together strongly suggest that the body odor of women who do not use hormonal contraceptives, changes across the phases of the menstrual cycle in perceivable ways and can be used as a potential cue to fertility.

When exposed to the body odor of women in different phases of their cycle, men can, not only discriminate between them and show a preference for highly fertile women, but they also increase the production of sex hormones, such as testosterone. Men's level of testosterone was shown to be higher when exposed to t-shirts worn by women during the ovulatory phase compared to those worn by women in the luteal phase or unworn [115]. However, Roney and Simmons [152] argued that this effect could be ascribed to the conscious knowledge of the receivers that they were smelling t-shirts worn by women, which could have induced them to visualize a woman, triggering the hormonal response. In a similar experiment that compared the level of testosterone when smelling the odor of women during ovulation vs. water, but without informing the participants about the source of the odor samples, no effect on testosterone levels was found [152].

A high level of testosterone has been related to the increase in mate-seeking behaviors in males [112,185], but data are inconclusive as to whether women can detect fluctuations in steroid hormones, like testosterone and cortisol, to drive their judgment of body odor attractiveness [144,189].

If hormones produce changes in body odor throughout the menstrual cycle of a woman, pregnancy is also expected to influence body odor, due to the increase of hormones such as estradiol and progesterone [194]. GC–MS analysis of sweat samples taken from pregnant and lactating women, revealed the presence of a distinctive profile of five volatile compounds, which were not found in non-pregnant women [196]. Habel et al. [62] conducted the first study about the discrimination of body odor attractiveness of pregnant vs. ovulating women. The odor from the ovulation condition was found to trigger a stronger neural response in areas of the brain related to the perception of female attractiveness; whereas the pregnancy odor activated mostly the medial frontal cortex, an area of the brain known to be related to empathic behaviors. However, due to the small sample size tested in this study, further explorations would be needed to confirm the significance of the results.

3.2. Age

The activity of the skin's secretory appendages, the apocrine, eccrine, and sebaceous glands, is age-dependent. Several studies have shown the attenuation of exocrine glands' function with aging, related to a general reduction in sweating (which can be delayed, though, by the regular, life-long practice of aerobic exercise; see [12]). The diminished secretions of eccrine glands were thought to be caused by a decrease in the number of sweat glands themselves [46]. A recent study, however, has demonstrated, using 3D digital reconstruction of X-ray micro-computed tomography (micro-CT) images, that the density and volume of eccrine glands did not differ between young (25–39 years) and old (61–71 years) subjects [43]. What changed was the morphological structure of the glands, with the secretory coil closer to the skin surface and the secretory duct more twisted in the old age group. The functional deterioration of the sweat glands is probably related to this structural change, and also to a decrease in the production of androgen hormones [46]. Similarly, prepubertal children were found to sweat less than young adults due to the lack of androgen hormones, a state which changes with the beginning of puberty [82,159]. The onset of androgens production with puberty also affects the secretion of sebaceous glands, which increases until adolescence and starts to decrease in old age (60–70 years) [46,136].

Besides these changes in sweat production with aging, different chemical compounds have also been identified in non-axillary skin secretions of different age groups. Haze et al. [72] analyzed samples taken from the back of t-shirts worn by Japanese subjects between 26 and 75 years old, using GC–MS. They found an increase of the unsaturated aldehyde 2-nonenal in subjects older than 40 years, most likely produced via the oxidative degradation of fatty acids in skin surface lipids. As the 2-nonenal is characterized by an unpleasant greasy and grassy odor, Haze et al. [72] proposed this compound to cause the change of body odor typical of old age.

Gallagher et al. [54] conducted a similar study but tested Caucasian subjects instead of Japanese ones (see [89]). Three VOCs were found to increase significantly with age, dimethylsulphone, benzothiazole, and nonanal, but not the 2-nonenal compound identified by Haze et al. [72]. Gallagher et al. [54] attributed the discrepancy to the extrinsic factor of different diets among the subjects of the studies. The higher consumption of fish typical of the Japanese culture might have caused the increase of unsaturated fatty acids in the skin lipids, which in turn produced a higher amount of 2-nonenal by oxidative degradation.

Given these changes in glandular function and sweat chemical compounds with aging, Mitro et al. [116] tested whether humans can perceive the variations of body odors with age and assign an age group (young, middle, and old) to the sampled body odors. They found that body odors from the old age group (75–95 years) were rated the least intense and as neither pleasant nor unpleasant, whereas the body odor from the middle age group (45–55) was rated the most intense and highly unpleasant, the latter being not significantly different from the young age group (20–30 years). With a two-alternative forced-choice (2AFC) task, Mitro et al. [116] determined that participants can significantly discriminate between body odors according to the different age groups.

3.3. Ethnicity

Genetics is another intrinsic source of variation in body odor. The secretion of odor precursors responsible for body odors from the apocrine glands is regulated by the protein-encoding gene ABCC11 (see Section 2.2.1). The occurrence of the SNP substitution was first shown to be responsible for a dry and white earwax phenotype, typical among the East Asian population with an AA homozygote genotype, but rarely found in Caucasians and Africans, who mostly show GA heterozygote or GG homozygote genotypes [142,206]. As ABCC11 transports a variety of metabolites also found in axillary sweat, Martin et al. [109] hypothesized that ABCC11 might play a role also in the secretion and transport of odorant molecules in axillary apocrine sweat, where the SNP substitution would cause a decrease in odorants' secretion. This hypothesis was tested and confirmed via chemical analysis of axillary sweat sampled from Asian and Caucasian donors having the different genotypes of ABCC11 [109]. Key odorant molecules known to produce the axillary odor, such as (*E*)−3M2H, 3H3MH, and 3M3SH, were found to be produced in significantly lower amounts by people with AA genotype, corresponding to the majority of the Asian donors. Reduced production of odorous compounds, however, does not necessarily mean that odor in individuals with the AA genotype is non-perceivable. Harker et al. [65] demonstrated that even though the intensity of axillary odor of Asian women with the AA genotype was significantly lower than that of Asian women with either the GG or GA genotype, their level of odor was still in the perceivable range.

