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The Effects of Sexual Orientation on Human Chemosensory Communication

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1. Abstract (German)

Die menschliche Partnerwahl hängt von einer Reihe von Faktoren ab. Neben Sympathie, gemeinsamen Interessen und interpersoneller Attraktivität scheint auch die chemosensorische Kommunikation über Körpergerüche einen Einfluss auf die Partnerwahl auszuüben. Einerseits scheint sowohl die Produktion als auch die Wahrnehmung von Körpergerüchen geschlechtsabhängig zu sein. Andererseits variieren hedonische Beurteilung und zentralnervöse Verarbeitung von Körpergerüchen in Abhängigkeit von der relativen genetischen Kompatibilität von Körpergeruchsspender und Wahrnehmendem. Die menschliche Partnerwahl hängt darüber hinaus von der sexuellen Orientierung ab. Es scheint daher sinnvoll anzunehmen, dass die sexuelle Orientierung auch die Wahrnehmung humaner Chemosignale beeinflusst. Nur wenige Studien haben sich bisher einer solchen Fragestellung angenommen. Die Ergebnisse dieser Studien deuten jedoch darauf hin, dass sowohl die hedonische Bewertung komplexer Körpergerüche als auch die zentralnervöse Verarbeitung einzelner Körpergeruchskomponenten mit der sexuellen Orientierung in Zusammenhang steht.

Die hier dargestellten Studien hatten zum Ziel, den Einfluss der sexuellen Orientierung auf die menschliche Chemokommunikation weiter zu untersuchen. Außerdem sollten sie erste Hinweise auf mögliche Verhaltenseffekte erbringen. Hierfür wurde zu Beginn der Einfluss der männlichen sexuellen Orientierung auf die Wahrnehmung von Androstenon, einer signifikanten Komponente des männlichen Körpergeruchs untersucht. Die folgenden Studien prüften Effekte von Geschlecht und sexueller Orientierung auf die zentralnervöse Verarbeitung menschlicher Chemosignale. In den abschließenden Studien wurde der Einfluss von sexueller Orientierung auf Mimikry untersucht, sowie der Effekt von chemosensorischen, auf Geschlecht und sexuelle Orientierung bezogene Kontextreizen.

Bei den verwendeten komplexen Körpergerüchen handelt es sich um Achselgeruchsproben, die mithilfe von in den Achselhöhlen befestigten Wattepads gewonnen wurden. Präsentiert wurden diese Körpergerüche, eingebettet in einen

konstanten Luftstrom, unter Verwendung eines 6-Kanal Olfaktometers (Burghart, Wedel, Deutschland).

Die erste Studie zeigt dass schwule im Vergleich zu heterosexuellen Männern sensitiver für Androstenon sind. Dieser Unterschied ist möglicherweise darauf zurückzuführen, dass schwule Männer häufiger mit männlichem Körpergeruch in Kontakt kommen und daher für Androstenon als bedeutsame Komponente dieses Körpergeruchs sensitiviert sind.

Die folgenden Studien zeigen anhand der Analyse von sowohl chemosensorisch ereigniskorrelierten Potentialen (CSEKPs) als auch der Stromdichteverteilungen in Antwort auf komplexe Körpergerüche einen generellen Vorteil von Frauen gegenüber Männern bei der zentralnervösen Verarbeitung komplexer Körpergerüche. Weiterhin zeigt sich eine bevorzugte Verarbeitung von Körpergerüchen potentieller Partner in Bezug auf das Geschlecht (bei lesbischen Frauen) und in Bezug auf Geschlecht und sexuelle Orientierung (bei schwulen und heterosexuellen Männern) auf der Ebene der frühen Stimulusenkodierung (P2 Latenz). Zusätzlich weisen lesbische Frauen und schwule Männer eine verstärkte späte, evaluative Verarbeitung des Körpergeruchs heterosexueller Männer auf, die als solche für beide Gruppen keine potentiellen Partner darstellen (P3 Amplitude).

Innerhalb der abschließenden Studien wurden per Elektromyographie mimische Reaktionen (Corrugator supercilii, involviert in Stirnrunzeln und Zygomaticus major, involviert in Lächeln) auf traurige und fröhliche Gesichter untersucht. Die chemosensorischen Stimuli wurden als soziale Kontextreize integriert. Ohne die Präsentation chemosensorischer Kontextreize zeigen Männer vor allem Mimikry auf traurige Frauengesichter, wobei dieser Effekt bei schwulen Männern verlängert sichtbar ist. Gegenüber traurigen männlichen Gesichtern, die ohne Kontextgeruch präsentiert werden, zeigen vor allem heterosexuelle Männer Gegen-Mimikry. Im Kontext vom Körpergeruch schwuler Männer allerdings zeigen alle Männer Mimikry auf traurige Gesichter. Ohne Kontextgeruch zeigt sich vor allem bei heterosexuellen Frauen Mimikry auf traurige Gesichter, unabhängig vom

Geschlecht des präsentierten Gesichts. Lesbische Frauen dagegen reagieren vor allem im Kontext von heterosexuell-weiblichem Körpergeruch mit Mimikry auf traurige Gesichter. Die Ergebnisse zeigen also Unterschiede in den mimischen Reaktionen auf Gesichtsausdrücke in Abhängigkeit von der sexuellen Orientierung, was möglicherweise auf Unterschiede in der Ausprägung von interpersoneller Empathie hinweist. Darüber hinaus unterstützen chemosensorische Kontextreize differentiell die mimische Reaktion, eventuell erklärbar durch Aktivierung von Motiven der Annäherung oder Bindung.

Zusammenfassend deuten die Ergebnisse darauf hin, dass menschlicher Körpergeruch Informationen darüber transportiert, ob eine Person einen potentiellen Partner in Bezug auf das Geschlecht und die sexuelle Orientierung darstellt. Außerdem ergaben sich erste Hinweise auf die Verhaltensrelevanz solcher Reize, da sie scheinbar Motive der Annäherung oder Bindung aktivieren. Es sind allerdings weitere Studien notwendig die das Wissen um die Verhaltenseffekte solcher chemosensorischen Signale im Kontext von menschlicher Partnerwahl erweitern.

2. Abstract (English)

Human mate choice is affected by a number of factors. In addition to sympathy, shared interests and interpersonal attractiveness, chemosensory communication via body odors has been assigned a role in human mate choice. Both the production as well as the perception of body odors have been shown to vary with gender. Moreover, the hedonic judgment as well as the central nervous processing of a specific body odor seem to be related to the relative genetic compatibility of the respective odor donor and the perceiver. As human mate choice, as a matter of course, varies with sexual orientation, it seems reasonable to assume that sexual orientation should affect the perception of human chemosensory signals. Few studies have addressed this issue so far, but these suggest sexual orientation to affect hedonic judgments of complex body odors as well as central nervous processing patterns in response to individual body odor compounds. Moreover, the hedonic evaluation of body odors has been shown to vary not only with the gender but also with the sexual orientation of the body odor donors.

The studies presented here were designed in order to further investigate sexual orientation related differences in human chemosensory communication, and to provide a first insight into their behavioral significance. First, effects of male sexual orientation on the perception of androstenone, a significant compound of male body odor were investigated. In the following studies, effects of gender and sexual orientation on the central nervous processing of gender and sexual orientation related chemosensory stimuli were investigated. The concluding studies examined both sexual orientation effects on facial mimicry and the effects of gender and sexual orientation related chemosensory context cues.

The complex body odors were composed of samples of axillary secretions, obtained by means of cotton pads attached to the armpits of the odor donors. The odors were presented via a 6-channel, constant-flow olfactometer (Burghart, Wedel, Germany).

Results of the first study show gay as compared to heterosexual men displaying a higher sensitivity for the odor of androstenone. This difference may arise from gay men's previous frequent encounters with male body odors, resulting in sensitization to androstenone, as it is a significant compound of the complex male body odor.

Within the following studies chemosensory event-related potentials and current source densities in response gender and sexual orientation related chemosensory stimuli were investigated. Results show a general advantage for females as compared to males in the processing of human chemosensory stimuli. Moreover, a processing advantage at the level of early stimulus encoding (P2 latency) for body odors obtained from potential partners in terms of gender (in lesbian women), and in terms of gender and sexual orientation (in men) is evident. Additionally, both gay men and lesbian women display pronounced processing of body odors obtained from individuals not constituting potential mates (heterosexual men) at the level of later stimulus evaluation (P3 amplitude).

Within the concluding studies facial reactions to sad and happy facial expressions were recorded via electromyography from the corrugator supercilii (involved in frowning) and zygomaticus major (involved in smiling) muscle regions. The chemosensory samples were introduced as social context odors. Without context odor, men show facial mimicry when presented with sad female faces, an effect that is especially prolonged in gay men. Muscle activity of heterosexual men when presented with sad male faces without context odor suggests a display of counter-mimicry. Facial mimicry when exposed to sad males faces only was observed when the faces were presented in the context of gay male body odor. Heterosexual women display facial mimicry in response to sad faces irrespective of the actor's gender. Lesbian women however show facial mimicry especially when presented with sad female faces in the context of heterosexual female body odor. These results show sexual orientation related differences in facial reactions to facial reactions, possibly

suggesting varying degrees of interpersonal empathy. Moreover, facial mimicry is facilitated by social context odors probably due to priming of affiliation motives.

In conclusion, the social chemosignal of human body odor has been shown to convey information about an individual being a poor or a eligible partner in terms of gender and sexual orientation, and that this information is detected by individuals exposed to the chemosignal. Moreover, a first lead as to the behavioral relevance of such social chemosignals has been observed, namely the priming of the motive to affiliate. However, more studies are needed that expand effects of gender and sexual orientation related chemosensory signals on further, in the context of mate choice relevant behaviors.

3. Theoretical and Empirical Background

Human chemosensory communication

In many non-human species, transmission of chemosensory signals is a crucial form of communication, mediating a variety of social behaviors, such as the recognition of conspecifics, dominance and aggression displays, and signaling mating characteristics (Wyatt, 2003). This form of communication has a number of advantages, as chemosensory signals may easily overcome physical barriers, may be transported by wind and water currents and thus cover long distances, and have generally low production costs. However, since early anatomists labeled humans as microsmatic animals (Zwaardemaker, 1895), the common misconception evolved that humans have a poorly developed sense of smell. It is widely believed that the dependence on auditory perception and trichromatic vision has significantly reduced human reliance on chemosensory communication (Gilad, Wiebe, Przeworski, Lancet & Paabo, 2004), but an increasing volume of research demonstrates that humans have sensitive and well-developed olfactory abilities capable of mediating social behavior (see Jacob, Zelano, Hayreh & McClintock, 2002).

In order for chemosensory communication to take place, individuals are required to produce chemical substances and to secrete these substances to the outside (Karlson & Lüscher, 1959). In humans, odorous substances are produced by the integument, the salivary glands, the accessory glands of the eye, and are found in urine, faces, sperm, and vaginal secretions. In everyday life, however, the most prevalent source of human body odor is the axilla. Axillary sweat is a conglomerate of secretions from the sebaceous, eccrine, apoeccrine, and apocrine glands (Cohn, 1994; Heckmann, Teichmann, Pause & Plewig, 2003), and its odorous components are basically comprised of steroids (Gower, Bird, Sharma & House, 1985; Gower & Ruparelia, 1993; Nixon, Mallet & Gower, 1988) and acids like (E)-3-methyl-2-hexenoic acid (Zeng et al., 1991) and isovaleric acid (Preti et al., 1987). Especially axillary steroids are supposed to exhibit communicative features, and thus 16-androstenes like androstenone (5-α-androst-16-en-3-one) and androstadienone (androsta-4,16,-

dien-3-one) are the most frequently investigated axillary compounds in humans (Bensafi, Brown, Khan, Levenson & Sobel, 2004; Bensafi, Tsutsui, Khan, Levenson & Sobel, 2004; Kirk-Smith & Booth, 1980). Indeed, androstenone has been shown to contribute significantly to at least male human body odor (Pause, Rogalski, Sojka & Ferstl, 1999).

Concerning the perception of 16-androstenes, considerable gender differences have been reported. While the majority of prepubescent children is able to detect androstenone (Schmidt & Beauchamp, 1988), significantly more males than females lose the ability during puberty (Dorries, Schmidt, Beauchamp & Wysocki, 1989). Moreover, the remaining osmic males become less sensitive to androstenone and androstadienone after puberty (Hummel, Krone, Lundström & Bartsch, 2005), whereas sensitivity in females increases (Dorries et al., 1989). Females also tend to vary in their judgment of androstenone's pleasantness during the course of their menstrual cycle (Hummel, Gollisch, Wildt & Kobal, 1991). Further, sex dimorphic effects on the level of central nervous processing were reported, in that females, but not males, exhibited anterior hypothalamic activation in response to androstadienone (Savic, Berglund, Gulyás & Roland, 2001).

In general, the perception of androstenone and androstadienone is altered by experience, as repeated exposure to both steroids leads to sensitization (Jacob, Wang, Jaffer & McPhee, 2006; Wysocki, Dorries & Beauchamp, 1989). On the other hand there is evidence that the sensitivity to androstenone (Keller, Zhuang, Chi, Vosshall & Matsunami, 2007; Knaapila et al., 2008; Wysocki & Beauchamp, 1984) and androstadienone is at least in part determined genetically. Only recently, a specific androstenone/androstadienone receptor was discovered, polymorphisms of which could account for differences in sensitivity (Keller et al., 2007).

Body odors in general, and axillary secretions in particular, have been demonstrated to convey a diversity of information. For instance, it has been known for some time, that humans are highly accurate at identifying individuals based solely on their body odors (Wallace, 1977). Shortly after birth, breast-fed infants

become familiar with, and respond preferentially to, their mother's unique odor signature (Cernoch & Porter, 1985; Russell, 1976). Mothers likewise recognize the characteristic scent of their newborn infants (Kaitz, Good, Rokem & Eidelman, 1987; Porter, Cernoch & Balogh, 1985; Russell, Mendelsohn & Peeke, 1982). Neuroimaging results demonstrated that olfactory based kin recognition recruits brain areas implicated in the coding of self-referent processing and kin recognition (Lundström, Boyle, Zatorre & Jones-Gotman, 2009). Moreover, it has been shown that individuals are able to identify their own body odors as well as body odors of peers and close friends (Mallet & Schaal, 1998; Olsson, Barnard & Turri, 2006). Analysis of the central nervous processes related to the perception of one's own body odor showed pronounced neuronal responses to chemosensory self- as compared to non-self signals (Pause, Krauel, Sojka & Ferstl, 1999). Concerning the level of acquaintance, smelling a friend's as opposed to a stranger's body odor has been demonstrated to activate specialized neuronal networks similar to what has previously been shown for familiar auditory and visual stimuli (Lundström, Boyle, Zatorre & Jones-Gotman, 2008). These results indicate a strong genetic impact on the production of body odors.

In addition to transmitting information about individual identity, body odors may communicate a person's emotional state. Individuals are able to distinguish fear-related body odors from happiness-related (Chen & Haviland-Jones, 2000) and neutral body odors (Ackerl, Atzmueller & Grammer, 2002). Moreover, in ambiguous situations, chemosensory anxiety signals have been shown to bias individuals toward interpreting facial expressions as more fearful (Zhou & Chen, 2009) and to diminish positive emotional priming of facial affect perception (Pause, Ohrt, Prehn & Ferstl, 2004). Further, chemosensory anxiety signals may pre-attentively prime defensive behavior, as they augment the startle reflex in humans (Pause, Adolph, Prehn-Kristensen & Ferstl, 2009; Prehn, Ohrt, Sojka, Ferstl & Pause, 2006). Concerning the level of central nervous processing, chemosensory signals obtained in situations eliciting an extreme level of stress have been shown to activate anxiety related brain networks (Mujica-Parodi et al., 2009). On the other hand, chemosensory

signals obtained in a more common anxiety evoking situation seem to automatically recruit brain areas involved in the processing of social emotional stimuli, and in the regulation of empathic feelings (Prehn-Kristensen et al., 2009). Thus production of body odors is not only genetically determined, but seems to be subject to endocrine regulation.

Human chemosensory signals have further been suggested to be involved in human reproduction and mate choice. First of all, gender influences the production of body odors, as those can be differentiated in dependence of their owner's sex (Doty, Orndorf, Leyden & Kligman, 1978; Schleidt & Hold, 1982). These gender differences may arise from higher concentrations of odorous 16-androstenes in male as compared to female body odor (Gower et al., 1985). Moreover, female body odors carry information about the individual women's reproductive state (Stern & McClintock, 1998), and are able to shift the time of menstrual cycle onset in other women to conform with the donor's cycle (McClintock, 1971; Preti, Cutler, Ramon Garcia, Huggins & Lawley, 1986). Specifically, female body odors may modulate the timing of ovulation in other women by changing the frequency of pulsatile secretion of luteinizing hormone (Shinohara, Morofushi, Funabashi & Kimura, 2001). Similar effects have been shown for male axillary secretions, as exposition to those enhances the regularity of menstrual cycles in women (Cutler et al., 1986), again possibly due to affecting pulsatile secretion of luteinizing hormone (Preti, Wysocki, Barnhart, Sondheimer & Leyden, 2003). Quality judgments also indicate a role for human body odor in reproduction. Men appear to detect menstrual cycle related changes in female body odor, as they judge body odors obtained around ovulation as more pleasant and sexy than body odors obtained during other phases of the menstrual cycle (Doty, Ford, Preti & Huggins, 1975; Singh & Bronstad, 2001). Thus, ovulation may not be concealed and men could use ovulation-linked odors in their mate selection. In women, on the other hand, preferences for body odors of symmetrical men, that is, men who evidence phenotypic markers of genetic benefits, are correlated with their probability of conception (Gangestad & Thornhill, 1998).

However, not only such endocrine regulated but also genetically determined mechanisms are implicated in the role chemosensory signals might play in human reproduction. Human mate selection may in part rely on chemosensory communication (Ober et al., 1997), as the individual body odor is associated with the allelic profile of the human leucocyte antigen (HLA; reviewed by Singh, 2001). Products of the HLA play a crucial role in immune recognition, and thus, HLA-heterozygote individuals may have a selective advantage under pathogen pressure (Brown, 1997). Indeed, preferences for body odors have been shown to be negatively associated with HLA-similarity (Jacob, McClintock, Zelano & Ober, 2002; Wedekind & Füri, 1997). Moreover, chemosensory event-related potentials (CSERPs) in response to the body odors of HLA-similar persons show pronounced amplitudes of the P3 component (Pause et al., 2006), indicating a high subjective stimulus significance and suggesting that body odors of HLA-similar persons might function as social warning signals, possibly reducing the likelihood of mating with HLA-similar individuals.

Taking into account the sex-dimorphic effects on the perception of even single molecular compounds of human body odor conveying information about their owner's gender, and the notion that human mate choice may to some extent rely on chemosensory cues, it seems reasonable to assume that sexual orientation should affect the perception of human chemosensory signals.

Human sexual orientation

Sexual orientation refers to the degree of sexual attraction to either men or women (Rahman & Wilson, 2003). About 2 to 10% of the population are reported to identify as homosexual (Binson et al., 1995; Diamond, 1993; Kinsey, Pomeroy & Martin, 1948; Kinsey, Pomeroy, Martin & Gebhard, 1953; Sell, Wells & Wypij, 1995). Thus, homosexuality represents a small but significant minority phenotype in humans, displaying a remarkable cross-cultural consistency (Whitam, 1983; Whitam, Daskalos, Sobolewski & Padilla, 1998). The distribution of sexual orientation appears

to be bimodal in men, whereas it is more variable in women, typically resulting in higher degrees of "bisexuality" (Bailey, Dunne & Martin, 2000; Pattatucci & Hamer, 1995). Homosexuality aggregates in families (Bailey et al., 1999; Pattatucci et al., 1995), and twin studies (Bailey & Pillard, 1991; Bailey, Pillard, Neale & Agyei, 1993) as well as pedigree studies (Hamer, Hu, Magnuson, Hu & Pattatucci, 1993; Turner, 1995) suggest that this familiality is partly genetic, especially proposing an effect of X-chromosomal genes.

Current theories concerning the etiogenesis of sexual orientation focus on the sexual differentiation of the brain. The X-chromosome has been shown to carry an overabundance of genes affecting the development and function of gonadal steroid receptors in the brain (Saifi & Chandra, 1999). In fact, sex-atypical differentiation of the brain has been evidenced by neuroanatomical (Allen & Gorski, 1992; LeVay, 1991; Scamvougeras et al., 1994; Swaab & Hofman, 1990) and neuropsychological findings (Gladue, Beatty, Larsson & Staton, 1990; Hall & Kimura, 1995; McCormick & Wittelson, 1994; Rahman, Wilson & Abrahams, 2003; Sanders & Wright, 1997). The prenatal androgen theory states that these patterns of findings result from hormonal exposure during critical periods of development. In this view, homosexuality in men is due to under-masculinisation (partial absence of androgenising effects) and in women due to over-masculinisation (excess in androgenising effects; Collaer & Hines, 1995; Ellis & Ames, 1987).

Concerning traditional behavioristic and psychodynamic models of sexual orientation development empirical support is all but non existent (Gonsiorek & Weinrich, 1991). One psychosocial theory that has received some attention during the last years is Bem's theory of "Exotic becomes Erotic" (Bem, 1996). This theory proposes a gender non-conforming temperament to cause alienation from same-sex peers, which leads the child to regard them as "exotic". During puberty the "exotic" same-sex peers become eroticized due to a "general arousal mechanism". However, overall Bem's theory has received little support (see for example Peplau, Garnets, Spalding, Conley & Veniegas, 1998).

Given the reduced reproductive success of homosexual individuals and the genetic component to sexual orientation, several evolutionary theories have tried to explain how such genes could be maintained within populations. The most frequently cited evolutionary theory draws on kin selection, stating that homosexual individuals may have helped their siblings to reproduce more successfully. This way, genes for homosexuality survive through sibling lineages (Wilson, 1975). However, this theory has been criticized to be based on weak assumptions and to not fit the anthropological record (Kirkpatrick, 2000). Another theory focuses on parental manipulation of offspring, such that parents induce homosexuality to make their offspring less competitive in reproductive roles as well as increase assistance towards reproducing siblings (Trivers, 1974). This theory too has been criticized, as it is at odds with the Darwinian notion of parental inclusive fitness (Archer, 1996; Gallup, JR., 1995). Within other evolutionary considerations regarding sexual orientation, higher levels of empathy (and lower levels of aggressiveness) in gay[1] as compared to heterosexual men are discussed as a possible explanation why genes linked to homosexuality were not selected against.

Miller (2000) has proposed that sexual orientation is influenced by a number of genes, and is maintained by a mechanism of balanced polymorphism. The respective genes should, during development, affect the sensitivity of the male brain to hormones which shift it in a feminine direction. Possessing single alleles causes greater interpersonal empathy and reduced aggressiveness in heterosexual men, whereas possessing several such alleles produces homosexuality. Traits of greater interpersonal empathy and reduced aggressiveness should increase reproductive success in heterosexual carriers, as women show a preference for such traits in their partners (Sprecher, Sullivan & Hatfield, 1994). In women, such genes might influence traits such as competitiveness as well as lesbianism. This theory has received some support, as indeed there is evidence that gay men are more empathic (Salais &

[1] Throughout this dissertation, the terms „gay men“ and “lesbian women” are used rather than “homosexual men” and “homosexual women”, following the “Guidelines to Reduce Bias in Language” of the “Publication Manual of the American Psychological Association” (2001)

Fischer, 1995; Sergeant, Dickins, Davies & Griffiths, 2006) and less aggressive (Gladue & Bailey, 1995) than heterosexual men, but lesbian and heterosexual women seemingly do not differ in their general self-reported aggressiveness (Gladue, 1991; Gladue et al., 1995).

Chemosensory communication in the context of sexual orientation

To date, few studies have addressed chemosensory communication with regard to sexual orientation. Concerning steroid compounds of human axillary secretions, Savic, Berglund and Lindström (2005) reported gay men displaying hypothalamic activation when smelling androstadienone, similar to the response pattern observed in heterosexual women, and differing from the activation pattern of heterosexual men. As opposed to heterosexual women, the brain response to androstadienone in lesbian women has been shown not to involve the anterior hypothalamus (Berglund, Lindström & Savic, 2006), although differences between lesbian and heterosexual women were not as clear-cut as differences between gay and heterosexual men.

With regard to complex body odors, differences in preferences related to the gender and sexual orientation of the perceivers and the odor donors have been reported (Martins et al., 2005). For example, gay men consistently preferred body odors of other gay men, whereas in heterosexual men as well as in lesbian and heterosexual women body odors of gay men were the least preferred. Lesbian and heterosexual women preferred body odors from heterosexual individuals, whereas heterosexual men preferred body odors from lesbian women and other heterosexual men. Moreover, the hedonic evaluation of body odors has been shown to vary with the sexual orientation of the odor donor (Sergeant, Dickins, Davies & Griffiths, 2007). Heterosexual women judged body odors of gay men as more pleasant than body odors of heterosexual men. So far, however, no data are available permitting deeper insight into the possible functional significance of complex body odors related to sexual orientation.

Aim and objectives of the present work

The aim of the studies presented here was to explore sexual orientation related differences in human chemosensory communication. This challenge was addressed by the following issues, forming the basis of the individual studies.

Within the first study, differences in the perception of androstenone between gay and heterosexual men were examined. The general idea behind this study was to establish in a relatively simple way possible effects of sexual orientation not only on subjective evaluation of but particularly on the objectively measurable sensitivity to human chemosensory signals. Androstenone was chosen due to the fact that it is the only body odor compound that has been demonstrated to hold a certain significance in conveying information about gender (Pause, Rogalski et al., 1999). Moreover, women and men differ in their sensitivity to androstenone (Dorries et al., 1989; Hummel et al., 2005), thus suggesting that any sexual orientation related differences should most likely be reflected in this dimension of perception. As sexual orientation in men seems to be distributed bimodally, whereas women seem to be more flexible in their sexual orientation (Bailey, Dunne & Martin, 2000; Pattatucci & Hamer, 1995), effects of sexual orientation were assumed to be most definite in men.

Having established that the perception of the chemosignal androstenone varies with sexual orientation, the next step was to examine the functional significance of such differences. To address this question, analysis of CSERPs in response to complex body odors constituted the method of choice. However, in order to form a sensible base for approaching sexual orientation related differences within CSERPs, variation of the central nervous processing of complex body odors according to the perceiver's gender had to be explored. Thus, within a pre-study (study 2), focusing on the chemosensory communication of human anxiety signals, gender effects on CSERPs as well as current source densities (CSDs) were analyzed.

As the results indeed showed pronounced gender related variations of the CSERPs and the CSDs in response to the presented body odors, the third and forth study dealt with the central nervous processing of complex human body odors in

homosexual and heterosexual men and women. In line with earlier results showing sexual orientation related effects on the hedonic evaluation of body odors both on the side of the odor perceivers and the odor donors (Martins et al., 2005; Sergeant, Dickins, Davies & Griffiths, 2007), chemosensory stimuli here were composed of body odors from gay and heterosexual men, as well as lesbian and heterosexual women. Specifically, study 3 examined the central nervous processing of complex body odors in gay and heterosexual men. Here, participants were presented with body odors of potential partners (gay male and heterosexual female body odors), and with heterosexual male body odor serving as a control odor. Within study 4, lesbian and heterosexual women were exposed to body odor obtained from lesbian women as well as heterosexual men, and with body odors obtained from heterosexual women, and central nervous processing was analyzed. For both studies it was hypothesized that the central nervous processing patterns in response to the presented body odors would vary with the sexual orientation of the participants. Moreover, since body odors of individuals that should be avoided as mates elicit pronounced P3 peaks (see Pause et al. 2006), it was hypothesized that participants would display such pronounced activation in response to body odors obtained from individuals not constituting potential mates in terms of gender and/ or sexual orientation

Studies 5 and 6 were designed in order to examine possible behavioral effects of chemosensory stimuli related to gender and sexual orientation. Drawing on the notion that empathy might have played a significant role in maintaining homosexual orientation during evolution (Miller, 2000), studies 5 and 6 focused for one on differences in empathy between heterosexual and homosexual individuals. Spontaneous facial mimicry in response to pictures of positive and negative facial affect was measured as a correlate of empathy (Sonnby-Borgström, 2002). Moreover, as body odors have been shown to activate brain regions associated with the processing of social emotional stimuli and in the regulation of empathic feelings (Prehn-Kristensen et al., 2009), and facial mimicry has been reported being subject to

social context (Lanzetta & Englis, 1989; Weyers, Mühlberger, Kund, Hess & Pauli, 2009), body odors related to gender and sexual orientation were here implemented as social context cues. Within study 5, gay and heterosexual men's facial mimicry responses to sad and happy facial expression with or without chemosensory context cues were examined. Body odors obtained from potential partners (gay male and heterosexual female body odor, respectively) were presented, and additionally, heterosexual male body odor was introduced as a control odor. In study 6, lesbian and heterosexual women were presented with the same facial expressions, again with or without chemosensory context cues. Here, body odors obtained from lesbian women and heterosexual men were presented, added by heterosexual female body odor as a control odor. It was hypothesized that homosexual and heterosexual individuals should differ in their facial mimicry, and that chemosensory context cues obtained from potential partners should facilitate facial mimicry.

All of the studies reported here were carried out in accordance with the Declaration of Helsinki. Additionally, study 2 was approved by the ethical committee of the Medical Faculty of the University of Kiel. The studies 3-6 were approved by the ethical committee of the German Society of Psychology (DGPs) and by the Lesbian and Gay Federation in Germany (Lesben- und Schwulenverband in Deutschland, LSVD).

4. Materials and Methods

Body odor compounds

Within the first study, participants' sensitivity to the body odor compounds androstenone (98%, Sigma-Aldrich, Germany, No. W50900) and isovaleric acid (99%, Sigma-Aldrich, Germany, No. 129542) were assessed. Isovaleric acid here served as a control stimulus, as humans possess specific isovaleric acid receptors (Menashe et al., 2007) as they possess specific receptors for androstenone (Keller et al., 2007) but in contrast to androstenone (Dorries et al., 1989; Hummel et al., 2005,) gender seemingly does not affect the perception of isovaleric acid (Menashe et al., 2007).

Complex body odors

The complex body odors presented in studies 2-6 were sampled by fixing cotton pads in the odor donors' armpits. For the second study, 49 donors (28 males) donated axillary sweat in two situations: In the anxiety condition, donors wore the cotton pads during one hour preceding an important oral examination in order to acquire an academic degree at the university. In the control condition, donors underwent one hour of ergometer training. For the studies 3-6, body odors were sampled over the course of one night from eleven lesbian women, eleven heterosexual women, 13 gay and 14 heterosexual men. Following the completion of collection, all sweat samples were pooled with respect to gender and donation condition (study 2) or with respect to the donors' gender and sexual orientation (studies 3-6). Each of the final homogenized samples was divided into small portions and stored at -20° C.

All body odor donors were required to be of European origin, non-smokers, and not to be under any acute or chronic medication. Further, they should not suffer from any neurological, psychiatric, endocrine or immunological disease. Female donors had to have a regular menstrual cycle. Moreover, in order to donate axillary sweat for the studies 3-6, female were required not to use hormonal contraception, and during donation had to be in the follicular phase (day 5 to day 10) of their menstrual cycle. For study 2, the donors' body-mass index had to range between 19.0

and 28.0 kg/m², for studies 3-6, the donors' body-mass index had to range between 17.5 and 30.0 kg/m². All donors were instructed to refrain from eating garlic, onions, asparagus, or any other spicy or aromatic food during 24 hours prior to odor donation. They were further advised to refrain from using deodorants within this timeframe, and to wash their armpits exclusively with an odorless medical soap (Eubos®, Dr. Holbein GmbH, Germany).

