On the Communicative Function of Body Odors: A Theoretical Integration and Review

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Abstract

Humans use multiple senses to navigate the social world, and the sense of smell is arguably the most underestimated one. An intriguing aspect of the sense of smell is its social communicative function. Research has shown that human odors convey information about a range of states (e.g., emotions, sickness) and traits (e.g., individuality, gender). Yet, what underlies the communicability of these states and traits via smell? We fill this explanatory gap with a framework that highlights the dynamic and flexible aspects of human olfactory communication. In particular, we explain how chemical profiles, associative learning (i.e., the systematic co-occurrence of chemical profiles with state- or trait-related information), and top-down contextual influences could interact to shape human odor perception. Our model not only helps to integrate past research on human olfactory communication but it also opens new avenues for future research on this fascinating, yet to date poorly understood, field.

Keywords

olfaction, communication, pheromones, associative learning, context

> I believe that odors have an altogether peculiar force, in affecting us through association—a force differing essentially from . . . the touch, the taste, the sight, or the hearing. (Poe, 1902/2009, p. 232)

This elegant early regard for the sense of smell as quoted in the epigraph stands in stark contrast to the relative scientific neglect and underestimation of a sense that fulfills a range of important functions in humans. Among these functions, the relatively well-known ones include avoiding environmental hazards and determining whether something is edible (Stevenson, 2010). A less well-recognized function of olfaction, however, is one that makes the sense of smell psychologically interesting—namely, its role in picking up social information from other humans. The range of social information conveyed this way is remarkably varied. Research has shown that body odors contain information ranging from relatively enduring characteristics, such as gender (Penn et al., 2007) and age (Mitro, Gordon, Olsson, & Lundström, 2012), to dynamic emotional states (e.g., de Groot, Smeets, Kaldewaij, Duijndam,

& Semin, 2012; Mujica-Parodi et al., 2009; Prehn, Ohrt, Sojka, Ferstl, & Pause, 2006; Zhou & Chen, 2009). Even though some of the characteristics that are communicable through human odors are known, what has remained unclear in the midst of the expanding literature is how a person is likely to receive social information from smell—an issue that is addressed here.

Answering the "how" question includes a discussion of whether human olfactory communication relies primarily on prewired mechanisms, learned associations, or a combination of these. More often than not, human olfactory communication has been explained in terms of a feature selected for by evolution (e.g., Gangestad & Thornhill, 1998; Pause, 2012; Schaal & Al Aïn, 2014; Weller, 1998). In this integrative review, we start by describing possible evolutionary pressures on human

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olfaction, only to balance the scale by supplementing this evolutionary viewpoint with a learning perspective—a framework that has already gained solid ground in the context of regular (nonhuman) odors (e.g., Herz, 2005; D. A. Wilson & Stevenson, 2006). Our aim is to place communication via smell in a broader context, to provide conceptual clarity, and to advance an integrative model from which human olfactory communication can be understood.

The Sense of Smell

Olfaction is a relatively poorly understood sense; yet, its plastic, implicit, and emotional nature furnishes psychological researchers with a fertile research soil. For one, odors have a known and proven strong associative nature (Herz, Beland, & Hellerstein, 2004). What is unique among the senses is that odor-related associations are extremely durable (e.g., Delaunay-El Allam, Soussignan, Patris, Marlier, & Schaal, 2010; Herz & Engen, 1996; Saive, Royet, & Plailly, 2015), making it appear as if "smells detonate softly in our memory like poignant land mines hidden under the weedy mass of years" (Ackerman, 1990, p. 5). Typically, odor-related associations are thought to be idiosyncratic (e.g., the perfume of a grandparent taking you back decades), but associations can also be consensual (e.g., religious individuals linking incense to a sensed presence). In such cases, odor-related associations are often implicit, providing people with a "rich unconscious background" (Sacks, 1985, p. 159); furthermore, certain smells can even motivate behavior outside of awareness (Holland, Hendriks, & Aarts, 2005). Because odors are primarily processed in limbic brain regions (Gottfried, 2006), odor-related associations can also be highly emotional (Chrea et al., 2009; Herz & Schooler, 2002), earning olfaction its label as the most emotional sense (see Ehrlichman & Bastone, 1992).

Compared with vision and hearing, however, olfaction has a long history of being underestimated. Smell lacks in finesse and discernment according to Aristotle, an idea that was maintained by later philosophers including Descartes, Kant, and Schopenhauer, who saw olfaction as vulgar, coarse, and inferior (see Le Guérer, 2002). Even though Nietzsche (1908/1967) appreciated the instinctual and veracious "animal" nature of the sense of smell, Freud (1930/1962) asked for repressing the uncivilized sensations evoked by a sense lacking abstraction, and he hypothesized that "the diminution of the olfactory stimuli seems . . . a consequence of man's raising himself from the ground" (p. 53). Whereas millions of years ago humans indeed faced a decline in the number of genes coding for odorant[1] receptors when they took their noses off the smell-rich ground (Rouquier, Blancher, & Giorgi, 2000), this decline is not related to a reduced sensory

capacity (e.g., Laska, Seibt, & Weber, 2000; for a review, see Shepherd, 2004).[2] The grounds by which the sense of smell has been depreciated in the Western world may lay in cultural causes. Whereas Western individuals have difficulties naming smells (Lorig, 1999; Olofsson & Gottfried, 2015a), the Jahai people in Malaysia, for whom smells are an everyday life necessity (Majid & Burenhult, 2014), can code smells in more abstract terms, and they name odors as easily as colors (Majid & Burenhult, 2014). Hence, the difficulty to name and think abstractly about smells, an apparent cause of its underappreciation in the Western world, seems a cultural rather than biological deficiency.

Strikingly, humans were estimated to be capable of discriminating more than a trillion odors, numbers that go well beyond people's ability to discriminate colors (2.3–7.5 million) and tones (~340,000; Bushdid, Magnasco, Vosshall, & Keller, 2014). Recently, doubt has been cast on the correctness of this estimation (Gerkin & Castro, 2015; Meister, 2015; for a reply, see Magnasco, Keller, & Vosshall, 2015); however, there are still other sources of evidence supporting the excellence of human smell abilities. In general, humans are remarkably good at detecting certain odorants at concentrations as low as three droplets in an Olympic-size swimming pool (Whisman, Goetzinger, Cotton, & Brinkman, 1978; also see Yeshurun & Sobel, 2010). Furthermore, humans share a skill with "supersmellers" such as rats and dogs—namely, that of tracking a scent through a field (J. Porter et al., 2007). In sum, in contrast to traditional views, the human sense of smell is per se not inferior to that of other species.

With supersmelling mammals such as rats, humans not only share a smell ability but also a common ancestor (O'Leary et al., 2013). The sense of smell forms a window to people's shared evolutionary past because brain regions devoted to odor processing are among the oldest brain structures to have developed in mammals (Pause, 2012). Because mammalian evolution was characterized by a rapid expansion of smell-related brain regions (Rowe, Macrini, & Luo, 2011), early mammals seemingly relied primarily on olfaction to determine what to approach and avoid, such as food and predators.