Extending on these studies, Prokop-Prigge et al. [141] analyzed the relationship between ethnicity, in terms of ABCC11 genotype, and the amount of axillary VOCs secretions, with the hypothesis that Asian participants (all but one AA homozygotes) would produce fewer odorants than Caucasians or African-Americans (all GG homozygotes). Via GC–MS analysis of axillary sweat samples collected from the donors, Prokop-Prigge et al. [141] found that the chemical profile did not differ qualitatively between ethnicities, meaning that the same VOCs were identified across the groups. The regulatory role of ABCC11 on odorants' production was found to be less clear-cut than previously thought. Indeed, even though Caucasian and African donors had all the same GG genotype, the authors observed significant differences in the amount of the 3M2H and another medium-chain VFA, 7-octenoic acid both significantly higher in African donors than Caucasian and lowest in Asians. These results indicate that the ethnic difference in body odors cannot be ascribed to the ABCC11 gene only, as its role in VOCs' production is still unclear. Further complexity in understanding the role of the axillary microbiome in odor production among ethnic groups was reported by Li et al. [101]. DNA analysis of samples from Hispanic, East Asian, and Caucasian donors, showed that the East Asian group had the highest amount of total bacteria and more *Staphylococcus hominis*, a bacteria related to malodor production. This result is in contrast with the finding that the East Asian population produces fewer odorant volatiles because of the prevalence of the AA genotype of ABCC11. The result was explained by speculating that it is probably not one single bacterium like *Staphylococcus hominis* that determines the body odor, as much as the microbiota as a whole [101].

Finally, Parma et al. [127] explored the question of whether such genetic differences among ethnicities are also perceivable. Donors and receivers of Caucasian and Afro-Portuguese origins were tested. Receivers were asked to rate the intensity, pleasantness, and familiarity of the body odor sampled from donors of both ethnicities, plus a no odor control condition. Receivers were instructed on the ethnic origin of the samples in one rating experiment and did a second rating without any information. Additionally, a two-alternative forced-choice task was performed to test if body odors could be discriminated based on ethnicity. Parma et al. [127] found no significant differences in the ratings of the perceptual features between the samples from the two ethnic groups, neither when no prior information was provided about the samples nor when receivers were primed to know that the body odor came from somebody of the same or different ethnicity. Also, the discrimination task was not above chance. However, Parma et al. [127] tested the perceptual difference between Caucasian and African donors, two ethnic groups more likely to share the same ABCC11 genotype [141]. It would thus be interesting to test if the difference in body odor is perceivable between East Asians and the Western populations, based on the known difference in genotype which has been shown to affect the quantitative production of odorant VOCs [109].

3.4. Emotional states and personality traits

3.4.1. Emotional states

Building on the ability of animals to chemosignal fear, stress, and alarm states, Chen and Haviland-Jones [18] conducted the first study to test whether humans are also able to communicate emotions via body odors. They induced in donors a fearful and a happy emotional state by exposing them to either a frightening movie or a comedy while collecting their axillary sweat with gauze pads. Receivers were asked to identify the "odors of people when they are happy" and the "odors of people when they are afraid". Women were able to discriminate above chance the happy odor of both women and men, whereas men could only distinguish the happy odor of women. Both women and men could discriminate above chance the fear odor of men only. Intensity and pleasantness of the stimuli were not measured, but since women were able to identify both the fearful and the happy odor, Chen and Haviland-Jones [18] ruled out the possibility that the discrimination was only based on differences in intensity and proposed that different emotional states can actually change the human body odor. Ackerl et al. [1] conducted a similar study about the chemosignaling of fear. A horror and a neutral movie were presented to donors to induce fear or a neutral state, respectively. A triple forced-choice experiment demonstrated that receivers were able to distinguish between the fear and the neutral odors significantly above chance. Even though the samples collected during the fear-inducing condition were not identified as fear per se, a qualitative difference was detected nonetheless, as the fear stimuli were rated significantly more odorous and less pleasant than the neutral condition. The relevance of the hedonic and intensity characteristics in the chemosignaling of emotions, however, is not clear, given that other studies did not find significant differences along these dimensions between stimuli [3,19,27,30,139,209]. This might suggest that the transmission of emotions via body odor occurs outside of the recipient's awareness. This hypothesis is supported by further evidence provided by neuroimaging studies showing activation of the amygdala, a brain area involved in emotional processing, in subjects exposed to stress sweat [117] and activation of the insula, related to feelings of empathy [140], without their conscious perception of qualitative differences compared to exercise sweat. Moreover, chemical analysis of fear, happy, and neutral body odors did not reveal any significant difference in the peak intensity of compounds usually related to odor, such as 3H3MH, indicating that odorous compounds might not be necessary for emotional chemosignaling [174].

Negative emotions, such as fear, stress, and anxiety, have received the most scientific attention, probably because humans display a

Table A1
Summary of the factors reviewed in the paper and the corresponding studies.

VOCs										Ketone, 6-phenylundecane, pentadecanoic acid, hexadecanoic acid, methylhexadecanoic acid, heptadecanoic acid, dialkyl ether, nonadecane, isopropyl hexadecanoate, 2-ethyl-hexyl-4-methoxy-cinnamate, docosane, 1-octyl-4methoxycinnamate		(R)/(*S*)−3-hydroxy-3-methylhexanoic acid ((R)/(*S*)−3H3MH), (R)/(*S*)−3-methyl-3-sulfanylhexan-1-ol ((R)/(*S*)-MSH)	
Hedonic property			Pleasantness	Intensity, pleasantness;		Masculinity-femininity; pleasantness, intensity, familiarity	Attractiveness, sexiness, healthiness, familiarity, intensity, pleasantness, masculinity, dominance, arousal					Sweat odor intensity, sulfur odor intensity, acid odor intensity, odor unpleasantness	
Cue		Own smell; male	Own vs partner; male vs female;	Male vs female	Male vs female								
Refs.	**Sex and hormones**	Russell [153]	Hold & Schleidt [77,162, 163]	Doty et al. [38]	Lindqvist [105]	Mutic et al. [119]	Carrito et al. [16]			Penn et al. [131]		Troccaz et al. [193]	
VOCs												1-dodecanol, 1–1′-oxybis octane, isocurcumenol, α-hexyl-cinnamic aldehyde, isopropyl myristate	
Hedonic property		Pleasantness, sexiness, intensity;	Pleasantness, sexiness, intensity;	Sexual attractiveness, intensity	Intensity, pleasantness, sexual attractiveness, femininity		Pleasantness, sexiness, intensity and physical attractiveness of the donor			Attractiveness			Facial attractiveness, pregnancy categorization
Cue		Fertile phase of the menstrual cycle	Follicular and luteal phase of the menstrual cycle	Use of contraceptive pill, day of menstrual cycle;	Menstrual, follicular, luteal phases of menstrual cycle;		High- and low-fertility phase of menstrual cycle; measurements of luteinizing hormone			Women's salivary oestradiol, progesterone, testosterone and cortisol levels		Pregnancy and lactation	Pregnancy and ovulation
Refs.	**Sex and hormones**	Thornhill & Gangestad [190]	Singh & Bronstad [172]	Kuukasjärvi et al. [95]	Havlíček et al. [67]		Gildersleeve et al. [59]			Lobmaier et al. [106]		Vaglio et al. [196]	Habel et al. [62]
VOCs		2- Nonenal, palmitoleic acid, vaccenic acid	Dimethylsulphone, benzothiazole, nonanal, hexyl salicylate, a-hexyl cinnamaldehyde			3M2H, HMHA, 3M3SH, 5a-androst- 16-en-3-one, 5a-androst-16-en-3a-ol	Sulfanylalkanols, 3M2H		3M2H, 3M3H, 7- and 2-octenoic acid				
Hedonic property				Pleasantness, intensity	**Ethnicity**		Malodor intensity				Intensity, pleasantness, familiarity, arousal	**Emotional states**	
Cue						ABCC11 genotypes	ABCC11 genotypes		ABCC11 genotypes				Fear, happy
Reference	**Age**	Haze et al. [72]	Gallagher et al. [54]	Mitro et al. [116]		Martin et al. [109]	Harker et al. [65]		Prokop-Prigge et al. [141]		Parma et al. [127]		Chen & Haviland-Jones [18]
VOCs			Aldehydes/ ketones, esters and cyclic molecules				**Personality traits**						

