



Review

Always follow your nose: The functional significance of social chemosignals in human reproduction and survival



Katrin T. Lübke*, Bettina M. Pause

Department of Experimental Psychology, University of Düsseldorf, Düsseldorf, Germany

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ABSTRACT

This article is part of a Special Issue “Chemosignals and Reproduction”

Across phyla, chemosensory communication is crucial for mediating a variety of social behaviors, which form the basis for ontogenetic and phylogenetic survival. In the present paper, evidence on chemosensory communication in humans, with special reference to reproduction and survival, will be presented. First, the impact of chemosignals on human reproduction will be reviewed. Work will be presented, showing how chemosensory signals are involved in mate choice and partnership formation by communicating attractiveness and facilitating a partner selection, which is of evolutionary advantage, and furthermore providing information about the level of sexual hormones. In addition to direct effects on phylogenetic survival, chemosignals indirectly aid reproductive success by fostering harm protection. Results will be presented, showing that chemosensory communication aids the emotional bond between mother and child, which in turn motivates parental caretaking and protection, leading to infant survival. Moreover, the likelihood of group survival can be increased through the use of stress-related chemosignals. Stress-related chemosignals induce a stress-related physiology in the perceiver, thereby priming a fight–flight–response, which is necessary for an optimum adaption to environmental harm. Finally, effects of sexual orientation on chemosensory communication will be discussed in terms of their putative role in stabilizing social groups, which might indirectly provide harm protection and foster survival. An integrative model of the presented data will be introduced. In conclusion, an outlook, focusing on the involvement of chemosensory communication in human social behavior and illustrating a novel approach to the significance of chemosensory signals in human survival, will be given.

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Contents

Introduction	135
The sources of human chemosignals	135
The perception of human chemosignals	136
The functional significance of social chemosignals in human reproduction	136
Chemosignals in human mate choice and sexuality	136
Chemosignals communicating sex hormonal status	137
The functional significance of human chemosignals in harm avoidance	137
Mother–infant bonding	137
Communication of threat	138
Human chemosignals and sexual orientation	139
Discussion	140
Acknowledgments	141
References	141

* Corresponding author at: Department of Experimental Psychology, University of Düsseldorf, Universitätsstraße 1, D-40225 Düsseldorf, Germany. Fax: +49 211 81 12019.
E-mail addresses: katrin.luebke@hhu.de (K.T. Lübke), bettina.pause@hhu.de (B.M. Pause).

Introduction

Across phyla, the transmission of chemical signals is a significant – if not the most significant – form of social communication. A diversity of species benefits from the multiple advantages of chemosensory communication. For example, chemical signals can easily overcome physical barriers, are still functional when other senses are blocked (such as in the dark or in a noisy environment), can be transported over long distances by wind or water current, may be conveyed to conspecifics quickly (high volatile molecules), may outlast the presence of their sender (low volatile molecules), and potentially have an enormous specificity (Bushdid et al., 2014), and their production costs (e.g. the amount of energy needed to produce and release a signal) are low (for an extensive review on chemosensory communication across phyla see Wyatt, 2014). Humans, however, seem to be an exception: Ever since humans have been classified as “microsmatic animals” (Turner, 1890), it seems somewhat commonly perceived that chemosensory senses in general were of minor importance for humans. However, from ancient times to modern cultures, humans have made use of fragrances not only within religious rituals, but also in order to mask or emphasize their own body odor (Pause, 2004b). The annual global perfume industry sales revenue reached 27.5 billion US dollars in 2012 (<http://www.statisticbrain.com/perfume-industry-statistics/>). This amount somewhat contradicts the idea of a general insignificance of chemical senses for humans. In fact, we will summarize work demonstrating that humans have sensitive and well-developed chemosensory abilities, capable of mediating social behaviors, and moreover, that humans are well-equipped for producing chemosensory signals. Apart from being regarded as microsmatic anyway, the fact that the significance of chemosensory communication in humans has been underestimated for quite a long time might be related to an additional advantage of chemosensory communication that reveals its effects especially in humans: Chemosensory social information may be mainly processed by the human brain at a subconscious level, and thus, like social information of other modalities, does not necessarily require conscious analysis (see Lundström and Olsson, 2010, and Pause, 2012 for overviews on the processing of human chemosignals).

In what follows, we will summarize evidence for human social communication via chemosignals, focusing complex molecule mixtures as present within body fluids. Chemical signals in social communication are usually mixtures of a variety of molecules (Wyatt, 2014). The term “pheromone” will be avoided in favor of terms such as “chemosensory signal” or “chemosignal”. To date, there is no general consensus among scientists on what constitutes a pheromone, especially regarding mammalian chemosensory communication (Doty, 2010; Wyatt, 2014). A signal, however, is definably a stimulus which, produced and released by a sender, transmits a message to a receiver. In contrast to a pure stimulus, like a common odor for example, which may or may not carry relevant information, a social signal always conveys specific information from one individual to another. We are going to focus on the transmission of chemosignals involved in successful reproduction, both directly and indirectly through harm avoidance. In this context, the latter spans from protection provided to offspring as a result of mother–infant bonding to protection provided to members of the social group by chemosensory communication of threat. These examples will show that chemical communication in humans aids survival by optimizing ontogenetic and phylogenetic strategies. After all, the evolution of *homo sapiens* may well have been driven by the development of chemosensory capacities, mediating social behavior specific to modern man (Bastir et al., 2011).