Further down the line of mammalian evolution, an important distinction with regard to the functionality of the sense of smell can be associated with whether the species is generalist or specialist (Herz, 2006; Rozin, 1976)—this dichotomous classification can ostensibly take integrated forms in different species depending on which functional domains (e.g., food intake, predator avoidance) are concerned. Generalists live in different environments, encounter different threats, and have access to a high (and dynamic) variety of food sources. Species that are predominantly specialist would profit more from a larger set of hardwired responses to

odorants than typical generalists such as humans (Herz, 2006; Köster, 2002; Rozin, 1976), whose survival chances have arguably increased by putting a somewhat larger emphasis on learning what odorants signify in terms of, for example, nutrition or danger.

In humans, odor learning is supported by data showing the early development of odor preferences and cross-cultural differences. Even before birth, the sense of smell is functional. Infants who are born prematurely (around 28–37 weeks of gestation) can detect (Sarnat, 1978) and discriminate (e.g., Marlier, Schaal, Gaugler, & Messer, 2001; Pihet, Schaal, Bullinger, & Mellier, 1996) odorants, as was indicated by their olfactory reflexes (e.g., sucking, arousal–withdrawal behavior, respiratory and facial responses; see Schaal, 2015). Odor preferences of newborns could have developed before birth because the mother's diet (e.g., garlic) was shown to "flavor" the sensory environment of the fetus (Mennella, Johnson, & Beauchamp, 1995). Indeed, compared with nonexposed neonates, babies of mothers who consumed alcohol, carrot juice, or anise during pregnancy responded more favorably to the respective substances (Faas, Spontón, Moya, & Molina, 2000; Mennella, Jagnow, & Beauchamp, 2001; Schaal, Marlier, & Soussignan, 2000). Neonates, prior to being breast- or bottle-fed, showed smiles to banana and vanillin odor, and they displayed disgust to shrimp and rotten egg odor (Steiner, 1974, 1979; cf. Soussignan, Schaal, Marlier, & Jiang, 1997, who noted an early predisposition to affectively process olfactory stimuli, albeit at a smaller scale than adults); however, these "innate" responses may already have been (partly) based on prenatal learning.

After birth, odor preferences are shaped by the culture or region in which a person is raised. In general, the more geographically close two individuals are, the more their odor preferences overlap (Chrea et al., 2004; Pangborn, Guinard, & Davis, 1988; Seo et al., 2011). Culture-specific experiences with foods or drinks enhance the pleasantness of the concomitant odor (Ayabe-Kanamura et al., 1998). Whereas Japanese individuals can tolerate the smell of dried fish and fermented soybeans, Western individuals find the smell of these unfamiliar products significantly more unpleasant, associating them with excrement and decay (Ayabe-Kanamura et al., 1998). Furthermore, cultural norms of body odor suppression arguably lower the pleasantness ratings of body odor in Japanese individuals compared with European individuals (Schleidt, Hold, & Attili, 1981). Obviously, there may also be cross-cultural or cross-regional similarities in the hedonic evaluation of everyday odors, which could in part be explained by these individuals experiencing the same odor (e.g., banana) in similar situations (e.g., a consumption setting) and eliciting a similar feeling (e.g., pleasant) and taste (e.g., sweet).

Indeed, associating odors with a basic taste (e.g., sweet) is one way in which odor preferences can be acquired (Stevenson, Prescott, & Boakes, 1995). In contrast to smells (e.g., Engen, 1988; but cf. Khan et al., 2007), people's liking for basic tastes is hardwired (Bartoshuk, 1989; Yarmolinsky, Zuker, & Ryba, 2009). Research has shown that odors paired with a hardwired sweet (vs. sour) taste were perceived as sweeter (vs. more sour; Stevenson et al., 1995). Sweet and fruity smells are generally agreed on as being highly pleasant, whereas the reverse is true for sour smells (Khan et al., 2007); yet, many acquired (e.g., culturally driven) preferences for sour taste exist (e.g., Japanese individuals and sour pickles). Odor preferences may not only emerge from pairings with taste but also through couplings with, for instance, (affect-laden) visual or tactile sensations (Baeyens, Wrzesniewski, De Houwer, & Eelen, 1996) and mere exposure (Balogh & Porter, 1986). Combined with genetic variations in odorant receptors (Keller, Zhuang, Chi, Vosshall, & Matsunami, 2007), various learning mechanisms can drive the development of odor preferences even before birth, with cultural factors further shaping these preferences. What has remained unclear is whether learning plays a similar role for odors that are psychologically relevant—namely, body odors.

Social Communication

The class of odors forming the main subject of the current contribution, body odors, can be set apart from most everyday odors by their capacity to simultaneously convey multiple social "messages." Notably, artificial odors such as perfumes can also contain social information; compared with a nonmeaningful perfume, the scent— but not image—of a personally meaningful perfume-induced activity in the amygdala–hippocampal region (Herz, 2011) can be associated with the retrieval of odor-related autobiographical memory (Masaoka, Sugiyama, Katayama, Kashiwagi, & Homma, 2012). Perfumes received scant attention and have not been used as a control condition in studies focused on body odors, which had long been considered as a communicative medium (McClintock, 1971). Nevertheless, neuroimaging studies have complemented numerous behavioral studies (e.g., de Groot et al., 2012; Prehn et al., 2006; Zhou & Chen, 2009) by revealing that body odors (vs. various control conditions) recruited social information processing regions (Lundström, Boyle, Zatorre, & Jones-Gotman, 2008), including the fusiform face area (Prehn-Kristensen et al., 2009) and a part of the mirror neuron system (inferior frontal gyrus; Lübke et al., 2014). Because the mirror neuron system is involved in achieving similarity of perspectives between a sender and a receiver, human odors can be effective as a medium for interpersonal

communication (e.g., Pause, 2012; Semin & de Groot, 2013). Achieving a common basis is an indispensable requirement for successful communication (Semin, 2007).

Admittedly, chemical communication is not as fast as visual or auditory communication. Before reaching a recipient's nose, odorants need to be produced, be released, and travel through the air (Wyatt, 2003). Yet, humans are among the most odoriferous of primates (Stoddart, 1990), and olfactory communication has certain unique advantages, with odorants being carried over long distances, crossing certain barriers, and signaling information even when the signaler has left (Wyatt, 2003). What has remained unclear is how an odorant recipient is capable of synchronizing perspectives with a sender on the basis of just chemicals. To this end, we advance a framework that is an attempt to capture the nature of this receiver capacity. First, we discuss different formal representations of the concept of pheromones[3] typically associated with olfactory communication and how these conceptualizations affect the search for human pheromones (cf. McClintock, 2000).

The Pheromone Problem

The term "pheromone" may invite thinking about a prewired one-to-one relationship between what a sender communicates and how a receiver responds. However, odorants emanating from the human body were argued not to be "keys" that "unlock" preprogrammed behavior (Doty, 2010). According to the original definition, *pheromones* are "substances . . . secreted to the outside by an individual and received by a second individual of the same species, in which they release a specific reaction" (Karlson & Lüscher, 1959, p. 55). This extremely flexible insect-based definition cannot be considered suitable for humans because it remains tacit about (a) what qualifies as a "substance" and whether pheromonal communication may be affected by (b) the context and (c) learning. These problems were realized early on, and multiple attempts were aimed at redefining the pheromone concept (e.g., Beauchamp, Doty, Moulton, & Mugford, 1976; Doty, 2010; Wyatt, 2014, 2015).