(*continued on next page*)

Table A1 (*continued*)

VOCs										Ketone, 6-phenylundecane, pentadecanoic acid, hexadecanoic acid, methylhexadecanoic acid, heptadecanoic acid, dialkyl ether, nonadecane, isopropyl hexadecanoate, 2-ethyl-hexyl-4-methoxy-cinnamate, docosane, 1-octyl-4methoxycinnamate			(R)/(*S*)−3-hydroxy-3-methylhexanoic acid ((R)/(*S*)−3H3MH), (R)/(*S*)−3-methyl-3-sulfanylhexan-1-ol ((R)/(*S*)-MSH)	
Hedonic property		Intensity, pleasantness		Intensity, pleasantness, unpleasantness, familiarity	Intensity, pleasantness	Intensity, pleasantness			Intensity, attractiveness, pleasantness	Attractiveness	Intensity, pleasantness, unpleasantness, familiarity	Pleasantness, intensity, familiarity	Intensity, masculinity, pleasantness, familiarity		
Cue		Fear, neutral	Fear, neutral, happy	Anxiety	Stress	Fear/ disgust; fear/happy/ neutral			Big five, dominance	Neuroticism, extraversion, dominance	Dominance/ aggression	Self-esteem	Cooperativeness		
Reference	**Emotional states**	Ackerl et al. [1]	Smeets et al. [174]	Pause et al. [129], Prehn et al. [139]	Dalton et al. [27]	De Groot et al. [30; 31; 34]			Sorokowska et al. [179; 180]	Sorokowska [178]	Adolph et al. [2]	Croijmans et al. [23]	Tognetti et al. [191]		
VOCs				Dimethyl trisulfide	Isovaleric acid	Phenylacetic acid; 3-hydroxy-4,5-dimethyl- 2 (5H)-furanone (sotolone)	Trimethylamine	Trans-3-methyl-2-hexenoic acid			**Diet**				
Hedonic property		Foul odor	Butcher shop; Baked brown bread; stale beer		Sweaty feet, dirty socks	Musty, sweaty locker room towels-like odor; maple syrup	Rotten fish	Peculiar odor	Intensity, pleasantness, health			Attractiveness, pleasantness, intensity	Attractiveness, pleasantness, intensity		
Cue		Scarlet fever	Yellow fever; Typhoid; tubercolosis	Skin ulcers/ fungating cancer wounds	Isovaleric acidemia	Phenylketonuria; maple syrup urine disease	Trimethylaminuria	Schizophrenia	Generalized sickness			Red meat	Garlic		
Refs.	**Diseases**	Honig et al. [78]	Pavlou & Turner [130]	Shirasu et al. [170]	Vockley & Ensenauer [198]	Cone [21]	Messenger et al. [114]	Smith & Sines [176]; Di Natale et al. [35] ; Gordon et al. [60]	Olsson et al. [126]; Regenbogen et al. [146]			Havlíček & Lenochova [69]	Fialová et al. [49]		
VOCs		3-hydroxy-4,5-dimethyl- 2 (5H)-furanone (sotolone)			**Hygiene habits**						**Climate**	Nonanal, Diphenyl ether, 3,7-Dimethyl-6-octanol,2-Ethyl hexanol, Eicosane, Tridecane, Octanal, Decanal, Isobornyl propionate, 3, 7-Dimethyl-2, 6-octandiol				
Hedonic property		Maple syrup	Liking, attractiveness, health, intensity	Pleasantness, attractiveness, femininity, intensity		Intensity, pleasantness	Pleasantness, intensity, familiarity	Pleasantness, intensity, attractiveness	Intensity, pleasantness, attractiveness						
Cue		Fenugreek	Diet rich in fruit and vegetables	Caloric intake restriction		Unscented antiperspirant	Fragranced body spray	Own vs assigned perfume	Shaving axillary hair			Moist and warm spring, dry and cold winter			
Refs.	**Diet**	Korman et al. [92], Yalçin et al. [205]	Zuniga et al. [211]	Fialová et al. [47]		Dalton et al. [27]	Croijmans et al. [23]	Lenochová et al. [99], Allen et al. [5]	Kohoutová et al. [91]			Zhang et al. [208]			

negative bias since infancy which serves an evolutionary adaptive purpose [197]. Moreover, the odor release of fear, stress, and anxiety likely share a common physiological mechanism that manifests in the rapid activation of the fight-or-flight stress response, during which the adrenalin release stimulates the secretions from the apocrine sweat glands [32,64]. A meta-analysis of the fear, stress, and anxiety chemosignaling literature has demonstrated a true effect with small to moderate size for the signaling process, but not for perceivable differences between emotional states [33].