The sources of human chemosignals

In humans, volatile chemosignals derive from several sources, e.g. urine, vaginal secretions, sperm, and lacrimal fluid. The axilla, however, is exceptionally equipped for producing volatile chemosignals. It

contains a variety of glands whose secretions contribute to a unique odorous chemosensory profile after being converted by resident bacteria. The relative warmth and humidity within the axilla support the growth of the bacterial culture, and enhance its enzymatic activity (Reichert et al., 1982). Further, the relatively high temperature aids in volatilizing odorous molecules. Another benefit for odor production is axillary hair, enlarging the surface for bacteria to reside in, and aiding the dispersion of odorous molecules. Of the primary cutaneous gland systems (apocrine, eccrine, apoeccrine, and sebaceous glands) present within the axilla (Heckmann et al., 2003), the secretions of the apocrine glands have been studied in more detail. In general, these glands are located within hairy body regions, that is, besides the axilla, the areola and the anogenital area (Hurley and Shelley, 1969; Robertshaw, 1985). However, their largest and most active variants reside within the axilla.

Whereas freshly collected apocrine secretion is odorless, incubation with the resident bacteria (coryneform bacteria, micrococci) results in the production of a characteristic odor (Labows et al., 1982; Leyden et al., 1981; Zeng et al., 1992, 1996a,b). Four classes of substances are known to contribute to this characteristic odor (Pause, in press). The olfactorily most dominant class is comprised of unsaturated or hydroxylated branched fatty acids, like 3-methyl-2-hexenoic acid (3M2H). These acids exist in abundance in axillary sweat, and contribute significantly to the typical axillary odor (Zeng et al., 1991). 3M2H is transported to the skin surface by apocrine secretion odor-binding proteins, and released by axillary bacteria (Spielman et al., 1995). Two other classes of major odor constituents within the human axillae are thio-alcohols (sulfanylalkanols), like 3-methyl-3-sulfanylhexan-1-ol (3M3SH; Hasegawa et al., 2004; Natsch et al., 2004; Troccaz et al., 2004), and short chain fatty acids, such as isovaleric acid. The latter is liberated by micrococci, and might contribute to a sweat-like odor (Leyden et al., 1981). The fourth class includes volatile steroids, such as 5 α -androst-16-en-3-one (androstene), 5 α -androst-16-en-3 α -ol (androstenol), and 4,16-androstadien-3-one (androstadienone; Gower et al., 1994; Nixon et al., 1988). Axillary coryneform bacteria convert the weakly odorous androstadienone into the stronger smelling androstene androstene (urineous odor) and androstenol (musky odor; Austin and Ellis, 2003; Gower et al., 1994). The odorous quality of axillary sweat as a whole is obviously affected by a specific variant of the ABCC11 gene, as individuals homozygous to this specific variant display significantly reduced numbers of odoriferous molecules of the aforementioned four classes, resulting in a very faint axillary odor (Martin et al., 2010). The ABCC11 gene is expressed in apocrine sweat glands and probably involved in the secretion of odor precursors (for more extensive reviews on axillary chemistry see Preti and Leyden, 2010; Wyatt, 2014; Wysocki and Preti, 2004).

There are numerous aspects arguing in favor of molecules resulting from axillary secretions being involved in within- and between-sex chemosensory communication in humans. Several elements of axillary odor production are prone to sex-hormonal influences. In detail, axillary hair grows during puberty and the cutaneous gland systems develop. While the sebaceous glands enlarge and sebum production increases in both sexes (Pochi et al., 1979), the secretory activity of the eccrine glands begins to differ between men and women. In contrast to women, the quantity secreted considerably increases during puberty in men (Kawahata, 1960; McCance, 1938; Rees and Shuster, 1981). Of special importance, the apocrine glands enlarge and mature to functionality with puberty (Kuno, 1956; Sato et al., 1987). Adult men feature larger apocrine glands than women, especially in axillary regions (Hurley and Shelley, 1969). The resident microflora also changes with puberty, resulting in a generally higher density of microbes within the male than in the female axilla (Marples, 1982; Somerville, 1969), and a differing composition of the bacterial culture. In the male axilla, coryneform bacteria are dominant, while within the female axilla, micrococci are the most prominent (Jackman and Noble, 1983). Accordingly, male and female axillary sweat also differs in its respective composition. It has been shown, that male compared to female axillary sweat contains

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