First, pheromones were initially redefined as consisting of one or, at most, a few odorant molecules (Beauchamp et al., 1976). However, this definition was broadened later to include multi-odorant pheromones (Wyatt, 2014). In fact, most animals, including various cockroach species and moths, communicate via multi-odorant pheromones (Wyatt, 2014). Even though we know that humans, like other mammals (e.g., Doty, 2010; Logan, 2015; Wyatt, 2015), produce hundreds of odorant molecules (e.g., Curran, Rabin, Prada, & Furton, 2005; Gallagher et al., 2008; Zeng, Leyden, Spielman, & Preti, 1996), what has remained unknown is whether a person responds to all, or many, odorant molecules or just to a small subset of odorant molecules. On the basis of pheromones that have been identified for other animals, we presume that if a human pheromone is identified, this pheromone is most likely a combination of multiple molecules.

Second, more recent pheromone definitions leave room for a potential contextual mediation of pheromone effects (Wyatt, 2014, 2015). A typical problem with the identification of human pheromones is high interindividual variability in odorant responding (Hudson & Distel, 2002; Köster, 2002) and certain failures to find predicted effects (e.g., Schank, 2006; H. C. Wilson, Kiefhaber, & Gravel, 1991; Yang & Schank, 2006; Ziomkiewicz, 2006).[4] Notably, even insect pheromonal communication was shown to be affected by contextual factors (e.g., Barrozo, Gadenne, & Anton, 2010), and at least one contextual factor (i.e., experimenter gender) has been revealed to affect human olfactory communication (Jacob, Hayreh, & McClintock, 2001). Experimenter gender is just one of the many (subtle) contextual factors that could affect human olfactory communication, and such contextual factors matter not only when a previously stored association is retrieved (decoding) but also when chemical components are "acquired" as a signature (encoding). The likelihood of finding systematic responses to human odorants is increased when researchers take note of the different contextual factors that could affect or have affected human olfactory communication at encoding and decoding stages.

A notable third aspect of modified pheromone definitions is that a large degree of genetic programming (e.g., Beauchamp et al., 1976; Doty, 2010) and at most little learning (e.g., Wyatt, 2014, p. 14) should be involved. Because even insects were shown to adjust their innate pheromonal mating strategies on the basis of experience (Keleman et al., 2012), it seems rather unlikely that complex mammals show innate responses to human odorants (cf. Doty, 2010). A potential exception may be the recent discovery of a breast odor that elicits invariant nipple search and sucking behavior in newborns (Schaal & Al Aïn, 2014).[5] Excluding this case, most responses to human odorants can arguably be explained by some form of learning (as detailed later). What is currently unknown is how much learning is involved in human olfactory communication and whether the quantity of learning exceeds the "little requirement for learning" definition as was stated for pheromones (cf. Wyatt, 2014, p. 14).

Even though the absence of learning was called the minimal condition of *innateness* (Samuels, 2002), many behaviors that seem innate are in fact only executed when certain developmental or environmental conditions are met (Mameli & Bateson, 2011). The problem of having to classify human pheromones on the basis of their

innateness can be sidestepped by defining pheromones as substances having a *species-wide effect* (Wyatt, 2014). Pheromones are contrasted to signature mixtures—namely, substances with informative properties (a) that may not be shared by all individuals and (b) that may be based on a different set of odorants for different individuals (Wyatt, 2014). What has remained unknown is whether the occasional systematicities in the way in which humans respond to each other's odorants (reviewed later) fit with the definition of a pheromone. We explore this possibility by highlighting the human capacity to develop shared associations with certain odorants. The framework furnished here is a way of explaining why consensual and experience-based responses to human odorants may appear innate.

Theoretical Integration: A Novel Framework

The search for human pheromones is complicated by human odorants being a rich information source. Like the features of a person's face, the odorant molecules identified as body odor can simultaneously convey multiple messages, with some messages resulting from more enduring properties than others. Enduring traits (e.g., gender, individuality) expectedly form the stable base of the perceived body odor, whereas dynamic elements (e.g., emotion, sickness) have the potential of being superimposed on this base profile.

Receivers can arguably detect these enduring traits and dynamic states in the body odor "Gestalt" stimulus because (a) distinctive *chemical profiles* (i.e., a set of odorant molecules in a fixed ratio) (b) have consistently and reliably been experienced together with state- or trait-related information embedded in the larger context, such that a systematic association was forged between the chemical profile on the one hand and state- or trait-related contextual information on the other hand. This learning hypothesis may explain why multiple individuals can show remarkably similar responses to odorants emanating from the human body. The actual attended-to message may be selected on the basis of the presence of a learned association, a recipient's internal state, or the context at hand.

In the next section, we develop this perspective in greater detail. An analytic distinction is made between the chemical stimulus (message) and what a receiver perceives. In passing, each of the previously mentioned problems regarding human pheromone communication (i.e., multicomponentiality of the stimulus, learning, and the context) is addressed with a view to opening new avenues for future research. The main focus is on factors influencing the odor experience of a receiver; yet, we start with the part where communication begins—namely, with the sender.

A tripartite model

The constant component: Chemical profiles consistent to a category. The perception of human body odor is based on a complex and dynamic stimulus that consists of multiple odorants in different concentrations. If reactions to these multicomponential social stimuli are learned, then certain *statistical regularities* must exist, such that a reliable association can be formed among one, a few, or multiple odorants (chemical profile) and co-occurring circumstances. Our first thesis is that a range of dynamic states and (relatively) enduring traits as part of these circumstances can be associated with chemical profiles that are sufficiently unique for these states and traits (e.g., gender is distinguishable with 75% accuracy on the basis of a specific set of odorant molecules; Penn et al., 2007). What also follows from this view is that any state or trait leading to a sufficiently distinctive chemical profile has the potential of being successfully chemically communicated in a relevant context.

The properties that are unique for chemical profiles are what we call *nonaccidental properties*, a term borrowed from visual object recognition theory (Kosslyn, 1994; Lowe, 1987a, 1987b). In vision research, nonaccidental properties refer to key elements of the object that remain constant to a category, despite certain variations in the stimulus. A chair, for instance, may be recognized by its seating and backrest; these elements are central to the chair concept, even though they may differ somewhat from chair to chair.

Whereas visual objects such as chairs can easily be identified and named, the power of olfaction was argued not to lie in explicit naming but in discrimination (Köster, 2002). Hence, we may fail to see slight differences in the chair's armrests, whereas two almost identical odorants can easily be discriminated (Pike, Enns, & Hornung, 1988). This discriminatory capacity may facilitate the implicit recognition, but not explicit identification, of the different chemical profiles "hidden" in the Gestalt stimulus.