Even though emotional odors are usually not directly perceivable in terms of hedonic and intensity characteristics, they still affect the cognitive performance, sensory processes, and physiological responses of the receiver. Pause et al. [129] showed that the chemosignal of anxiety, collected before an academic examination, decreased the positive priming of neutral face perception by female participants, but it did not affect the negative priming. Using the same methodology of anxiety sweat collection, Prehn et al. [139] demonstrated a significant increase in startle reflex from recipients of the anxiety chemosignal, evidence of the activation of a withdrawal behavior. This effect was found to be independent of the sex of the donors [128]. Long exposure (20 min) to anxiety chemosignals induced during a high rope course resulted in a significant increase in self-reported anxiety of recipients, outside of their conscious awareness of qualitative differences between anxiety and control conditions [3]. Stress chemosignals can even negatively affect the social judgment of other people [27].

Fear body odor was shown to act upon ambiguous situations by increasing cautiousness and vigilance when processing ambiguous words [19] and by judging an ambiguous face as fearful [209]. The authors from both studies, excluded an effect of the difference in perceived pleasantness, intensity, or quality between the odor conditions, indicating that the observed change in behavior and alertness cannot be ascribed to a difference in the sensorial qualities of the stimuli. Chen et al. [19] suggested that what is picked up by receivers is a consequence of the neurochemical changes happening when experiencing fear, and according to Zhou and Chen [209], such chemical input is associated with fear, even though mostly unconsciously, to increase evolutionary fitness.

De Groot et al. [30] reached similar conclusions when demonstrating the occurrence of emotional contagion of fear and disgust. Receivers exposed to axillary odors collected during a state of fear or disgust revealed congruent facial expressions (i.e., fear or disgust), and either sensory acquisition in case of fear or sensory rejection for disgust (however, [42] found decreased inhalation of fear sweat compared to control sweat). These findings of emotional contagion were later replicated and extended from Western Caucasian to East Asian receivers, who mimicked a facial expression of fear or happiness when exposed to fear or happiness body odors, respectively [34], hinting at an ethnocultural universality of emotional chemosignaling. As the reactions of the receivers were not related to the sensory perception of pleasantness or intensity of the stimuli, the authors concluded that the states of fear and disgust are each characterized by distinctive chemical profiles that emanated from people experiencing such emotions. A first insight into the chemical composition of fear sweat was given by Smeets et al. [174]. Samples of axillary sweat produced while experiencing fear, happiness, and calmness (i.e. neutral state) were collected and analyzed via GC–MS to determine their chemical composition. Fear sweat was found to be significantly distinct from neutral sweat, with fear being characterized by the presence of chemical compounds such as aldehydes and ketones, while neutral sweat showed higher amounts of esters and cyclic molecules. The chemical composition of the happy sweat was less straightforward, resulting in two sub-clusters, overlapping either with the fear or the neutral cluster. Even though the chemistry of happiness is still to be resolved, De Groot et al. [31] have demonstrated that people can chemosignal happiness by showing that receivers mimicked the happy state in their facial expressions and in a more global visual processing style. The ability to communicate emotions via body odor was further identified to play a role in relationship maintenance, by promoting mutual understanding and responding to the emotional needs of a partner [107]. For a recent review on the olfactory communication of emotions, limitations of current methodologies, and future approaches, we refer the reader to Roberts *et al.* [151].

3.4.2. Personality traits

Certain emotions are related to specific personality trait domains. For example, neuroticism is characterized by a prevalence of negative emotions such as anxiety, self-consciousness, anger, and irritability [200]. Because negative emotions are subject to chemosignaling, it is reasonable to assume that enduring personality traits revealed by such emotions are also communicable via body odor. Based on this assumption and on the previous research on personality traits that have a neurophysiological connection [17,40,112,210], Sorokowska et al. [180] conducted the first study to investigate the perception of the Big Five personality dimensions and dominance through body odor. The authors found moderate but significant correlations between the self-assessed personality traits of the donors and receivers' ratings for neuroticism, dominance, and extraversion, whereas agreeableness, conscientiousness, and openness to experience were not accurately perceived. This study suggests that only personality traits that are more related to emotions and provide a physiological response can be communicated via body odor, and vice versa. Moreover, personality traits related to fear and anxiety, such as neuroticism, can be discerned already during childhood [177]. In a follow-up study, Sorokowska [178] investigated the assessment accuracy of neuroticism, dominance, and extraversion when presented with either only body odor cues, only images of faces, or both. Body odor cues alone could provide accurate information to judge dominance and neuroticism, while extraversion was judged significantly more accurately when relying on visual face cues. The combination of visual and olfactory cues increased the assessment accuracy only in the case of extraversion, while it decreased it when judging neuroticism and dominance, indicating that increasing the availability of information does not necessarily improve accurate personality assessment. Why that is the case and why only for certain personality traits, is still to be determined, but a possible influence factor to form a first impression of personality could be the attractiveness of the body odor. Sorokowska [178] proposed that the agreement between receivers on the judgment of neuroticism and dominance could be mediated by the perceived attractiveness of the odors. Dominance is a personality trait that women in the fertile phase of the menstrual cycle find attractive in men [71] and it can be accurately perceived not only from natural body odor but also when personal fragranced cosmetic products are used [179]. The chemosensory communication of dominance was also demonstrated to happen in relation to competition under the ecological condition of a badminton match [2].

Dominance and neuroticism are not the only personality traits that can be transmitted via body odor. Croijmans et al. [23] demonstrated the chemosignaling of self-esteem, such that female receivers rated body odors of males with high self-reported self-esteem as more pleasant and less intense than those of male donors with low self-esteem.

Recently, the chemosignaling of cooperativeness has also been investigated [191]. The cooperativeness of male donors was assessed via the public good game task, while receivers were asked to identify the cooperative smell by selecting high-cooperative potential partners and avoiding low-cooperative ones in the public good game, based on their body odor only. The stimuli were further rated for selfishness, pleasantness, intensity, masculinity, and familiarity. The results showed that only female but not male receivers could detect the level of cooperativeness of the donors since they were able to choose the high-cooperative potential partners. The hedonic qualities of the odor stimuli were found to be unrelated to the level of cooperativeness of the donors, indicating that the perception of cooperativeness might happen on an unconscious level.

4. Extrinsic factors

4.1. Diseases

Various infectious and metabolic diseases are known to affect body odor, making it a powerful diagnostic tool [11,103,171]. In order to employ changes in body odors as diagnostic biomarkers, VOCs related to specific infectious and metabolic diseases have been identified [130, 143,171].