Body odors were administered according to Kobal (Kobal, 2003). Samples were filled into glass chambers of a constant flow (2*3 channel-) olfactometer (OM6b, Burghart, Wedel, Germany, see Fig. 1). In the olfactometer, the glass tubes (see Fig. 1) containing the body odor samples were stored in a warm-water chamber, and the stimuli were delivered to the participants through a teflon tube. Chemosensory stimuli were presented birhinally by independent airstreams (100 ml/s). The temperature of the airflow at the exit of the olfactometer was 37° C and the relative humidity was set above 80%. Thus, the chemosensory but not the mechano- or thermosensory receptors in the nasal mucosa were activated.

Figure 1. left side: olfactometer OM6b, right: side glass tube prepared for body odor samples.

Pictures of facial affect

Within the studies 5 and 6, color pictures of happy and sad male and female faces were selected from the Karolinska Directed Emotional Faces database (KDEF, Lundqvist, Flykt & Öhman, 1998). The KDEF is a set of totally 4900 pictures of human facial expressions. It contains 70 (35 male) individuals displaying seven different emotional expressions (neutral, happy, angry, afraid, disgusted, sad, surprised), with each expression viewed from five different angles. The amateur actors modeling the facial expressions were between 20 and 30 years of age and wore no beards, mustaches, earrings, eyeglasses and no visible makeup. Actors were instructed to try to evoke the emotion that was to be expressed, and to try to make the expression strong and clear, while maintaining naturalness. Within a pre-study, 64 individuals (41 female, mean age 31.2 years, SD = 13.5, range 18-65 years) had selected those male and female actors, that according to their opinion, displayed the respective emotion at best. The pictures of the best six actors of each gender per emotion were selected, and presented in frontal view (see Fig. 2).

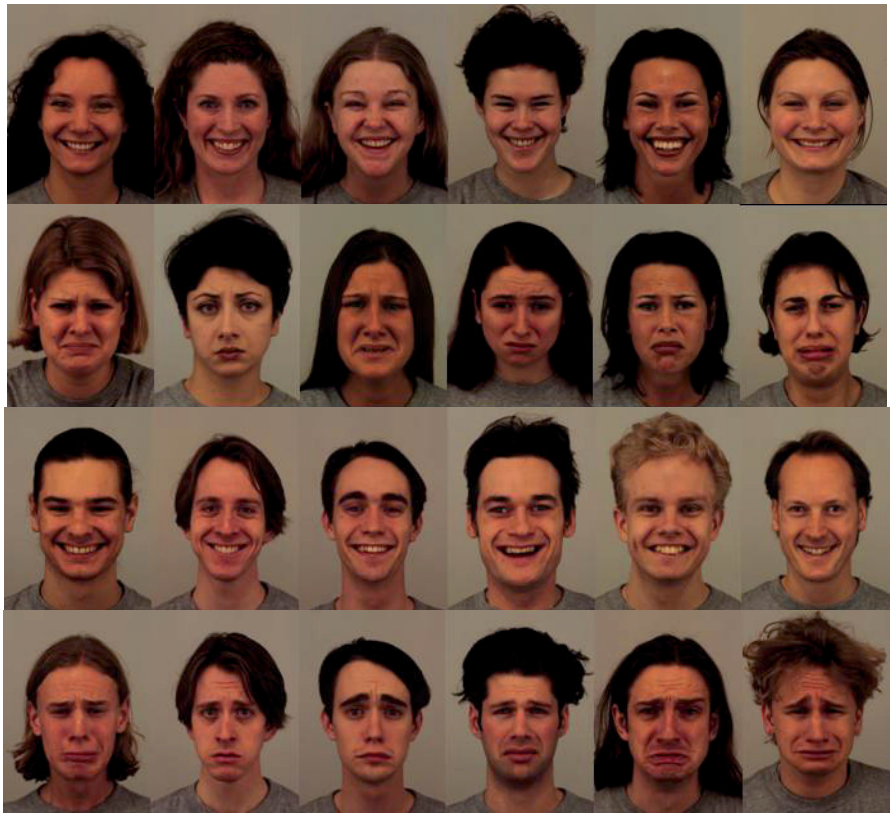

Figure 2. Pictures of male and female facial affect presented in studies 5 and 6.

Olfactory threshold tests

For the olfactory threshold tests carried out in study 1, 16 concentration steps of each androstenone and isovaleric acid were prepared. Androstenone was dissolved in 1,2-propanediol (99 %, Sigma-Aldrich, Germany, No. 134368). A concentration of 1.25 mg/ml was used as the highest concentration that was diluted 1:2 (v/v) for each consecutive step. Dilution steps were prepared that way rather than in decimal log steps due to the fact that sensitivity for androstenone is not normally but trimodally distributed in the population (Bremner, Mainland, Khan & Sobel, 2003; Wysocki & Beauchamp, 1991). In the lowest concentration 0.04 μg androstenone was diluted in 1 ml 1,2-propanediol. For isovaleric acid, diethyl phthalate (≥ 96%, Sigma-Aldrich, Germany, No. 80080) was used as the solvent. An 1:2 (v/v) dilution was the highest concentration which was diluted in half decimal log steps for each consecutive concentration. In the lowest concentration isovaleric acid was diluted 1:63,000,000 (v/v).

Thresholds were measured according to a two-alternative forced-choice single-staircase detection procedure (Doty & Laing, 2003). With this method, the odor concentrations are presented near the perception threshold in ascending and descending series. When seven staircase reversal points are obtained the procedure is finished and the geometric mean of the last four reversals is used as the threshold estimate.

Chemosensory event-related potentials

In order to obtain CSERPs, and to allow for CSD mapping, the EEG in the present studies was recorded with 8 mm Ag/AgCl electrodes from 60 (study 2, in reference to the left earlobe) and 61 (studies 3 and 4, with average reference) scalp positions, according to the extended 10-20 system (see Fig. 3). For analysis of the CSERPs, these electrode sites were subdivided into nine areas by averaging adjacent electrodes in anterior, central, and posterior areas for the left and right hemisphere as well as for midline electrodes.

CSERPs were used to investigate the time course of central nervous processing of complex body odors with a high time-resolution, and to subdivide different steps of information processing by analyzing different components (for an overview on the event-related potential technique in general see Luck, 2005). In order to determine the relative amount of neuronal activity engaged in stimulus processing, amplitudes of components related to early (N1, P2) and late (P3) stimulus processing were analyzed. In order to determine the speed of stimulus processing, latencies of the same components were examined.

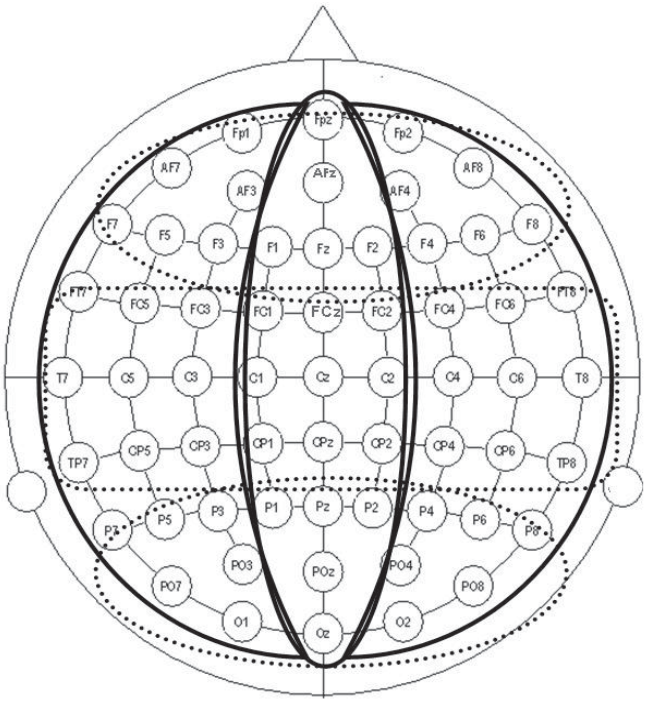

Figure 3. Schematic representation of the electrode array, with the electrodes assigned to the nine electrode pools.

The CSERP structurally resembles the event-related potentials (ERP) to acoustic or visual stimuli (Pause, Sojka, Krauel & Ferstl, 1996), with the early components (N1, P2) featuring more exogenous characteristics and the later component (P3) being more endogenous in nature. Thus, early components are typically affected by stimulus characteristics such as intensity, whereas the P3 reflects stimulus encoding and is modulated by subjective stimulus meaning, selective attention and expectation

(Pause, 2002). However, early components have also been reported to vary with attention (Krauel, Pause, Sojka, Schott & Ferstl, 1998). Within the current studies, the early components of the CSERP were detected between 300 and 700 ms after stimulus onset, whereas the P3 was detected between 700 and 1100 ms after stimulus onset. The overall longer latency of the CSERP components as compared to visual or auditory ERPs is probably explained by the finding that olfactory receptor neurons respond to stimulation with a latency of 140 – 570 ms (Firestein & Werblin, 1989).

Current source density

Within studies 2-4, CSD was used to provide insight as to the neocortical sources of the measured voltage. The CSD transform replaces the voltage values at electrodes that have valid head coordinates with the current source density at this points. It is calculated by applying the spherical LaPlace operator to the voltage distribution on the surface of the head at a fixed point in time (Perrin, Pernier, Bertrand & Echallier, 1989). Because the voltage distribution is recorded at a finite set of discrete electrodes, the spherical spline interpolation is used to estimate the entire voltage distribution. Due to the fact that current from deep brain sources dissipates widely over the entire scalp, CSD is insensitive for these sources, and preferentially emphasizes superficial current sources.

Facial electromyography

Measurement of facial electromyographic (EMG) activity in studies 5 and 6 was carried out in order to evaluate the extend of facial mimicry in response to pictures of facial affect. It has been found consistently that people, when presented with pictures of positive or negative facial expressions, tend to mimic those expressions spontaneously, rapidly and without the involvement of conscious cognitive processing (Dimberg, 1982; Dimberg, 1997; Dimberg, Thunberg & Elmehed, 2000). EMG was recorded on the left side of the face using bipolar miniature Ag/AgCl electrodes (inner diameter: 5 mm). The left side of the face was chosen because

emotional facial reactions are more pronounced on the left side as compared to the right side of the face (Dimberg & Petterson, 2000), which is in line with the notion that the motor cortex of the right brain hemisphere is predominantly involved in the control of spontaneously evoked emotional reactions (contralateral motor control; for an overview see Davidson & Hugdahl, 1995). Activity from the areas of the Musculus corrugator supercilii and of the Musculus zygomaticus major was recorded: Corrugator activity results in knitting of the brow, resembling negative facial affect display (sad or angry), whereas the zygomaticus pulls the lip corner up and back to form a smile.

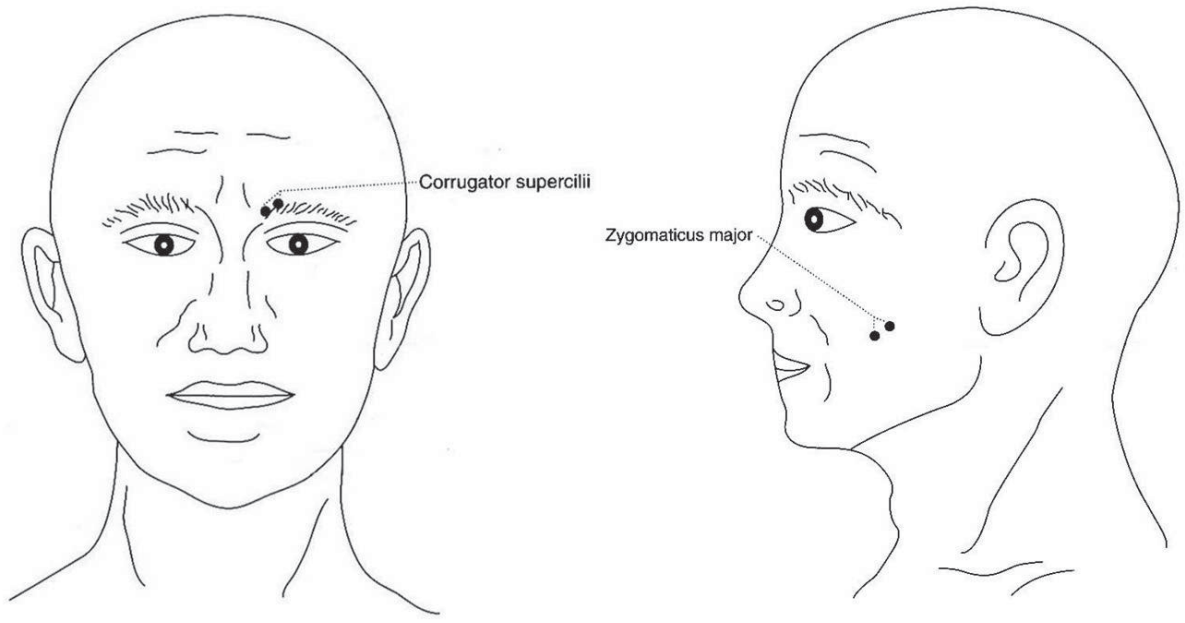

Figure 4. Electrode placements for recording of corrugator supercilii and zygomaticus major activity. Graphic adopted from (Fridlund & Cacioppo, 1986).

For recording of corrugator activity, one electrode was affixed directly above the brow on an imagery line that transverses the inner commissure of the eye, and the second electrode was positioned 1 cm lateral to, and slightly superior to, the first on the border of the eyebrow. Zygomaticus activity was recorded by placing one electrode midway between the corner of the mouth and the preauricular depression and placing the second electrode 1 cm inferior and medial to the first (see Fig.4; see Fridlund et al., 1986).

Emotional self-ratings

Throughout the here presented studies, participants reported their experienced emotion when presented with the chemosensory stimuli and the pictures of facial affect by means of the Self-Assessment Manikin (SAM; Bradley & Lang, 1994). This language-free, pictographic rating scale covers three dimensions of emotional experience, namely valence, arousal, and dominance (see Fig. 5). Indications on the dimension of valence may vary between -4, indicating negative emotion, and +4, indicating positive emotion. Self-description on both the arousal and dominance scales may vary between 1, indicating low levels of experienced arousal and dominance, and 9, indicating high levels of experienced arousal and dominance.

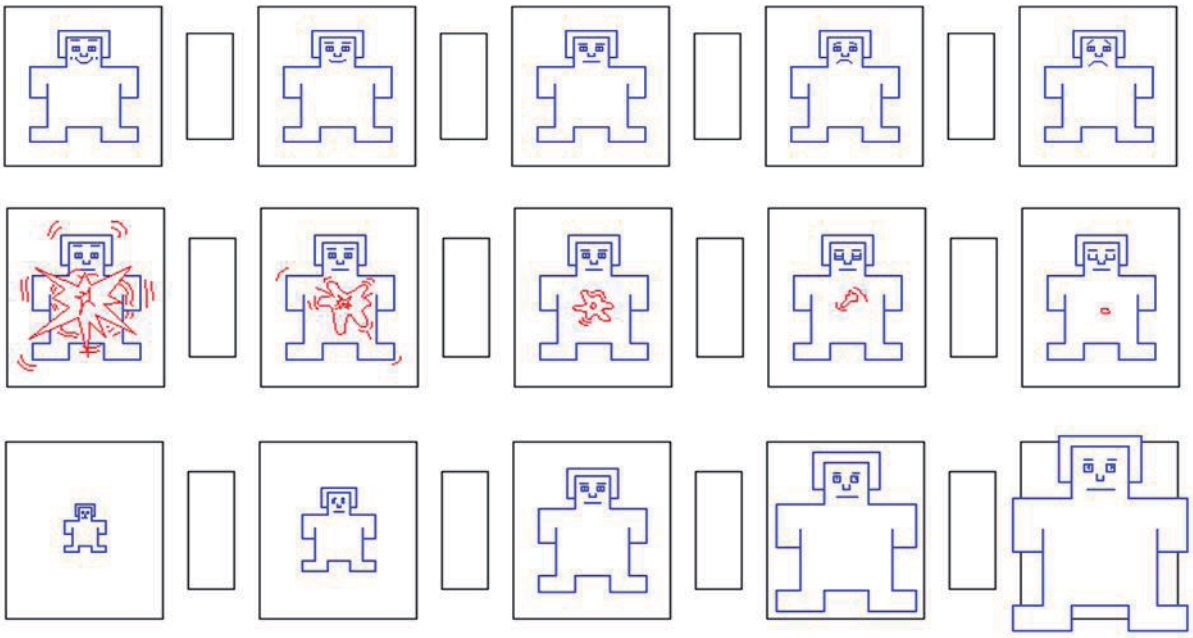

Figure 5. SAM scale. The first row depicts the emotional dimension of valence (-4 to +4), the second row depicts arousal (9 to 1), the third row illustrates dominance (1 to 9).

5. Overview of the Studies

Study 1: Effects of male sexual orientation on the perception of androstenone

Lübke, K., Schablitzky, S. & Pause, B. M. (2009). Male sexual orientation affects sensitivity to androstenone. *Chemosensory Perception, 2,* 154-160.

Within study 1, differences between gay and heterosexual men in their sensitivity to androstenone were examined. Moreover, effects of male sexual orientation on the hedonic evaluation and the reported emotion when presented with androstenone were investigated. Isovaleric acid served as a control odor. The sample consisted of 13 self-identified gay and 14 heterosexual men, differing not only in their self-description of sexual orientation, but also in correlates such as childhood-gender nonconformity (as assessed via the Childhood Gender Identity/ Gender Role Questionnaire; Zucker et al., 2006) or their adult gender role (as assessed by the Bem Sex Role Inventory; Schneider-Düker & Kohler, 1988). In addition, heterosexual men displayed higher degrees of homophobia than homosexual men (as assessed by means of the Modern Homophobia Scale; Raja & Stokes, 1998).

Olfactory thresholds were measured according to a two-alternative forced-choice single-staircase detection procedure (Doty et al., 2003). Odor ratings on perceived intensity, pleasantness, unpleasantness, and familiarity were obtained via four different visual analog scales. Concerning emotional responses, participants indicated their experienced valence, arousal, and dominance while smelling androstenone and isovaleric acid by means of the SAM.

Results show gay men displaying higher sensitivity to androstenone than heterosexual men, whereas no differences are observed concerning isovaleric acid. However, gay and heterosexual men do not differ in their hedonic evaluation or experienced emotion when presented with either odor. A post-hoc exploratory analysis of possible relationships between androstenone perception and the correlates of sexual orientation as well as homophobia reveal a positive relationship

between the perceived unpleasantness and intensity of androstenone and a masculine gender role as well as homophobia.

The observed difference in the perception of androstenone related to sexual orientation is in line with earlier studies demonstrating similar differences for preference ratings of complex body odors (Martins et al., 2005) as well as central nervous activation patterns in response to androstadienone (Savic et al., 2005). Following the idea that androstenone is a social chemosignal, as it transmits information about people's sex (Pause et al., 1999), the current results match findings of sexual orientation related differences reported for visual social stimuli. Functional magnetic resonance imaging showed heterosexual men and homosexual women responding more to female faces, whereas homosexual men and heterosexual women responded more to male faces (Kranz & Ishai, 2006). Like within the current study, these effects did not extend to the level of conscious evaluation.

The higher sensitivity to androstenone of gay as compared to heterosexual men could reflect an acquired sensitization to androstenone due to repeated exposure to complex male body odor. Sensitization due to exposure has been shown for androstenone (Wysocki et al., 1989) and, as discussed, androstenone seems to be an important substrate within male body odor (Pause et al., 1999). However, a genetic influence cannot be ruled out (Keller et al., 2007; Knaapila et al., 2008; Wysocki et al., 1984), and it may be the subject of further studies to explore a possible linkage between genes that influence androstenone receptor expressions and genes possibly related to sexual orientation.

A positive relationship between personal discomfort with gay men and a masculine gender role on one hand, and the perceived intensity and unpleasantness of androstenone on the other hand was observed. This may suggest that more homophobic men, who may also display a more masculine gender role, do not get in close contact with other men. Thus, they are less familiar with male body odor and judge androstenone as rather strong and unpleasant. Positive correlations between

familiarity and hedonic judgments of common odors have been shown within different populations (Ayabe-Kanamura et al., 1998; Distel et al., 1999).

Study 2: Gender effects on central-nervous processing of human chemosensory anxiety signals

Pause, B. M., Lübke, K., Laudien, J. H. & Ferstl, R. (2010). Intensified neuronal investment in the processing of chemosensory anxiety signals in non-socially anxious and socially anxious individuals. *PLoS One, 5*, e10342. Verfügbar unter: doi:10.1371/journal.pone.0010342.

Within the pre-study to the studies 3 and 4, gender effects on the central nervous processing of human chemosensory anxiety signals were examined. An additional experiment was carried out in order to explore effects of social anxiety on brain responses to the same chemosignals. Participants in experiment 1 were 28 (16 male) right-handed individuals, participants in experiment 2 were 16 (8 male) likewise right-handed, socially anxious individuals. Chemosensory stimuli were presented in an oddball paradigm (stimulus duration = 0.5 s; inter-stimulus interval = 9 s) of two blocks of 100 trials each (25 deviant and 75 standard stimuli, pseudo-randomized order). The EEG was recorded from 60 scalp locations. For analysis, the N1 and the P2 peak of the CSERP were detected and CSD maps were calculated.

In experiment 1, the amplitude of the P3 peak and the corresponding centrally located activation (as revealed by the CSDs) is generally larger in women than in men, who do not show reliable CSERPs in response to either stimulus. Furthermore, in female participants the P3 peak appears with a larger amplitude in response to chemosensory anxiety stimuli as compared to chemosensory control stimuli, associated with a medial frontal activation visible in the CSDs. Experiment 2 shows pronounced early processing of chemosensory anxiety signals in socially anxious participants.

The processing of axillary odors clearly recruited stronger neuronal activity in women than in men. The intense neuronal processing of body odor signals in women was accompanied by a differential response to the two chemosensory stimuli not observed in men. To date reported results concerning gender differences in the sensitivity to chemosensory anxiety signals (Chen et al., 2000; Mujica-Parodi et al., 2009; Pause et al., 2004; Prehn-Kristensen et al., 2009; Zhou et al., 2009), in response to common odors (Oloffson & Nordin, 2004; Stuck et al., 2006), and in response to emotional stimuli in general (Orozco & Ehlers, 1998; Rozenkrants & Polich, 2008) have been inconsistent. However, the stimuli administered in the present study were undetectable for the most part. The current results then suggest that gender effects on the processing of social emotional stimuli are most pronounced when those feature a weak perceptional salience (Li, Yuan & Lin, 2008; Schirmer, Striano & Friederici, 2005). Concerning the neuronal sources of activity in response to anxiety signals, women mainly recruited medial frontal brain areas, which have been shown to be activated in response to potentially harmful odors (Laudien, Wencker, Ferstl & Pause, 2008). With regard to the level of social anxiety, the here reported results are in line with a perceptional bias towards social and threat related information in socially anxious individuals (Kolassa et al., 2009; Kolassa & Miltner, 2006).

Studies 3 and 4: Effects of sexual orientation on the central nervous processing of gender and sexual orientation related chemosensory stimuli

Lübke, K., Hoenen, M. & Pause, B. M. (submitted). Accelerated processing of social chemosignals obtained from potential partners in regards to gender and sexual orientation. *Cerebral Cortex*.

Within the present studies, effects of sexual orientation on the central nervous processing of gender and sexual orientation related body odors in men (study 3) and women (study 4) were examined. The samples consisted of 28 (14 gay) male and 28 (14 lesbian) female participants. During EEG recording, 90 stimuli were presented

(stimulus duration = 0.5 s; inter-stimulus interval = 18-22 s), with 30 presentations of each body odor [heterosexual male, gay male (study 4: lesbian female), heterosexual female]. The EEG was recorded from 61 scalp locations. For analysis, the N1, P2 and P3 peak of the CSERP were detected and CSD maps were calculated. Further, participants reported their experienced emotion when presented with the body odors by means of the SAM.

Both men and women report feelings of unhappiness when presented with heterosexual male body odor whereas they report feelings of happiness when presented with female body odors. In response to gay male body odor, gay men display a shorter latency of the P2 peak than heterosexual men. The reverse pattern is observable in response to heterosexual female body odor. Further, gay men show a pronounced amplitude of the P3 peak in response to heterosexual male body odor. The corresponding CSD maps shows neuronal activation predominantly originating from medial frontal and left parietal areas in gay men. Lesbian as compared to heterosexual women show shorter P2 latencies in response to female body odors, the effect being prominent in response to the body odor of heterosexual women. Additionally, lesbian women display the largest P3 amplitude in response to heterosexual male body odor, accompanied by a pronounced medial frontal and medial parietal activity.

The present results indicate a processing advantage at the level of early stimulus encoding (P2 latency) for body odors obtained from potential partners in terms of gender (in lesbian women), and in terms of gender and sexual orientation (in men). For one, this accelerated processing may be attributed to previous frequent encounters with body odor produced by (potential) partners, as repeated exposure to a chemosensory stimulus has been shown to result in shortened latencies of early CSERP components, such as the P2 (Boulkroune, Wang, March, Walker & Jacob, 2007; Pause, Sojka, Krauel, Fehm-Wolfsdorf & Ferstl, 1996). Further, the observed effects may be related to attentional processes, as shorter P2 latencies in response to attended compared to non-attended chemosensory stimuli have been reported

(Krauel et al., 1998). Here, presentation of body odors of potential partners may have led individuals to allocate relatively more attention to these stimuli.

The pronounced P3 amplitude in response to heterosexual male body odor observed in both lesbian women and gay men is in line with the idea that body odors may function as potent social warning signals in the context of mate choice. A similarly larger P3 amplitude has been shown in response to body odors taken from HLA-similar persons (who should be avoided as potential mates) compared to the response to body odors from HLA-dissimilar persons (Pause et al., 2006). The neuronal activity correlated to the P3 peak was strongest in medial frontal and parietal areas. Activation in parietal areas may represent attentional processes (for an overview see Behrmann, Geng & Shomstein, 2004), whereas medial prefrontal activation could be related to flexible physiological adjustments in socially relevant situations (Damasio, 1994). As medial frontal activation has further been reported to be related to the perception of potentially harmful odors (Laudien et al., 2008), the observed pattern of activation might also correspond to the negative evaluation of heterosexual male body odor. Seemingly, whereas on a subjective level all participants reported negative feelings when smelling heterosexual male body odor, predominantly lesbian women and gay men showed corresponding physiological response patterns.

Studies 5 and 6: Effects of sexual orientation on facial mimicry with and without social context odors related to gender and sexual orientation

Lübke, K., Riether, N. & Pause, B. M. (submitted). Sexual orientation and related social chemosensory context cues affect facial mimicry. *Journal of Personality and Social Psychology*.

Within the present studies, effects of sexual orientation on empathy and facial mimicry in men (study 5) and women (study 6) were examined. Moreover, effects of social context odors on facial mimicry were investigated. Eleven gay and twelve

heterosexual men participated in study 5, and the sample in study 6 consisted of twelve lesbian and eleven heterosexual women. Participants self-rated their empathy by means of the Saarbrücker Persönlichkeitsfragebogen (SPF; Paulus, 2009). The EMG was recorded from the corrugator supercilii and zygomaticus major muscle regions while pictures of happy and sad male and female faces were presented. In studies 5 and 6, pictures of both male and female actors were presented without any context body odor. Additionally, in study 5, male faces were paired with heterosexual as well as gay male context body odor, and pictures displaying female faces were presented with heterosexual female context body odor. In study 6, female faces were presented with lesbian as well as heterosexual female context body odor, whereas male faces were presented in the context of heterosexual male body odor. Participants reported their experienced emotion when presented solely with the body odors and when presented with pictures of facial expression, both with and without context odors, by means of the SAM.

In study 5, gay men describe themselves as slightly more empathic than heterosexual men. The participants report more negative feelings when exposed to heterosexual male body odor as compared to gay male or heterosexual female body odors. Concerning facial muscle activity, men display stronger corrugator activity in response to sad as compared to happy female faces (500-1000 ms after picture onset. This effect was prolonged in gay men (1000-1500 ms after picture onset). In addition, all men report to experience unhappiness when presented with sad female faces and happiness when presented with happy female faces. A facial muscle response corresponding to mimicry to male faces only was observed with gay male context odor (500-1000 ms after picture onset). Without context odor, heterosexual men show stronger zygomaticus activity when presented with sad than when exposed to happy male faces, whereas gay men tend to show the reversed pattern (1500-2000 ms after picture onset).

Results of study 6 show lesbian women describing themselves as more empathic than heterosexual women. All women indicate experiencing feelings of

unhappiness when presented with heterosexual male body odor, whereas they indicate positive feeling when presented with female body odors. Concerning facial muscle activity, all women display stronger corrugator activity in response to sad as compared to happy faces irrespective of the actor's gender (1500-2000 ms after picture onset). In heterosexual women, this effect occurs even earlier (1000-2000 ms after picture onset). In lesbian women, a corresponding effect is evident early in response to female faces in the context of heterosexual female body odor (500-1500 ms after picture onset). All women report feelings of happiness when presented with happy faces, and feelings of unhappiness, when presented with pictures of sad facial affect.

The data suggest that both men and women display facial reactions to facial expressions, and that these are not only affected by the sexual orientation of the participants, but also by the gender of the person displayed, and further by chemosensory social context cues, comprised of human body odors. The observed stronger corrugator activation when exposed to negative compared to positive facial affect in men and women, indicating facial mimicry, is well in line with the current literature (see for example Dimberg et al., 2000; Dimberg, Thunberg & Grunedal, 2002; Sonnby-Borgström, Jönsson & Svensson, 2008). Moreover, data of the current studies suggest participants to experience emotional contagion which also has been reported repeatedly (Hess & Blairy, 2001; Sonnby-Borgström, 2002; Sonnby-Borgström & Jönsson, 2004). So far, for men to display a higher tendency for mimicking female facial affect has not been reported. However, in the current study this effect was especially prolonged in gay men, which may account for the divergent results compared to earlier studies. Moreover, heterosexual men showed facial muscle activity congruent with counter-mimicry. Studies directly relating empathy to facial mimicry have reported participants low in empathy to show increased zygomaticus muscle activity when presented with pictures of negative facial affect (Sonnby-Borgström, 2002). Thus it seems likely that the observed tendency for counter-mimicry is an indication of a lower level of empathy in heterosexual men,

especially as gay men showed the opposite response pattern. This notion fits well with the fact that gay men reported higher levels of empathy and further were more prone to display facial mimicry than heterosexual men.

The facilitation of facial mimicry in the context of gay male body odor is in line with evolutionary theories concerning the persistence of homosexual orientation. It has been proposed that homosexuality was not selected against because it aided same-sex affiliation and alliance formation (Kirkpatrick, 2000; Muscarella, 1999; Muscarella, 2000). As behavioral mimicry shares a bidirectional relationship with rapport and affinity (see Lakin, Jefferis, Cheng & Chartrand, 2003), a possible interpretation of the current data hints at priming of affiliation motives by gay male body odors.

The fact that lesbian women displayed facial mimicry predominantly when presented with female faces in the context of heterosexual female body odor is in line with neuroimaging studies showing pronounced neuronal activation in lesbian women when exposed to visual (Kranz et al., 2006) and chemosensory female social signals (Berglund et al., 2006). Together these results suggest that female social stimuli hold a certain significance for lesbian women. Given the link between behavioral mimicry and affiliation (Lakin et al., 2003), the present findings might reflect that lesbian women tend to affiliate specifically with other women, whereas heterosexual women show no gender-related differential response. Moreover, in lesbian women, female body odor might facilitate the tendency to affiliate.