The discriminative potency of olfaction, the likelihood of nonaccidental properties, and the highly associative nature of the sense of smell culminate in our second thesis, which is about odor learning. The idea of odor learning has been well-established in the field of common (nonhuman) odor perception (e.g., Engen, 1988; Hermans & Baeyens, 2002; Herz, 2005; Stevenson et al., 1995; D. A. Wilson & Stevenson, 2006), and we argue that learning theories can also be applied to human olfactory communication.

Odor learning. Because certain odorants produced by the human body (e.g., during a state of fear) may be emitted distinctively and repeatedly in similar (i.e., fear-inducing) contexts, this regularity can forge an association between the distinctive chemical pattern (i.e., related to fear) and the generic (i.e., fear-inducing) features of

the comparable situations. Multiple individuals can experientially extract the chemical profile of fear and associate it with fear-related information, and these potentially socially shared associations do not need conscious awareness to be formed (cf. Degel, Piper, & Köster, 2001).

Both anecdotal and empirical evidence support the human capacity to associate odorants with information if the connection is credible (Todrank, Byrnes, Wrzesniewski, & Rozin, 1995). For instance, posters tried to warn Japanese citizens in World War II about phosgene bombs by pointing to their hay-like smell (Stevenson, 2010). Initially neutral odors can be disliked quickly when paired with a negative verbal label (Herz & von Clef, 2001), when associated with adverse physiological effects (Van den Bergh et al., 1999), or when humans were led to believe that the odor is noxious (Dalton, 1996). Even two initially indistinguishable odorants could become discriminable through aversive learning (Li, Howard, Parrish, & Gottfried, 2008). These are but a few specific examples of odor learning related to negative outcomes, but implicit learning also extends to positive outcomes (e.g., Degel et al., 2001). Examples such as these have been captured in broader theories of odor learning (Hermans & Baeyens, 2002; Stevenson & Boakes, 2003; D. A. Wilson & Stevenson, 2006).

One of these theories, odor object theory (D. A. Wilson & Stevenson, 2006), has already gained considerable traction outside the field of human olfactory communication. What this theory posits is that complex odorant mixtures (e.g., coffee) can be stored in memory as "objects" or templates (D. A. Wilson & Stevenson, 2006). A stable, background-detached odor representation of a complex mixture such as coffee arises from feature extraction and object synthesis (D. A. Wilson & Stevenson, 2006). Like vision, olfactory perception is synthetic, which means that odorant mixtures are treated as a unitary object rather than an analytical combination of the individual elements[6] (e.g., Gottfried, 2010; Stevenson & Wilson, 2007; Weiss et al., 2012; D. A. Wilson, 2009). The presence of synthetic (holistic) odor objects is supported by performance data showing the difficulty humans have detecting more than a few unique odorants in a multi-odorant mixture (e.g., Livermore & Laing, 1998) and by neuroimaging data (e.g., Gottfried, 2010; Olofsson & Gottfried, 2015a; cf. Majid, 2015; for an integrated perspective, see Olofsson & Gottfried, 2015b).

By the same token, the multi-odorant stimulus produced by the body may be encoded as a single body odor object. The Gestalt stimulus expectedly consists of several individual analytical elements, such as chemical profiles representing different dynamic states or enduring traits. These individual chemical profiles may be "selected" during a decoding phase with the help of top-down contextual information.

The dynamic component: Contextual influences. Each of the previously stored chemical profiles may be activated on the basis of top-down processes that are initiated by the context. For instance, a given situation (e.g., smoke coming out of the toaster during breakfast) limits the number of likely correlated events (i.e., the toast is on fire). In a similar vein, access to visual cues or verbal labels (e.g., body odor vs. cheddar cheese) constrains expectations about the odorant that is most likely to be encountered in a mixture (De Araujo, Rolls, Velazco, Margot, & Cayeux, 2005), and this predictive feedback helps to refine the initially holistic representation of the odor object (Olofsson & Gottfried, 2015a). Not only did contextual information drive odor perception but a person's internal state (e.g., hunger, satiety) was also shown to influence the perceived pleasantness of a multicomponent stimulus (i.e., peanut butter; Howard & Gottfried, 2014; for a similar perspective, see Yeshurun & Sobel, 2010). Hence, dynamic situational factors—such as the context at hand (e.g., the experimental environment), a person's internal states (e.g., hunger, emotions, hormone levels), traits (e.g., gender, personality), and cognitions (e.g., verbal instructions pointing to the source of the odor, people's awareness about being influenced by an odor)—affect olfactory processing at the level of *decoding*; yet, many of these features may also have contributed to shaping olfactory representations during *encoding*. Indeed, situations form an integral part of the perceptual experience of a person (Yeh & Barsalou, 2006); predicting how a situation will unfold is essential for human survival because it prepares individuals for adequate goal-directed action and feelings without the necessity of conscious awareness (e.g., Barsalou, 2005a, 2005b). A full match between the situation (i.e., the broader context, a person's level of awareness, traits, and internal states) during encoding and decoding allows for observing "situated" odor-based behavior that may go unnoticed when odorants are presented in novel or irrelevant settings.

Recapitulation

On the basis of three main elements—multicomponentiality, associative learning, and contextual influences—we have advanced a broad and dynamic framework from which human odor perception may be understood. First, body odor is a stimulus consisting of several chemical profiles that are more or less uniquely relatable to certain states (e.g., emotions) and traits (e.g., individuality; see Figure 1). That is, these chemical profiles have nonaccidental properties, such that one odorant or a set of them could gain informative and predictive value through their frequent and reliable coupling to state- or trait-related situational information, and templates of these chemical profiles may be stored (learned). Because of the synthetic
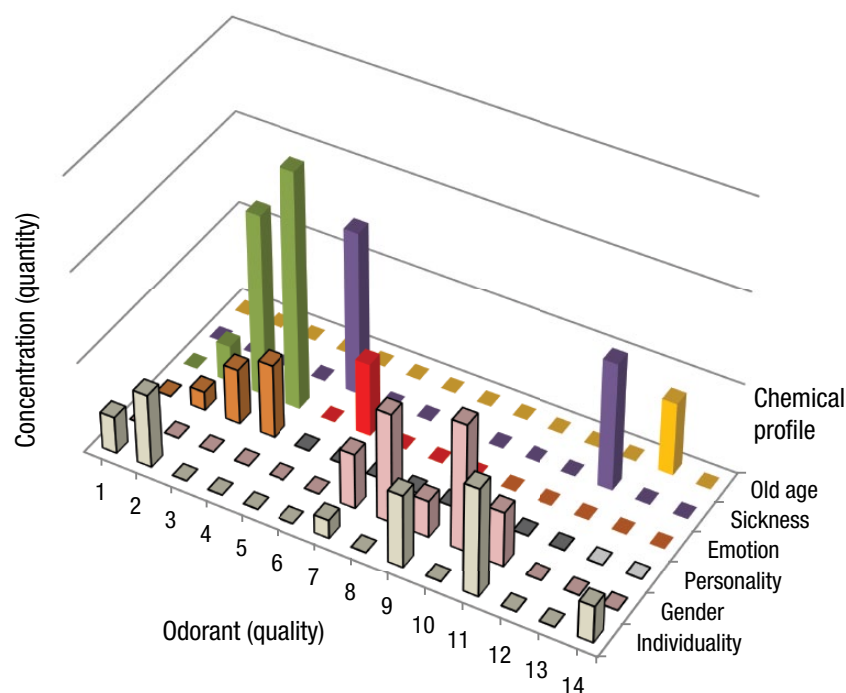
Fig. 1. Schematic representation of the multi-odorant Gestalt stimulus perceived as body odor. Fictitious concentrations (quantities) of odorants (qualities) forming distinguishable chemical profiles are depicted that can become indicative of certain states and traits (for a conceptually similar figure, cf. Schaal, 2008; Wyatt, 2010, 2014). Individuality, gender, and personality are the more stable, enduring traits (black outline) on which the dynamic factors emotion, sickness, and old age may be superimposed (no outline). Some chemical profiles (e.g., gender, emotions) may be further subdivided into subprofiles (e.g., male–female; fear–happiness). A certain overlap within and across chemical profiles may exist, given that there are sufficient defining features for any state or trait (i.e., nonaccidental properties). Top-down factors (e.g., a person's internal state, context) may highlight a chemical (sub) profile (e.g., fear) that is nested in the multicomponential Gestalt stimulus.