4.1.1. Infectious diseases

Cutaneous infections that affect skin odor include scarlet fever [78], typhoid fever, characterized by a baked-bread odor, tuberculosis, causing the odor of stale beer, and yellow fever, producing the odor of a butcher shop [130]. Fungating tumors can cause skin ulcers, and cutaneous wounds infected by bacteria that emit a characteristic foul, rotting smell, mainly caused by the compound dimethyl trisulphide [170]. Other infectious diseases with tell-tale odors that do not concern the skin directly are diphtheria, with a sweetish and putrid breath odor [183], cholera, an intestinal infection causing sweet-smelling feces [55], and bacterial vaginosis, accompanied by a characteristic odor of rotten fish caused by trimethylamine [203].

4.1.2. Metabolic disorders

Metabolic disorders cause the accumulation of metabolites due to enzyme deficiencies and abnormal chemical reactions. When such metabolites are odorous compounds, metabolic disorders produce distinctive odors. Isovaleric acidemia causes a smell from skin and sweat described as sweaty feet [198]. Phenylketonuria produces an accumulation of phenylacetate, found to be the cause of a musty, sweaty locker room towels-like odor [21]. In trimethylaminuria, known also as fish odor syndrome, the oxidation of trimethylamine is impaired causing the excretion of rotten fish smell from sweat, urine, breath, and reproductive fluids [114]. As hinted by the name, maple syrup urine disease is characterized by an odor similar to maple syrup or caramelized sugar in sweat, urine, and ear wax [21]. The deficiency of insulin typical of diabetes, causes an excess of ketones released in breath and urine with a sweet odor due to acetone [13].

4.1.3. Psychiatric disorders

Besides metabolic and infectious diseases, psychiatric disorders, especially schizophrenia, have also been associated with a ‘peculiar smell’ [176], whose biomarkers were first associated with (E)−3M2H, an idea later discarded [207], and are now still unclear [35,60,134].

4.1.4. Chemosignaling of sickness

Olsson et al. [126] investigated whether the body odor of people in a state of generalized sickness could be distinguished from a healthy state. Furthermore, to test if the chemosignaling happens at the early stage of the sickness for the receivers to avoid contamination, sweat samples were collected 4 h after the activation of the innate immune system via the injection of lipopolysaccharide (LPS). Receivers rated the sick body odors as significantly more unpleasant, intense, and unhealthy. Since the LPS treatment had a small effect on the health ratings, the authors argued that health was not directly perceived but rather inferred from the pleasantness of the odors. The decrease in perceived pleasantness was not related to the odor intensity, as confirmed by the GC–MS analysis of the samples showing that the overall amount of VOCs was lower in the LPS condition compared to the healthy one. In a follow-up study, Regenbogen et al. [146] found a main effect of odor in liking ratings of sick and healthy faces, such that regardless of the face condition, when paired with sick odor, they were liked significantly less than the control odor. Moreover, olfactory stimuli of sickness were found to increase the activation of the neural pathways related to odor processing.

These results were recently replicated by Sarolidou et al. [155], who further found that the disliking and avoidance behavior triggered by sickness cues were enhanced in people with a higher perceived vulnerability to disease and health anxiety. These findings taken together support the idea that an inflammatory response in the body causes a characteristic odor.

4.2. Diet

An experiment showing that dogs can discriminate between the body odors of monozygotic twins who followed different diets [73] is usually referred to as an indication that there is an effect of diet on human body odor.

Control protocols for sweat donors usually concern the avoidance of external factors that can influence their odor profile, namely the use of scented beauty products, smoking, intense physical exercise, and the consumption of certain odorous foods. As noted by Havlíček and Lenochova [70], the list of ‘forbidden’ foods is usually replicated in olfaction research with minor variations, but only a few studies have addressed which foods actually affect body odor. Meat consumption, for example, is usually not controlled for, but Havlíček and Lenochova [69] showed that consumption of red meat affects male body odor attractiveness. Using a within-subjects design, donors were randomly assigned to a meat or non-meat condition and then switched for the second round. Female receivers rated intensity, pleasantness, sexual attractiveness, and masculinity. Odors collected in the non-meat condition were judged significantly more pleasant, attractive, and less intense than the meat condition.

In a similar study, Fialová et al. [49] investigated the effect of garlic consumption on male body odor attractiveness. The rated attributes of pleasantness, attractiveness, masculinity, and intensity were not significantly different between the garlic and non-garlic condition when donors consumed the recommended daily dosage of garlic. However, with double the amount of garlic, the samples of body odor collected in the garlic condition were judged to be significantly more attractive and pleasant and less intense and masculine than the control condition. This unexpected increase in hedonic attributes was speculated to be due to the numerous health benefits of garlic, especially its antibacterial and antioxidant characteristics [49]. From an evolutionary viewpoint, the preference for body odors that signal healthy individuals could be explained by the sexual selection of healthy potential partners [48].

The ingestion of fenugreek seeds before delivery or during breastfeeding is responsible for a strong maple syrup-like body odor in newborns and infants [92,205], leading to a misdiagnosis of maple syrup urine disease. The aroma of fenugreek is mainly due to the volatile compound 4,5-dimethyl-3-hydroxy-2[5H]-furanone or sotolone, which was also found to be present in the urine of patients with maple syrup urine disease [137].

Understanding the effect of specific foods, however, does not tell the whole story of how daily eating habits affect body odor holistically. Zuniga et al. [211] investigated the hedonic effect of a diet rich in fruits and vegetables, the staples of a healthy diet, on male body odor. Participants were not restricted in their food choices during the sweat collection period but they were asked to report their dietary data next to a spectrophotometric analysis of their skin yellowness, regarded as an objective measurement of carotenoid levels and therefore of fruit and vegetable intake. Female receivers judged the health, attractiveness, intensity, and liking of the sweat samples. The hedonic evaluation of the samples was positively correlated with the level of skin yellowness, which was predicted by lower consumption of meat, and higher consumption of eggs, tofu, and vegetables. Contrary to the findings of Havlíček and Lenochova [69], Zuniga et al. [211] found that meat intake was associated with a more pleasant and less intense smell. This difference is likely ascribable to the different amounts of meat consumed in the two studies, indicating that a moderate meat intake can improve body odor while excessive consumption has the opposite effect. Zuniga et al. [211] also found that the consumption of fats and oils was related

to a more pleasant smell, likely due to the liposoluble property of carotenoids which increases their absorption, whereas carbohydrates and seafood produced odors judged as significantly less pleasant.