6. General Discussion

Together, the studies reported here suggest a significant role for sexual orientation in human chemosensory communication. Sexual orientation has been shown to affect the perception of body odor compounds as well as the central nervous processing of complex body odors. Moreover, not only has a link between sexual orientation and interpersonal empathy been demonstrated, but also the effect of both gender related visual social cues and gender and sexual orientation related chemosensory social cues on its behavioral correlate. Factors that may account for the observed pattern of results may be related to learning as well as genetic influences. As discussed, experience affects chemosensory perception, since repeated exposure to a chemosensory stimulus has been shown to result in enhanced sensitivity (Dalton, Doolittle & Breslin, 2002; Jacob et al., 2006) as well as in shifts of hedonic evaluation (Jacob et al., 2006; Wang, Chen & Jacob, 2003), and changes in central nervous processing patterns (Boulkroune et al., 2007; Pause et al., 1996). On the other hand, odor perception, especially concerning body odor compounds, has been shown to be at least in part genetically determined (Keller et al., 2007; Knaapila et al., 2008; Wysocki et al., 1984). Concerning sexual orientation several family (Bailey et al., 1999; Pattatucci et al., 1995), twin (Bailey et al., 1991; Bailey et al., 1993) as well as pedigree studies (Hamer et al., 1993; Turner, 1995) have suggested a genetic component of sexual orientation. However, a possibly shared genetic basis for sexual orientation and odor perception remains to be investigated.

Within the current studies, the observed effects of sexual orientation were generally more pronounced in men as compared to women. As reported, female sexual orientation is considered more variable (Bailey et al., 2000; Pattatucci et al., 1995) and women are presumed to display greater erotic plasticity than men (Baumeister, 2000). The results of the current study correspond to this notion.

Importantly, patterns of central nervous responses have been shown not only to vary with the gender and the sexual orientation of the perceiving individual but also with the gender and the sexual orientation of the odor donors. Similarly, facial

mimicry was affected not only by gender but sexual orientation related chemosensory cues. In line with earlier findings demonstrating differences in the hedonic evaluation of complex body odors with regard to the sexual orientation of the odor donors (Martins et al., 2005; Sergeant et al., 2007), these results suggest that even the production of body odors varies with sexual orientation.

Within a first study following this dissertation, the subjective evaluation of body odors related to gender and sexual orientation was further examined. Moreover, it addressed the issue whether individuals are able to correctly assign the presented body odors to the group of individuals (gay male, heterosexual male, lesbian female or heterosexual female odor donors) they were obtained from. Preliminary results not only point at sustained effects of gender and sexual orientation concerning subjective ratings of the different body odors, but also suggest that individuals indeed are able to correctly identify the body odors (Lübke, Riether, Hoenen & Pause, in preparation). A second study was designed to review the assumption of sexual orientation as a seemingly unidimensional construct by designing a multi-item questionnaire, validated for the German language area. Preliminary results suggest that "sexual orientation" may indeed be comprised of several dimensions (Lübke, Kok, Niebuhr & Pause, in preparation).

In conclusion, the social chemosignal of human body odor has been shown to convey information about a potential partner being a poor or a eligible match in regards to gender and sexual orientation, and that this information is detected by individuals exposed to the chemosignal. Moreover, a first lead as to the behavioral relevance of such social chemosignals has been observed, namely the priming of the motive to affiliate. Together, this research may have broadened the knowledge on phylogenetically ancient mechanisms of mate choice in humans. However, more studies are needed that expand effects of gender and sexual orientation related chemosensory signals on other behaviors relevant in the context of mate choice, and to clarify the mechanisms of especially female intrasexual chemosensory communication.

7. References

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9. Original Research Articles

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Male Sexual Orientation Affects Sensitivity to Androstenone

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Abstract Androstenone has often been discussed as a human social chemosignal, as it is one of the major contributing substances to the human body odor for which humans possess specific receptors. Here, we investigated whether male sexual orientation influences the perception of androstenone. Sensitivity to androstenone, subjective ratings of intensity, pleasantness, unpleasantness, and familiarity of the odor, as well as self-reported emotional responses (valence, arousal, dominance) to the odor were assessed in 13 homosexual and 14 heterosexual men. Isovaleric acid served as a control substance. Homosexual men displayed significantly higher olfactory sensitivity to the odor of androstenone than heterosexual men ($p<0.05$), but they did not differ from heterosexual men in their sensitivity to isovaleric acid ($p>0.25$). Moreover, both groups did not differ in their judgments of or in their emotional response to androstenone or isovaleric acid. The current results indicate that men's sexual orientation significantly impacts the perception of androstenone but that this effect does not necessarily extend to subjective judgments.

Keywords Androstenone · Body Odor · Chemosensory Communication · Olfactory Sensitivity · Olfactory Threshold · Sexual Orientation

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Introduction

In many non-human species, chemosensory communication is crucial for mediating social behaviors, such as the recognition of conspecifics, communication of stress, and mating behavior (Wyatt 2003). Also, in humans, evidence increases that human body odor and especially axillary secretions convey a variety of social information, for example related to the degree of acquaintance (Lundström et al. 2008), the immunogenetic profile (Pause et al. 2006), or the endocrine status (Stern and McClintock 1998).

Single molecules that are thought to contribute significantly to the characteristic axillary odor in humans are, among others, (*E*)-3-methyl-2-hexenoic acid (Zeng et al. 1991), short-chain fatty acids like isovaleric acid (Preti et al. 1987), and 16-androstenes (Gower and Ruparelia 1993; Nixon et al. 1988). Because they are supposed to possess communicative features, androstenone and androstadienone are the most frequently investigated 16-androstenes in humans (Bensafi et al. 2004; Kirk-Smith and Booth 1980). Men display significantly higher levels of axillary androstenone (Gower et al. 1985) and plasma androstadienone than women (Brooksbank et al. 1969).

Sensory thresholds for androstenone and androstadienone are distributed tri- and bimodally, respectively, within the population. To both steroids, some individuals are highly sensitive; others are moderately sensitive (Lundström et al. 2003; Wysocki and Beauchamp 1991). In case of androstenone, some individuals even display specific anosmia, with rates varying from 11% up to 75% (Bremner et al. 2003). This diversity may be explained by the fact that androstenone produces a concentration-dependent trigeminal stimulation (Boyle et al. 2006).

Perception of androstenone and androstadienone is altered by experience, as repeated exposure to androstadie-

none (Jacob et al. 2006) as well as androstenone leads to sensitization (Wysocki et al. 1989). On the other hand, there is evidence that sensitivity to androstenone (Keller et al. 2007; Knaapila et al. 2008; Wysocki and Beauchamp 1984) and androstadienone is at least in part determined genetically. Only recently, a specific androstenone/androstadienone receptor was discovered, polymorphisms of which could account for differences in sensitivity (Keller et al. 2007).

There are considerable sex differences concerning the perception of androstenone and androstadienone. While almost all prepubescent children are able to detect androstenone (Schmidt and Beauchamp 1988), significantly more men than women lose the ability during puberty (Dorries et al. 1989). Moreover, the remaining osmic men become less sensitive to androstenone and androstadienone after puberty (Hummel et al. 2005). While women become more sensitive to androstenone during puberty (Dorries et al. 1989), they also tend to vary in their judgment of androstenone's pleasantness during the course of the menstrual cycle (Hummel et al. 1991). Further, sex dimorphic effects on central nervous processing level were reported, in that women, but not men, exhibited anterior hypothalamic activation in response to androstadienone (Savic et al. 2001).

Moreover, perception of androstadienone has been shown to vary with sexual orientation as well. Homosexual men exhibited anterior hypothalamic activation similar to that of heterosexual women when presented with androstadienone, the pattern of activation differing significantly from that of heterosexual men (Savic et al. 2005). In contrast to heterosexual women, homosexual women did not process androstadienone by the anterior hypothalamus (Berglund et al. 2006). In addition, even the preference for complex body odors seems to differ with sex and sexual orientation (Martins et al. 2005).

Isovaleric acid is, like androstenone and androstadienone, a compound of human body odor for which humans possess specific receptors (Menashe et al. 2007). However, Menashe et al. (2007) reported no sex-related effects on the perception of isovaleric acid or the distribution of its receptor genotypes.

The aim of the present study was to examine whether the perception of androstenone varies with the sexual orientation. Androstenone was chosen over androstadienone because results strongly indicate that it contributes significantly to at least male complex human body odor (Pause et al. 1999), which yet remains to be investigated for androstadienone.

Here, we tested heterosexual and homosexual men's sensitivity for androstenone as well as their subjective ratings of the odor and their subjective emotional response. Isovaleric acid served as a control because—like androstenone—it is a compound of human body fluids, but perception-related sex differences seem to be restricted to androstenone. Consequently, sexual orientation should affect the perception of androstenone but not of isovaleric acid.

Sexual orientation and its correlates were assessed by means of self-ratings and questionnaires.

Materials and Methods

Participants

Male homosexual and heterosexual participants were recruited via advertisement at the university and at local gay bars. Transsexual men were asked not to apply for participation.

As assessed in a semi-structured interview, only 34 of the initial 87 applicants were in good health, nonsmokers, were not under acute or long-term medication, had not had any surgery known to influence olfactory perception, did not suffer from any somatic or mental disease, and reported no drug abuse. Four of the remaining participants were excluded because they showed a tendency towards social conformity [as measured with the lie scale of the German Eysenck-Personality Inventory (EPI; Eggert 1974)]. Another three participants described themselves as bisexual [by means of a visual analog scale for description of sexual orientation (VAS-SO) or a German version of the Multidimensional Scale of Sexuality (MSS; Berkey et al. 1990)] and thus were excluded from participation.

Of the final 27 participants (age 18–40 years, M=25.42, SD=5.48), 13 participants were identified as homosexual and 14 as heterosexual by their indications on the VAS-SO and the MSS. Accordingly, both groups differed significantly in their self description via the VAS-SO [$t(25)=-60.856$; $p<0.001$]. There were no differences in age between the heterosexual (M=24.36, SD=3.00) and the homosexual group [M=26.54, SD=7.25; $t(16)=1.007$, $p>0.25$; Welch test (Welch 1947)]. Homosexual men reported more childhood gender nonconformity than heterosexual men [German version of the Recalled Childhood Gender Identity/Gender Role Questionnaire (RCGIR; Zucker et al. 2006); $t(25)=-3.839$, $p<0.01$, one-sided test]. Moreover, the homosexual participants described their adult gender role as more feminine than the heterosexual participants [Bem Sex-Role-Inventory (BSRI; Schneider-Düker and Kohler 1988); $t(25)=-2.541$, $p<0.01$, one-sided test]. In addition, heterosexual men displayed a higher degree of homophobia than homosexual men [German version of the Modern Homophobia Scale (MHS, Raja and Stokes 1998); "personal discomfort with gay men": $t(17)=-3.342$, $p<0.01$; Welch test; "institutional homophobia towards gay

men": $t(13)=-2.356$, $p<0.05$; Welch test, see Table 1]. However, both samples did not differ in their attitude towards deviance or changeability of male homosexuality [MHS, $t(20)=-0.536$, $p>0.50$; Welch test].

Participants gave written informed consent and were paid for participation. The study was carried out in accordance with the ethical guidelines of the American Psychological Association.

Odor Detection Thresholds

Sixteen concentration steps of each androstenone (5-α-androst-16-en-3-one, 98%, Sigma-Aldrich, Germany, no. W50900) and isovaleric acid (99%, Sigma-Aldrich, no. 129542) were prepared for the threshold tests. Androstenone was dissolved in 1,2-propanediol (99 %, Sigma-Aldrich, no. 134368). A concentration of 1.25 mg/ml was used as the highest concentration that was diluted 1:2 (*v*/*v*) for each consecutive step. In the lowest concentration, 0.04 μg androstenone was diluted in 1 ml. For isovaleric acid, diethyl phthalate (≥96%, Sigma-Aldrich, no. 80080) was used as the solvent. A 1:2 (*v*/*v*) dilution was the highest concentration which was diluted in half decimal log steps for each consecutive concentration. In the lowest concentration, isovaleric acid was diluted 1:63,000,000 (*v*/*v*).

Thresholds were measured according to a two-alternative forced-choice single-staircase detection procedure (Doty and Laing 2003). With this method, the odor concentrations are presented near the perception threshold in ascending and descending series. When seven staircase reversal points are obtained, the procedure is finished, and the geometric mean of the last four reversals is used as the threshold estimate.

Odor Ratings

Participants rated both odors with regard to perceived intensity (0=not detectable, to 10=extremely intensive), pleasantness (0=not at all pleasant, to 10=extremely pleasant), unpleasantness (0=not at all unpleasant, to 10=extremely unpleasant), and familiarity (0=not at all familiar, to 10=extremely familiar) on four different visual analog scales for the description of odors (VAS-O, 10 cm). As positive and negative emotions are processed by different neuronal networks within the human brain (for an overview, see LeDoux 2002), pleasantness and unpleasantness were assessed separately. For the ratings, participants were presented with the fifth dilution step of androstenone (78.13 μg/ml) and isovaleric acid (1:200 *v*/*v*).

Subjective Emotional Responses

Participants indicated their experienced pleasure (−4 to +4), arousal (1 to 9), and dominance (1 to 9) while smelling androstenone and isovaleric acid by means of the language-free Self-Assessment Manikin (SAM; Bradley and Lang 1994). Again, androstenone was presented in a concentration of 78.13 μg/ml and isovaleric acid in a dilution of 1:200 *v*/*v* (see odor ratings). The SAM scores were calculated as difference values compared to participants' emotional states at the beginning of the session (baseline measurement).

Questionnaires

In order to define participants' sexual orientation, three VAS-SO (10 cm) were used, ranging from "homosexual" to "heterosexual," "not at all homosexual" to "completely homosexual," and "not at all heterosexual" to "completely heterosexual," respectively. In addition, participants completed a German version of the MSS, which contrasts six proposed categories of bisexuality, as well as categories related to heterosexuality, homosexuality, and asexuality. It includes ratings of the behavioral and cognitive/affective components of sexuality.

Table 1 Mean scores and group differences on the Recalled Childhood Gender Identity/Gender Role Questionnaire, the Bem Sex Role Inventory and the Modern Homophobia Scale

	Homosexual men (n=13)		Heterosexual men (n=14)		
	M	SD	*M*	SD	
Recalled Childhood Gender Identity/Gender Role Questionnaire	3.63	0.47	4.23	0.33	$t(25)=-3.839$**
Bem Sex Role Inventory	−1.57	2.10	0.30	1.71	$t(25)=-2.541$**
Modern Homophobia Scale: Personal Discomfort	1.21	0.24	1.81	0.63	$t(17)=-3.342$**
Modern Homophobia Scale: Institutional Homophobia	1.41	0.26	1.49	0.50	$t(13)=-2.356$*
Modern Homophobia Scale: Deviance/Changeability	1.00	0.00	1.30	0.48	$t(20)=-0.536$

Group differences on the modern homophobia scale were calculated by means of the Welch test

M mean, *SD* standard deviation

*$p<0.05$; **$p<0.01$

A German version of the RCGIR was used to measure recalled gender-typed behavior during childhood (at the age up to 12 years). Five response alternatives per item (scored from 1 to 5) cover a range from gender-conform to gender-nonconform behavior (lower values indicate more childhood gender nonconformity).

In order to assess participants' current gender role, the German reconstruction of the BSRI was used. This instrument consists of adjectives reflecting character traits either socially desirable for men (masculinity scale) or for women (femininity scale). Scores equal to or above 2.025 resemble a masculine gender role, whereas scores equal to or below −2.025 refer to a feminine gender role. Values between −1 and 1 indicate an androgynous gender role, and values between the gender-typed and the androgynous category refer to either a masculine or a feminine tendency.

Via a German version of the MHS, participants' attitudes towards gay men were assessed. The scale comprises items reflecting the factors "personal discomfort" with gay men, "institutional homophobia" towards gay men, and "deviance/changeability" of male homosexuality. Higher values reflect more pronounced homophobia (five-point scale).

Procedure

Participants attended two sessions, during the first of which they indicated their sexual orientation (VAS-SO, MSS) and had their tendency towards social conformity (EPI) and homophobia (MHS) assessed. At the beginning of the second session, participants rated their emotional state (SAM, baseline measurement). Afterwards, threshold tests were carried out, and participants' subjective ratings of the odors (VAS-O) and their emotional response hereto (SAM) were recorded. As the order of presentation does not affect group differences, participants were always presented with androstenone first. In addition, participants described their adult (BSRI) and childhood gender role (RCGIR). These sessions lasted about 2 h (M=120 min, SD=26 min), and room temperature was kept constant (M=22 °C, SD=1 °C). Participants were tested individually.

Data Analysis

Analysis was based on ten participants per group only. Seven participants (three homosexual men, four heterosexual men) had to be excluded from analysis because they were not able to detect the highest concentration of androstenone and were thus labeled "anosmic."

Differences between the homosexual and heterosexual groups within the threshold data as well as within the subjective data were analyzed by means of repeated measures analysis of variance (ANOVA) with "odor" as within-subject factor and "sexual orientation" as between-subjects factor. Subsequently, significant group differences were analyzed by means of independent-sample t tests. An alpha level of 0.05 was used for all statistical analyses.

Results

Olfactory Thresholds

The ANOVA revealed a significant "odor" by "sexual orientation" interaction (F[1,18]=5.514; p<0.05; f=0.554). Follow-up t tests showed that homosexual men displayed lower androstenone thresholds than heterosexual men (t[18]=2.333; p<0.05, Cohen's d=1.04, see Fig. 1), with a mean threshold of 8.45 (SD=2.85) resembling a lower odor concentration than the mean threshold of the heterosexual group (M=5.55, SD=2.85). Both groups did not differ in their thresholds for isovaleric acid (t[18]=0.177, p>0.25, see Fig. 1).

Moreover, the ANOVA revealed a significant main effect of the factor "odor" (F[1,18]=84.748; p<0.001, f=2.171] with participants displaying higher sensitivity to isovaleric acid (M=12.54, SD=1,40) than to androstenone (M=7.00, SD=3.09).

Odor Ratings

Neither ANOVA concerning the subjective ratings showed a significant "sexual orientation" by "odor" interaction (all p values>0.10) or a significant main effect of the factor "sexual orientation" (all p values>0.25).

ANOVAs concerning intensity and unpleasantness both revealed a significant main effect of the factor "odor" (intensity: F[1,18]=14.005; p<0.05; f=0.883; unpleasant-

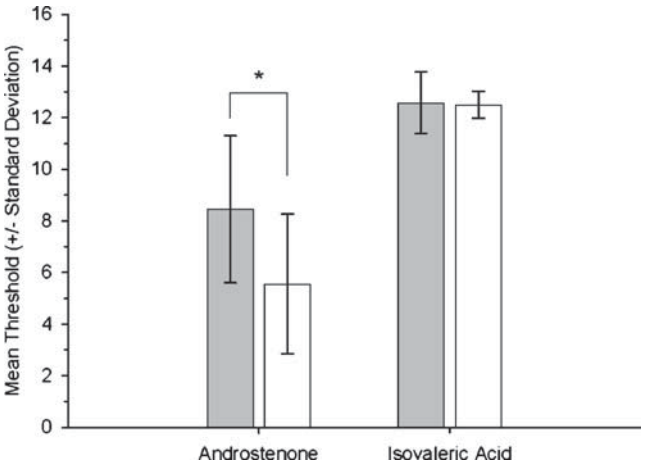

Fig. 1 Androstenone and isovaleric acid thresholds of homosexual (*gray bars*) and heterosexual (*white bars*) men. Note that higher values correspond to higher sensitivity; *p<0.05

ness: $F[1,18]=6.390$; $p<0.05$, $f=0.596$), with isovaleric acid being rated as more intensive ($M=8.60$, SD=1.70) and more unpleasant ($M=7.83$, SD=2.18) than androstenone (intensity: $M=6.18$, SD=2.54; unpleasantness: $M=6.00$, SD=2.93). Overall, pleasantness of both androstenone ($M=2.67$, SD=1.72) and isovaleric acid ($M=1.91$, SD=2.10) was rated relatively low. Both odors were rated as moderate familiar (androstenone: $M=4.00$, SD=3.43; isovaleric acid: $M=4.56$, SD=2.95).

Subjective Emotional Response

ANOVAs concerning participants' emotional response to the odors revealed no significant main effects of either "odor" or "sexual orientation" and no significant interaction of both factors (all p values>0.10).

Participants indicated feeling less happy ($M=-2.25$, SD=1.74), less dominant ($M=-1.55$, SD=1.54), and slightly more aroused ($M=0.60$, SD=2.09) in response to androstenone as compared to the baseline measurement. In response to isovaleric acid compared to baseline, participants described themselves as less happy ($M=-2.70$, SD=2.62), slightly more aroused ($M=0.95$, SD=2.21), and slightly less dominant ($M=-0.90$, SD=1.94).

Exploratory Data Analysis

Post hoc, an exploratory analysis of possible relationships between the assessed components of odor perception (sensitivity, ratings, and emotional response) and correlates of sexual orientation as well as homophobia was carried out.

Analysis revealed that the more participants indicated personal discomfort with gay men (MHS), the more intensive ($r=0.467$, $p<0.05$) and unpleasant ($r=0.450$, $p<0.05$) androstenone was judged. Moreover, there was a significant positive correlation between ratings of masculinity (BSRI) and rated unpleasantness of androstenone ($r=0.472$, $p<0.05$).

Discussion

Homosexual men display higher olfactory sensitivity than heterosexual men to androstenone, a putative social chemosignal in humans ($p<0.05$). However, sensitivity to a control odor (isovaleric acid) was not affected by differences in sexual orientation. In addition, correlative data suggest a positive relationship between perceived unpleasantness and intensity of androstenone and a masculine gender role as well as homophobia (all p values<0.05). According to self descriptions, the sexual orientation of the homosexual participants was significantly different from the sexual orientation of the heterosexual participants ($p<0.001$). Moreover, homosexual men remembered a higher degree of childhood gender nonconformity ($p<0.01$), indicated a less masculine adult gender role ($p<0.01$), and expressed homophobia to a lesser degree than heterosexual men (personal discomfort with gay men: $p<0.01$; institutional homophobia towards gay men: $p<0.05$).

Differences related to sexual orientation have been shown for preference ratings of complex body odors (Martins et al. 2005) as well as central nervous activation patterns in response to androstadienone (Savic et al. 2005). Extending these findings, the current data show that also the sensitivity to androstenone, a major component of human body odor, is related to sexual orientation. Together, these data suggest qualitative differences in the perception of human body odor and some of its specific components as a function of sexual preferences. As androstenone in particular is discussed as a substance contributing significantly to male but not female body odor (Pause et al. 1999), it most likely conveys social information especially about people's sex. Similar sexual-orientation-related differences have been reported for visual social stimuli. Kranz and Ishai (2006) presented heterosexual and homosexual men and women with pictures of male and female faces. Functional magnetic resonance imaging revealed that heterosexual men and homosexual women responded more to female faces, whereas homosexual men and heterosexual women responded more to male faces. On the other hand, subjective ratings of the faces did not differ between these groups, which corresponds well to the current results, indicating that the perception of visual and putative chemosensory social stimuli varies with sexual orientation but that this effect does not necessarily extend to subjective judgments. However, as subjective ratings are prone to greater noise than psychophysical data, the nonsignificant results in the present study could also be due to the relatively small sample size. In order to increase the internal validity of the study, the 27 participants were recruited particularly carefully out of 87 applicants. Hence, the possibility cannot be ruled out that differences within the subjective ratings might be observed within a larger sample, resulting in more statistical power. However, even within this selected sample, the size of the effect of sexual orientation on androstenone sensitivity was considerably large (Cohen's $d=1.04$).

For the control odor isovaleric acid, no differences with regard to the sexual orientation were observed, neither in sensitivity nor in subjective ratings or emotional response. Due to the fixed order of testing, possible fatigue effects could have reduced potential group differences. However, as participants displayed a much higher sensitivity for isovaleric acid than for androstenone ($p<0.001$), the occurrence of fatigue effects seems not to be likely.

There are at least three factors that could account for the observed difference in androstenone sensitivity between heterosexual and homosexual men. As discussed, thresholds as well as subjective judgments may in part be genetically determined (Keller et al. 2007; Knaapila et al. 2008; Wysocki and Beauchamp 1984). Future studies may explore if variations of the androstenone receptor genotype can account for the relatedness between androstenone perception and sexual orientation in men.

Another factor important for androstenone perception seems to be the hormonal status; as the olfactory threshold changes during puberty, pleasantness judgments vary with the female menstrual cycle, and men and women show significant differences in their ability to smell androstenone (Dorries et al. 1989; Hummel et al. 1991, 2005; Schmidt and Beauchamp 1988). Within this rationale, homosexual men's higher sensitivity to androstenone as compared to heterosexual men may originate from hormonal differences between those groups. Within studies concerned with male homosexuality, testosterone is the most investigated hormone, with some authors reporting higher (Brodie et al. 1974) and others reporting lower (Loraine et al. 1971) testosterone levels in homosexual men compared to heterosexual men. Results of a more recent study revealed no significant differences within testosterone levels at all (Neave et al. 1999). In addition to this inconsistency, an influence of particularly the testosterone level on androstenone perception is yet not known.

The third factor influencing the perception of androstenone is learning. As sensitization due to experience has been shown for androstenone (Wysocki et al. 1989) and androstenone seems to be an important substrate within the human body odor (Pause et al. 1999), the greater sensitivity to androstenone of the homosexual men compared to the heterosexual men could reflect an acquired sensitization to androstenone due to repeated exposure to the complex male body odor.

It is not yet known if there are any behavioral correlates for the enhanced sensitivity to androstenone displayed by the homosexual men. To our knowledge, there is only one experimental study with a homosexual sample in which behavior in response to androstenone, in this case local preference, was observed (Pause 2004). Results demonstrated that homosexual men and heterosexual women showed similar local preferences for a chair treated with androstenone compared to an untreated chair. This behavior was positively correlated to androstenone sensitivity. These results could suggest that, within persons favoring a male partner, a higher sensitivity to androstenone is related to some kind of approach behavior towards the source of the odor.

Even though subjective judgments of androstenone did not vary on a group level, our results suggest that a greater extent of personal discomfort towards homosexual men correlates with a more intensive and unpleasant androstenone rating, which also correlates with a more masculine gender role. More homophobic men who may also display a more masculine gender role may not get in close contact with other men. As a consequence, they are less familiar with male body odor and judge androstenone as rather strong and unpleasant. Correlations between familiarity and hedonic judgments of common odors have been shown within different populations (Ayabe-Kanamura et al. 1998; Distel et al. 1999).

As mentioned in the introduction, androstenone thresholds are not normally distributed within the population. Nevertheless, group differences within androstenone thresholds were analyzed parametrically. The Student's t test is considered to be quite robust against deflection from normality, and the sample sizes as well as the variances within the samples were equal (see Cohen 1965). Performing the corresponding nonparametric Mann–Whitney U test on the androstenone threshold data would have yielded similar results like the t test (U=22.50; p<0.05).

Conclusions

Men's sexual orientation has a significant impact on their sensitivity for a putative human social chemosignal carrying information about people's sex. These results support findings of other studies showing sexual-orientation-related differences in the perception of human visual social stimuli also conveying information about people's sex. Neither the effects of sexual orientation on the perception of chemosensory social stimuli nor its effects on the perception of visual social stimuli extend to the level of conscious evaluation. Future research should examine if and how such differences in the perception of social clues in general and the perception of androstenone in particular translate into behavior.

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Intensified Neuronal Investment in the Processing of Chemosensory Anxiety Signals in Non-Socially Anxious and Socially Anxious Individuals

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Abstract

Background: The ability to communicate anxiety through chemosensory signals has been documented in humans by behavioral, perceptual and brain imaging studies. Here, we investigate in a time-sensitive manner how chemosensory anxiety signals, donated by humans awaiting an academic examination, are processed by the human brain, by analyzing chemosensory event-related potentials (CSERPs, 64-channel recording with current source density analysis).

Methodology/Principal Findings: In the first study cerebral stimulus processing was recorded from 28 non-socially anxious participants and in the second study from 16 socially anxious individuals. Each individual participated in two sessions, smelling sweat samples donated from either female or male donors (88 sessions; balanced session order). Most of the participants of both studies were unable to detect the stimuli olfactorily. In non-socially anxious females, CSERPs demonstrate an increased magnitude of the P3 component in response to chemosensory anxiety signals. The source of this P3 activity was allocated to medial frontal brain areas. In socially anxious females chemosensory anxiety signals require more neuronal resources during early pre-attentive stimulus processing (N1). The neocortical sources of this activity were located within medial and lateral frontal brain areas. In general, the event-related neuronal brain activity in males was much weaker than in females. However, socially anxious males processed chemosensory anxiety signals earlier (N1 latency) than the control stimuli collected during an ergometer training.

Conclusions/Significance: It is concluded that the processing of chemosensory anxiety signals requires enhanced neuronal energy. Socially anxious individuals show an early processing bias towards social fear signals, resulting in a repression of late attentional stimulus processing.

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Introduction

Within all major taxa stress responses to danger are associated with the release of chemical stress signals, which induce physiological stress adaptations within surrounding conspecifics [1–6]. Different sensory systems seem to be specialized to process chemosensory stress signals in mammals (the main olfactory system, trace-amine-associated receptors, the vomeronasal organ, Grueneberg ganglion cells [see 7–10]).

In humans, the processing of chemosensory anxiety signals in the insula, precuneus, cingulate cortex, and in the fusiform cortex [11] has been discussed to resemble a contagion of the feeling of anxiety between the signal sender and the signal perceiver. However, the chemical communication of an extreme level of psychological and physiological stress (first time sky diving) results in a rather restricted activation of the amygdala [12]. Furthermore, in the context of chemosensory stress signals, the perceptual acuity for social safety cues is reduced [13], whereas the perceptual acuity for social cues of danger is increased [12,14]. On a behavioral level, chemosensory stress signals of conspecifics augment defensive reflexes (startle) in humans [15,16] and rats [17,18]. However, the attentional capacities for the identification of sweat stimuli donated by anxious subjects appear to be limited [19,20].

Very recently it has been shown, that the priming of withdrawal reflexes in the context of chemosensory anxiety signals is intensified in non-clinical socially anxious participants [15]. Thereby, it is suggested that socially anxious people might process such signals with a stronger neuronal investment than non-socially anxious people. As it is generally agreed that social phobia is associated with a bias in the processing of social information [21], an intensified neuronal processing of social fear signals might be highly disorder-specific [22].

In the present study, axillary sweat served as the anxiety signal and was collected from 49 students (28 males) while awaiting an oral examination at the university. The chemosensory control stimulus was composed of a sweat sample from the same participants while participating in an ergometer training. Upon completion of collection, all sweat samples were pooled with regard to the respective donation conditions and the donor's sex.

Each of the four final homogenized samples was divided into small portions of 0.4 g and stored at −20°C. For the EEG data recording, the small portions were filled into the glass bottles of the olfactometer and renewed after each experiment. In detail, the sweat donors and the sampling procedure are described elsewhere [11].

The aim of the first experiment was to investigate in a highly time-sensitive manner (analyzing chemosensory event-related potentials; CSERPs) whether and how chemosensory anxiety signals are processed by the brain. In the second experiment non-clinical highly socially anxious participants were investigated. In order to increase the statistical power of this first time-sensitive investigation of neuronal processing of anxiety sweat, the first experiment was analyzed independently of the second experiment. However, as a result, it will not be possible to directly compare the CSERPs of non-socially anxious and socially anxious participants. It was hypothesized that chemosensory anxiety signals in general are processed advantageously by the human brain (experiment 1). In addition, the processing of chemosensory anxiety signals in socially anxious participants should resemble their attentional bias towards potential social threat (experiment 2).