and coarse aspects of odor perception, however, it may be difficult to detect one of the several unique chemical profiles in a Gestalt stimulus. To hone in on the best matching template in any given situation, people may profit from the added specificity of top-down information sources (e.g., contextual information, their internal state). It is this two-way and iterative process that makes body odor perception dynamic and situated.

Communication via Body Odor: A Review of the Evidence

Although the role of learning in human olfactory communication still must be elucidated, what is known is that *systematicities* exist in the responses of a receiver to particular odorants produced by a sender. The current state of affairs regarding these systematicities is reviewed from the perspective of the novel framework proposed here. Thus, in the current review, we complement existing reviews on the social communicative function of human odors (Doty, 2010; Pause, 2012; Schaal & Porter, 1991;

Stevenson, 2010; Stoddart, 1990; Wysocki & Preti, 2004) by focusing on the interaction among odor learning, the role of context, and the potential compounds responsible for driving these remarkably systematic effects.

Communicability of enduring characteristics

Before highlighting research that gained increasing attention over the last decade—namely, chemical communication of dynamic emotional states—we report evidence for the nonaccidental properties, and thus communicability, of enduring features—namely, individuality, gender, and age.[7]

A unique "odorprint." The smell of individuality is strongly determined by genotype. Dynamic elements such as diet and hygiene are known to influence body odor (Havlíček & Roberts, 2009); yet, genotype is what contributes to unique and stable odorprints, enabling people to discriminate among individuals (Penn et al.,

2007), kin and non-kin, and—potentially—good versus bad mates.

Research has shown that genetic factors contribute to relatively stable chemical profiles that can be observed for the same individual over different days (Kuhn & Natsch, 2009). The odorants emitted in the armpit region by monozygotic twins are almost identical (Kuhn & Natsch, 2009); when these twins followed the same diet, even highly trained tracking dogs could not discriminate their scent (Hepper, 1988). Hence, environmental factors including food intake and hygiene further shape the genotype-mediated composition and, therefore, identity of body odor.

The relative stability of individual odorant profiles facilitates the speed and ease of odor identity learning. Among the most frequently encountered odorant profiles are those of kin, especially early in life. Within the well-researched field of odor-based kin recognition, the relation between mother and child has most frequently been examined (R. H. Porter, 1998). Strikingly, mothers (90%) needed only 10–60 min of postpartum contact to correctly identify the scent of their own baby versus other neonates (Kaitz, Good, Rokem, & Eidelman, 1987; also see R. H. Porter, Cernoch, & McLaughlin, 1983). Newborns orient to and prefer their own mother's armpit odor over that of other mothers (Cernoch & Porter, 1985) but only if close contact with the mother's skin was achieved through breastfeeding (vs. bottle feeding).

Odor preferences of newborns are shaped even before birth because neonates have been shown to be attracted to the scent of their own (vs. another newborn's) amniotic fluid (e.g., Schaal, Marlier, & Soussignan, 1995). Prenatal experience may also explain why newborns show odor-induced suckling behavior that seems innately tuned to breast odor (e.g., Logan et al., 2012; R. H. Porter & Winberg, 1999; Schaal, 2005; Varendi & Porter, 2001; cf. Schaal & Al Aïn, 2014).

Robust evidence (see, e.g., Cernoch & Porter, 1985; Schaal, Marlier, & Soussignan, 1998) supports the neonatal capacity to recognize and like the chemical signature of their mother but not father. Newborns learn their mother's signature early (i.e., before or shortly after birth), and odor associations are long lasting (Delaunay-El Allam et al., 2010). The importance of neonatal olfactory learning has been suggested to lie primarily in promoting adequate feeding behavior (e.g., Schmidt & Beauchamp, 1992)—a function also observed in other mammals (Schaal et al., 2009).

Genetic factors related to the production of species-specific odorants have been shown to govern sexual selection. For instance, mice prefer the odor of potential mates with a dissimilar immune gene profile, thereby preventing inbreeding and endowing offspring with better (i.e., more heterogeneous) equipment to fight pathogens (K. Yamazaki, Beauchamp, Singer, Bard, & Boyse, 1999; K. Yamazaki et al., 1976). Pioneering research showed that humans also prefer the body odor embedded in t-shirts worn by people with dissimilar immune system–related gene profiles (Wedekind & Füri, 1997; Wedekind, Seebeck, Bettens, & Paepke, 1995); yet, a state-of-the-art review cited mixed evidence in favor of odor-driven immunity-related mate selection (Havliček & Roberts, 2009). Even though the odorants produced by the human body are influenced by genotype (Kuhn & Natsch, 2009), the relation among genes that are specifically related to immunity and armpit odorants could not be established (Natsch, Kuhn, & Tiercy, 2010); moreover, no genetic evidence was obtained for immunity-based mate selection in humans (Derti, Cenik, Kraft, & Roth, 2010). What is still unknown is how body odor preferences translate into actual mate selection, and what complicates matters is that preferences fluctuate as a function of dynamic factors, including menstrual cycle phase (Havliček & Roberts, 2009).

Indeed, multiple studies have shown that during the fertile phase of the menstrual cycle, women prefer the body odor embedded in t-shirts worn by more symmetrical men (e.g., Gangestad & Thornhill, 1998; Rikowski & Grammer, 1999; Thornhill & Gangestad, 1999; Thornhill et al., 2003); this effect has been ascribed to peak levels of female-typical hormones (Garver-Apgar, Gangestad, & Thornhill, 2008). Facial and bodily symmetries are indicators of "good genes" (Geary, Vigil, & Byrd-Craven, 2004), and good genes may be expressed in body odorants as well. However, there is currently an ongoing debate (Gangestad, 2016; Gildersleeve, Haselton, & Fales, 2014; Harris, Pashler, & Mickes, 2014; Wood, 2016) about the validity of fertility-based odor preferences because critics have pointed to publication bias and imprecise fertility estimates (Wood, Kressel, Joshi, & Louie, 2014). In sum, research on menstrual cycle–based odor preferences for genetically fit males should be interpreted with caution.