A different aspect of a healthy diet that can be inferred from body odor in animals [58,135], is adequate caloric intake. Fialová et al. [47], therefore, tested whether a state of complete caloric intake restriction would negatively affect the quality of human body odor as assessed by receivers of the opposite sex. Male receivers rated pleasantness, attractiveness, femininity, and intensity of female body odor samples collected during three different conditions, i.e., while following their usual diet, during 48 h of fasting, and after the restoration of caloric intake. No significant differences in the hedonic judgment of the sweat samples were found between the usual diet and the fasting conditions, whereas the odor samples from the eating restoration condition were rated significantly more pleasant and attractive and less intense than the other two conditions. This result was explained by the health benefits of short-term fasting, thus in line with the theory of the chemosignaling of an individual's health state.

4.3. Hygiene habits

Roberts et al. [149] dubbed people, especially the WEIRD ones (Western, educated, industrialized, rich, and democratic), the "deodorized apes", because of their painstaking attempts to erase their natural body odor and replace it with more socially acceptable artificial fragrances. As daily hygienic habits are directed to constantly trying to cover one's body odor, it is no surprise that control protocols for sweat donors are always concerned with forbidding the use of fragranced products, be it deodorant or laundry detergent.

The use of fragranced grooming products is known to boost confidence, both self-perceived and perceived by others. Higuchi et al. [76] found that the body language of females during an interview was judged as more self-confident and attractive when they were wearing perfume than when they were not. Roberts et al. [150] demonstrated similar results for men, whose self-confidence already increased 15 min after applying deodorant and kept growing for the following 48 h. A female panel asked to judge the non-verbal behavior of these men from videos, rated the men who used deodorant as significantly more attractive than those who were wearing a body spray lacking fragrance and antimicrobial properties. Note that in these two studies, raters were never exposed to the body odor of people wearing or not wearing fragrances, they were only judging their body language based on visual input. But if non-verbal behavior and self-perception are both influenced by masking one's natural body odor, what happens to chemosignaling? Dalton et al. [27] addressed the question of whether an unscented antiperspirant could block the stress chemosignal and induce a more positive social judgment. Indeed, receivers exposed to the treated stress sweat judged women presented in videos during a stressful situation as significantly more confident, trustworthy, and competent than when exposed to untreated stress sweat. Croijmans et al. [23] showed that the self-esteem and attractiveness of male contestants on a dating show were rated significantly higher by female receivers when they were exposed to sweat masked by a fragranced body spray compared to natural body odor, independent of the level of self-esteem of the donors.

Even though the use of fragrances can change the socio-communication of certain emotions and personality traits, fragrances are usually chosen purposely to suit and match one's natural body odor, such that when people apply a random fragrance assigned to them, their body odor is perceived less pleasant and less attractive than when they apply their favorite fragrance [99] and it can even be discriminated more accurately [5]. Sorokowska et al. [179] found that the use of scented products could mask the chemosignaling of neuroticism, but not dominance. This indicates that people tend to choose scented products that boost their desirable characteristics (i.e., dominance) and attenuate or even hide the undesirable ones (i.e., neuroticism). Allen et al. [4] investigated the effect of the application of people's own deodorant on perceived masculinity and femininity. They found that the effect was dependent on the sex of both the donor and the receiver. Female receivers rated the masculinity of men higher when a fragrance was applied, but not significantly more than in the natural body odor condition. In contrast, both male and female receivers rated female body odor as significantly more feminine in the fragranced condition. These results again indicate that fragranced products are designed to increase desirable properties, in this case, femininity in women, and keep low the not-so-desirable characteristics, since extreme masculinity in men may not be perceived positively [147].

Besides applying scented products, another widespread hygienic practice consists in shaving the axillary hair. The function of axillary hair has been proposed to be retention of the chemical compounds released from the apocrine glands [20], such that hair removal was found to eliminate axillary odor up to 24 h after shaving in men [168]. Similarly, Kohoutová et al. [91] found that the odor of shaved male underarms was more attractive and pleasant and less intense than unshaved ones from the same person. However, this effect was only temporary and it was dependent on whether the donor shaved his axillary hair regularly or had never shaved them. The positive hedonic effect of shaving the armpits for those who had never done it before was found to last only one week, whereas if the axillae were regularly shaved, the effect lasted up to six weeks.

4.4. Climate

Thermal stimuli like a hot environment and/or physical exercise and physical labor activate the thermoregulatory function of the eccrine sweat glands (see Sections 3.1 and 3.1.1). It is well known that during exposure to an environment with high or increasing temperatures, sweat production increases to allow heat loss via evaporation [9,53,63,124]. Moreover, Lenochova et al. [98], while studying the effect of freezing odor samples on their quality perception, observed that higher environmental temperature can increase the perceived intensity of body odors by changing the volatility of the odor molecules. Pressure and humidity are other climatic variables that can affect both body temperature (and therefore sweat production) [169] and smell sensitivity [94]. However, the effect of climate (e.g., humid, dry, or cold) and seasonal changes on body odor variations has been largely overlooked, aside from a brief mention of the difference in the number of thermally-activated eccrine glands in cold vs hot climates [66]. The only notable exception is a study aimed at identifying chemical compounds emanating from the arm skin [208]. The chemical analysis was conducted in China, both during a moist and warm spring and a dry and cold winter, to assess the effect of humidity and temperature on the chemical fingerprint of skin odor. A seasonal effect was found such that the amount of secreted VOCs changed between winter and spring.

Lam et al. [96] point out that while studies on odor production and perception are usually conducted on European and North American subjects, i.e., people living in a rather temperate climate, more attention should be paid to the Asian, especially the East Asian, population. While Asians might have a genetic predisposition to produce less odor compared to Caucasians and Africans (see Section 3.3), the hot and humid tropical climate in which they live can increase their sweat and (mal)odor production.

With anthropogenic climate change modifying the patterns of weather on a global scale, we suggest that future research should focus more on the impact of the extrinsic factor climate, keeping especially in mind how climate change is affecting and will affect body odor variations.

5. Discussion

In this paper, we provided a review of the intrinsic and extrinsic factors known in literature to affect body odor variations (Fig. 1). While the overview might suggest these factors act in isolation, in reality, they

interact which may complicate understanding their singular contributions. Ethnicity for example closely relates to culture, which includes also the typical diet of and climate in the area of residence, as well as different culturally approved hygiene habits. Shared extrinsic factors, like climate or diet, when living in the same area and eating together, have also been proposed as a possible explanation for the greater similarity in the chemical and perceptual profile of body odor between click friends compared to random dyads of people [145].