Methods

Study 1: Non-socially anxious participants

Participants. Twenty-eight right-handed participants (16 males) were investigated. They were on average 24.7 years of age (SD = 4.3, range = 19–38). As there are differences in the chemosensory perception of self and non-self [23], only those participants were selected who did not previously act as sweat donor. None of the participants suffered from any physical (self-report) or mental disease (as assessed with the Structured Clinical Interview for DSM-IV, SKID, German Version; [24]), and none reported using chronic or acute medication. All participants scored low in social anxiety (M = 11.07, SD = 3.30, according to the Social Interaction Anxiety Scale, SIAS; [25]). Participants who described themselves as medium or high socially anxious (SIAS > 16) were excluded from the study. In addition, the participants scored low in depression (M = 3.50, SD = 3.33, according to the Beck Depression Inventory, BDI, German Version; [26]) and reported a medium interest in social activities (M = 2.59, SD = 0.46, according to the agreeableness scale of the Big Five personality inventory, NEO-FFI; [27]). All of them reported to be non-smokers and to be of European origin. All female participants had a regular menstrual cycle (+/− 3 days). All participants gave written, informed consent and were paid for their participation. Both studies were carried out in accordance with the Declaration of Helsinki and were approved by the ethical committee of the Medical Faculty of the University of Kiel.

Olfactory hyposmia screening. Prior to EEG recording, all participants were screened for general hyposmia. For this purpose, the participants were requested to identify a bottle containing phenyl-ethyl alcohol [99%, Fluka, Germany, 1:200 (*v/v*) diluted in 1,2-propanediol] in a set of three bottles, with the remaining two bottles containing the same volume of solvent (two consecutive trials). No participant had to be excluded due to general hyposmia.

Stimulus presentation. For the recording of detection performance, stimulus ratings, and EEG activity, the chemosensory stimuli were presented according to the method described by Kobal [28], using a constant flow, six channel olfactometer (OM6b, Burghart Messtechnik GmbH, Wedel, Germany). Both nostrils were stimulated simultaneously, and accordingly, both air streams (100 ml/s each) were controlled by separate mass flow meters. In the olfactometer, the glass tubes containing the stimuli were stored in a warm-water chamber, and the stimuli were delivered (duration = 0.5 s) to the participants through a teflon tube. The temperature of the gas flow at the exit of the olfactometer was 37°C and the relative humidity was set above 80%. White noise of 80 dB (A) was presented binaurally over earplugs (Etymotic Research, ER3-14A), in order to prevent the participants from hearing the switching valves of the olfactometer.

Stimulus detection. To determine participants' detection performance of the chemosensory anxiety signal (anxiety sweat) and the chemosensory control stimulus (sport sweat), participants had to select the most intense stimulus from a series of three stimuli, with the remaining two blank odors consisting of pure cotton pad. This procedure was carried out twice. Participants who failed once to detect the chemosensory signal (the anxiety or the sport signal) were defined as non-detectors.

Procedure. All participants were tested individually in two separate sessions. During both sessions, they completed an identical experimental protocol, with the exception that either sweat donated by male or female persons was presented. The order of these sessions was balanced across participants.

Prior to the EEG recording, participants practiced the velopharyngeal closure technique [29]. The EEG was recorded during an olfactory oddball paradigm consisting of two blocks of 100 trials each (25 deviant chemosensory stimuli in a train of 75 standard stimuli). The stimuli were presented in pseudo-randomized order (with the first three trials being standards) for 0.5 s with an inter stimulus interval (ISI) of 9 s. In each of the two blocks, the standard stimulus was either the anxiety or the sport stimulus, with the order of these blocks counterbalanced across participants. The participants were instructed to avoid eye movements and to silently count the total number of odor presentations (deviants and standards).

Data Recording, Reduction and Analysis. The EEG was recorded in reference to the left ear lobe with Ag/AgCl electrodes (inner diameter 6 mm) from 60 scalp locations and the ear lobes, using an electrode cap (EasyCap GmbH, Germany). Two additional electrodes were placed near the right eye (3 cm above, inside the vertical pupil axis and 1.5 cm below, outside the vertical pupil axis) for the recording of vertical and horizontal eye movements. The impedance of the electrodes was always below 11 kΩ.

The physiological data were recorded, amplified, and filtered with the Aquire software (Version 4.2, NeuroScan Inc., Virginia, USA) using sampling rates of 200 Hz, a low-pass filter of 40 Hz (24 dB/ octave) and a 50 Hz notch filter. The ground was connected at FCz.

Offline, EEG signals were re-referenced to linked ear lobes, baseline corrected (0–1000 ms before stimulus onset), and high pass filtered (0.2 Hz, 24 dB/ octave). The data were then corrected for eye movements [30]. In addition, trials contaminated by any further artifacts (amplitudes between −50 and +50 μV) within the first 1400 ms after odor presentation were eliminated from the analysis. Subsequently, a zero phase shift digital low pass filter (Butterworth-filter, 7 Hz, 24 dB/ octave) was applied. The 60 scalp electrode positions were subdivided into nine areas, and a mean peak for each of these regions was calculated by averaging adjacent electrodes in anterior, central, and posterior areas for the left and right hemisphere as well as for midline electrodes [sagittal line: anterior (A), central (C), posterior (P); transversal line: left (L), midline (M), right (R); sagittal by transversal: AL: Fp1, AF7, AF3, F7, F5, F3; AM: Fpz, F1, Fz, F2; AR: Fp2, AF4, AF8, F4, F6, F8; CL: FT7, FC5, FC3, T7, C5, C3, TP7, CP5, CP3; CM:FC1, FC2, C1, Cz, C2, CP1, CPz, CP2; CR: FC4, FC6, FT8, C4, C6, T8, CP4, CP6, TP8; PL: P7, P5, P3, PO7, PO3, O1; PM: P1, Pz, P2,

POz, Oz; PR: P4, P6, P8, PO4, PO8, O2]. In relation to the baseline period two separate peaks were differentiated within predefined latency windows (N1: 350–500 ms, P3: 700–900 ms; as the odors were perceived at the threshold level and with a low distinctiveness, it was refrained from dividing the P3 into different subcomponents [see 31]).

A five-way ANOVA was calculated [factors: Chemosensory Condition (anxiety condition, sport condition), Sex of Donor (male, female), Sex of Perceiver (male, female), Sagittal Line (anterior, central, posterior) and Transversal Line (left, midline, right)]. Subsequently, nested effects were calculated in accordance with Page and coworkers [32]. However, due to the small number of deviant stimuli and the poor signal-to-noise ratio for deviant stimuli, only CSERPs in response to standard stimuli were analyzed. An alpha level of $p<0.05$ was used for all statistical tests. Huynh-Feldt corrected degrees of freedom were calculated and corrected p-values are reported. The presentation of the CSERP results will focus on the effects including the chemosensory condition, and only significant results will be reported. Current Source Density (CSD) maps were calculated using a spherical spline model ([33], order of splines: $m = 4$, maximal degree of legendre polynominals $= 20$).

Study 2: Socially anxious participants

Participants. Socially anxious participants were 16 (8 male) students of the University of Kiel (mean age $= 21.94$ years, SD $= 2.05$, range $= 20–26$). All socially anxious participants scored 22 or higher on the SIAS ($M = 29.31$, SD $= 6.07$). However, they described themselves as not being depressed (BDI: $M = 5.31$, SD $= 3.20$) and reported a medium tendency for being compassionate and cooperative towards others (agreeableness scale of the NEO-FFI: $M = 2.45$, SD $= 0.38$). None of them suffered from any physical (self-report) or mental disease (SKID), and none reported using chronic or acute medication. All of them were dextrals, non-smokers and of European origin, and none of them participated previously as sweat donor. No participant had to be excluded due to general hyposmia. All participants gave written, informed consent and were paid for their participation.

Procedure. The procedure and analyses followed the same protocol as in experiment 1.

Results

Study 1: Non-socially anxious participants

Stimulus detection. Some participants were able to detect an odor of single sweat samples (either male anxiety, or female anxiety, or male sport, or female sport). However, no participant was able to olfactorily detect both chemosensory stimuli of both donor genders (Table 1). The detection rates did not significantly vary between the two odor conditions or the sex of the sweat donor (binomial tests), or with the sex of the perceiver (Fisher test). As the chemosensory stimuli were not detectable for most of the participants, it was refrained from analyzing any odor ratings.

CSERPs. In female participants the P3 peak appeared with a larger amplitude in response to chemosensory anxiety stimuli as compared to chemosensory control stimuli [Fig. 1a; Chemosensory Condition by Sex of Perceiver: $F(1, 26) = 6.30$, $p = 0.019$, f (Cohen's f) $= 0.49$, Power $= 0.67$; nested effects: Chemosensory Condition in female participants: $F(1, 26) = 5.29$, $p = 0.030$, $f = 0.45$, Power $= 0.60$].

Male participants did not show reliable CSERPs in response to either stimulus (Fig. 1a). Accordingly, the P3 amplitude was generally larger in females than in males [Sex of Perceiver: $F(1, 26) = 10.87$, $p = 0.003$, $f = 0.65$, Power $= 0.89$]. This sex effect was evident at all three transversal electrode lines, but most pronounced at midline electrode positions [Sex of Perceiver by Transversal: $F(2, 52) = 7.84$, $p = 0.001$, $f = 0.55$, Power $= 0.94$].

The N1 component was not affected by the donation condition or the sex of the perceiver, and none of the components varied with the sex of the donor. The chemosensory condition did not affect the latency of any component.

CSDs. At the time of the maximum P3 amplitude (805 ms–810 ms), females showed much stronger neuronal activation than males in response to both chemosensory stimuli (Fig. 2). In females, centrally located neuronal activity was related to either odor source, whereas medial frontal activation was specifically associated with the perception of chemosensory anxiety signals. The prefrontal activation appears with a left sided dominance between 400 and 600 ms after stimulus onset and reappears between 700 and 900 ms with a medial dominance. After 900 ms the frontal activity vanishes. However, the non-specific central activation can be observed 500 ms after stimulus onset and remains with slight local changes for about 1 s (see Supplementary Material, Video S1).

Table 1. Odor detection performances (number/ percentages of participants who could detect single odors or combinations of odors).

Odour source	Sex of the odor donor	Number of odors	Non-anxious participants (N = 28)		Socially anxious participants (N = 16)	
			N	%	N	%
Anxiety sweat	Male	1	5	18	3	19
	Female	1	6	21	7	44
	Male and female	2	2	7	1	6
Sport sweat	Male	1	4	14	5	31
	Female	1	8	29	3	19
	Male and female	2	1	4	1	6
Anxiety and sport sweat	Male and female	4	0	0	0	0

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Study 2: Socially anxious participants

Stimulus detection. As within Study 1, the chemosensory stimuli were difficult to detect. No participant was able to detect all of the four olfactory stimuli (Table 1). The detection rates did not significantly vary with the chemosensory condition, the sex of the sweat donor (binomial tests), or with the sex of the perceiver (Fisher test). As the chemosensory stimuli were not detectable for most of the participants, odor ratings were not analyzed.

CSERPs. The amplitude of the N1 component in socially anxious female participants was larger in response to chemosensory stimuli donated during the anxiety condition than in response to chemosensory stimuli donated in the sport control condition above posterior scalp regions [Chemosensory Condition by Sex of Perceiver by Sagittal: $F(2, 28) = 5.93$, $p = 0.009$, $f = 0.74$, Power $= 0.84$; nested effects: Chemosensory Condition by Sagittal within female participants: $F(2, 28) = 5.94$, $p = 0.009$, $f = 0.65$, Power $= 0.84$; Chemosensory Condition within female subjects within posterior electrode positions: $F(1, 15) = 5.49$,

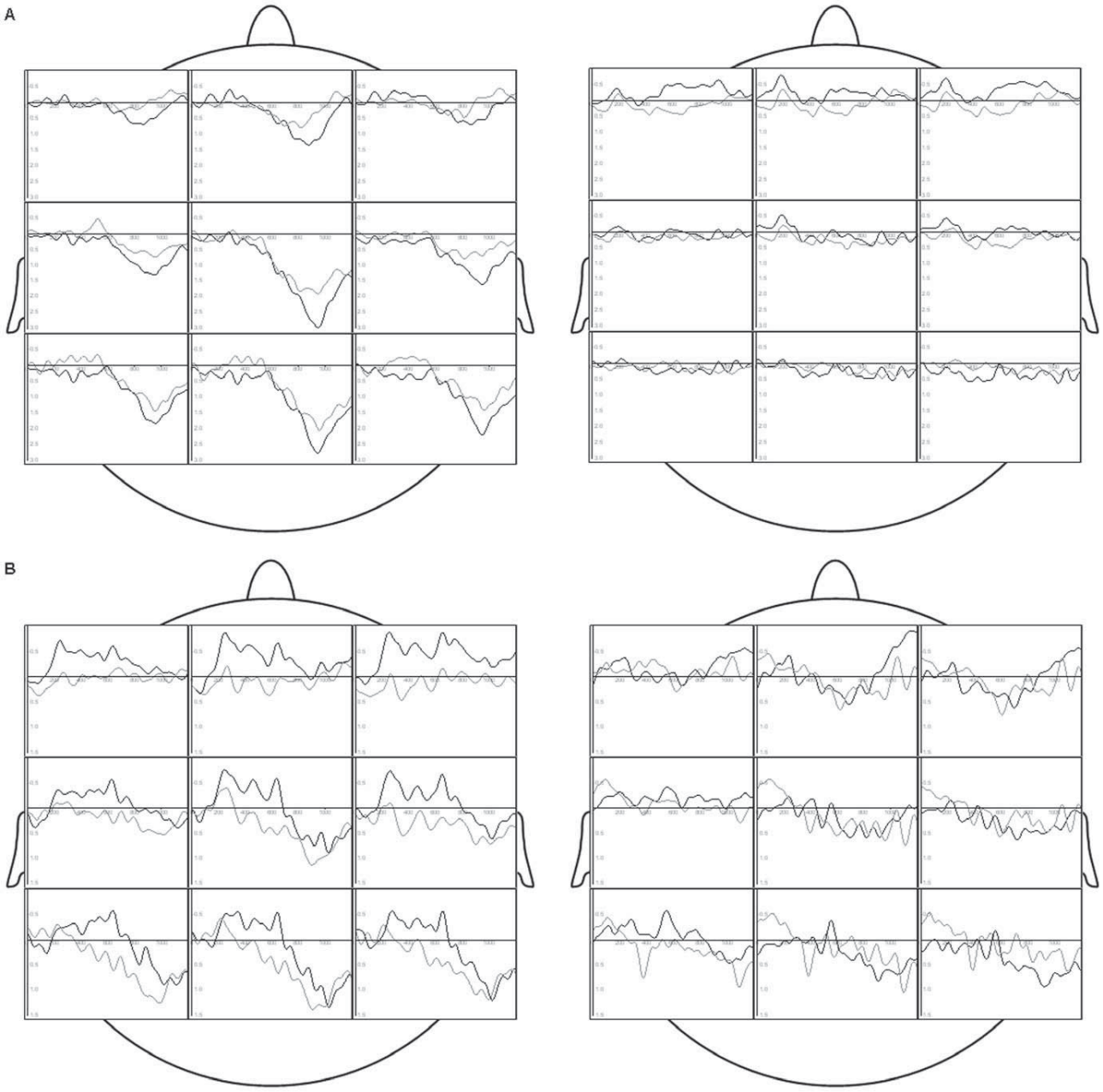

Figure 1. Grand Averages. (A) Grand Averages of the CSERPs of non-socially anxious female (left; N = 12, 24 sessions) and male (right; N = 16, 32 sessions) participants in response to sweat donated during the anxiety condition (black line) and the sport control condition (grey line) at pooled electrode positions (anterior left, anterior midline, anterior right, central left, central midline, central right, posterior left, posterior midline, posterior right). (B) Grand Averages of the CSERPs of socially anxious female (left; N = 8, 16 sessions) and male (right; N = 8, 16 sessions) participants in response to sweat donated during the anxiety condition (black line) and the sport control condition (grey line) at pooled electrode positions (see Fig. 1A).
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$p = 0.033$, $f = 0.61$, Power $= 0.59$] as well as at posterior left electrode positions [Chemosensory Condition by Sex or Perceiver by Sagittal by Transversal: $F\ (4, 56) = 4.22$, $p = 0.011$, $f = 0.55$, Power $= 0.90$; nested effects: Chemosensory Condition by Sagittal by Transversal within female participants: $F\ (4, 56) = 4.85$, $p = 0.006$, $f = 0.59$, Power $= 0.94$; Chemosensory Condition by Sagittal within female participants within left electrode positions: $F\ (2, 30) = 10.36$, $p < 0.001$, $f = 0.83$, Power $= 0{,}98$; Chemosensory Condition by Sagittal within female participants within midline electrode positions: $F\ (2, 30) = 4.04$, $p = 0.032$, $f = 0.52$, Power $= 0.68$; Chemosensory Condition within female participants within left electrode positions within posterior electrode positions: $F\ (1, 15) = 10.73$, $p = 0.005$, $f = 0.85$, Power $= 0.86$; see Fig. 1b].

In socially anxious participants, the N1 latency was shorter in response to chemosensory stimuli donated during the anxiety condition as compared to chemosensory stimuli donated during the sport control condition [Chemosensory Condition: $F\ (1, 14) = 9.80$, $p = 0.007$, $f = 0.84$, Power $= 0.83$]. This effect was more pronounced in male than in female participants [Chemosensory

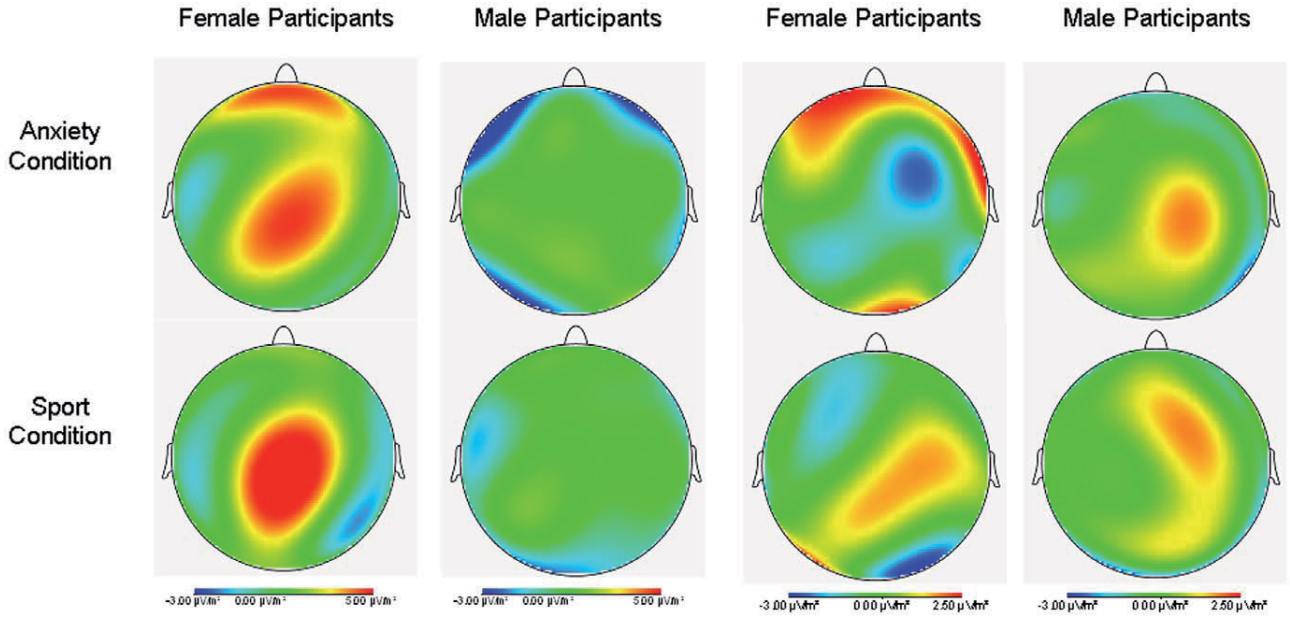

Figure 2. Current Source Density (CSD) maps. Neuronal processing of chemosensory anxiety signals and sport control stimului plotted as CSD maps. The two left columns show the CSDs of non-socially anxious female and male participants plotted for the time point of the maximum P3 amplitude. The two right columns show the CSDs of socially anxious female and male participants plotted for the time point of the maximum N1 amplitude. Blue colors represent a weaker magnitude (neuronal sinks) and red colors represent a stronger magnitude of CSD (neuronal sources).
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Condition by Sex of Perceiver: $F(1, 14) = 6.71$, $p = 0.021$ $f = 0.69$, Power $= 0.83$; nested effects: Chemosensory Condition within male participants: $F(1, 14) = 16.37$, $p = 0.001$, $f = 1.08$, Power $= 0.96$].

The amplitude and latency of the P3 were not affected by the chemosensory condition. The sex of the odor donor did not affect either component.

CSDs. At the time point of the maximum N1 amplitude (435–440 ms after valve activation), socially anxious female participants show stronger brain activations across left and right frontal scalp areas in response to chemosensory anxiety signals than in response to the control stimuli (Fig. 2). The frontal activity starts about 300 ms with a right sided maximum, and about 400 ms after stimulus onset with an additional left sided maximum. The frontal activity vanishes briefly at about 500 ms after valve activation and reappears between 500 and 700 ms with a medial maximum (see Supplementary Material, Video S2). During the entire time period of the CSERP no frontal neuronal sources can be detected in socially anxious females smelling sport sweat. Instead, the chemosensory control stimuli are processed by centrally located neocortical brain areas, between 400 and 600 ms after valve activation (Fig. 2).

Discussion

Study 1: Non-socially anxious participants

The EEG data reveal that the processing of chemosensory anxiety signals engages significantly more neuronal resources than the chemosensory processing of sport sweat. Thereby, the results are in line with recent brain imaging studies [11,12], demonstrating that the processing of chemosensory anxiety or stress signals requires more neuronal resources than the processing of body odor signals sampled in a non-emotional control condition. While the chemosensory stimuli used in the brain imaging studies were perceived to have a weak odor, most of the participants in the present experiment could not detect an odor when presented with the sweat samples. Therefore, the present study strongly supports the conclusion drawn by Mujica-Parodi et al. [12] and Prehn-Kristensen et al. [11], that the neuronal processing of chemosensory anxiety signals is not consciously mediated.

The processing of axillary odors unequivocally recruited stronger neuronal activity in females than in males. The intense neuronal processing of body odor signals in females was accompanied by a differential response to the two chemosensory stimuli within the P3 latency range. So far, two studies reported females to respond more sensitively than males to chemosensory anxiety signals [13,20], whereas other studies did not find any gender differences [11,12,15]. However, no study described a processing advantage for chemical signals of emotions in male participants. Even though a larger late positivity within the ERP in females has been observed in response to common odors [34] and socially relevant information (facial expressions of emotions; [35]), null effects of gender in emotional stimulus processing have also been reported (odors: [36]; emotional stimuli: [37]). Here, it is postulated that sex effects in the processing of emotional stimuli are most pronounced for social emotional stimuli [38] and most importantly, for emotional stimuli with a weak perceptional salience [39,40]. In accordance with this assumption, the stimuli administered in the present study were perceived subliminally by most of the participants. A comparable strong effect of gender was only found for the perception of subliminally presented facial expressions in the context of chemosensory anxiety signals [13].

Within the P3 latency range, females showed neuronal activity in response to both body odors above central brain areas. Additional medial frontal activation predominantly occurred in response to the anxiety signals. Recently, it was demonstrated by CSD analysis that neuronal activity located in medial frontal brain areas is most prominent in the P3 latency window and in response to potentially harmful odors [41]. In general, medial prefrontal activation is the most common observation in emotional activation

studies [42] and may be related to flexible physiological adjustments in (socially) relevant situations [43], as well as to the integration of sensory and cognitive information in order to adjust physiological activity [44].

Study 2: Socially anxious participants

Even though most of the socially anxious participants could not smell the chemosensory stimuli, the processing of anxiety-related chemosignals was faster and recruited more neuronal resources than the processing of sport-related chemosignals. Similar to non-socially anxious participants, the large potentials in response to chemosensory anxiety signals could be observed in female participants only. However, the faster processing of chemosensory anxiety signals was more pronounced in males.

Individuals scoring high in social phobia engage neuronal investment in the processing of chemosensory anxiety signals at an earlier processing level (N1) than non-socially anxious participants (P3). It has repeatedly been reported that social anxiety is characterized by a bias towards social and threat related information at an early level of information processing. Especially the P1 component of the visual ERP is increased in socially anxious participants during the processing of human faces [45,46]. This processing advantage occurs most distinctly in response to negative or angry facial expressions [47,48]. It is in line with the present study that the early processing advantage for negative social stimuli in social phobia patients is accompanied by a reduced late stimulus processing [46]. Hereby, it is indicated that attentional avoidance follows the initial orientation towards negative social information.

It has repeatedly been reported that the processing of neutral (e.g. [49]), negative (e.g. [50]), or angry faces (e.g. [51]) in social phobia requires an increased neuronal activity within the amygdala. However, just recently it could be shown that the increased amygdala activity seems rather to be related to the processing of angry than of fearful faces, and does not differentiate between generalized anxiety and social phobia [22]. In contrast, patients with social phobia but without generalized anxiety recruit more neuronal resources during the processing of fearful faces, especially in frontal brain regions (middle frontal gyrus/frontal polar cortex, BA 10; lateral frontal cortex, BA 46). The CSD maps of the present study indicate that socially anxious individuals engage similar brain circuits during the processing of chemosensory anxiety signals. However, in the present study, the degree of general anxiety was not obtained and therefore, could be confounded with social anxiety. Instead, as socially anxious and non-anxious participants scored low in depression and medium in social interest, it was excluded that the present effect of social anxiety is biased by the degree of depression or social interest.

General discussion

In combination, both studies demonstrate that distinct emotional states, like anxiety, are communicated chemosensorily. Especially in females, the processing of chemosensory anxiety signals requires more neuronal activity than the processing of body odor donated in an emotionally neutral condition. In socially anxious males, the processing of anxiety related chemosignals is faster than the processing of the control stimuli. Thus, the here reported results are in line with previous studies, indicating a chemosensory transmission of anxiety or stress-related experience in humans [11,12,14]. Most importantly, the present study could demonstrate that understanding the phenomenon of chemosensory communication of anxiety may have important applied consequences. Participants scoring high in social anxiety are at risk to develop social phobia, one of the most common anxiety disorders, with a lifetime prevalence of 12.6% [52]. As social phobia is a powerful risk factor for subsequent depressive illness and substance abuse [53], the explanation of its pathogenesis is of special importance. In the present study, socially anxious participants showed a processing advantage for chemosensory anxiety signals already at a very early level of stimulus processing. Therefore, in the future, this knowledge could gainfully be integrated into behavioral therapy of social anxiety.

It should be noted, that the effects reported here could be demonstrated even though the chemosensory stimuli were applied repeatedly (200 times) and with relatively short ISIs (9s) in each EEG session. Repeated odor stimulation would result in a strong habituation and thus a strong reduction of the CSERP amplitudes [28,54]. However, recent research indicates that chemosensory alarm signals are not processed in olfactory, but in separate sensory systems [8,10]. Accordingly, it has been reported that the response to social chemosignals is less prone to effects of habituation than the response to common odors [55]. For example, rodents respond to a continuous exposure to chemosensory alarm signals of consepecifics with a 40 min lasting autonomic stress response (increase in body temperature [56]).

Finally, as only anxiety related signals were investigated in the present study, it can not be ruled out whether the here reported effects are emotion specific or related to the perception of social distress signals in general. More studies are needed, exploring as to whether other basic emotions like anger, disgust or happiness chemosensorily induce specific physiological adaptations in the perceiver. In sum, the research on chemosensory communication of emotions may broaden the knowledge about phylogenetically ancient emotions in humans, offering a new method to define basic emotions in humans and understanding emotion related disorders.

Supporting Information

Video S1 Time course (0–1200 ms after valve activation) of the current source density distribution in non-socially anxious females (N = 12), perceiving chemosensory anxiety signals from male and female donors. Blue colors represent a weaker magnitude (neuronal sinks) and red colors represent a stronger magnitude of CSD (neuronal sources). Left sided, the voltage distribution is plotted as a grand average at Cz across the same female participants.
Found at: doi:10.1371/journal.pone.0010342.s001 (1.16 MB MP4)

Video S2 Time course (0–1200 ms after valve activation) of the current source density distribution in socially anxious females (N = 8), perceiving chemosensory anxiety signals from male and female donors. Blue colors represent a weaker magnitude (neuronal sinks) and red colors represent a stronger magnitude of CSD (neuronal sources). Left sided, the voltage distribution is plotted as a grand average at Cz across the same female participants.
Found at: doi:10.1371/journal.pone.0010342.s002 (1.30 MB MP4)

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Author Contributions

Conceived and designed the experiments: BMP RF. Performed the experiments: JHL. Analyzed the data: KL. Wrote the paper: BMP.

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Accelerated processing of social chemosignals obtained from potential partners in regards to gender and sexual orientation

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Abstract

Sexual orientation affects preferences for human body odor and cerebral processing of its components. Here, we investigate in a time-sensitive manner the processing of body odors by gay compared to heterosexual men, and lesbian compared to heterosexual women by analyzing chemosensory event-related potentials (CSERPs).

Cerebral processing (64-channel recording of CSERPs, current source density analysis) of gay and heterosexual male and heterosexual female body odor was recorded from 28 (14 gay) men, and processing of lesbian and heterosexual female and heterosexual male body odor was recorded from 28 (14 lesbian) women.

Gay and heterosexual men showed shorter P2-latencies in response to body odors of potential partners (gay male and female body odors, respectively). Moreover, gay men displayed the largest P3-peak in response to heterosexual male body odor, the activity originating from medial frontal and left parietal brain areas. Lesbian women responded with shorter P2-latencies than heterosexual women to female body odors, and showed the most pronounced P3-peak in response to male body odor. This activation originated from medial frontal and parietal brain areas. These findings demonstrate early processing advantages for potential partners' chemosignals, and, at the level of later stimulus evaluation, enhanced processing of chemosignals from individuals not constituting potential mates.

Introduction

It is well known that social behavior is mediated by chemosensory communication in many non-human species, (Wyatt 2003), and evidence is increasing that humans are also capable of chemosensory communication. Body odor, and especially axillary secretions have been demonstrated to convey information about individual identity (Porter 1999; Mallet and Schaal 1998), reproductive state (Stern and McClintock 1998), affect (Mujica-Parodi et al. 2009; Pause et al. 2010), or the level of acquaintance (Lundström et al. 2008). Moreover, human mate selection may in part rely on chemosensory communication (Ober et al. 1997), as individual body odor is associated with the allelic profile of the human leucocyte antigen (HLA). Chemosensory event-related potentials in response to body odors of HLA-similar persons show pronounced amplitudes of the P3 component (Pause et al. 2006), indicating high subjective stimulus significance. These results suggest that body odors of HLA-similar persons might function as social warning signals, possibly reducing the likelihood of mating with HLA-similar individuals. Furthermore, preferences for body odors are negatively associated with HLA-similarity (Wedekind and Füri 1997, Jacob et al. 2002).

In addition to the immunogenetic profile, gender also influences the production of body odors, as those can be differentiated in dependence of their owner's sex (Doty et al. 1978; Schleidt and Hold 1982). These gender differences may arise from higher concentrations of odorous 16-androstenes in male as compared to female body odor (Gower et al. 1985). On the other hand, gender has been shown to affect the perception of body odor compounds such as 16-androstenes (e.g. androstenone, androstadienone). In addition to gender differences in sensitivity to androstenone (Dorries et al. 1989, Hummel et al. 2005), sex dimorphic effects on the central nervous processing level have been reported: Women, but not men, exhibit anterior hypothalamic activation in response to androstadienone (Savic et al. 2001). Furthermore, recent data show intensified central-nervous processing of complex human body odors in women compared to men (Pause et al. 2010).

Sexual orientation also seems to influence body odor production and its perception. Gay men are more sensitive to androstenone than are heterosexual men (Lübke et al. 2009). Moreover, when smelling androstadienone, gay men display hypothalamic activation similar to that of heterosexual women, differing from the activation pattern of heterosexual men (Savic et al. 2005). As opposed to heterosexual women, the brain response of lesbian women to androstadienone does not involve the anterior hypothalamus (Berglund et al. 2006). Concerning complex body odors, results suggest that an individual's gender and sexual orientation have some impact on perception of and responses to body odors. Preference judgments and hedonic ratings of body odors strongly vary depending on the gender and sexual orientation of both the perceiver and the donor of the body odor (Martins et al. 2005, Sergeant et al. 2007).