Gender. Individuality was not the only source for differences in chemical profiles because the specific odorants that humans produce and the quantity thereof are also affected by gender. For instance, body odors sampled by means of t-shirts or underarm compresses could be assigned significantly more often than chance to the correct gender category, with the odorant samples of men generally being judged as stronger and less pleasant (armpit odor: Doty, Orndorff, Leyden, & Kligman, 1978; t-shirt odors: Hold & Schleidt, 1977; Schleidt, 1980; Schleidt et al., 1981; Sorokowska, Sorokowski, & Szmajke, 2012; cf. Doty, Green, Ram, & Yankell, 1982, who found similar effects for breath odor). Chemical analysis revealed qualitative differences: Gender could be correctly classified with 75% accuracy on the basis of 12

odorants (see Penn et al., 2007, for a list). Arguably, both qualitative and quantitative differences contribute to the perceived pleasantness of the body odor (cf. Schleidt, 1980); yet, humans have the capacity to associate certain (concentrations of) odorants with the categories male and female (Zeng et al., 1991, 1996).

Age. In addition to individuality and gender, another factor that can chemically be expressed is old age. Age estimations of a stranger's body odor (i.e., sampled with t-shirts) were positively correlated with the stranger's actual age (Sorokowska et al., 2012). Participants also performed greater than chance in discriminating, labeling, and selecting the armpit odor of old individuals (75– 95 years) compared with younger people (Mitro et al., 2012). Chemical analysis showed evidence for a greasy and grassy-smelling odorant (2-nonenal) in Japanese people more than 40 years of age (Haze et al., 2001; S. Yamazaki, Hoshino, & Kusuhara, 2010). Researchers using Western samples generally did not replicate the Asian findings (e.g., Curran et al., 2005), although Gallagher et al. (2008) found a somewhat related odorant (nonanal) to be present in the body odor of older adults. What these findings mean from the perspective of our associative model is that individuals from different cultures may have associated different odorants with the concept of old age.

Summary. The reported evidence shows that odorants produced by the human body can differ as a function of individuality, gender, and age. Arguably, body odor becomes informative to a recipient when he or she has (implicitly) associated specific chemical profiles with a certain individual, gender, or age. Receivers may (implicitly) respond to a particular type of olfactory information (e.g., gender) once contextually this type of information has been made salient to them (e.g., via experimental instructions: "Pick out the odor you perceive as belonging to a woman"). This argument is further strengthened in the next section, in which we focus on the olfactory communication of dynamic states.

Communicability of dynamic states

Sickness. A recent study showed that body odor can contain a sickness cue (Olsson et al., 2014). Exposure to the t-shirt of a sick individual was associated with higher ratings of unhealthiness (but also unpleasantness, intensity) compared with unworn t-shirts and t-shirts of individuals who were only led to believe they were ill (Olsson et al., 2014). The exact components responsible for this effect are currently unknown. Having to provide a rating of healthiness may have focused the attention of participants in top-down fashion on the sickness signature in the Gestalt stimulus, although future research needs to support this.

Emotions. Besides sickness, another communicable dynamic factor is emotional state. Next, we briefly review research on the chemical communication of emotions—a field that has gradually expanded since the start of this century (Chen & Haviland-Jones, 2000). When dealing with the chemical communication of emotions, one first needs a grounding of what is meant with emotions and how they can be communicated. What has generally been used as a theoretical anchor in emotional chemo-signaling research is a discrete emotion perspective, in which emotions are seen as having a universal and discrete form (e.g., fear, disgust, anger) that emerge from a person's biological heritage (e.g., Ekman, 1992; Izard, 2007; Panksepp, 2007). The consensual responses to emotion-related body odors are typically said to reflect discrete emotions. Because the typical chemosignaling study isolates the body odor (i.e., the armpit odor) of the sender before presentation to a receiver, receivers lack relevant audiovisual contextual input to label their experience in specific emotion terms. In the absence of relevant contextual information, the reactions to emotion-related body odor may be unspecific to a discrete emotion such as fear. The measures used in chemosignaling studies to target fear (e.g., startle reflex, facial electromyography, brain imaging) may alternatively reflect a general state of high arousal and negative valence (e.g., Hess & Fischer, 2013; Lang, 1995; Larsen, Norris, & Cacioppo, 2003; Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012; Mauss & Robinson, 2009; Russell & Barrett, 1999).

Subjective measures, for instance, indicated that receivers exposed to fear odor from the armpit region selected general (high arousal) negative valence words to describe the odor (Ackerl, Atzmueller, & Grammer, 2002), their own situation (Albrecht et al., 2011), and characteristics of a third person (Dalton, Mauté, Jaén, & Wilson, 2013), rather than the emotion-specific terms "anxious," "fearful," or "stressed." However, the lack of consensus in describing what the smell induced may also be explained by humans having difficulty describing odors and their effects (Lorig, 1999; Olofsson & Gottfried, 2015a). To target implicit effects that cannot be verbalized, researchers should provide recordings of the brain and behavior that complement self-report measures.

What studies have shown with regard to behavior is that exposure to fear odor sampled from the armpit region increased vigilance (e.g., Chen, Katdare, & Lucas, 2006; de Groot et al., 2012; de Groot, Smeets, & Semin, 2015). Vigilant behavior ranged from increased caution during a word choice task (Chen et al., 2006), to higher accuracy on an easy visual search task (de Groot et al., 2012), to faster overall classifications of facial expressions (de Groot, Smeets, & Semin, 2015). With regard to brain activity, exposure to armpit odor from anxious/fearful individuals resulted in higher event-related potentials at various time points (e.g., Adolph, Meister, & Pause, 2013;

Pause, Lübke, Laudien, & Ferstl, 2010) and increased amygdala activity (Mujica-Parodi et al., 2009). Whereas these combined findings point to sensory acquisition processes, a state of vigilance associated with fear (Susskind et al., 2008), an alternative explanation is not ruled out—namely, that individuals processed arousing and motivationally salient information unspecific to fear (e.g., Goossens et al., 2009; Sander, Grafman, & Zalla, 2003).

By measuring facial expressions via electromyography, the next set of studies aimed to find whether emotion-related armpit odor would induce *emotional contagion* (Hatfield, Cacioppo, & Rapson, 1993). What these studies have consistently shown is that exposure to fear odor from the armpit elicited a facial expression of fear (*medial frontalis* muscle activity—lifting the eyebrow; de Groot, Semin, & Smeets, 2014a, 2014b; de Groot et al., 2012; de Groot, Smeets, Rowson, et al., 2015) or negative affect (*corrugator supercilii* muscle activity—furrowing the brow; de Groot et al., 2014a, 2014b; de Groot, Smeets, & Semin, 2015). Furthermore, exposure to the armpit odor of happy individuals (i.e., the other end of the valence dimension) resulted in a facial expression of genuine happiness (cf. Ekman, Friesen, & Hager, 2002) and a more global perceptual focus (de Groot, Smeets, Rowson, et al., 2015) that have been associated with positive mood (e.g., Gasper & Clore, 2002). Even though emotional expressions of receivers apparently "matched" the emotional state of the sender, the question is whether facial mimicry becomes more specific than positive and negative affect in the absence of relevant (social) contextual information (see Hess & Fischer, 2013, for a review).