Genetic factors, like sex and ethnicity, make individual body odor, or at least part of it, unique and stable [148] enough to be used for biometric identification [26,80]. Curran et al. [26] distinguished three layers of the human scent profile: the *primary odor*, roughly corresponding to intrinsic factors reviewed here; the *secondary odor*, which includes extrinsic factors of diet and environment; and the *tertiary odor*, referring to hygiene habits, especially scents applied from outside the body, like soap and perfume. Of these three layers, Curran et al. [26] proposed that the primary odor is the one containing VOCs whose uniqueness and stability allow for individual identification. Chemical analysis of axillary sweat of different people showed that the ratio pattern of compounds varied significantly more between than within individuals, making the analysis of scent profile a valid method to identify people, for example in forensic applications [25,26].

Besides genetic factors, other intrinsic and extrinsic factors can affect variations in individual body odors, namely age, personality, emotions, diseases, climate, and dietary and hygiene habits.

Given the role that these factors can play in shaping individual body odors, their effect should always be taken into account when conducting chemosensory research. Some of the factors are usually accounted for in the control protocols to try to limit their influence. In these protocols, the attention is generally focused exclusively on extrinsic factors, i.e., diet, hygiene, absence of diseases, and lifestyle habits like smoking and exercise. Among the intrinsic factors, sex might be used to screen donors, since males are known to produce more sweat than females, while the other factors tend to be overlooked. Based on the evidence reviewed here, we suggest integrating the preparatory protocols already in place for sweat donors with a systematic assessment of the influencing factors. This could be, for example, implemented by administrating a questionnaire to sweat donors to measure their dietary and hygiene habits, their personality and emotional state at the moment of the experiment, the phase of the menstrual cycle for females, etc. This could be coupled with a food log or the use of fragranced products log to ensure the proper following of the preparatory protocol. Measuring the factors influencing individual variation of axillary odor presents further relevant implications for human chemosensory research. It would facilitate studies' comparison and replication, it would offer additional insights into the experimental data allowing to draw better-informed conclusions, and it could help improve the ecological validity of the studies.

Future research should further focus on the interaction among these factors since in daily life people do not adhere to control protocols and all the intrinsic and extrinsic factors can always be present together. For example, is there a factor whose valence or subconscious signal overcomes the others, or do they all contribute equally to the odor signature? Is the contribution context-dependent? This would increase the ecological validity of chemosignaling studies. A first step in this direction was taken by Gaby and Zayas [52], whose study on social judgment relied on receivers assessing the "diplomatic" odor, i.e., with no change of diet or hygienic habits, of senders sitting next to the receivers, instead of a t-shirt patch or cotton pad presented in a jar or via an olfactometer.

All the factors reviewed in this paper make up the information that can be transmitted between people during daily social interactions and are mostly perceived unconsciously. Olfactory perception in general, and chemosignaling in particular, usually take place implicitly, outside of awareness. In fact, people usually do not pay attention and do not actively perceive all the odorant molecules and odor objects contained in every inhale they take, unless these odorants deviate, positively or negatively, from routine and expectations enough to attract attention [84,93,173]. This is at the base of the "Misfit Theory of Spontaneous Conscious Odor Perception" (MITSCOP) formulated by Köster et al. [93], which states that "almost all odors are incidentally and unconsciously associated with the situation in which they occur and are stored as implicit expectations" and that "an incidentally learned odor will not be spontaneously perceived consciously if it fits our implicit expectations in the situation".

Emotional and behavioral responses to odors seem to not require or are even impacted by conscious perception and identification of the odor source [93,102]. Li et al. [102] found that human faces were judged less likable when people were exposed to a subthreshold unpleasant odor compared to a pleasant one, and when they were completely unaware of the presence of the odor. On the contrary, for people who could sense an odor even without being able to judge its valence, pleasantness did not affect the likeability ratings of the faces. Thus, conscious odor perception was demonstrated to remove the effect of unconscious information processing on social judgment.

The behavioral impact of odors as a function of the degree of consciousness is complex, and both unconscious as well as consciously perceived odors have an important function. What is interesting is the increased importance that conscious (self-) perception of axillary odor has gained over time, especially in Western industrialized society, with the "deodorized ape" [149] spending great efforts to get rid of the odor of axillary sweat. This is how cues can even clash: even a positive cue or signal, such as the emotion of happiness, can be embedded in and communicated via smelly sweat. We'd like to coin this phenomenon as the 'happy-stink paradox'. Therefore, future work is needed to systematically distinguish between factors that affect body odor in a conscious, perceivable way from chemosignals that cannot be consciously related to any qualitative or hedonic property of the odor but nonetheless trigger a subconscious behavioral, physiological, or cognitive response.

6. Conclusions

A large corpus of research has demonstrated the various factors driving body odor variation. Some of this research has focused on consciously detectable body odor, its sensory dimensions, and how they differ in relation to identifiable causal factors. Other research has focused on body odor's signaling function which is presumed to be unconscious, identifying variables that are causally related to eliciting different behavioral effects in perceivers, but without much clarification of potential sensory differences between these odors that could drive the different social behaviors. In general, most studies employ procedures for trying to source body odor with as few "contaminants" as possible via strict protocols controlling behavior, diet, and product use in sweat odor donors. Such practices, however understandable, may impede a more ecological and comprehensive understanding of body odor, and of the role of the various drivers identified here, as well as of their interactions on body odor differences. We suggest that future research should apply an integrative approach in which all these factors are assessed systematically instead of being dismissed, such that their individual and combined contribution can be better understood.

Declaration of Competing Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Appendix

Table A1

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Corrigendum to 'Intrinsic and extrinsic factors affecting axillary odor variation. A comprehensive review' Physiology & Behavior, Volume 270 (2023), 114307

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This article contains a few typographical errors that the authors would like to rectify here.

The authors regret to point out that during typesetting Table A1 was reoriented making it less readable and more difficult to understand. The Table is reported here with the correct orientation.

In addition, the authors would like to point out that in the caption of Fig. 2 ',olecules' should be 'molecules'.

On line 3 of section 4.4 Climate, the text should read 'see Sections 2.1 and 2.1.1' instead of 'see Sections 3.1 and 3.1.1'.

The authors would like to apologise for any inconvenience caused.

Table 1
Summary of the factors reviewed in the paper and the corresponding studies.