As human body odor seems to convey information concerning the compatibility of a potential mate, which is processed within the central nervous system (Pause et al. 2006), and preferences for body odors depend on the sexual orientation of the odor donor and of the perceiver (Martins et al. 2005), we sought to determine whether chemosensory event-related potentials (CSERPs) vary in response to body odors in regards to the sexual orientation of the perceiving individual or to the kind of body odor presented.

The studies reported here were designed to investigate differences in the central-nervous processing of human body odors in men and women related to sexual orientation. It was hypothesized that gay compared to heterosexual men as well as lesbian compared to heterosexual women would display differing patterns of central nervous activation in response body odors obtained from potential partners. Since body odors of individuals that should be avoided as mates elicit pronounced P3 peaks (see Pause et al. 2006), it was hypothesized that participants would display such pronounced activation in response to body odors obtained from individuals not constituting potential mates in terms of gender and/ or sexual orientation. Therefore, two studies were conducted. The first study was designed in order to investigate

sexual orientation related differences in men's central nervous processing of heterosexual female and gay male body odors as chemosensory signals obtained from potential partners, while heterosexual male body odor was introduced as a control odor. Within the second study, differences between lesbian and heterosexual women in the central nervous processing of body odors obtained from lesbian women and heterosexual men were examined, with body odor of heterosexual women being presented as a control odor.

Study 1: Male Participants

Materials and Methods

Participants

Participants were recruited via newspaper advertisement and advertisement at the university and at local gay bars. Thirty right-handed men (15 gay men) participated in the experiment however, data from one heterosexual and one gay male participant had to be excluded from analysis due to pronounced EEG artifacts (see EEG data reduction), resulting in a total of 28 participants. None of these participants reported a history of chronic medication, of neurological, psychiatric, endocrine or immunological diseases or diseases related to the upper respiratory tract. All participants reported to be of European origin and none of them showed a tendency towards social conformity [as measured with the lie scale of the German Eysenck-Personality Inventory (EPI, Eggert 1974)]. Four heterosexual and five gay male participants reported being regular smokers, and the groups did not differ in their smoking behavior ($P = 1.000$, Fisher's Exact Test). Participants had a mean age of 28.5 years (SD = 7.2; range = 20-44 years), and there were no age differences for heterosexual and gay male participants [$T(26) = 1.56$, $P > 0.10$]. No participant had previously acted as sweat donor.

Participants' sexual orientation was assessed by means of the Kinsey scales of sexual behavior and sexual fantasies (Kinsey et al. 1948) as well as by means of visual analog scales for describing homosexuality and heterosexuality. According to their self-description (see

Tab. 1), heterosexual and gay male participants differed significantly on both Kinsey scales [behavior scale: $T(13) = 60.35$, $P < 0.001$, Welch-Test (Welch 1947); fantasy scale: $T(23) = 32.29$, $P < 0.001$, Welch-Test], as well as on both visual analogue scales (homosexuality: $T(18) = 31.49$, $P < 0.001$, Welch-Test, heterosexuality: $T(18) = -41.12$, $P < 0.001$, Welch-Test].

- Table 1 -

Participants gave written informed consent and were paid for their participation. Both of the studies reported here, including the sweat sampling procedures, were carried out in accordance with the Declaration of Helsinki and approved by the ethical committee of the German Society of Psychology (DGPs). Additionally both studies were approved by the Lesbian and Gay Federation in Germany (Lesben- und Schwulenverband in Deutschland, LSVD).

Chemosensory stimuli

Axillary sweat was sampled by cotton pads over the course of one night from 11 heterosexual women, 13 gay and 14 heterosexual men. The donors indicated their sexual orientation on visual analog scales for describing homosexuality (ranging from 0 = “not homosexual” to 10 = “homosexual”) and heterosexuality (ranging from 0 = “not heterosexual” to 10 = “heterosexual”). Both heterosexual men and women differed significantly from gay men in their self-description on both scales [men, homosexuality: $T(25) = 62.17$, $P < 0.001$, men, heterosexuality: $T(25) = -58.77$, $P < 0.001$, women, homosexuality: $T(22) = 46.93$, $P < 0.001$, women, heterosexuality: $T(22) = -41.45$, $P < 0.001$].

Donors were on average 26.1 years old (SD = 5.6, range = 18-42), and there were no differences in age between heterosexual men (M = 24.4, SD = 3.0), heterosexual women (M = 27.7, SD = 5.9) and gay men [M = 26.5, SD = 7.3, $F(2,35) = 1.19$, $P > 0.250$].

All donors reported being of European origin, and denied any acute or chronic medication. Furthermore, no donor indicated suffering from any neurological, psychiatric, endocrine, or immunological disease, or using drugs. Their body-mass-index ranged from 18.5 to 29.1 kg/m^2 (M = 23.4, SD = 3.1), and all of them were non-smokers. Female donors reported having a regular menstrual cycle and denied use of hormonal contraception. Of the female donors, seven reported to regularly shave their axillary hair (missing data: 4). Concerning the male odor donors, seven gay (missing data: 1) and six heterosexual men (missing data: 2) reported to regularly shave their axillary hair. Accordingly, female donors differed from heterosexual male donors in their shaving habits ($P = 0.044$, Fisher's Exact Test), whereas female and gay male donors ($P > 0.100$, Fisher's Exact Test) as well as gay male and heterosexual male donors did not ($P = 1.000$, Fisher's Exact Test). The donors were instructed to refrain from eating garlic, onions, asparagus, or any other spicy or aromatic food during the 24 hours prior to the odor donation. They were further advised to refrain from using deodorants within this timeframe, and to wash their armpits exclusively with an odorless medical soap (Eubos®, Dr. Holbein GmbH, Germany). Female donors were required to be in the follicular phase of their menstrual cycle (day 5 to day 10 of the menstrual cycle). All donors gave written informed consent, and were paid for their donation.

Following the completion of collection, all sweat samples were pooled with respect to the donor's sex and, in case of male donors, with respect to their sexual orientation. Each of the final three homogenized samples were divided into small portions of 0.3 g and stored at -20 °C.

Self ratings of emotions

In order for the participants to indicate their experienced emotions when smelling the body odors, they were presented with three glass bottles containing one portion of 0.3 g cotton pad worn by either heterosexual men, gay men, or heterosexual women. Participants indicated their experienced emotional valence (-4 to +4), arousal (1 to 9), and dominance (1 to 9) while smelling the body odors by means of the language-free Self-Assessment Manikin (SAM, Bradley and Lang 1994).

Olfactory hyposmia screening

Prior to EEG recording, all participants were screened for general hyposmia. For this purpose, the participants were required to identify a bottle containing phenyl-ethyl alcohol [99%, Fluka, Germany, 1:100 (*v/v*) diluted in diethyl phthalate] from a set of three bottles in two consecutive trials, with the remaining two bottles containing the same volume of solvent. No participant had to be excluded due to general hyposmia.

Stimulus presentation

For the recording of the EEG activity and stimulus detection performance, chemosensory stimuli were presented according to the method described by Kobal (2003), using a constant-flow (100 ml/s; stimulus duration = 0.5 s), six channel olfactometer (OM6b, Burghart, Wedel, Germany). Both nostrils were stimulated simultaneously, and accordingly, both air streams were controlled by separate mass flow meters. In the olfactometer, the glass tubes containing the stimuli were stored in a warm-water chamber, and the stimuli were delivered to the participants through a teflon tube. The temperature of the air flow at the exit of the olfactometer was 37 °C and the relative humidity was set above 80%. White noise of 80 dB (A) was presented binaurally over earplugs (Etymotic Research, ER3-14A), in order to prevent the participants from hearing the switching valves of the olfactometer.

Stimulus detection

To determine participants' detection performance of the three body odors, participants were required to indicate within a given timeframe after stimulus presentation whether or not they believed they had detected an odor. Detection performance was calculated as percentage of detected from presented odors.

Procedure

All participants were tested individually in two separate sessions. Within the first session, participants indicated their emotional responses to the odors.

Prior to the EEG recording in the second session, participants practiced the velopharyngeal closure technique (Pause et al. 1999), and were instructed to avoid eye and body movements. During EEG recording, 90 stimuli were presented, with 30 presentations of each body odor (heterosexual male, gay male, heterosexual female). The stimuli were presented in a previously randomized, fixed order (with the restriction that the same stimulus could be presented no more than three times in a row). At the beginning of each trial, a fixation cross was presented on a screen for 5.5 s, and odors were presented for 0.5 s, 2 s – 3 s seconds after cross-onset (randomized). Subsequent to the fixation cross, the screen turned black for 2 – 4 s (randomized), followed by the question "Did you smell anything?" appearing on the screen for 3 s. Within this timeframe, participants were able to indicate their answer by pressing a mouse-button (left = yes, right = no). Afterwards, again a black screen was again presented for 0.5 s, followed by a presentation of a picture with slightly positive valence, taken from the International Affective Picture System (IAPS, Lang et al. 1997) lasting 4 s. These pictures were presented in order to keep the participants alert during the relatively long interstimulus intervals (18-22 s, randomized). The trials ended with the presentation of another black screen, lasting 1 s - 5 s (randomized).

Data Recording, Reduction and Analysis

The EEG was recorded in reference to the average across all electrodes with Ag/AgCl electrodes (inner diameter 6 mm) from 61 scalp locations using an electrode cap (EasyCap GmbH, Germany). Two additional electrodes were placed near the right eye (3 cm above, inside the vertical pupil axis and 1.5 cm below, outside the vertical pupil axis) for the recording of vertical and horizontal eye movements. The impedance of the electrodes was usually below 10 and always below 20 kΩ.

The physiological data were recorded, amplified, and filtered with the BrainVision Recorder software (Brain Products GmbH, Munich, Germany) using a sampling rate of 250 Hz, a low-pass filter of 40 Hz (24 dB/ octave) and a 50 Hz notch filter.

Offline, EEG signals were high pass filtered (0.05 Hz, 24 dB/ octave), afterwards corrected for eye movements (Gratton et al. 1983) and baseline-corrected. Subsequently, trials contaminated with artifacts (due to sweating, movements, or pronounced alpha-activity) were eliminated. Data of one heterosexual and one gay male participant were excluded from further analysis due to less than 10 of 30 trials in one or more odor condition being free of artifacts, resulting in a total of 28 participants. Prior to averaging, signals were low pass filtered (7 Hz, 24 dB/ octave). The 61 scalp electrode positions were then subdivided into nine areas, and a mean peak for each of these regions was calculated by averaging adjacent electrodes in anterior, central, and posterior areas for the left and right hemisphere as well as for midline electrodes [sagittal line: anterior (A), central (C), posterior (P); transversal line: left (L), midline (M), right (R); sagittal by transversal: AL: Fp1, AF7, AF3, F7, F5, F3; AM: Fpz, AFz, F1, Fz, F2; AR: Fp2, AF4, AF8, F4, F6, F8; CL: FT7, FC5, FC3, T7, C5, C3, TP7, CP5, CP3; CM:FC1, FCz, FC2, C1, Cz, C2, CP1, CPz, CP2; CR: FC4, FC6, FT8, C4, C6, T8, CP4, CP6, TP8; PL: P7, P5, P3, PO7, PO3, O1; PM: P1, Pz, P2, POz, Oz; PR: P4, P6, P8, PO4, PO8, O2]. In relation to the baseline period three separate peaks were differentiated within

predefined latency windows (N1: 350-600ms, P2: 500-700ms, P3: 700-1100ms; see Pause and Krauel 2000).

For the EEG data, a four-way ANOVA was calculated [factors: Body Odor (gay male, heterosexual male, heterosexual female), Sexual Orientation of the Perceiver (gay male, heterosexual male), Sagittal Line (anterior, central, posterior) and Transversal Line (left, midline, right)]. For the rating data and the detection performance, two-way ANOVAs were calculated [factors: Body Odor (gay male, heterosexual male, heterosexual female), Sexual Orientation of the Perceiver (gay male, heterosexual male)]. Subsequently, nested effects were calculated in accordance with Page and colleagues (2003). An alpha level of $P < 0.05$ was used for all statistical tests, except for the exploratory analysis of the EEG data, in which the alpha level was $P < 0.10$. Huynh-Feldt corrected degrees of freedom were calculated and corrected p-values are reported. Current Source Density (CSD) maps were calculated using a spherical spline model (Perrin et al., 1989; order of splines: m = 4, maximal degree of legendre polynominals = 20).

Results

Self ratings of emotions

Participants indicated feeling neither happy nor unhappy in response to the body odors (M = 0.08, SD = 0.72), and reported middling arousal (M = 4.63, SD = 1.36) and dominance (M = 5.45, SD = 0.93).When smelling heterosexual female body odor, participants reported to feel happier (M = 0.82, SD = 1.42) than when smelling heterosexual male body odor [M = -0.68, SD = 1.70; Body Odor $F(2,52) = 6.48$, $P < 0.005$, $f = 0.500$, Power = 0.889, Heterosexual Male compared to Female Body Odor $T(27) = -4.23$, $P < 0.001$]. No differences were observed concerning emotional responses on the arousal or dominance level. Moreover, the sexual orientation of the participants had no effect on the emotional self ratings.

Stimulus detection

Data of four participants (two gay men) had to be excluded from the analysis due to an insufficient number of trials responded to (10% or more missing responses to any body odor). The remaining participants detected on average 51.77% (SD = 22.96) of the presented body odors, with heterosexual male body odor being detected in 54.76% (SD = 27.28), gay male body odor being detected in 52.93% (SD = 23.54), and female body odor being detected in 47.63% (SD = 27.72) of the cases. Gay men detected the body odor of heterosexual men more often (M = 67.00%, SD = 27.63%) than did heterosexual men [M = 42.52%, SD = 21.56%; Body Odor by Sexual Orientation $F(2,44) = 9.17$, $P < 0.001$, $f = 0.645$, Power = 0.967, nested effects: Sexual Orientation within Heterosexual Male Body Odor $F(1,22) = 5.85$, $P < 0.05$].

CSERPs

Latencies

For an overview of the ANOVA results concerning the latencies, see Table 2.

- Table 2 -

Scalp distribution

In male participants the N1 peak appeared with the shortest latency at midline electrode positions [M = 464.95 ms, SD = 25.37 ms; Transversal $F(2,52) = 3.81$, $P < 0.05$, $f = 0.383$, Power = 0.668], significantly differing from left electrode positions [M = 481.14 ms, SD = 22.68 ms; $T(27) = -3.21$, $P < 0.005$]. The peak of the P3 component appeared with a longer latency at posterior electrode positions [M = 920.46 ms, SD = 53.69 ms; Sagittal $F(2,52) = 7.94$, $P < 0.005$, $f = 0.553$, Power = 0.943] as compared to central [M = 899.79 ms; SD = 43.56 ms; $T(27) = 3.22$, $P < 0.005$] and anterior electrode positions [M = 870.06 ms; SD =

49.82 ms; $T(27) = 2.09$, $P < 0.05$]. Moreover, the P3 peak showed a longer latency in central compared to anterior areas [$T(27) = 2.66$, $P < 0.05$].

Effects of Body Odor and Sexual Orientation of the Perceiver

When presented with gay male body odor, gay men displayed a shorter P2 latency (M = 560.86 ms, SD = 55.54 ms) than heterosexual men (M = 604.57 ms, SD = 44.57 ms) at central right-electrode positions. Heterosexual men, on the other hand, showed a shorter P2 latency (M = 589.43 ms, SD = 58.61) than gay men (M = 630.86 ms, SD = 39.33 ms) in response to heterosexual female body odor at central-right electrode positions [Sexual Orientation of the Perceiver by Body Odor by Sagittal by Transversal $F(4,104) = 3.51$, $P < 0.05$, $f = 0.297$, Power = 0.869, nested effects: Sexual Orientation of the Perceiver by Body Odor by Sagittal within Right Electrode Positions $F(4,104) = 3.12$, $P < 0.05$, Sexual Orientation of the Perceiver by Body Odor within Right Electrode Positions within Central Electrode Positions $F(2,52) = 4.55$, $P < 0.005$, Sexual Orientation of the Perceiver within Right Electrode Positions within Central Electrode Positions within Body Odor of Gay Men $F(1,26) = 5.28$, $P < 0.05$, Sexual Orientation of the Perceiver within Right Electrode Positions within Central Electrode Positions within Body Odor of Heterosexual Women $F(1,26) = 4.82$, $P < 0.05$]. The effect of heterosexual men (M = 588.67 ms, SD = 21.76) showing a shorter P2 latency than gay men (M = 619.33 ms, SD = 27.25 ms) when presented with heterosexual female body odor extended to all central scalp regions [Sexual Orientation of the Perceiver by Body Odor by Sagittal $F(4,104) = 3.51$, $P < 0.05$, $f = 0.363$, Power = 0.849, nested effects: Sexual Orientation of the Perceiver by Body Odor within Central Electrode Positions $F(2,52) = 8.38$, $P < 0.005$, Sexual Orientation within Central Electrode Positions within Body Odor of Heterosexual Women $F(1,26) = 10.82$, $P < 0.005$].

Neither the N1 nor the P3 latency differed with respect to the sexual orientation of the perceiving participants or the kind of body odor presented.

Amplitudes

For an overview of the ANOVA results concerning the amplitudes see Table 3. Figures 1a and 1b display the CSERP characteristics of gay men (Fig. 1a) and heterosexual men (Fig. 1b) within the nine electrode pools.

- Fig. 1a, Fig. 1b -

- Table 3 -

Scalp distribution

The amplitude of the N1 was smaller at midline (M = -0.26 μV, SD = 0.45 μV) than at left (M = -0.58 μV, SD = 0.42 μV) and right electrode positions [M = -0.58 μV, SD = 0.49 μV; Transversal $F(2,52) = 4.25$, $P < 0.05$, $f = 0.404$, Power = 0.718, Left compared to Midline Electrode Position $T(27) = -3.21$, $P < 0.005$, Right compared to Midline Electrode Positions $T(27) = -2.25$, $P < 0.05$]. The P2 peak appeared with a larger amplitude at midline (M = 0.97 μV, SD = 0.65 μV) than at left (M = 0.36 μV, SD = 0.41 μV) and right electrode positions [M = 0.30 μV, SD = 0.48 μV; Transversal $F(2,52) = 11.49$, $P < 0.001$, $f = 0.664$, Power = 0.991, Left compared to Midline Electrode Position $T(27) = 3.55$, $P < 0.005$, Right compared to Midline Electrode Positions $T(27) = 3.91$, $P < 0.005$]. Moreover, the P2 peak was larger at posterior-left (M = 0.96 μV, SD = 1.18 μV) than at central-left electrode positions [M = -0.03 μV, SD = 0.59 μV; Transversal by Sagittal $F(4,104) = 3.03$, $P < 0.05$, $f = 0.343$, Power = 0.787, nested effects: Sagittal within Left Electrode Positions $F(2,52) = 4.06$, $P < 0.05$, Posterior-Left compared to Central-Left Electrode Positions $T(27) = 4.36$, $P < 0.001$]. The P3 component showed a larger peak at posterior electrode positions [M = 1.93 μV, SD = 1.42 μV; Sagittal $F(2,52) = 14.07$, $P < 0.001$, $f = 0.735$, Power = 0.998] as compared to central [M = 0.58 μV, SD = 0.54 μV; $T(27) = 5.26$, $P < 0.001$] and anterior electrode positions [M = -0.30 μV, SD = 1.72 μV; $T(27) = 3.91$, $P < 0.005$]. Additionally, the P3 peak was larger at

central compared to anterior electrode positions [$T(27) = 2.31$, $P < 0.05$]. Moreover, the P3 peak was most distinct at midline electrode positions [M = 1.42 μV, SD = 0.74 μV; Transversal $F(2,52) = 17.27$, $P < 0.001$, $f = 0.815$, Power = 1.000], differing significantly from left [M = 0.43 μV, SD = 0.63 μV; $T(27) = 4.38$, $P < 0.001$] and right electrode positions [M = 0.37 μV; SD = 0.65 μV; $T(27) = 4.69$, $P < 0.001$]. Analysis of a Transversal by Sagittal interaction revealed both the Transversal and the Sagittal main effects being stable throughout all factor levels [Transversal by Sagittal $F(4,104) = 5.11$, $P < 0.01$, $f = 0.443$, Power = 0.960].

Effects of Body Odor and Sexual Orientation of the Perceiver

The amplitude of the P3 component was larger in response to the body odor of gay men (M = 0.84 μV, SD = 0.40) than in response to body odors of both heterosexual men (M = 0.67 μV, SD = 0.25 μV) and women [M = 0.70 μV; SD = 0.31 μV; Odor $F(2,52) = 5.17$, $P < 0.01$, $f = 0.446$, Power = 0.804, Body Odor of Gay Men compared to Body Odor of Heterosexual Men $T(27) = 2.88$, $P < 0.01$, Body Odor of Gay Men compared to Body Odor of Heterosexual Women $T(27) = 2.51$, $P < 0.05$]. As analysis of the P3 properties had shown that its peak was not only most prominent at central- and posterior-midline electrode positions, but even featured a reversed polarity at anterior electrode positions (see analysis above, see Fig. 1a, 1b), an exploratory analysis within central- and posterior-midline areas was performed. At central-midline electrode positions, gay men displayed the largest P3 amplitude in response to heterosexual male body odor (M = 2.22 μV, SD = 1.94 μV), trending towards a difference from heterosexual female (M = 1.50 μV, SD = 1.81) and gay male body odor [M = 1.59 μV, SD = 1.67 μV; Body Odor $F(2,26) = 3.46$, $P < 0.05$; $f = 0.516$, Power = 0.595; Gay Male Body Odor compared to Heterosexual Male Body Odor $T(13) = -2.07$, $P = 0.054$; Heterosexual Female Body Odor compared to Heterosexual Male Body Odor $T(13) = -2.12$, $P = 0.059$]. At posterior-midline electrode, no differential responses to the body odors were observed in gay men. Moreover, within both of these scalp areas, representing the maximum

P3 amplitude, heterosexual men did not show differential responses to the presented body odors ($P > 0.250$).

The amplitudes of the N1 and P2 component were unaffected by the sexual orientation of the perceiving participant and the kind of body odor presented.

CSDs

At the time of the maximum P3 amplitude (896 ms), gay men showed much stronger neuronal activation than heterosexual men in response to all three body odors presented (Fig. 2). In gay men, medial frontal and left parietal activity was related to either odor, but was the strongest in response to heterosexual male body odor. Heterosexual men did not show any particular differences in activation patterns related to the kind of body odor presented.

- Fig. 2 -

Study 2: Female Participants

Materials and Methods

Participants

Lesbian and heterosexual female participants were recruited via newspaper advertisement and advertisement at the university and at local gay bars. Thirty right-handed women (15 lesbian women) participated in the experiment, however, data from one heterosexual and one lesbian woman had to be excluded from analysis due to noticeable artifacts in the EEG recording (see EEG data reduction). All of the remaining 28 participants met the same criteria as the participants in study one. Additionally, the female participants reported having a regular menstrual cycle, and were not using any hormonal contraceptives. Lesbian and heterosexual women did not differ in their menstrual cycle phase, neither at the time of the first nor at the

time of the second session (*P*s = 1.000, Fisher's Exact Test). Four heterosexual and three lesbian participants reported being regular smokers, and both groups did not differ in their smoking behavior (*P* = 1.000, Fisher's Exact Test). The participants had a mean age of 29.5 years (SD = 7.2; range = 20-45 years), and heterosexual and lesbian women did not differ in age [$T(26) = 0.31$, $P > 0.25$]. Neither participant had previously acted as sweat donor. Participants' sexual orientation was assessed the same way as in study one. According to their self-description (see Tab. 4), heterosexual and lesbian participants differed significantly on both Kinsey scales [behavior scale: $T(13) = 50.84$, $P < 0.001$, Welch-Test; fantasy scale: $T(26) = 16.03$, $P < 0.001$], as well as on both visual analog scales (homosexuality: $T(26) = 48.70$, $P < 0.001$, heterosexuality: $T(14) = -43.14$, $P < 0.001$, Welch-Test].

Participants gave written informed consent and were paid for their participation.

- Table 4 -

Chemosensory stimuli

Axillary sweat was sampled from the same heterosexual male and female donors as in study one. Here, sweat samples additionally were obtained from 11 lesbian women, instead of gay men (see study 1). Sweat donation followed the same protocol as in study one, and the donors met the same criteria. Both heterosexual men and women differed significantly from lesbian women in their self-description on the visual analog scales for describing homosexuality and heterosexuality [men, homosexuality: $T(23) = 46.52$ $P < 0.001$, men, heterosexuality: $T(23) = -52.33$, $P < 0.001$, women, homosexuality: $T(20) = 36.46$, $P < 0.001$, women, heterosexuality: $T(22) = -37.02$, $P < 0.001$].

Donors were on average 26.1 years old (SD = 5.4, range = 19-42), and there were no differences in age between heterosexual men (M = 24.4, SD = 3.0), heterosexual women (M = 27.7, SD = 5.9) and lesbian women [M = 26.6, SD = 6.9, $F(2,33) = 1.29$, $P > 0.250$].

Their body-mass-index ranged from 18.5 to 29.0 kg/m^2 (M = 23.3, SD = 3.1), and all of them were non-smokers. Of the lesbian odor donors, eight reported to regularly shave their axillary hair (missing data: 3). Accordingly, female donors did not differ in their shaving habits (P = 1.000, Fisher's Exact Test), whereas both lesbian (P = 0.042, Fisher's Exact Test) and heterosexual female donors (P = 0.044, Fisher's Exact Test) differed from male donors in their shaving habits.

Procedure

The procedure followed the same protocol as in experiment one, except for presenting body odor of lesbian women instead of body odor of gay men.

Data Recording, Reduction and Analysis

Data recording, reduction, and analysis followed the same protocol as in study one. Subsequent to artifact rejection, data of one lesbian and one heterosexual woman were excluded from further analysis due to less than 10 of 30 trials in one or more odor condition being free of artifacts, resulting in a total of 28 (14 lesbian) female participants.

Results

Self ratings of emotion

Women reported neither particularly positive nor negative feelings when presented with the body odors (M = 0.07, SD = 1.03), and indicated middling arousal (M = 4.10, SD = 1.29) and dominance (M = 5.49, SD = 1.17).When smelling lesbian (M = 1.00, SD = 1.83) and heterosexual female body odor (M = 0.79, SD = 1.55), women described themselves as happier than when smelling heterosexual male body odor [M = -1.57, SD = 1.83; Body Odor $F(2,52) = 20.41$, $P < 0.001$, $f = 0.886$, Power = 1.000, Male compared to Lesbian Body Odor $T(27) = -4.72$, $P < 0.001$, Male compared to Heterosexual Female Body Odor $T(27) = -4.77$, P

< 0.001]. When smelling the body odor of both heterosexual men (M = 4.79, SD = 1.93) and women (M = 4.36, SD = 1.65), heterosexual women reported more arousal than when smelling lesbian body odor [M = 3.00, SD = 1.41; Body Odor by Sexual Orientation $F(2,52) = 3.96$, $P < 0.05$, $f = 0.390$, Power = 0.685, nested effects: Body Odor within Heterosexual Women $F(2,52) = 3.73$, $P < 0.05$, Lesbian compared to Heterosexual Female Body Odor within Heterosexual Women $T(13) = -2.56$ $P < 0.001$, Lesbian compared to Heterosexual Male Body Odor within Heterosexual Women $T(27) = -2.53$, $P < 0.05$]. No differences were observed concerning emotional self ratings on the dominance level.

Stimulus detection

Due to technical problems, detection data of four heterosexual women were not recorded. The remaining female participants detected on average 47.18% (SD = 12.68) of the presented body odors, with heterosexual male body odor being detected in 56.20% (SD = 26.64), lesbian body odor being detected in 47.63% (SD =17.75), and heterosexual female body odor being detected in 37.72% (SD = 13.80) of the cases. Both body odors of heterosexual men (M = 56.20%, SD = 26.64%) and lesbian women (M = 47.63%, SD = 17.75%) were detected more often than the body odor of heterosexual women [M = 37.72%, SD = 13.80%; Body Odor $F(2,44) = 5.25$, $P < 0.05$, $f = 0.489$, Power = 0.807, Heterosexual Female compared to Lesbian Female Body Odor $T(27) = -2.36$, $P < 0.05$, Heterosexual Female compared to Heterosexual Male Body Odor $T(27) = -3.29$, $P < 0.005$]. Detection rates did not vary with respect to the sexual orientation of the perceiving women.

CSERPs

Latencies

For an overview of the ANOVA results concerning the latencies, see Table 5.

- Table 5 -

Scalp distribution

In female participants the N1 peak appeared with the shortest latency at midline electrode positions [M = 464.90 ms, SD = 21.81 ms; Transversal $F(2,52) = 3.29$, $P < 0.05$, $f = 0.355$, Power = 0.599], significantly differing from left electrode positions [M = 477.32 ms, SD = 20.65 ms; $T(27) = -8.39$, $P < 0.01$]. The P2 latency was shorter above anterior (M = 582.71 ms, SD = 26.83 ms) compared to central (M = 600.79 ms, SD = 20.76 ms) and posterior scalp regions [M = 604.94 ms, SD = 14.53 ms; Sagittal $F(2,52) = 3.52$, $P < 0.05$, $f = 0.545$, Power = 0.937, Anterior compared to Central Electrode Positions $T(27) = -2.53$, $P < 0.05$, Anterior compared to Posterior Electrode Positions $T(27) = -3.35$, $P < 0.005$]. The latency of the P3 peak was longer at posterior (M = 919.16 ms, SD = 68.61 ms) and at central (M = 911.19 ms, SD = 41.86 ms) than at anterior electrode positions [M = 873.00 ms, SD = 60.56 ms; Sagittal $F(2,52) = 4.28$, $P < 0.05$, $f = 0.405$, Power = 0.722, Anterior compared to Central Electrode Positions $T(27) = -3.05$, $P < 0.01$, Anterior compared to Posterior Electrode Positions $T(27) = -2.17$, $P < 0.05$].

Effects of Body Odor and Sexual Orientation of the Perceiver

In response to the body odors in general, heterosexual women (M = 459.71 ms, SD = 44.24 ms) displayed a shorter latency of the N1 component than lesbian women (M = 504.86 ms, SD = 39.40 ms) at central-right electrode positions [Sexual Orientation of the Perceiver by Transversal by Sagittal $F(4,104) = 3.51$, $P < 0.05$, $f = 0.368$, Power = 0.849, nested effects: Sexual Orientation of the Perceiver by Sagittal within Right Electrode Positions $F(2,52) = 3.82$, $P < 0.05$, Sexual Orientation of the Perceiver within Right Electrode Positions within Central Electrode Positions $F(1,26) = 8.13$, $P < 0.01$]. The P2 peak in heterosexual women appeared with a shorter latency (M = 585.49 ms, SD = 19.84 ms) as compared to lesbian

women (M = 600.03 ms, SD = 15.03 ms) at right electrode positions [Sexual Orientation of the Perceiver by Transversal $F(2,52) = 3.52$, $P < 0.05$, $f = 0.368$, Power = 0.631, nested effects: Sexual Orientation of the Perceiver within Right Electrode Positions $F(1,26) = 4.78$, $P < 0.05$]. In response to female body odors, lesbian women showed shorter latencies of the P2 component at left electrode positions (lesbian body odor: M = 586.67 ms, SD = 20.09 ms; heterosexual female body odor: M = 579.05 ms, SD = 29.40) than heterosexual women (lesbian body odor: M = 595.81 ms, SD = 23.42 ms; heterosexual female body odor: M = 613.24 ms, SD = 34.12), the effect being especially prominent in response to body odor of heterosexual women [Sexual Orientation of the Perceiver by Body Odor by Transversal $F(4,104) = 4.00$, $P < 0.05$, $f = 0.359$, Power = 0.828, nested effects: Sexual Orientation of the Perceiver by Body Odor within Left Electrode Positions $F(2,52) = 4.00$, $P < 0.010$, Sexual Orientation of the Perceiver within Left Electrode Positions within Body Odor of Heterosexual Women $F(2,52) = 4.00$, $P < 0.010$]. Neither the sexual orientation of the perceiving women nor the kind of body odor presented exerted any effects on the latency of the P3 component.