Another study was conducted to test whether armpit odor produced during two different negative emotions (fear and disgust) would result in emulating these discrete states, as evidenced by multiple outcome measures (i.e., facial electromyography, sniffing behavior, eye movements, visual search; de Groot et al., 2012). Whereas fear was expected to be characterized by increased visual field size, enhanced visual search, and deeper inhalations (sensory acquisition), the reverse action pattern was predicted for disgust (sensory rejection); these patterns would follow the respective facial expressions of fear and disgust (Susskind et al., 2008). Whereas exposure to the armpit odor of fearful individuals induced a slight lifting of the eyebrow and vigilance (e.g., showing enhanced performance on an easy visual search task; de Groot et al., 2012), the armpit odor of disgusted individuals induced nose wrinkling and affected indicators of sensory rejection (e.g., fewer eye fixations). These findings seem to support the communication of discrete emotions through smell. However, rather than reflecting mimicry, the reaction to disgusted individuals' armpit odor may have been based on the higher unpleasantness and intensity of this stimulus (de Groot et al., 2012); yet, higher unpleasantness may be part of the "signal." In sum, what has been consistently shown is that exposure to fearful individuals' armpit odor evokes sensory acquisition processes, most notably vigilant behavior (e.g., Chen et al., 2006; Mujica-Parodi et al., 2009).

On the basis of our framework, we presume that if the chemical profiles are sufficiently nonoverlapping, consistent, and reliable for a specific emotion (e.g., fear, disgust), information about these specific emotional states can be tied to these chemical profiles. Multiple individuals can then extract the natural relation between a specific emotion-related chemical profile and other-modality information in the situation in which this profile is typically encountered, explaining the consensual responses to emotion-related odors. In line with this perspective, individuals having a greater sensitivity to particular information in the environment (e.g., emotions) may form strong(er) associations between a certain (e.g., emotion-related) chemical profile and (e.g., emotion-related) other-modality contextual information.

Research has shown that certain populations display a greater sensitivity to emotion-related chemosignals. Because women are generally more sensitive to emotional signals (Brody & Hall, 2000) and have a better sense of smell (e.g., Brand & Millot, 2001), they were expected to respond more strongly to emotion-related body odors. Curiously, men responded most strongly to female armpit odor, regardless of emotion (de Groot et al., 2014a); only women emulated the emotional state of the sender after exposure to emotion-specific armpit odor (de Groot et al., 2014a). These findings are complemented by brain recording studies, which showed more emotional involvement when women (vs. men) were exposed to armpit odor from individuals with anxiety (Pause et al., 2010), including greater activity in the superficial nucleus of the amygdala (Radulescu & Mujica-Parodi, 2013).

In a similar vein, individuals with social anxiety are more sensitive to negative social information, including what is chemically communicated. Individuals with high social anxiety showed stronger startle responses in the presence of armpit odor from individuals with anxiety (Adolph et al., 2013; Pause, Adolph, Prehn-Kristensen, & Ferstl, 2009). Electroencephalogram recordings showed that women with social anxiety, in particular, responded to anxiety armpit odor with higher alertness (Pause et al., 2010) and increased motivated attention (Adolph et al., 2013). Individuals with social anxiety are generally more sensitive to emotion-related information. These individuals have a greater capacity associating certain emotion-specific chemical profiles with emotional outcomes. This finding has been identified in the context of human chemical communication, by means of the specific behavioral repertoire and recruitment of neural resources in these sensitive

individuals, preparing them for adequate goal-directed action by cueing that something important is going on.

Emotion-related body odor thus affects various individuals to a different extent. Receivers arguably respond to the most salient information in the Gestalt stimulus, and what is most salient depends on the receiver's implicit associations, a person's state, and the context at hand. The experimental task may determine whether a participant exposed to a fearful person's armpit odor displays cautious or risky behavior. Whereas fear odor recipients spent more time on a cognitively demanding task to increase their accuracy on a lexical decision task (Chen et al., 2006), they made more risky decisions during a risk-behavior game (Haegler et al., 2010). What these opposing response patterns demonstrate is that responses to fear odor (from the armpit) can flexibly be attuned to the experimental context.

Curiously, when fear odor was presented together with fear-inducing horror clips, the facial expression related to fear was stronger than when fear was induced via just one source (de Groot et al., 2014b). Hence, each of the modalities added its part to the fear percept. Even though an interaction was not observed, we presume that a more or less full-blown and discrete fear experience would occur in ecologically valid settings that allow for a more natural coupling between (a set of) odorants and audiovisual information.

What future researchers need to address is whether there are distinctive and stable emotion-related chemical profiles within the complex multi-odorant mixture that have the potential of eliciting species-wide responses. For instance, natural selection may have favored those individuals who could detect "fearomones" (a term probably coined first by Quinn, 2004); fearomone-detecting individuals were arguably better protected from harm than nondetectors and had higher chances of passing on their genes. Research could reveal whether this capacity is still observed today across different contexts, in individuals of different ages, belonging to different cultures.

General Summary and Conclusion

In sum, this integrative review highlights the complex, associative, and situated nature of human olfactory communication. First, body odor contains multiple sources of information at the same time. The perception of body odor is actually based on various chemical (sub)profiles that are specific (nonaccidental) to a certain state or trait. Through associative learning, multiple individuals may have extracted these relations. Eventually, human odorants become a medium by means of which information about dynamic states (e.g., emotions and sickness) and enduring characteristics (e.g., age, gender, individuality, personality) can be transferred from a sender to a receiver. Because odorants are typically perceived holistically, top-down information from the context may help to focus on the various unique (sub)profiles nested in a mixture. Hence, although body odor initially conveys coarse multifarious information, receivers can respond to specific information that is most salient to them. What is salient is determined in part by top-down factors, such as the context at hand, the goals of the receiver, and existing associations with the odorants.

The application of an associative learning perspective to human olfactory communication leads to a range of testable hypotheses concerning the development (and maintenance) of these associations. What has already been shown is that associative learning, next to mere exposure, can induce top-down changes in the perception (e.g., enhanced sensitivity) of odorants, causing two initially indistinguishable odorants to become discriminable (Li et al., 2008). In a similar vein, we presume that chemical profiles can become discriminable after learning that these profiles consistently and reliably co-occur with state- or trait-related information. The vision that this perspective opens is that the range of transferable information via smell is limited only by the amount of chemical profiles that reliably co-occur with defining contextual features. Eventually, one could predict consensual reactions to certain odor compounds by charting how often odorants co-occur with certain state- or trait-related information. In future studies, researchers could additionally determine (a) at what age certain state- or trait-related associations with odorants emerge (e.g., what are the effects of hormonal changes in puberty?), (b) how many couplings are necessary for learning to occur, and (c) how resistant to change these associations are. What current research on human olfactory communication nevertheless suggests is that associative learning is likely; strong(er) reactions to certain chemical profiles are often only observed in specific (sub)populations.