Reference ***Sex and hormones***	**Cue**	**Hedonic property**	**VOCs**
Russell [153]	Own smell; male		
Hold & Schleidt [77] [162] [163]	Own vs partner; male vs female	Pleasantness	
Doty et al. [38]	Male vs female	Intensity, pleasantness	
Lindqvist [105]	Male vs female		
Mutic et al. [119]		Masculinity-femininity; pleasantness, intensity, familiarity	
Carrito et al. [16]		Attractiveness, sexiness, healthiness, familiarity, intensity,	

(*continued on next column*)

Table 1 (*continued*)

Reference ***Sex and hormones***	**Cue**	**Hedonic property**	**VOCs**
		pleasantness, masculinity, dominance, arousal	
Penn et al. [131]			Ketone, 6-phenylundecane, pentadecanoic acid, hexadecanoic acid, methylhexadecanoic acid, heptadecanoic acid, dialkyl ether, nonadecane, isopropyl hexadecanoate, 2-ethyl-hexyl-4-methoxy- cinnamate, docosane, 1-octyl-4methoxycinnamate
Troccaz et al. [193]		Sweat odor intensity, sulfur odor intensity, acid odor intensity, odor unpleasantness	R)/(S)-3-hydroxy-3-methylhexanoic acid ((R)/(S)-3H3MH), (R)/(S)-3-methyl-3-sulfanylhexan-1-ol ((R)/(S)-MSH)
Thornhill & Gangestad [190]	Fertile phase of the menstrual cycle	Pleasantness, sexiness, intensity	
Singh & Bronstad [172]	Follicular and luteal phase of the menstrual cycle	Pleasantness, sexiness, intensity	
Kuukasjärvi et al. [95]	Use of contraceptive pill, day of menstrual cycle	Sexual attractiveness, intensity	

(*continued on next page*)

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Table 1 (*continued*)

Reference	Cue	Hedonic property	VOCs
Sex and hormones			
Havlíček et al. [67]	Menstrual, follicular, luteal phases of menstrual cycle	Intensity, pleasantness, sexual attractiveness, femininity	
Gildersleeve et al. [59]	High- and low-fertility phase of menstrual cycle; measurements of luteinizing hormone	Pleasantness, sexiness, intensity and physical attractiveness of the donor	
Lobmaier et al. [106]	Women's salivary oestradiol, progesterone, testosterone and cortisol levels	Attractiveness	
Vaglio et al. [196]	Pregnancy and lactation		1-dodecanol, 1-1′-oxybis octane, isocurcumenol, α-hexyl-cinnamic aldehyde, isopropyl myristate
Habel et al. [62]	Pregnancy and ovulation	Facial attractiveness, pregnancy categorization	
Age			
Haze et al. [72]			2- Nonenal, palmitoleic acid, vaccenic acid
Gallagher et al. [54]			Dimethylsulphone, benzothiazole, nonanal, hexyl salicylate, a-hexyl cinnamaldehyde
Mitro et al. [116]		Pleasantness, intensity	
Ethnicity			
Martin et al. [109]	ABCC11 genotypes		3M2H, HMHA, 3M3SH, 5a-androst-16-en-3-one, 5a-androst-16-en-3a-ol
Harker et al. [65]	ABCC11 genotypes	Malodor intensity	Sulfanylalkanols, 3M2H
Prokop-Prigge et al. [141]	ABCC11 genotypes		3M2H, 3M3H, 7- and 2-octenoic acid
Parma et al. [127]		Intensity, pleasantness, familiarity, arousal	
Emotional states			
Chen & Haviland-Jones [18]	Fear, happy		
Ackerl et al. [1]	Fear, neutral	Pleasantness, intensity	
Smeets et al. [174]	Fear, neutral, happy		Aldehydes/ketones, esters and cyclic molecules
Pause et al. [129], Prehn et al. [139]	Anxiety	Pleasantness, intensity, unpleasantness, familiarity	
Dalton et al. [27]	Stress	Pleasantness, intensity	
De Groot et al. [30; 31; 34]	Fear, disgust; fear, happy, neutral	Pleasantness, intensity	
Personality traits			
Sorokowska et al. [179; 180]	Big five, dominance	Intensity, attractiveness, pleasantness	
Sorokowska [178]	Neuroticism, extraversion, dominance	Attractiveness	
Adolph et al. [2]	Dominance, aggression	Intensity, pleasantness, unpleasantness, familiarity	
Croijmans et al. [23]	Self-esteem	Pleasantness, intensity, familiarity	
Tognetti et al. [191]	Cooperativeness	Intensity, masculinity, pleasantness, familiarity	
Diseases			
Honig et al. [78]	Scarlet fever	Foul odor	
Pavlou & Turner [130]	Yellow fever; typhoid; tuberculosis	Butcher shop; baked brown bread; stale beer	
Shirasu et al. [170]	Skin ulcers, fungating cancer wounds		Dimethyl trisulfide
Vockley & Ensenauer [198]	Isovaleric acidemia	Sweaty feet, dirty socks	Isovaleric acid
Cone [21]	Phenylketonuria; maple syrup urine disease	Musty, sweaty locker room towels-like odor; maple syrup	Phenylacetic acid; 3-hydroxy-4,5-dimethyl-2(5H)-furanone (sotolone)
Messenger et al. [114]	Trimethylaminuria	Rotten fish	Trimethylamine
Smith & Sines[176]; Di Natale et al. [35] ; Gordon et al. [60]	Schizophrenia	Peculiar odor	Trans-3-methyl-2-hexenoic acid
Olsson et al. [126]; Regenbogen et al. [146]	Generalized sickness	Intensity, pleasantness, health	
Diet			
Havlíček & Lenochova [69]	Red meat	Attractiveness, pleasantness, intensity	
Fialová et al. [49]	Garlic	Attractiveness, pleasantness, intensity	
Korman et al. [92], Yalçin et al. [205]	Fenugreek	Maple syrup	3-hydroxy-4,5-dimethyl- 2(5H)-furanone (sotolone)
Zuniga et al. [211]	Diet rich in fruit and vegetables	Liking, attractiveness, health, intensity	
Fialová et al. [47]	Caloric intake restriction	Pleasantness, attractiveness, femininity, intensity	
Hygiene habits			
Dalton et al. [27]	Unscented antiperspirant	Pleasantness, intensity	
Croijmans et al. [23]	Fragranced body spray	Pleasantness, intensity, familiarity	
Lenochová et al. [99]; Allen et al. [5]	Own vs assigned perfume	Pleasantness, intensity, attractiveness	
Kohoutová et al. [91]	Shaving axillary hair	Pleasantness, intensity, attractiveness	
Climate			
Zhang et al. [208]	Moist and warm spring, dry and cold winter		Nonanal, Diphenyl ether, 3,7-Dimethyl-6-octanol,2-Ethyl hexanol, Eicosane, Tridecane, Octanal, Decanal, Isobornyl propionate, 3, 7-Dimethyl-2, 6-octandiol

(*continued on next column*)