Amplitudes

For an overview of the ANOVA results concerning the amplitudes see Table 6. Figures 3a and 3b display the CSERP characteristics of lesbian women (Fig. 3a) and heterosexual women (Fig. 3b) within the nine electrode pools.

- Fig. 3a, Fig. 3b -

- Table 6 -

Scalp distribution

The peak of the N1 component appeared with a smaller amplitude above midline (M = -0.42 μV, SD = 0.39 μV) as compared to left (M = -0.82 μV, SD = 0.50 μV) and right scalp regions [M = -0.85 μV, SD = 0.51 μV; Transversal $F(2,52) = 7.67$, $P < 0.005$, $f = 0.544$, Power = 0.935, Left compared to Midline Electrode Position $T(27) = -3.15$, $P < 0.005$, Right compared to Midline Electrode Positions $T(27) = -3.63$, $P < 0.005$]. The P2 peak was most pronounced at midline (M = 1.16 μV, SD = 0.61 μV), being larger than at left (M = 0.40 μV, SD = 0.65 μV) and right electrode positions [M = 0.31 μV, SD = 0.40 μV; Transversal $F(2,52) = 20.45$, $P < 0.001$, $f = 0.886$, Power = 1.000, Left compared to Midline Electrode Position $T(27) = -5.33$, $P < 0.001$, Right compared to Midline Electrode Positions $T(27) = -5.56$, $P < 0.001$], which was evident above anterior as well as central and posterior scalp regions [Transversal by Sagittal $F(4,104) = 5.54$, $P < 0.005$, $f = 0.462$, Power = 0.973]. The P3 component showed a larger peak at posterior electrode positions [M = 2.21 μV, SD = 1.54 μV; Sagittal $F(2,52) = 23.89$, $P < 0.001$, $f = 0.959$, Power = 1.000] as compared to central [M = 0.77 μV, SD = 0.44 μV; $T(27) = 4.93$, $P < 0.001$] and anterior electrode positions [M = -0.31 μV, SD = 1.23 μV; $T(27) = 5.03$, $P < 0.001$]. Additionally, the P3 peak was larger at central compared to anterior electrode positions [$T(27) = 4.19$, $P < 0.001$]. Moreover, the P3 peak was most distinct at midline electrode positions [M = 1.99 μV, SD = 0.83 μV; Transversal $F(2,52) = 53.46$, $P < 0.001$, $f = 1.435$, Power = 1.000], differing significantly from left [M = 0.28, μV, SD = 0.56 μV; $T(27) = 8.39$, $P < 0.001$] and right electrode positions [M = 0.39 μV, SD = 0.54 μV $T(27) = 8.49$, $P < 0.001$]. Analysis of a Transversal by Sagittal interaction revealed both the Transversal and the Sagittal main effects being stable throughout all factor levels [Transversal by Sagittal $F(4,104) = 9.68$, $P < 0.001$, $f = 0.610$, Power = 1.000].

Effects of Body Odor and Sexual Orientation of the Perceiver

Lesbian women displayed the most pronounced P3 amplitude in response to the body odor of heterosexual men (M = 1.14, μV, SD = 0.68 μV), with a larger amplitude as compared to the responses to heterosexual (M = 0.74, μV, SD = 0.25 μV) and lesbian (M = 0.81, μV, SD = 0.39 μV) female body odors [see Fig. 3a; Sexual Orientation of the Perceiver by Body Odor $F(2,52) = 4.68$, $P < 0.05$, $f = 0.425$, Power = 0.762, nested effects: Body Odor within Lesbian Women $F(2,52) = 6.23$, $P < 0.005$, Body Odor of Heterosexual Men compared to Body Odor of Lesbian Women within Lesbian Women $T(13) = 2.19$, $P < 0.05$, Body Odor of Heterosexual Men compared to Body Odor of Heterosexual Women within Lesbian Women $T(13) = 2.41$, $P < 0.05$]. Heterosexual women did not show differential responses to the body odors presented ($P > 0.250$). Thus, in lesbian women an exploratory analysis within central- and posterior-midline electrode positions was performed, as the P3 peak was not only most prominent in these areas, but, like in male participants, even featured a reversed polarity at anterior electrode positions (see analysis above, see Fig. 2a, 2b). Within central-midline electrode positions, lesbian women showed the largest P3 peak in response to heterosexual male body odor (M = 3.71 μV, SD = 2.34 μV), differing from the response to lesbian body odor (M = 2.07 μV, SD = 1.27 μV) and further trending towards a difference from the response to heterosexual female body odor [M = 2.29 μV, SD = 1.63 μV; Body Odor $F(2,26) = 3.88$, $P < 0.05$; $f = 0.547$, Power = 0.649; Lesbian Body Odor compared to Heterosexual Male Body Odor $T(13) = -2.317$, $P < 0.05$; Heterosexual Female Body Odor compared to Heterosexual Male Body Odor $T(13) = -1.872$, $P = 0.084$]. Similar effects, though only with a tendency towards statistical significance, were observed within posterior-midline electrode positions, with lesbian women showing the largest P3 peak when presented with heterosexual male body odor (M = 3.95 μV, SD = 2.57), differing from the P3 amplitude in response to lesbian (M = 2.80 μV, SD = 2.42) and heterosexual female body odor [M = 2.83 μV, SD = 2.12 μV; Body Odor $F(2,26) = 2.69$, $P = 0.087$; $f = 0.453$, Power = 0.486; Lesbian Body Odor

compared to Heterosexual Male Body Odor $T(13) = -2.161$, $P < 0.05$; Heterosexual Female Body Odor compared to Heterosexual Male Body Odor $T(13) = -2.155$, $P = 0.051$].

The amplitudes of the N1 and P2 component were unaffected by the sexual orientation of the perceiving participant and the kind of body odor presented.

CSDs

At the time of the maximum P3 amplitude (900 ms), lesbian women showed stronger neuronal activation than heterosexual women in response to all three body odors presented (Fig. 4). In lesbian women, medial frontal and medial parieto-occipital activity was related to either odor, but was the strongest in response to male body odor. Heterosexual women did not display any specific differences in activation patterns related to the kind of body odor presented.

- Fig. 4 -

Discussion

The present studies showed both men and women reporting feelings of unhappiness when presented with heterosexual male body odor and reporting feelings of happiness when presented with female body odors. During EEG recording, male participants detected the presented body odors on average in 51.77 % (SD = 22.96) of the cases, and female participants detected them on average 47.18 % (SD = 12.68) of the time, suggesting that the odors in general were perceived as being relatively weak.

The EEG data reveal faster processing of gay male body odor in gay men than in heterosexual men at a level of early stimulus encoding (P2), and, conversely, faster processing

of female body odor in heterosexual men as compared to gay men. Moreover, lesbian women as compared to heterosexual women exhibit faster processing of female body odors. Concerning later, evaluative stages of odor processing (P3), gay men as well as lesbian women display strong neuronal activity in response to body odor of heterosexual men. Therefore, in both women and men, the speed as well as the strength of the neuronal responses to the body odors is related to the sexual orientation of the perceiver and the kind of body odor presented. These results are in line with recent brain imaging studies demonstrating that the processing of body odor components depends on sexual orientation (Berglund et al. 2006; Savic et al. 2005) and extend other findings showing that the preference for human body odors is influenced by the sexual orientation of the perceiver as well as the sexual orientation of the odor donor (Martins et al. 2005; Sergeant et al. 2007).

P2-latency differences between gay and heterosexual men as well as lesbian and heterosexual women are specific for responses to body odors obtained from potential partners, or, in case of female participants, to body odors of the preferred gender, indicating a processing advantage for the respective odors. This accelerated processing could be due to previous frequent encounters with body odor produced by (potential) partners. Repeated exposure to a chemosensory stimulus has been shown to result in enhanced sensitivity (Dalton et al. 2002; Jacob et al. 2006) as well as in shifts of hedonic evaluation (Jacob et al. 2006; Wang et al. 2003), attributed to stimulus-induced plasticity of the olfactory system (Mainland et al. 2002). Moreover, repeated exposure affects the central nervous processing of chemosensory stimuli, resulting for example in shortened latencies of early CSERP components, such as the P2 (Boulkroune et al. 2007; Pause et al. 1996a). Another possible underlying mechanism may be the level of allocated attention to the stimulus. Previous research has shown shorter latencies of the P2 component when the chemosensory stimuli were attended to, than when attention was deflected from the stimuli (Krauel et al. 1998). Here, presentation of body odors of heterosexual women may have led heterosexual men to

allocate more attention to this stimulus than gay men did, and, on the other hand, presentation of body odors of gay men may have driven gay men to be more attentive than heterosexual men. In lesbian women, presentation of female body odors may have caused heightened attention.

The exploratory analysis of P3-relevant scalp areas revealed that gay men responded with the most pronounced P3 peak to body odor of heterosexual men. Lesbian women also displayed the strongest P3-response to the body odor of heterosexual men. In the context of mate choice, this is in line with the idea that body odors may function as potent social signals. Recent research examining the processing of body odors as a function of human leucocyte antigen (HLA) similarity has shown that body odors taken from HLA-similar persons (who should be avoided as potential mates) elicit larger P3 amplitudes than body odors from HLA-dissimilar persons (Pause et al. 2006). This indicates that such body odors hold a certain significance for the perceiving individual, probably constituting a social warning signal which could eventually reduce the likelihood of mating with HLA-similar individuals. Thus, the current results hint at a similar mechanism operating on a broader group level, regarding the potential for an individual to be an eligible mate in terms of both gender and sexual orientation. Moreover, analysis of the CSD within the P3 latency window in gay men revealed the most pronounced neuronal activity in response to heterosexual male body odor, specifically in medial frontal and left parietal areas. Lesbian women showed a similar pattern of electrical activation when presented with heterosexual male body odor. Activation in parietal areas may represent attentional processes (for an overview see Behrmann et al. 2004), whereas medial prefrontal activation in general could be related to flexible physiological adjustments in socially relevant situations (Damasio 1994). Moreover, medial prefrontal activation might indicate a negative evaluation of heterosexual male body odor, as medial frontal activation has been reported to be related to the perception of potential harmful odors (Laudien et al. 2008) and in fact, within the current studies male and female participants

reported feelings of unhappiness exclusively when presented with heterosexual male body odor. Seemingly, whereas on a subjective level all participants reported negative feelings when smelling heterosexual male body odor, predominantly lesbian women and gay men showed corresponding physiological response patterns.

All male participants displayed the largest P3 amplitude in response to body odor of gay men. However, the P3 peak was most prominent above central- and posterior-midline scalp areas, (see Fig. 1a, 1b), which is well in line with the current literature (Pause et al. 1996b; Pause and Krauel 2000). Taking into account the results of the exploratory analysis within these areas (see above), the main effect of the body odor most likely originates from frontal and temporal electrode positions, where an actual P3 peak is not present at all.

Concerning the scalp topography of the CSERP, the amplitude of the N1 component was smaller at midline than at lateral electrode positions in both male and female participants. The P2 peak, on the other hand, appeared with a larger amplitude at midline than at left and right electrode position, and furthermore, was larger at posterior-left than at central-left electrode positions in male participants. In women, the P2 peak did not vary with the sagittal line. Several studies have shown that the N1 in response to olfactory stimuli shows a medial parietal dominance (Hummel and Kobal 1992; Pause et al. 1997), and that the P2 shows a medial frontal dominance (Laudien et al. 2006; Laudien et al. 2008), suggesting that the body odors presented here were most probably not processed primarily as odors. In fact, recent brain imaging studies have demonstrated that body odors are processed by specialized neuronal networks which differ significantly from networks processing perceptually similar common odors (Lundström et al. 2008; Prehn-Kristensen et al. 2009). The peak of the P3 component was most distinct at posterior-midline electrode positions, and hence could be separated from the early positivity (P2). This finding is in line with earlier observations showing a parietal maximum of this component, which is considered to reflect subjective stimulus significance (Donchin and Coles 1988; Pause et al. 1996b; Polich and Criado 2006).

Together, both studies reported here demonstrate that the processing of socially relevant chemosensory stimuli depends on the sexual orientation of the perceiver. Furthermore, depending on the sexual orientation of the perceiver, patterns of central nervous responses are differentially affected by the gender and the sexual orientation of the odor donors, indicating that the production of body odors not only varies with gender but may vary with sexual orientation as well. Corresponding effects have been reported for gender-related visual social signals, showing that the pattern of central nervous activation in response to male and female faces depends on the sexual orientation of the perceiver (Kranz and Ishai 2006). As for visual social cues related to sexual orientation, gay men and lesbian women have been shown to be more accurate than heterosexuals in judging others' sexual orientation on the basis of brief observations of nonverbal behavior (Ambady et al. 1999).

Although the current study indicates that sexual orientation affects the processing of body odors in both genders, the pattern of results varies between male and female perceivers. Whereas the speed of the early processing differs significantly between gay and heterosexual men when they are presented with body odors of potential partners, the results are not as clear-cut within the female participants. Interestingly, female sexual orientation is considered more variable (Bailey et al. 2000; Pattatucci and Hamer 1995) and women are presumed to display greater erotic plasticity than men (Baumeister 2000). The results reported here correspond to this notion.

As discussed, experience with the chemosensory stimuli may account for some of the observed differences related to sexual orientation of the perceiver. Nevertheless, genetic influences cannot generally be ruled out. Odor perception, especially concerning body odor compounds, has been shown to be at least in part genetically determined (Keller et al. 2007; Knaapila et al. 2008; Wysocki and Beauchamp 1984), and several family (Bailey et al. 1999; Pattatucci and Hamer 1995), twin (Bailey and Pillard 1991; Bailey et al. 1993) and pedigree studies (Hamer et al. 1993; Turner 1995) have suggested a genetic component of sexual

orientation. However, it remains speculative whether the genetic basis of both odor perception and sexual orientation may be associated.

In conclusion, within the context of mate choice, the social chemosignal of human body odor seems not only to convey information about a potential partner being a poor or a eligible match on an individual level (by the similarity of the immunogenetic profile, Pause et al. 2006), but also on a broader group level. The research on chemosensory communication of gender and sexual orientation may thus broaden the knowledge on phylogenetically ancient mechanisms of mate choice in humans.

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Tables

Table 1

Self description of sexual orientation in male participants (study 1)

	Gay Male Participants			Heterosexual Male Participants		
	M	SD	Range	M	SD	Range
Kinsey Scale: Behavior***	5.86	0.36	5-6	0.00	0.00	0-0
Kinsey Scale: Fantasy***	5.57	0.51	5-6	0.14	0.36	0-1
Visual Analog Scale: Homosexuality***	9.07	0.94	7.6-10.0	0.34	0.45	0.0-1.4
Visual Analog Scale: Heterosexuality***	0.63	0.75	0.0-2.1	9.74	0.35	8.7-10.0

Notes. Kinsey Scales range from 0 (“exclusively heterosexual”) to 6 (“exclusively homosexual”), Visual Analog Scale on Homosexuality ranges from 0.0 (“not homosexual”) to 10.0 (“homosexual”), Visual Analog Scale on Heterosexuality ranges from 0.0 (“not heterosexual”) to 10.0 (“heterosexual”); ***: $p < 0.001$.

Table 2

ANOVAs on the latencies of the CSERPs: Effects in male participants (study 1)

	Transversal	Body Odor by Sagittal by Transversal	SO by Body Odor by Sagittal	SO by Body Odor by Sagittal by Transversal	Sagittal	SO by Sagittal by Transversal
N1	* M < L	** Nested Effects: n.s.	–	–	–	–
P2	–	–	* HetMP < GayMP in HetF in C	* HetMP < GayMP in HetF in CR, GayMP < HetMP in GayM in CR	–	–
P3	–	–	–	–	** A < C < P	* Nested Effects: n.s.

Notes. Sagittal line: A=anterior, C=central, P=posterior. Transversal line: L=left, M=midline, R=right. Body Odor: GayM=gay male, HetM = heterosexual male, HetF=heterosexual female, SO=Sexual Orientation of the Perceiver: GayMP=gay male participant, HetMP=heterosexual male participant. n.s. = non-significant, *p < 0.05, ** p < 0.01.

Table 3

ANOVAs on the amplitudes of the CSERPs: Effects in male participants (study 1)

	Transversal	Sagittal by Transversal	Body Odor	Sagittal	Transversal
N1	* (L=R) > M	–	–	–	–
P2	*** M > (L=R)	* PL > CL	–	–	–
P3	–	** PL > CL > AL, PM > CM > AM, PR > (CR = AR)	** GayM > (HetM=HetF)	*** P > C > A	** M > (L=R)

Notes. Sagittal line: A=anterior, C=central, P=posterior. Transversal line: L=left, M=midline, R=right. Body Odor: GayM=gay male, HetM = heterosexual male, HetF=heterosexual female, SO=Sexual Orientation of the Perceiver: GayMP=gay male participant, HetMP=heterosexual male participant. *p < 0.05, ** p < 0.01, *** p < 0.001.

Table 4

Self description of sexual orientation in female participants (study 2)

	Lesbian Female Participants			Heterosexual Female Participants		
	M	SD	Range	M	SD	Range
Kinsey Scale: Behavior***	5.79	0.43	5-6	0.00	0.00	0-0
Kinsey Scale: Fantasy***	5.21	1.05	3-6	0.29	0.47	0-1
Visual Analog Scale: Homosexuality***	9.68	0.67	7.5-10.0	0.25	0.28	0.0-1.0
Visual Analog Scale: Heterosexuality***	0.40	0.79	0.0-2.3	9.79	0.21	9.4-10.0

Notes. Kinsey Scales range from 0 (“exclusively heterosexual”) to 6 (“exclusively homosexual”), Visual Analog Scale on Homosexuality ranges from 0.0 (“not homosexual”) to 10.0 (“homosexual”), Visual Analog Scale on Heterosexuality ranges from 0.0 (“not heterosexual”) to 10.0 (“heterosexual”); ***: $p < 0.001$.

Table 5

ANOVAs on the latencies of the CSERPs: Effects in female participants (study 2)

	Transversal	SO by Sagittal by Transversal	Sagittal	SO by Transversal	SO by Body Odor by Transversal
N1	* M < L	* HetFP < LesFP in CR	–	–	–
P2	–	–	** A < (C=P)	* HetFP < LesFP in R	* LesFP < HetFP in HetF in L
P3	–	–	* A < (C=P)	–	–

Notes. Sagittal line: A=anterior, C=central, P=posterior. Transversal line: L=left, M=midline, R=right. Body Odor: LesF=lesbian female, HetM = heterosexual male, HetF=heterosexual female, SO=Sexual Orientation of the Perceiver: LesFP=lesbian female participant, HetFP=heterosexual female participant. *$p < 0.05$, ** $p < 0.01$.

Table 6

ANOVAs on the amplitudes of the CSERPs: Effects in female participants (study 2)

	Transversal	Sagittal by Transversal	SO by Body Odor	Sagittal
N1	**	–	–	–
	(L=R) > M			
P2	***	**	–	–
	M > (L=R)	AM > (AL=AR),		
		CM > (CL=CR), PM >		
		(PL=PR),		
P3	***	***	*	***
	M > (L=R)	PL > CL > AL,	HetM > (LesF=HetF) in	P > C > A
		PM > CM > AM,	LesFP	
		PR > CR > AR		

Notes. Sagittal line: A=anterior, C=central, P=posterior. Transversal line: L=left, M=midline, R=right. Body Odor: LesF=lesbian female, HetM = heterosexual male, HetF=heterosexual female, SO=Sexual Orientation of the Perceiver: LesFP=lesbian female participant, HetFP=heterosexual female participant. *$p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Figure legends:

Figure 1. (a) Grand Averages of the CSERPs of gay men in response to gay male (light grey line), heterosexual male (black line), and heterosexual female (dark grey line) body odors at pooled electrode positions (anterior left, anterior midline, anterior right, central left, central midline, central right, posterior left, posterior midline, posterior right; abscissa: ms, ordinate: μV). **(b)** Grand Averages of the CSERPs of heterosexual men in response to gay male (light grey line), heterosexual male (black line), and heterosexual female (dark grey line) body odors at pooled electrode positions (see Fig. 1a).

Figure 2. Neuronal processing of the body odors plotted as Current Source Density (CSD) maps. The first row shows the CSDs of gay men in response to gay male body odor (first column), heterosexual male body odor (second column), and heterosexual female body odor (third column), each plotted for the time point of the maximum P3 amplitude (at 896 ms). The second row shows the CSDs of heterosexual men in response to gay male body odor (first column), heterosexual male body odor (second column), and heterosexual female body odor (third column), each plotted for the time point of the maximum P3 amplitude (at 896 ms). Blue colors represent a weaker magnitude (neuronal sinks) and red colors represent a stronger magnitude of CSD (neuronal sources).

Figure 3. (a) Grand Averages of the CSERPs of lesbian women in response to lesbian female (light grey line), heterosexual male (black line), and heterosexual female (dark grey line) body odors at pooled electrode positions (anterior left, anterior midline, anterior right, central left, central midline, central right, posterior left, posterior midline, posterior right; abscissa: ms, ordinate: μV). **(b)** Grand Averages of the CSERPs of heterosexual women in response to

lesbian female (light grey line), heterosexual male (black line), and heterosexual female (dark grey line) body odors at pooled electrode positions (see Fig. 4a).

Figure 4. Neuronal processing of the body odors plotted as Current Source Density (CSD) maps. The first row shows the CSDs of lesbian women in response to lesbian female body odor (first column), heterosexual female body odor (second column), and heterosexual male body odor (third column), each plotted for the time point of the maximum P3 amplitude (at 900 ms). The second row shows the CSDs of heterosexual women in response to lesbian female body odor (first column), heterosexual female body odor (second column), and heterosexual male body odor (third column), each plotted for the time point of the maximum P3 amplitude (at 900 ms). Blue colors represent a weaker magnitude (neuronal sinks) and red colors represent a stronger magnitude of CSD (neuronal sources).