Following that line of reasoning, members from different cultures can be found to have different associations with similar odor compounds or similar associations based on different odor compounds. For instance, 2-nonenal was found as the old-age odorant in Japanese samples (Haze et al., 2001; S. Yamazaki et al., 2010); yet, a different set of odorants was related to the smell of older adults in Western samples (Curran et al., 2005; Gallagher et al., 2008). In future studies, researchers could indicate whether members from different cultures have learned to associate different odorants with the older adult concept.

Cultural factors can obviously interact with genetic factors in shaping odor–information associations. For instance, a genetic variation expressed in the workings of sweat glands causes Asian individuals to produce less intense body odor than, for instance, Caucasian individuals (Martin et al., 2010; Schaal & Porter, 1991). The

"associability" of the genetically predetermined less intense Asian odor may then further be culturally undermined, for example, in Japanese individuals having strong cultural norms of body odor suppression (Schleidt et al., 1981), and in Chinese Americans who adhere to their country of origin's norms of emotional restrictiveness to maintain social harmony (e.g., Soto, Levenson, & Ebling, 2005). In these cases, a combination of genetic and cultural factors could result in Chinese and Japanese individuals (i.e., at least those unfamiliar with members from other cultures) being affected less strongly by, for instance, emotion-related body odor than culturally more expressive and stronger odor-producing Caucasian individuals. What further complicates the design is the possibility that not only the body odor production capacity but also the receiver capacity may differ as a function of genes and culture. This example illustrates the dynamic and situated nature of human olfactory communication.

Human communication takes place in a social context (Smith & Semin, 2004, 2007), and human olfactory communication is no exception. In previous studies, researchers presented isolated body odor to receivers, who then lacked relevant contextual information to make sense of their experience. These artificial settings have nevertheless been highly important initial steps that critically reduced the impact of possible extraneous variables to observe an effect of a specific experimental variable on a range of outcome measures. However, because odor perception is holistic (e.g., Gottfried, 2010; Olofsson & Gottfried, 2015a), humans may experience difficulty detecting individual elements (e.g., gender, age, emotions) in a "mixture" when top-down factors are absent (e.g., relevant contextual information, a person's state). To examine the role of top-down factors in body odor perception, researchers could manipulate the state of participants to see whether congruent state-related information is detected more easily in a mixture. In addition, the context can be manipulated (e.g., through the presence of another person or virtual reality) to observe whether attention can be heightened to certain features in the body odor as a function of changing elements of the situation.

Because the current framework is focused on the culture- and context-dependent development of associations with body odor, it provides an insight into how similarity of perspectives between a sender and a receiver—an indispensable requirement for successful communication (Semin, 2007)—can be achieved through smell. Next to the senses of vision, hearing, and touch, olfaction can provide researchers with diverse social information. We conceive of the human ability to quickly couple odorants to information (e.g., about emotions) and adaptive action tendencies (e.g., fight–flight behavior) as evolutionarily useful. Whether individuals actually develop

these associations is something that depends, *inter alia*, on the situations these individuals will typically encounter. Such a learning perspective should cover the largest portion of human olfactory communication, which depends on locally adapted olfactory abilities. However, similar to what was observed in insects (Keleman et al., 2012), learning-dependent processes might also cooperate with learning-independent processes. Partially hardwired responses to human odorants may especially be found in critical stages of life, such as newborns relying on a potential pheromone in the mother's breast odor to locate food (e.g., Schaal & Al Aïn, 2014).

The prerequisite of innateness is what makes defining human odorants as pheromones problematic because innateness is often (implicitly) conceptualized as the absence of learning (Samuels, 2002); yet, many seemingly innate behaviors are only performed when certain developmental or environmental conditions are met (Mameli & Bateson, 2011). Instead of defining pheromones by their innateness, it may be more fruitful to examine the number of people showing a shared association with a certain set of human odorants, and whether these associations are based on a fixed set of odorants (Wyatt, 2014). For substances to be classified as pheromones rather than signature mixtures (cf. Wyatt, 2014, p. 14), future researchers should determine (a) whether a sufficient number of people share the association and (b) whether consensual associations are, in fact, based on the same (vs. different) set(s) of odorants. From our framework, a pheromone is intelligible as a distinct chemical profile nested within the multicomponential Gestalt stimulus, which multiple individuals—in more or less invariant form—have associated with state- or trait-related information; exposure to this chemical profile elicits consensual (context-dependent) responses in receivers. Because humans belong to different cultures causing them to be exposed to different (levels of) odorants during their life, we presume that a complex culture-dependent mix of odorant–information associations exists, which should make it easier to find so-called signature mixtures than species-wide pheromones. Nevertheless, this is an empirical question; like other animal species, humans have the potential to develop pheromone-like consensual associations with human odorants.

To conclude, dozens of studies have already shown some of the consensual responses to body odor, and the literature is still growing at a steady rate. However, what the researchers of these studies have not yet focused on, unlike what is explained by the integrative model advanced here, is the potential mechanism that could drive these consensual responses. Here, we provide a framework that is designed to fill this explanatory gap by furnishing a theory on olfactory communication that highlights the

dynamic and flexible aspects of human olfactory communication. By addressing (a) the multifaceted nature of body odor, (b) associative learning mechanisms, and (c) contextual influences, our tripartite model not only helps to integrate past research on human olfactory communication but it also opens new avenues for future research on this remarkable topic.

Notes

1. The word *odorant* is used to refer to the specific molecules before they are translated into a smell by the central nervous system; the smell sensation is referred to as *odor*.

2. The interested reader is also referred to research showing anatomical evidence that modern humans (*Homo sapiens*) have evolved relatively larger olfactory structures than another large-brained representative of the *Homo* line (*Homo neanderthalensis*); these larger olfactory structures are related to higher olfactory functions, such as relating odorants to socially relevant cognitive processes (Bastir et al., 2011). Hence, adopting an erect posture is not per se related to regressed olfactory capabilities.

3. The terms "pheromone" and "chemosignal" have often been used interchangeably. To avoid needless complexity, we basically treat these terms as similar. Actual definitions can be found in the next section, where pheromones are contrasted to signature mixtures on the basis of several criteria, and in the General Summary section.

4. Obviously, there are more null results than those reported in the cited studies. These studies focused on replicating the phenomenon of olfactory-mediated menstrual synchrony (McClintock, 1971)—research that has been criticized on methodological, statistical, and theoretical grounds (e.g., H. C. Wilson, 1992).

5. The authors themselves have been reluctant to call this an example of a pheromone; they stated that intra-amniotic experience with these or similar compounds could (partly) have driven the postnatal effect (Doucet, Soussignan, Sagot, & Schaal, 2009; Schaal & Al Aïn, 2014).

6. By comparison, the perception of sound is not synthetic but analytic. That is, each individual tone can possibly be analyzed separately.

7. There is also empirical evidence showing that certain personality traits (e.g., neuroticism, extraversion) can be conveyed by body odor (e.g., Sorokowska et al., 2012), perhaps through their associated frequently experienced emotions of fear and happiness, respectively. Furthermore, sexual information was also said to be transferable by means of body odor; this conclusion was based on a significant increase in hypothalamus activity compared with "neutral" body odor and a "putative" sex pheromone (Zhou & Chen, 2008).

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