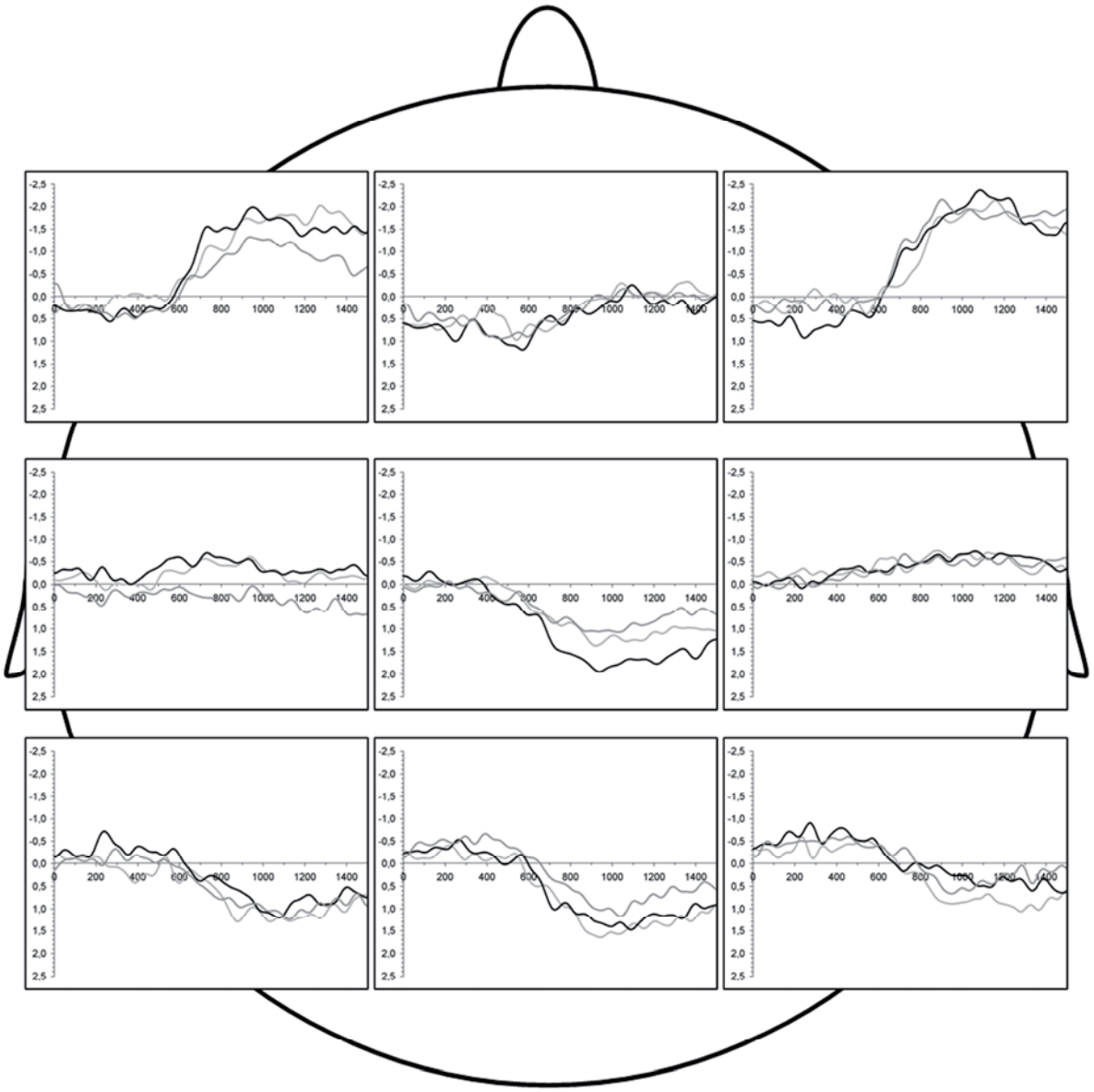

Fig. 1 a

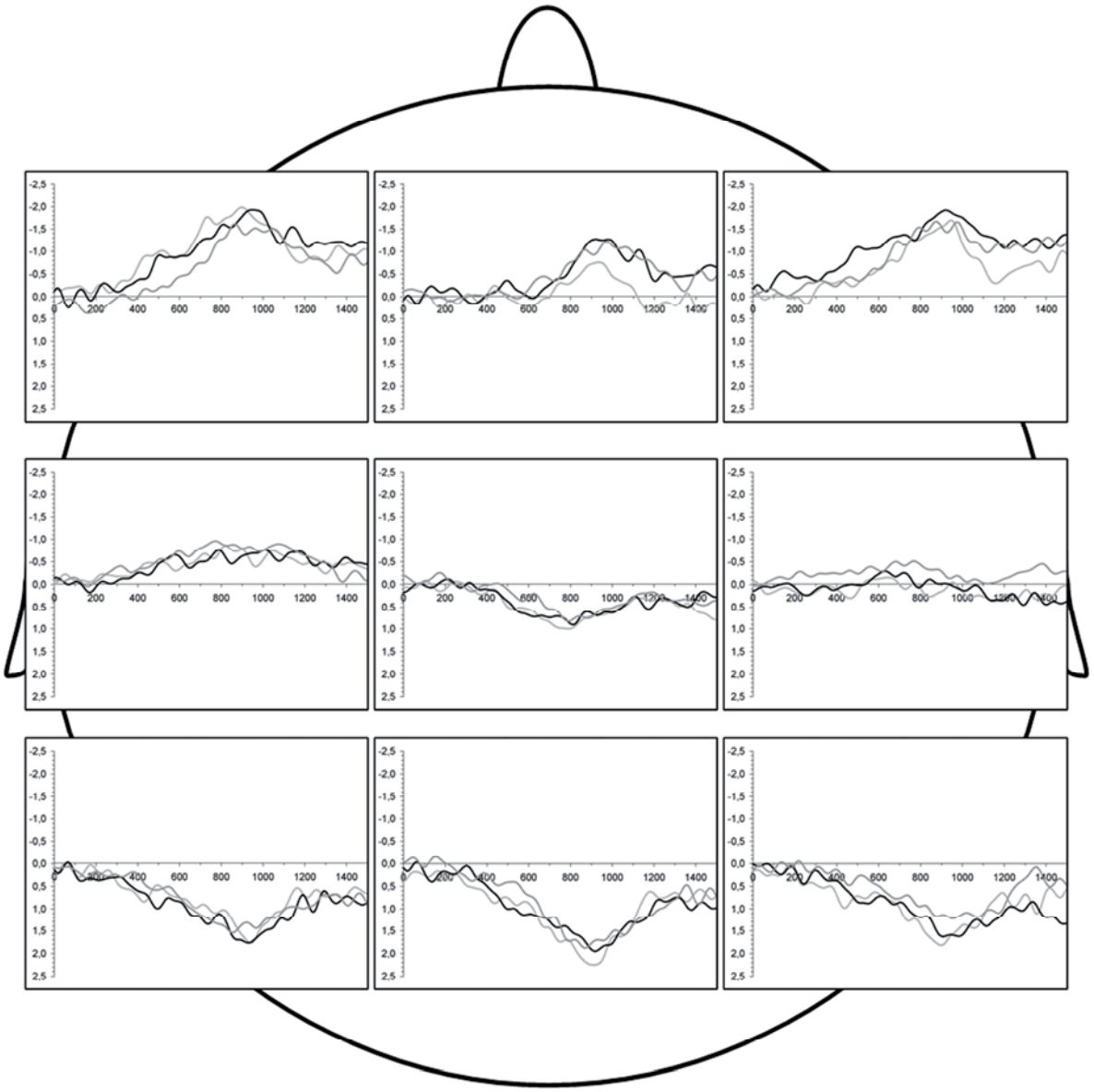

Fig. 1 b

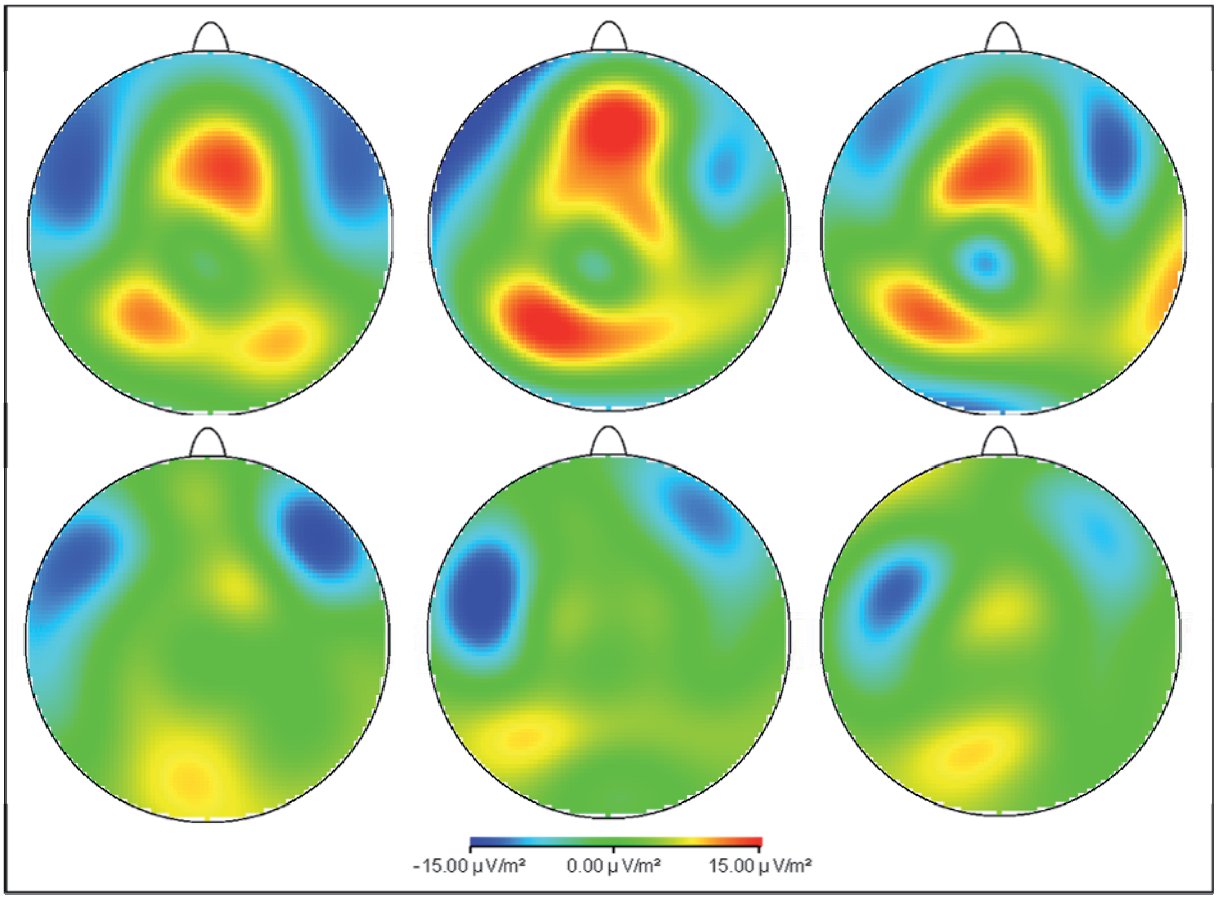

Fig. 2

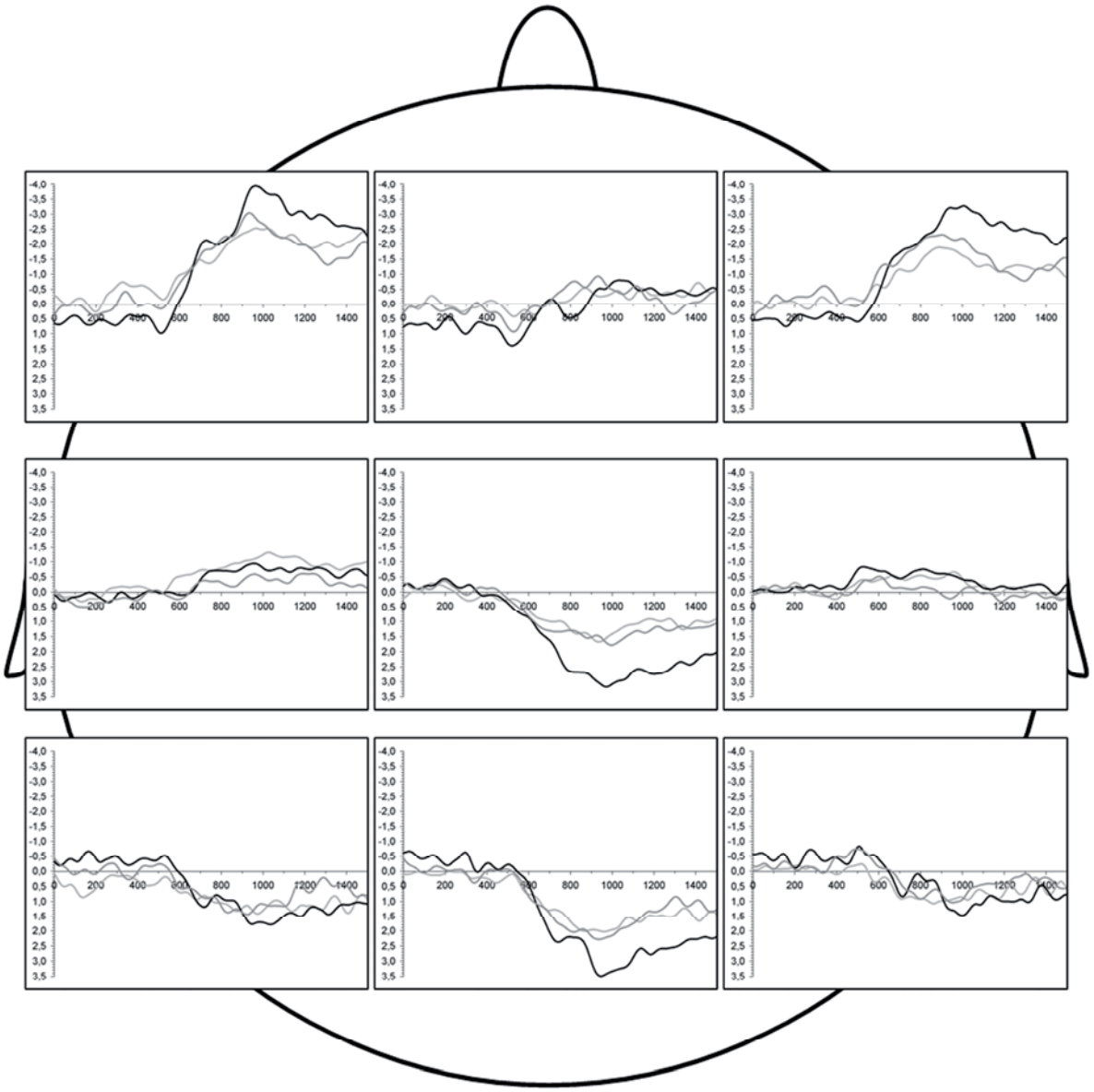
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Fig. 3a

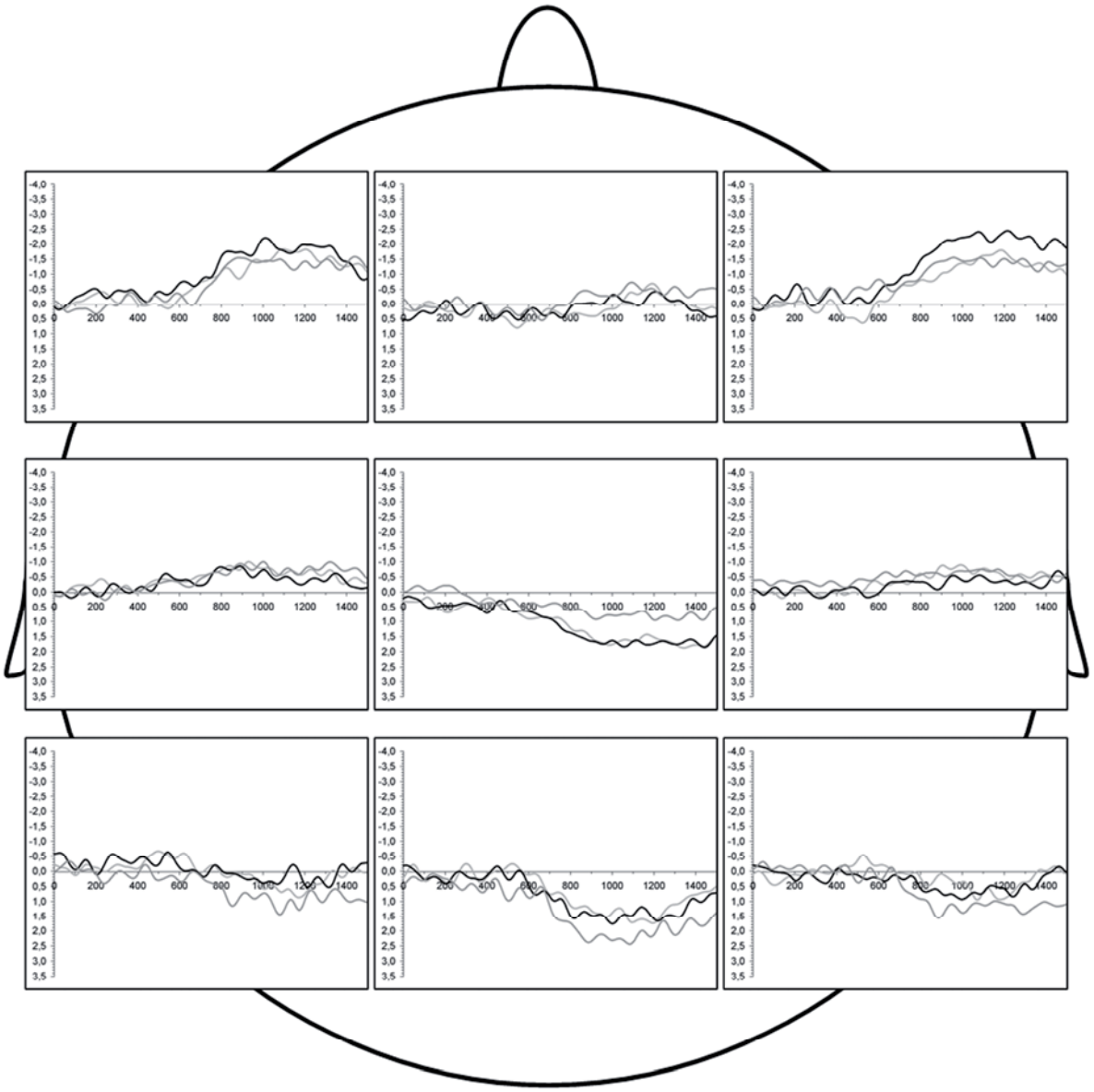
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Fig. 3b

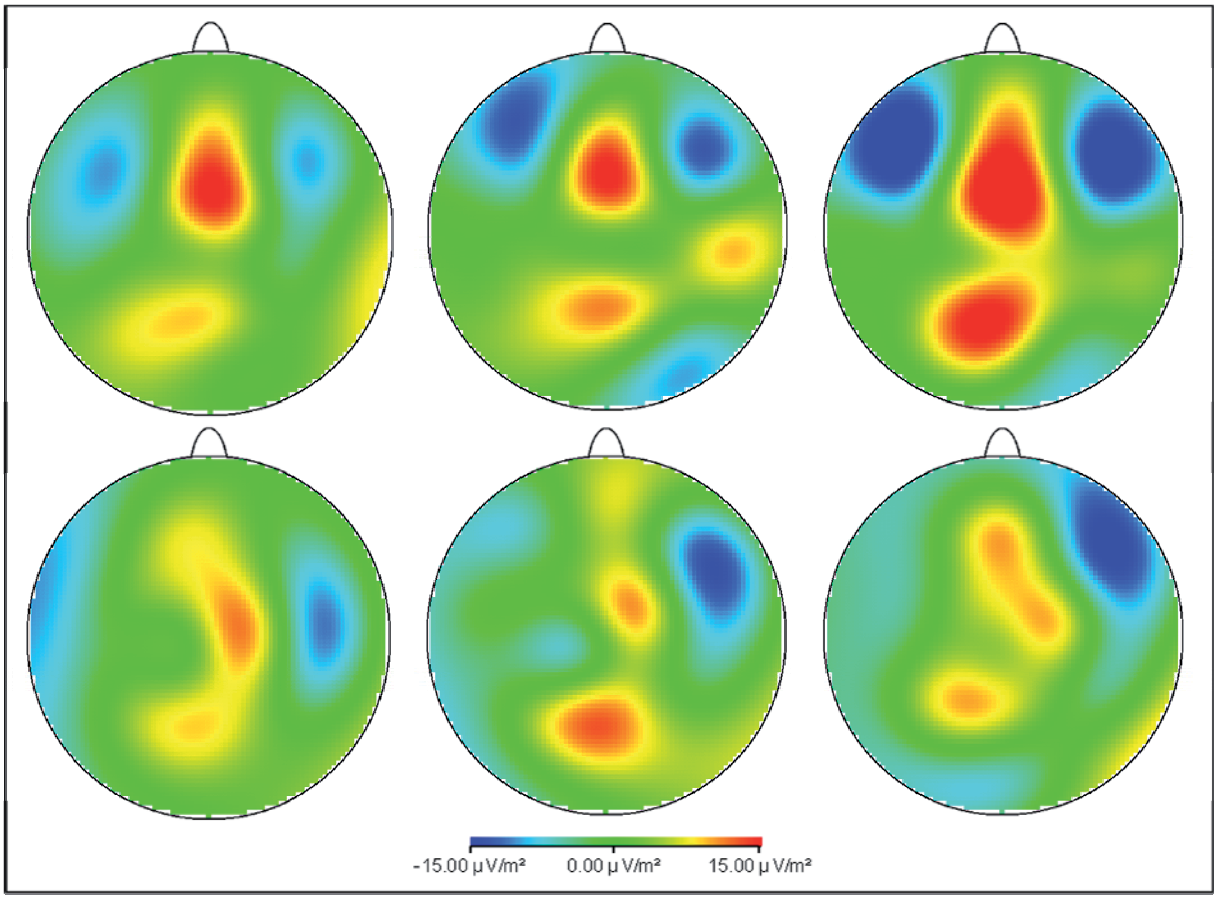

Fig. 4

General information concerning the original research article:

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Sexual Orientation and Related Social Chemosensory Context Cues Affect Facial Mimicry

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Abstract

Here, we investigate differences in facial mimicry related to sexual orientation, and the effects of human body odors as chemosensory context cues.

Facial electromyographic activity from corrugator supercilii and zygomaticus major muscle regions in response to happy and sad faces of 23 (11 gay) men (study 1) and 22 (12 lesbian) women (study 2) was recorded. In addition to the exclusive presentation of the faces, in study 1 gay and heterosexual male and heterosexual female body odors were presented simultaneously with faces of the corresponding gender. In study 2, lesbian and heterosexual female and heterosexual male body odors were presented.

Men responded with stronger corrugator activity to sad as compared to happy female faces (500-1000 ms after picture onset). This effect was prolonged in gay men (1000-1500 ms after picture onset). A corresponding differential corrugator response to male faces was observed with gay male context odor (500-1000 ms after picture onset). In addition, heterosexual men displayed stronger zygomaticus activity when presented with sad as compared to happy male faces (1500-2000 ms after picture onset). Heterosexual women displayed stronger corrugator activity in response to sad as compared to happy faces irrespective of the actor's gender (1000-2000 ms after picture onset). In lesbian women, a corresponding effect was evident in response to female faces in the context of heterosexual female body odor (500-1500 ms after picture onset).

The results are discussed with respect to possible differences in empathy and activation of affiliation motives.

Introduction

When presented with pictures of positive or negative facial expressions, people tend to mimic those expressions spontaneously and rapidly (Dimberg, 1982; Dimberg & Thunberg, 1998; Dimberg, Thunberg, & Grunedal, 2002). This facial mimicry is detectable by electromyography (EMG) of facial muscular activity. Typically, zygomaticus major activation, indicating smiling, is observed when individuals are presented with positive facial expressions (happy faces), and corrugator supercilii activation, indicating frowning, is observed when individuals are exposed to negative facial expressions (angry or sad faces; Dimberg, 1982; Sonnby-Borgström, Jönsson, & Svensson, 2008).

A correlation between interpersonal empathy and mimicry has been reported (Sonnby-Borgström, 2002), and some authors even argue that mimicry may not only be linked to, but may be the source of empathy (Chartrand & Bargh, 1999). Results of a number of studies suggest that women may be more empathic than men. Gender differences favoring women are evident in self-reports on empathy (Baron-Cohen & Wheelwright, 2004; Eisenberg & Lennon, 1983), but also in behavioral measures such as the decoding of non-verbal emotional cues (see Hall, Carter, & Horgan, 2000; McClure, 2000 for reviews) and in brain networks supporting empathy (Schulte-Rüther, Markowitsch, Shah, Fink, & Piefke, 2008). Concerning facial mimicry, results indicate that women show more pronounced mimicry than men (Dimberg & Lundquist, 1990) and, moreover, report higher levels of emotional contagion than men (Sonnby-Borgström et al., 2008). Besides being subject to gender differences, empathy is purported to vary with sexual orientation as well. Within evolutionary considerations regarding sexual orientation, higher levels of empathy (and lower levels of aggressiveness) in gay as compared to heterosexual men is discussed as a possible explanation why genes linked to homosexuality have not been selected against. Miller (2000) argues that several genes may affect the sensitivity of the male brain to hormones which shift it in a feminine direction during development. Possessing several such alleles produces homosexuality, whereas single

alleles cause greater interpersonal empathy and reduced aggressiveness, which may be adaptive traits. Indeed there is evidence that gay men are more empathic (Salais & Fischer, 1995; Sergeant, Dickins, Davies, & Griffiths, 2006) and less aggressive (Gladue & Bailey, 1995) than heterosexual men. To date no studies are available regarding possible differences in empathy between lesbian and heterosexual women.

Facial imitation has been reported to vary with the gender of the person displaying the facial expression (Lundqvist, 1995; Vrana & Gross, 2004). Social context also modifies facial mimicry, for example the induction of a competitive situation may evoke counter mimicry (Lanzetta & Englis, 1989), even if the context is only nonconsciously primed (Weyers, Mühlberger, Kund, Hess, & Pauli, 2009). Body odors have been shown to constitute potent social signals. For example, visual emotion perception is modulated in the context of human chemosensory anxiety signals (Pause, Ohrt, Prehn, & Ferstl, 2004; Zhou & Chen, 2009). Moreover, the chemosensory perception of human anxiety appears to automatically recruit empathy-related neuronal sources (Prehn-Kristensen et al., 2009). In addition to emotional states, immunogenetic profile (Jacob, McClintock, Zelano, & Ober, 2002; Pause et al., 2006; Wedekind & Füri, 1997), gender (Schleidt & Hold, 1982; Doty, Orndorf, Leyden, & Kligman, 1978) and most probably sexual orientation (Martins et al., 2005; Sergeant, Dickins, Davies, & Griffiths, 2007) are communicated chemosensorily in humans. However, no behavioral effects of such gender and sexual orientation related chemosignals have been reported so far.

In order to examine possible effects of chemosensory context cues related to gender and sexual orientation and sexual orientation itself on facial mimicry, two studies were conducted. The first study examined heterosexual and gay men's facial mimicry without social context odor as compared to the context of chemosensory signals obtained from potential partners (gay male and heterosexual female body odor, respectively). Additionally, heterosexual male body odor was introduced as a control odor.

Within the second study, lesbian and heterosexual women's facial mimicry was examined, either without context odor or when presented with body odors obtained from lesbian women and heterosexual men. Here, heterosexual female body odor served as a control odor.

Study 1: Male Participants

Aim

Study 1 was designed to investigate the effect of male sexual orientation on facial mimicry and empathy and furthermore to investigate possible differences in facial mimicry in the social context of gender and sexual orientation related body odors. It was hypothesized that gay men as compared to heterosexual men should show more pronounced facial mimicry and display higher levels of empathy. In addition, context body odors of potential partners should enhance facial mimicry.

Materials and Methods

Participants

Participants were recruited via newspaper advertisement and advertisement at the university and at local gay bars. Thirty right-handed men participated in the experiment, however, data from seven participants had to be excluded from analysis due to pronounced breathing artifacts (see EMG data reduction), resulting in a total of 23 participants (11 gay men, 12 heterosexual men). None of these participants reported a history of neurological, psychiatric, endocrine or immunological diseases or diseases related to the upper respiratory tract, and all denied chronic medication use. All participants reported being of European origin and none of them showed a tendency towards social conformity [as measured with the lie scale of the German Eysenck-Personality Inventory (EPI, Eggert, 1974)]. Four heterosexual and three gay

male participants reported being regular smokers, and the groups did not differ in their smoking behavior (p = 1.000, Fisher's Exact Test). The participants had a mean age of 27.5 years (SD = 6.5; *range* = 20-44 years), and heterosexual and gay male participants did not differ in age [$t(21) = 1.02$, $p > .250$]. No participant had previously acted as a sweat donor. Participants' sexual orientation was assessed by means of the Kinsey scales of sexual behavior and sexual fantasies (Kinsey, Pomeroy, & Martin, 1948) as well as by means of visual analog scales for describing homosexuality and heterosexuality (see Tab. 1). According to their self-description, heterosexual and gay male participants differed significantly on both Kinsey scales [behavior scale: $t(10) = 65.00$, $p < .001$, Welch-Test (Welch, 1947); fantasy scale: $t(15) = 32.02$, $p < .001$, Welch-Test], as well as on both visual analog scales [homosexuality: $t(21) = 26.88$, $p < .001$; heterosexuality: $t(21) = -39.97$, $p < .001$].

Participants gave written informed consent and were paid for participation. Both current studies, including the sweat sampling procedures, were carried out in accordance with the Declaration of Helsinki and approved by the ethical committee of the German Society of Psychology (DGPs). Additionally both studies were approved by the Lesbian and Gay Federation in Germany (Lesben- und Schwulenverband in Deutschland, LSVD).

- Tab. 1 -

Self-reported Empathy

In order to assess participants' empathy, the "Saarbrücker Persönlichkeitsfragebogen" (SPF, Paulus, 2009), a German version of the Interpersonal Reactivity Index (IRI, Davis, 1980) was used. The SPF assesses four aspects of empathy: Perspective-Taking (the individual's tendency to adopt others' point of view), Fantasy (the individual's ability to project themselves into the feelings of a fictional character), Empathic Concern (feelings of concern or sympathy towards others), and Personal Distress (feelings of anxiety and distress in

response to distress experienced by others). The scores on each scale vary between 4 and 20, with higher scores corresponding to greater levels of self-reported empathy.

Presentation of Facial Stimuli

Color pictures of happy and sad male and female faces (frontal view) were selected from the Karolinska Directed Emotional Faces database (KDEF, Lundqvist, Flykt, & Öhman, 1998). Within a preliminary study, 64 persons (41 female, mean age 31.2 years, *SD* = 13.5, *range* 18-65 years) had selected those male and female actors that, according to their opinion, best displayed the respective emotion. The pictures of the six highest-rated actors of each gender were selected for each emotion. During the EMG recording, pictures were presented on a screen for the duration of 2000 ms. Each picture showing a male actor, irrespective of the emotion displayed, was presented three times, once without any context body odor, once with a heterosexual male body odor as context, and once with gay male body odor as context. Pictures displaying female faces were presented twice, once without any context odor and once with a heterosexual female context body odor.

Ratings of the experienced emotion when presented with pictures of facial affect

In between presentation of the faces, participants indicated their experienced emotional valence (-4 to +4), arousal (1 to 9), and dominance (1 to 9) while looking at the pictures by means of the language-free Self-Assessment Manikin (SAM, Bradley & Lang, 1994).

Chemosensory Stimuli

Axillary sweat was sampled by cotton pads over the course of one night from 11 heterosexual women, and 13 gay and 14 heterosexual men. The donors indicated their sexual orientation on visual analog scales for describing homosexuality (ranging from 0 = “not homosexual” to 10 = “homosexual”) and heterosexuality (ranging from 0 = “not heterosexual” to 10 =

"heterosexual"). Both heterosexual men and women differed significantly from gay men in their self-description on both scales [men, homosexuality: $t(25) = 62.17$, $p < .001$; men, heterosexuality: $t(25) = -58.77$, $p < .001$; women, homosexuality: $t(22) = 46.93$, $p < .001$; women, heterosexuality: $t(22) = -41.45$, $p < .001$].

Donors were on average 26.1 years old (*SD* = 5.6, *range* = 18-42), and there were no differences in age between heterosexual men (*M* = 24.4, *SD* = 3.0), heterosexual women (*M* = 27.7, *SD* = 5.9) and gay men [*M* = 26.5, *SD* = 7.3; $F(2, 35) = 1.19$, $p > .250$].

All donors reported being of European origin, and denied acute or chronic medication. Furthermore, no donor indicated suffering from any neurological, psychiatric, endocrine, or immunological disease, or drug use. Their body-mass-index ranged from 18.5 to 29.1 kg/m^2 (*M* = 23.4, *SD* = 3.1), and all of them were non-smokers. Female donors reported having a regular menstrual cycle and denied use of hormonal contraception. Of the female donors, seven reported regularly shaving of axillary hair (missing data: 4). Concerning the male odor donors, seven gay (missing data: 1) and six heterosexual men (missing data: 2) reported regularly shaving their axillary hair. Accordingly, female donors differed from heterosexual male donors in their shaving habits ($p = .044$, Fisher's Exact Test), whereas female and gay male donors ($p > .100$, Fisher's Exact Test) as well as gay male and heterosexual male donors did not ($p = 1.000$, Fisher's Exact Test). The donors were instructed to refrain from eating garlic, onions, asparagus, or any other spicy or aromatic food during the 24 hours prior to the odor donation. They were further advised to refrain from using deodorants within this timeframe, and to wash their armpits exclusively with an odorless medical soap (Eubos®, Dr. Holbein GmbH, Germany). Female donors were required to be in the follicular phase of their menstrual cycle (day 5 to day 10 of the menstrual cycle). All donors gave written informed consent, and were paid for their donation.

Following the completion of collection, all sweat samples were pooled with respect to the donor's sex and, in case of male donors, with respect to their sexual orientation. Each of

the final three homogenized samples was divided into small portions of 0.3 g and stored at -20 °C.

Ratings of the Experienced Emotion when Presented with Body Odors

In order for the participants to rate their emotional response to the body odors, they were presented with three glass bottles containing one portion of 0.3 g cotton pad worn by either heterosexual men, gay men, or heterosexual women. Participants indicated their experienced emotional valence (-4 to +4), arousal (1 to 9), and dominance (1 to 9) while smelling the body odors by means of the SAM.

Olfactory Hyposmia Screening

Prior to EMG recording, all participants were screened for general hyposmia. For this purpose, the participants were required to identify a bottle containing phenyl-ethyl alcohol [99%, Fluka, Germany, 1:100 (*v/v*) diluted in diethyl phthalate] from a set of three bottles in two consecutive trials, with the remaining two bottles containing the same volume of solvent. No participant had to be excluded due to general hyposmia.

Olfactory Stimulus Presentation

For the recording of the EMG activity, chemosensory stimuli were presented according to the method described by Kobal (2003), using a constant-flow (100 ml/s; stimulus duration = 2600 ms), six channel olfactometer (OM6b, Burghart, Wedel, Germany). Both nostrils were stimulated simultaneously, and accordingly, both air streams were controlled by separate mass flow meters. In the olfactometer, the glass tubes containing the stimuli were stored in a warm-water chamber, and the stimuli were delivered to the participants through a teflon tube. The temperature of the air flow at the exit of the olfactometer was 37 °C and the relative humidity was set above 80%. Presentation of the olfactory stimuli started 600 ms prior to picture

presentation, and lasted until the end of picture presentation (2000 ms). White noise of 80 dB (A) was presented binaurally over earplugs (Etymotic Research, ER3-14A), in order to prevent the participants from hearing the switching valves of the olfactometer.

Procedure

All participants were tested individually. Prior to the EMG recording, participants practiced inhaling after a countdown as soon as "Please inhale" was presented on the screen, and to keep inhaling for the duration of picture presentation (for a total of 3000 ms). To verify correct inhalation, one respiration belt (BP-BM-10, Brain Products GmbH, Munich, Germany) was fixed around the thorax and one was fixed around the abdomen, and breathing cycles were recorded.

During EMG recording, 60 pictures were presented, comprised of 18 sad male faces, 18 happy male faces, 12 sad female faces, and 12 happy female faces. The stimuli were presented in a previously randomized, fixed order (with the restriction that the same stimulus combination, e.g. "sad female face without context odor" may be presented no more than two times in a row). At the beginning of each trial, a visual countdown from three to one lasting 3000 ms was presented to prepare the participants for inhalation. Afterwards, "Please inhale" was presented for 1000 ms, followed by the respective picture lasting 2000 ms. Subsequently, the screen turned black for 2000 to 3000 ms (randomized), followed by a consecutive presentation of the three SAM scales (valence, arousal, dominance) for 3500 ms each, separated by black screens lasting 500 ms. During presentation of each SAM scale, participants were able to indicate their emotional response by moving a cursor on the respective 9-point scale. The trials ended with another black screen lasting 1000 to 2000 ms (randomized).

Data Recording, Reduction and Analysis

Facial EMG activity was measured bipolarly on the left side of the face (Dimberg & Petterson, 2000) with miniature Ag/AgCl electrodes (inner diameter: 5 mm; GE Healthcare, Munich, Germany). Before being attached over the corrugator supercilii and zygomaticus major muscle regions (Fridlund & Cacioppo, 1986), the electrodes were filled with Signa electrode paste (Parker Laboratories Inc., New Jersey, USA). To reduce impedance, electrode sites were cleaned with alcohol and mildly rubbed with electrode paste. Muscle activity was recorded, amplified, and filtered with the BrainVision Recorder software (Brain Products GmbH, Munich, Germany) using a sampling rate of 2000 Hz, a low-pass filter of 500 Hz (24 dB/ octave), a high-pass filter of 20 Hz (24 dB/ octave, van Boxtel, 2001), and a 50 Hz notch filter. Breathing cycles were recorded with a low-pass filter of 40 Hz (24 dB/ octave) but without any high-pass filter.

Offline, raw data were first inspected for correct inhalation. Trials including odor presentation were only kept for analysis if participants started inhaling no later than 300 ms prior to picture presentation and continued inhaling for at least 1700 ms during picture presentation. This way, only such trials were kept for analysis in which participants perceived the context odors for the entire duration of picture presentation (for an overview on the time course of central nervous odor processing see Kobal & Hummel, 1991; Pause, 2005). Data from three heterosexual and four gay male participants had to be excluded from analysis, because they failed to inhale correctly in at least three of the six presentations of any stimulus combination that included a context odor, resulting in a total of 23 participants. Subsequently, data were rectified, low-pass filtered (8 Hz, 24 dB/ octave), and segmented according to the respective stimulus combinations. Data were then collapsed over trials and baseline-corrected. Here, the last second prior to picture presentation served as baseline.

For the statistical analysis, mean muscle activity during four periods was calculated: 0-500 ms, 500-1000 ms, 1000-1500 ms, and 1500-2000 ms of picture presentation. Four

separate ANOVAs were performed for each time period and each muscle region, which were also applied to the ratings of emotional responses to the pictures. However, two gay male participants failed to indicate their emotional response to one or more stimulus combination in more than 50% of the cases and thus were excluded from analysis, resulting in a total of 21 participants. To investigate the effects of the depicted emotion, the gender of the presented face, and the sexual orientation of the participants on both facial mimicry and the reported emotion when presented with pictures of facial affect (not testing possible effects of the context odors), one three-way ANOVA was calculated [factors: Picture Gender (male, female), Emotion (happy, sad), Sexual Orientation of the Participant (gay male, heterosexual male)]. In order to examine possible effects of social context odors, three separate three-way ANOVAs were calculated: Within the first ANOVA, possible effects of gay male context body odor were examined [factors: Gay Male Context Odor (male faces with gay male body odor, male faces without context odor), Emotion (happy, sad), Sexual Orientation of the Participant (gay male, heterosexual male)]. Within the second ANOVA, effects of heterosexual male context body odor were analyzed [factors: Heterosexual Male Context Odor (male faces with heterosexual male body odor, male faces without context odor), Emotion (happy, sad), Sexual Orientation of the Participant (gay male, heterosexual male)]. The third ANOVA was calculated in order to examine possible effects of heterosexual female context odor [factors: Heterosexual Female Context Odor (female faces with heterosexual female body odor, female faces without context odor), Emotion (happy, sad), Sexual Orientation of the Participant (gay male, heterosexual male)]. Subsequently, nested effects were calculated in accordance with Page, Braver, and Kinnon (2003). Huynh-Feldt corrected degrees of freedom were calculated and corrected *p*-values are reported. With regard to the analysis of both muscle activity and emotional responses to the pictures, only effects containing the factor "Emotion" are reported. Concerning the analysis of the individual odors' effects, only effects that additionally include the factor Context Odor are reported.

Participants' reports of emotion when presented with the body odors as measured by the SAM were analyzed by a two-way ANOVA [factors: Body Odor (gay male, heterosexual male, heterosexual female), Sexual Orientation of the Perceiver (gay male, heterosexual male)]. Again, nested effects were calculated (Page et al., 2003), Huynh-Feldt corrected degrees of freedom were calculated and corrected *p*-values are reported.

Results

Self-reported Empathy

On the subscales of Fantasy ($M = 13.61$, $SD = 2.25$), Perspective-Taking ($M = 13.83$, $SD = 1.99$) and Empathic Concern ($M = 13.26$, $SD = 1.66$), participants scored slightly above medium, whereas on the subscale of Personal distress they scored below medium ($M = 10.13$, $SD = 1.66$). The difference between gay and heterosexual men on the subscale of Perspective-Taking approached significance [$t(21) = 1.48$, $p = .076$; one-sided test], with gay men describing themselves as more empathic ($M = 14.46$, $SD = 1.97$) than heterosexual men did ($M = 13.35$, $SD = 1.91$).

Ratings of the Experienced Emotion when Presented with Body Odors

Participants rated their emotional valence as negative ($M = -0.74$, $SD = 1.63$) when presented with heterosexual male body odor, differing significantly from a slightly positive rating when presented with heterosexual female body odors [$M = 0.91$, $SD = 1.44$; Body Odor $F(2, 42) = 5.65$, $p = .010$, $f = 0.519$, Power = .835; Heterosexual Male Body Odor compared to Heterosexual Female Body Odor $t(22) = -4.750$, $p < .001$]. Moreover, when presented with heterosexual female body odor ($M = 6.00$, $SD = 1.21$), men reported experiencing greater dominance than when presented with heterosexual ($M = 5.22$, $SD = 1.41$) or gay male ($M =$ 5,04, $SD = 1.40$) body odors [Body Odor $F(2, 42) = 4.81$, $p = .013$, $f = .478$, Power = .767; Heterosexual Male Body Odor compared to Heterosexual Female Body Odor $t(22) = -2.274$,

p = .033; Gay Male Body Odor compared to Heterosexual Female Body Odor $t(22)$ = -3.140, p = .005]. No effects were observed concerning the arousal ratings.

Ratings of the Experienced Emotion when Presented with Pictures of Facial Affect

Effects of emotion, gender, and sexual orientation

When presented with happy faces, participants indicated a positive emotional valence (M = 1.28, SD = 0.77), differing significantly from the negative emotional valence experienced (M = -1.05, SD = 0.82) when presented with sad faces [Emotion $F(1, 19) = 48.48$, $p < .001$, f = 1.600, Power = 1.000]. Participants described themselves as unhappier when presented with sad female faces (M = -1.25, SD = 0.80) compared to sad male (M = -0.85, SD = 0.97) faces [Picture Gender by Emotion $F(1, 19) = 10.52$, p = .004, f = 0.744, Power = 0.867; nested effects: Picture Gender within Sad Faces $F(1, 19) = 6.27$, p = .022]. No effects were observed concerning the arousal or dominance dimensions.

Effects of "gay male context odor"

No effects involving gay male context odor were observed on valence, arousal, or dominance.

Effects of "heterosexual male context odor"

The effect that men reported feelings of positive affect when presented with happy faces compared to sad faces was also observed when male faces were presented with (happy: M = 1.09, SD = 0.93; sad = M = 0.15, SD = 0.94) and without (happy: M = 1.12, SD = 0.94; sad: M = -0.85, SD = 0.97) contemporaneous presentation of heterosexual male body odor [Emotion by Heterosexual Male Context Odor $F(1, 19) = 12.50$, p = .002, f = 0.811, Power = .842; nested effects: Emotion within Male Faces without Context Odor $F(1, 19) = 28.04$, $p <$ .001; Emotion within Male Faces with Heterosexual Male Context Odor $F(1, 19) = 14.29$, $p <$ .001]. However, exposure to heterosexual male body odor diminished this effect, because

when presented with sad male faces in the context of this odor, participants reported less negative feelings than without heterosexual male context odor [M = -0.85, SD = 0.97; Heterosexual Male Context Odor by Emotion $F(1, 19) = 12.50$, $p = .002$, $f = 0.811$, Power = .842; nested effects: Heterosexual Male Context Odor within Sad Faces $F(1, 19) = 21.30$, $p < .001$]. No effects were observed concerning the arousal or dominance dimensions.

Effects of "heterosexual female context odor"

Heterosexual men indicated higher arousal levels when presented with happy female faces (M = 5.17, SD = 1.30) compared to sad female faces [M = 4.56, SD = 1.48; Emotion by Heterosexual Female Context Odor by Sexual Orientation of the Participant $F(1, 19) = 10.40$, $p = .004$, $f = 0.740$, Power = .863; nested effects: Emotion by Heterosexual Female Context Odor within Heterosexual Male Participants $F(1, 19) = 12.91$, $p = .002$; Emotion within Heterosexual Male Participants within Female Faces without Heterosexual Female Context Odor $F(1, 20) = 5.01$, $p = .037$]. In the context of heterosexual female body odor, this effect was weakened, as heterosexual men then reported experiencing less arousal when presented with happy female faces (M = 4.59, SD = 1.09) compared to the presentation of happy female faces without the context odor [M = 5.17, SD = 1.30; Heterosexual Female Context Odor by Sexual Orientation of the Participant by Emotion $F(1, 19) = 10.40$, $p = .004$, $f = 0.740$, Power = .863; nested effects: Heterosexual Female Context Odor by Sexual Orientation of the Participant within Happy Faces $F(1, 19) = 12.91$, $p = .002$; Heterosexual Female Context Odor within Happy Faces within Heterosexual Men $F(1, 20) = 5.01$, $p = .037$]. Analysis of valence and dominance ratings did not yield any significant effects.

Facial EMG: Corrugator Supercilii

Effects of emotion, gender, and sexual orientation

Within the period of 500-1000 ms, all participants showed stronger muscular activity when presented with sad female faces (M = 0.22 μV, SD = 0.57 μV) than when presented with happy female faces [M = -0.16 μV, SD = 0.64 μV; Emotion by Picture Gender $F(1, 21) = 6.73$, $p = .017$, $f = 0.567$, Power = .695; nested effects: Emotion within Female Faces $F(1, 21) = 6.86$, $p = .016$]. In response to male faces, no significant differential muscle activity was observed. Analysis of muscular activity within the periods of 0-500 ms, 1000-1500 ms, and 1500-2000 ms did not yield any significant effects.

Effects of "gay male context odor"

Whereas without social context odors participants only displayed significant corresponding facial muscle activity when presented with pictures of females, within the context of gay male body odor participants also showed stronger corrugator activity when presented with sad male faces (M = 0.27 μV, SD = 0.62 μV) as compared to happy male faces (M = -0.13 μV, SD = 0.57 μV) within 500-1000 ms after picture onset [Emotion by Gay Male Context Odor $F(1, 21) = 5.38$, $p = .031$, $f = 0.506$, Power = .598; nested effects: Emotion within Male Faces with Gay Male Body Odor $F(1, 21) = 10.89$, $p = .003$]. Within the periods of 0-500 ms, 1000-1500 ms, and 1500-2000 ms after picture onset no significant effects were observed.

Effects of "heterosexual male context odor"

Analysis concerning heterosexual male context odor did not yield significant effects in any time-period.

Effects of "heterosexual female context odor"

The observed effect of all participants showing corresponding facial muscle activity when presented with female faces within 500-1000 ms after picture onset was extended by gay men displaying stronger muscular activity when presented with sad female faces (M = 1.50 µV, SD = 2.14 µV) as compared to happy female faces (M = -0,03 µV, SD = 0.80 µV) within 1000-1500 ms after picture onset [Emotion by Heterosexual Female Context Odor by Sexual Orientation of the Participants $F(1, 21) = 6.97$, $p = .015$, $f = 0.576$, Power = .709; nested Effects: Emotion by Heterosexual Female Context Odor within Gay Male Participants $F(1, 21) = 7.47$, $p = .012$, Emotion within Gay Male Participants within Female Faces without Context Odor $F(1, 22) = 4.39$, $p = .048$]. However, presentation of heterosexual female context body odor diminished this effect in gay men, as no significant differential muscle activity was observed in this condition. Analysis did not reveal any effects within 0-500 ms, 500-1000 ms or 1500-2000 ms after picture onset.

Facial EMG: Zygomaticus Major

Effects of emotion, gender, and sexual orientation

Heterosexual men showed stronger muscular activity when presented with sad (M = 0.22 µV, SD = 1.25 µV) than when presented with happy (M = -0.52 µV, SD = 1.52 µV) male faces within 1500-2000 ms after picture onset [see Fig. 1; Sexual Orientation of the Participants by Emotion by Picture Odor $F(1, 21) = 4.48$, $p = .046$, $f = 0.478$, Power = .522; nested effects: Sexual Orientation of the Participants by Emotion within Male Faces $F(1, 21) = 5.31$, $p = .032$; Emotion within Male Faces within Heterosexual Male Participants $F(1, 21) = 4.76$, $p = .041$]. On a descriptive level, gay men showed the opposite pattern (see Fig. 1), displaying stronger zygomaticus activity when presented with happy male faces (M = 0.14 µV, SD = 0.74 µV) compared to sad male faces (M = -0.25 µV, SD = 0.86). Analysis within the time periods of 0-500 ms, 500-1000 ms, and 1000-1500 ms did not yield any significant effects.

- Fig. 1 -

Effects of "gay male context odor"

The effect of heterosexual men showing stronger zygomaticus activity when presented with sad (M = 0.22 μV, SD = 1.25 μV) than when presented with happy (M = -0.52 μV, SD = 1.52 μV) male faces within 1500-2000 ms after picture onset also was evident within the analysis of gay male context odor effects [Sexual Orientation of the Participants by Emotion by Gay Male Context Odor $F(1, 21) = 4.45$, $p = .047$, $f = 0.461$, Power = .520; nested effects: Sexual Orientation of the Participants by Emotion within Male Faces without Context Odor $F(1, 21) = 5.31$, $p = .032$; Emotion within Male Faces without Context Odor within Heterosexual Male Participants $F(1, 21) = 4.76$, $p = .041$]. However, gay male context odor reduced this effect, as no significant differential zygomaticus activity was observed when gay male body odor was presented.

Effects of "heterosexual male context odor"

Analysis concerning heterosexual male context odor did not yield significant effects in any time-period.

Effects of "heterosexual female context odor"

No significant effects involving heterosexual female context odor were observed in any time-period.

Discussion

When presented exclusively with the body odors, all male participants report more negative feelings when exposed to heterosexual male body odor as compared to gay male or heterosexual female body odors. When exposed to pictures of facial affect without contemporaneous presentation of body odors, participants indicate feelings of happiness when presented with pictures of happy facial affect, and report feelings of negative emotional valence when presented with sad faces, an effect that is especially prominent when participants are exposed to female faces. Concerning facial muscle activity, men display stronger corrugator supercilii activity in response to sad as compared to happy female facial expressions. This effect was prolonged in gay men. When presented with sad male faces, heterosexual men show stronger zygomaticus major activity than when exposed to happy male faces. In the context of gay male body odor, however, all participants respond with stronger corrugator activity when presented with sad than when presented with happy male facial expressions. These data suggest that men display facial reactions to facial expressions, and that these are not only affected by sexual orientation, but also by the gender of the person displayed, and further by chemosensory social context cues, comprised of human body odors.

The observed pronounced corrugator activity in response to expressions of negative facial affect, suggesting a display of facial mimicry, is well in line with the current literature (see for example Dimberg & Petterson, 2000; Dimberg et al., 2002; Sonnby-Borgström et al., 2008). Moreover, the subjective reports of experienced emotional valence matching the displayed affect might indicate emotional contagion, an effect that has repeatedly been shown when individuals were presented with static (Sonnby-Borgström, 2002; Sonnby-Borgström & Jönsson, 2004; Sonnby-Borgström et al., 2008) as well as dynamic (Hess & Blairy, 2001) emotional facial expressions. However, a higher tendency for men to display facial mimicry or report emotional contagion especially when presented with pictures of females has not been reported so far. In general, gender effects on the side of the individual posing the facial

expression have been rarely studied. Vrana and Gross (2004) reported that individuals show more negative facial expressions when presented with pictures of females modeling joyful and angry expressions as compared to presentation of males displaying the same expressions, indicated by more corrugator and less zygomaticus activity. Results from other studies indicate no differences in facial muscle responses to male as opposed to female emotional faces (Dimberg & Lundquist, 1990). Within the present study, facial mimicry to female faces was especially prolonged in gay male participants, a fact that may account for the divergent results compared to earlier studies since these studies did not report the sexual orientation of the participants. Together with the higher self-described empathy of gay as compared to heterosexual men, the present results hint at higher levels of interpersonal reactivity within gay as compared to heterosexual men.

Interestingly, heterosexual men showed stronger zygomaticus major muscle activity when exposed to sad as compared to happy male faces, indicating a display of counter mimicry. Negative attitudes towards individuals modeling facial expressions have been reported to be associated with counter mimicry (Likowski, Mühlberger, Seibt, Pauli, & Weyers, 2008), as well as non-shared pertinent social identity (Bourgeois & Hess, 2008). Moreover, induction of a competitive situation may result in counter mimicry (Lanzetta & Englis, 1989; Weyers et al., 2009). However, within the current design there was no reason for especially heterosexual men to experience competition or develop a negative attitude towards the male actors modeling the emotional expressions. It seems more likely that the observed tendency to smile when presented with a negative emotional facial expression is an indication of a lower level of empathy in heterosexual men, especially as gay men showed the opposite response pattern. Studies directly relating empathy to facial mimicry have yielded results supporting this notion, as participants low in empathy showed increased zygomaticus muscle activity in response to pictures of negative facial affect (Sonnby-Borgström, 2002). As within the current study, these differences did not extend to reported emotional contagion.

Mimicry to male faces seems to be facilitated in the context of gay male body odor, which is in line with findings demonstrating that facial reactions to facial expressions are affected by social cues (Bourgeois & Hess, 2008; McHugo, Lanzetta, & Bush, 1991). Even though no results concerning effects of chemosensory social cues on facial mimicry have been reported so far, it has been shown that human chemosensory anxiety signals activate brain areas involved in the processing of social emotional stimuli, as well as areas involved in the regulation of empathic feelings (Prehn-Kristensen et al., 2009). Whether non-emotional chemosignals like those used in the current study evoke similar central nervous response patterns remains to be investigated. However, a facilitation of facial mimicry by social chemosignals specifically obtained from gay men is in line with evolutionary theories concerning the persistence of gay male sexual orientation. It has not only been proposed that differences in empathy may account for the perseverance of homosexual orientation (Miller, 2000), but also that homosexuality has not been selected against because it aided same-sex affiliation and alliance formation (Kirkpatrick, 2000; Muscarella, 1999; Muscarella, 2000). Behavioral mimicry shares a bidirectional relationship with rapport and affinity (see Lakin, Jefferis, Cheng, & Chartrand, 2003), such that rapport facilitates mimicry, and mimicry increases rapport. Even subliminal priming of the goal to affiliate with another person enhances behavioral mimicry (Lakin & Chartrand, 2003). Taking into account this link between affiliation and mimicry, and the evolutionary considerations concerning gay male sexual orientation, a possible interpretation of the current data hints at a priming of affiliation motives by gay male body odors.

Study 2: Female Participants

Aim

In study 2, the effect of female sexual orientation on empathy and facial mimicry in the social context of gender and sexual orientation related to body odors was investigated. It was hypothesized that lesbian and heterosexual women should differ in facial mimicry and self-reported levels of empathy. Moreover, context body odors of potential partners should facilitate facial mimicry.

Materials and Methods

Participants

Lesbian and heterosexual female participants were recruited via newspaper advertisement and advertisement at the university and at local gay bars. Thirty right-handed women participated in the experiment, however, data from eight women had to be excluded from analysis due to noticeable breathing artifacts during the EMG recording (see EMG data reduction). All of the remaining 22 participants (12 lesbian and 10 heterosexual women) met the same criteria as the participants in study one. Additionally, the female participants reported having a regular menstrual cycle, and were not using any hormonal contraceptives. Lesbian and heterosexual women did not differ in their menstrual cycle phase (ps > .250, Fisher's Exact Test). Two heterosexual and three lesbian participants reported being regular smokers, and accordingly, the groups did not differ in their smoking behavior (p = 1.000, Fisher's Exact Test). The participants had a mean age of 28.9 years (SD = 6.9; *range* = 20-45 years), and heterosexual and lesbian women did not differ in age [$t(20) = -0.24$, $p > .25$]. No woman had previously acted as a sweat donor.

Participants' sexual orientation was assessed the same way as in study one. According to their self-description (see Tab. 2), heterosexual and lesbian participants differed significantly on

both Kinsey scales [behavior scale: $t(11) = 51.91$, $p < .001$, Welch-Test; fantasy scale: $t(20) = 12.79$, $p < .001$], as well as on both visual analog scales [homosexuality: $t(13) = 34.47$, $p < .001$, Welch-Test; heterosexuality: $t(12) = -43.67$, $p < .001$, Welch-Test]. Participants gave written informed consent and were paid for participation.

- Tab. 2 -

Presentation of Facial Stimuli

The procedure including the presentation of facial stimuli followed the same protocol as in study one, except for the fact that each picture showing a female model was presented three times, once without any context body odor, once with a heterosexual female context body odor, and once with lesbian female body odor as context. Pictures displaying male faces were presented twice, once without any context odor and once with a heterosexual male context body odor.

Chemosensory Stimuli

Axillary sweat was sampled from the same heterosexual male and female donors as in study one. In the present study, sweat samples were additionally obtained from eleven lesbian women, instead of gay men (see study 1). Sweat donation followed the same protocol as in study one, and the donors met the same criteria. Both heterosexual men and women differed significantly from lesbian women in their self-description on the visual analog scales for describing homosexuality and heterosexuality [men, homosexuality: $t(23) = 46.52$, $p < .001$; men, heterosexuality: $t(23) = -52.33$, $p < .001$; women, homosexuality: $t(20) = 36.46$, $p < .001$; women, heterosexuality: $t(22) = -37.02$, $p < .001$].

Donors were on average 26.1 years old (*SD* = 5.4, *range* = 19-42), and there were no differences in age between heterosexual men (*M* = 24.4, *SD* = 3.0), heterosexual women (*M* = 27.7, *SD* = 5.9) and lesbian women [*M* = 26.6, *SD* = 6.9, $F(2, 33) = 1.29$, $p > .250$]. Their body-mass-index ranged from 18.5 to 29.0 kg/m^2 (*M* = 23.3, *SD* = 3.1), and all of them were non-smokers. Of the lesbian odor donors, eight reported regularly shaving their axillary hair (missing data: 3).Female donors did not differ in their shaving habits ($p = 1.000$, Fisher's Exact Test), whereas both lesbian ($p = .042$, Fisher's Exact Test) and heterosexual female donors ($p = .044$, Fisher's Exact Test) differed from male donors in their shaving habits.

Data Recording, Reduction and Analysis

Data recording and reduction followed the same protocol as in study one. Subsequent to the inspection for correct inhalation, data from five heterosexual and three lesbian women had to be excluded from analysis, because they failed to inhale correctly in at least three of the six presentations of any stimulus combination that included a context odor. Data of the remaining 22 participants were analyzed.

With regard to the ratings of the experienced emotion when presented with pictures of facial affect, two lesbian women and one heterosexual woman were excluded from analysis because they failed to indicate their emotional response to one or more stimulus combination in more than 50% of the cases, resulting in a total of 19 participants.

Statistical analysis also followed the same protocol as in study one, with the exception that instead of effects of gay male context body odor effects of lesbian female context body odor were analyzed.

Results

Self-Reported Empathy

Female participants scored slightly above medium on the dimensions of Fantasy (M = 13.82, SD = 2.22), Perspective-Taking (M = 14.73, SD = 2.57) and Empathic Concern (M = 13.82, SD = 1.74), whereas they scored medium on the dimension of Personal distress (M = 12.00, SD = 2.43). Lesbian women scored higher (M = 15.92, SD = 2.39) than heterosexual women (M = 13.30, SD = 1.20) on the subscale of Perspective-Taking [$t(20) = 2.719$, $p = .007$, one-sided test] as well as on the subscale of Empathic Concern [lesbian women: M = 14.42, SD = 1.93; heterosexual women: M = 13.10, SD = 1.20; $t(20) = 1.875$, $p = .038$, one-sided test].

Ratings of the Experienced Emotion when Presented with Body Odors

Women indicated feelings of unhappiness when presented with heterosexual male body odor (M = -1.59, SD = 1.84), but reported experiencing feelings of happiness when exposed to lesbian (M = 1.27, SD = 1.80) as well as heterosexual female body odor [M = 1.05, SD = 1.59]. No effects were observed concerning arousal or dominance ratings.

Ratings of the Experienced Emotion when Presented with Pictures of Facial Affect

Effects of emotion, gender, and sexual orientation

Female participants rated their experienced emotional valence as positive when presented with happy faces (M = 1.16, SD = 0.72), differing significantly from the reported negative emotional valence when presented with sad faces [M = -1.04, SD = 0.82; Emotion $F(1, 17) = 66.07$, $p < .001$, $f = 1.969$, Power = 1.000]. This effect was evident when presented with male (sad: M = -0.96, SD = 0.81; happy: M = 0.94, SD = 0.70) as well as female faces [sad: M = -1.12, SD = 0.88, happy: M = 1.38, SD = 0.82; Emotion by Picture Gender $F(1, 17) = 20.85$, $p < .001$, $f = 1.108$, Power = .990; nested effects: Emotion within Male Faces $F(1, 17) = 47.94$, $p < .001$, Emotion within Female Faces $F(1, 17) = 78.53$, $p < .001$]. Moreover, female

participants reported greater positive emotional valence when presented with happy female (M = 1.38, SD = 0.82) as compared to happy male faces [M = 0.94, SD = 0.70; Picture Gender by Emotion $F(1, 17) = 20.85$, $p < .001$, f = 1.108, Power = .990; nested effects: Picture Gender within Happy Faces $F(1, 17) = 15.68$, $p = .001$]. No significant effects were observed concerning arousal or dominance ratings.

Effects of context odors

Analysis of possible effects of the presented context odors on emotional responses did not yield significant results, neither concerning valence, nor concerning arousal or dominance ratings.

Facial EMG: Corrugator Supercilii

Effects of emotion, gender, and sexual orientation

All female participants showed stronger muscular activity when exposed to sad faces (M = 0.57 µV, SD = 0.78 µV) as compared to happy faces (M = 0.30 µV, SD = 1.03 µV) within 1500-2000 ms after picture onset [Emotion $F(1, 20) = 4.33$, $p \leq .050$, f = 0.465, Power = .507]. In heterosexual women, this effect was already present within the period of 1000-1500 ms after picture onset [see Fig 2.; sad: M = 0.61 µV, SD = 0.91 µV; happy: M = 0.18 µV, SD = 0.98 µV; Emotion by Sexual Orientation of the Participants $F(1, 20) = 5.26$, $p = .033$, f = 0.513, Power = .587; nested effects: Emotion within Heterosexual Female Participants $F(1, 20) = 5.45$, $p = .030$]. No effects within the other time periods were observed.

- Fig. 2 -

Effects of "lesbian female context odor"

No significant effects were observed in any time-period.

Effects of "heterosexual female context odor"

Whereas without context odor especially heterosexual women responded with corresponding facial muscle activity to male and female faces within 1000-1500 ms after picture onset (see above), in the context of heterosexual female body odor predominantly lesbian women (see Fig. 3) showed stronger muscular activity to sad (M = 0.79 µV, SD = 0.86 µV) than to happy female faces [M = -0.01 µV, SD = 0.80 µV; Emotion by Heterosexual Female Context Odor by Sexual Orientation of the Participant $F(1, 20) = 8.27$, $p = .009$, $f = 0.644$, Power = .779; nested effects: Emotion by Heterosexual Female Context Odor within Lesbian Female Participants $F(1, 20) = 10.04$, $p = .005$; Emotion within Lesbian Female Participants within Female Faces with Heterosexual Female Body Odor $F(1, 21) = 11.15$, $p = .003$]. Moreover, in lesbian women this effect also was also observed within the earlier time-frame of 500-1000 ms [see Fig. 3; sad: M = 0.57 µV, SD = 0.60 µV; happy: M = 0.18 µV, SD = 0.62 µV; Emotion by Heterosexual Female Context Odor by Sexual Orientation of the Participant $F(1, 20) = 7.50$, $p = .013$, $f = 0.613$, Power = .739; nested effects: Emotion by Heterosexual Female Context Odor within Lesbian Female Participants $F(1, 20) = 10.69$, $p = .004$; Emotion within Lesbian Female Participants within Female Faces with Heterosexual Female Body Odor $F(1, 21) = 7.01$, $p = .015$]. No effects were observed within the first 500 ms after picture onset and within 1500-2000 ms after picture onset.

- Fig. 3 -

Effects of "heterosexual male context odor"

Analysis did not yield any significant effects in either time period.

Facial EMG: Zygomaticus Major

No significant effects were observed in any time-period.

Discussion

The present results show lesbian women describing themselves as more empathic than heterosexual women. When merely exposed to the body odors, all women report experiencing feelings of unhappiness when presented with heterosexual male body odor, whereas they report positive feelings when presented with lesbian and heterosexual female body odor.

Concerning presentation of facial expressions without any context odor, women indicate experiencing feelings of happiness when presented with happy facial expressions, and experiencing feelings of negative affect when presented with sad facial expressions. Moreover, when presented with happy female faces, women report experiencing even more happiness than when exposed to happy male faces. With regard to facial muscle activity, all women respond with stronger corrugator supercilii activity to sad as compared to happy facial expressions, irrespective of the model's gender. In heterosexual women, this effect occurred even earlier. When presented with female faces in the context of heterosexual female body odor, especially lesbian women responded with stronger corrugator activity to sad as compared to happy faces. These results indicate that in women facial reactions to facial expression vary with sexual orientation. Moreover, in lesbian women, these reactions are not only subject to the gender of the person displayed, but affected by social chemosensory context cues.

Stronger corrugator supercilii activation, in response to pictures of negative facial affect, indicating a display of facial mimicry, is well documented (see for example Dimberg & Petterson, 2000; Dimberg et al., 2002; Sonnby-Borgström et al., 2008), and the current results are in line with this literature. Additionally, results suggest women experiencing

emotional contagion, as their reported affect on the dimension of valence is congruent with the presented facial expressions (Hess & Blairy, 2001; Sonnby-Borgström et al., 2008). No specific activation of the zygomaticus major muscle was observed when participants were presented with happy faces. This result somewhat contrasts the current literature, since especially women have been reported to show strong imitation particularly of joyful facial expressions (Dimberg & Lundquist, 1990). These divergent results may be accounted for by methodological differences. Within the current study, pictures of both positive and negative facial affect were presented in a pseudo-randomized order, whereas Dimberg and Lundquist presented blocks of negative and positive facial expressions. There is evidence that presenting pictures of different facial affects in randomized order as opposed to a block-design results in some kind of orienting response visible in facial EMG. This response especially affects the zygomaticus major muscle, confounding with the mimicry response (Dimberg, 1996).

Despite the fact that lesbian women described themselves as more empathic on the SPF, they did not express more facial mimicry than heterosexual women in general. While heterosexual women displayed facial mimicry regardless of the gender of the person modeling the facial expression, lesbian women showed facial mimicry predominantly when presented with female faces in the context of heterosexual female body odor, a pattern not observed in heterosexual women. In addition, lesbian as well as heterosexual women reported feelings of happiness when presented with female body odors. Recent neuroimaging studies suggest that lesbian women display pronounced central nervous activity when presented with pictures of female faces (Kranz & Ishai, 2006), whereas heterosexual women respond more to male faces. Other imaging studies have shown that lesbian women differ from heterosexual women in their pattern of brain activation in response to an odorous estrogen-like steroid, which the authors present as a human female pheromone (Berglund, Lindström, & Savic, 2006). Together with the current study these results suggest that female chemosensory as well as female visual social stimuli hold a certain significance for lesbian women. Given the link

between behavioral mimicry and affiliation (Lakin & Chartrand, 2003; Lakin et al., 2003), the present findings might suggest that lesbian women tend to affiliate with other women, and that female body odors facilitate this tendency. However, it remains to be investigated in further studies why this effect does not extend to lesbian female body odor

General Discussion

Together, both studies suggest an effect of sexual orientation in both men and women on self-reported empathy. However, in which way this effect translates into behavior in terms of facial mimicry, is subject to gender related visual social cues as well chemosensory social cues related to gender and sexual orientation. Regarding both presented studies, men's facial mimicry differed in more aspects with regard to sexual orientation than did women's. These results correspond to the notion that male sexual orientation is considered as more stable (Bailey, Dunne, & Martin, 2000; Pattatucci & Hamer, 1995) and that men are presumed to display less erotic plasticity than women (Baumeister, 2000), which supports more clear-cut sexual orientation related differences in men than in women.

The fact that the chemosensory context cues presented in the current study differentially affected facial mimicry demonstrates that not only gender but also sexual orientation is chemosensorily communicated in humans. Communication of sexual orientation via body odors has been suggested by rating studies reporting differences in the hedonic evaluation of homosexual and heterosexual male and female body odors (Martins et al., 2005; Sergeant et al., 2007). However, to our knowledge the present studies are the first to show behavioral effects of such chemosensory signals. Further studies are needed to clarify their behavioral significance, especially with regard to female intrasexual chemosensory communication.

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Tables

Table 1

Self description of sexual orientation in male participants (study 1)

	Gay Male Participants			Heterosexual Male Participants		
	M	*SD*	*Range*	*M*	*SD*	*Range*
Kinsey Scale: Behavior***	5.91	0.30	5-6	0.00	0.00	0-0
Kinsey Scale: Fantasy***	5.64	0.51	5-6	0.08	0.29	0-1
Visual Analog Scale: Homosexuality***	9.19	0.84	7.6-10.0	0.48	0.72	0.0-2.3
Visual Analog Scale: Heterosexuality***	0.46	0.47	0.0-1.6	9.64	0.61	7.8-10.0

Notes. Kinsey Scales range from 0 (“exclusively heterosexual”) to 6 (“exclusively homosexual”), Visual Analog Scale on Homosexuality ranges from 0.0 (“not homosexual”) to 10.0 (“homosexual”), Visual Analog Scale on Heterosexuality ranges from 0.0 (“not heterosexual”) to 10.0 (“heterosexual”); ***: $p < 0.001$.

Table 2

Self description of sexual orientation in female participants (study 2)

	Lesbian Female Participants			Heterosexual Female Participants		
	M	*SD*	*Range*	*M*	*SD*	*Range*
Kinsey Scale: Behavior***	5.83	0.39	5-6	0.00	0.00	0-0
Kinsey Scale: Fantasy***	5.25	1.14	3-6	0.30	0.48	0-1
Visual Analog Scale: Homosexuality***	9.49	0.80	7.5-10.0	0.37	0.27	0.1-1.0
Visual Analog Scale: Heterosexuality***	0.57	0.89	0.0-2.3	9.71	1.20	9.4-10.0

Notes. Kinsey Scales range from 0 (“exclusively heterosexual”) to 6 (“exclusively homosexual”), Visual Analog Scale on Homosexuality ranges from 0 (“not homosexual”) to 10 (“homosexual”), Visual Analog Scale on Heterosexuality ranges from 0 (“not heterosexual”) to 10 (“heterosexual”); ***: $p < 0.001$.

Figure legends

Figure 1. Zygomaticus activity in heterosexual (top) and gay (bottom) male participants in response to happy (black line) and sad (grey line) male faces presented without context odor; abscissa: ms, ordinate: μV.

Figure 2. Corrugator activity in heterosexual female participants in response to happy (black line) and sad (grey line) faces presented without context odor; abscissa: ms, ordinate: μV.

Figure 3. Corrugator activity in lesbian participants in response to happy (black line) and sad (grey line) female faces in the context of heterosexual female body odor; abscissa: ms, ordinate: μV.

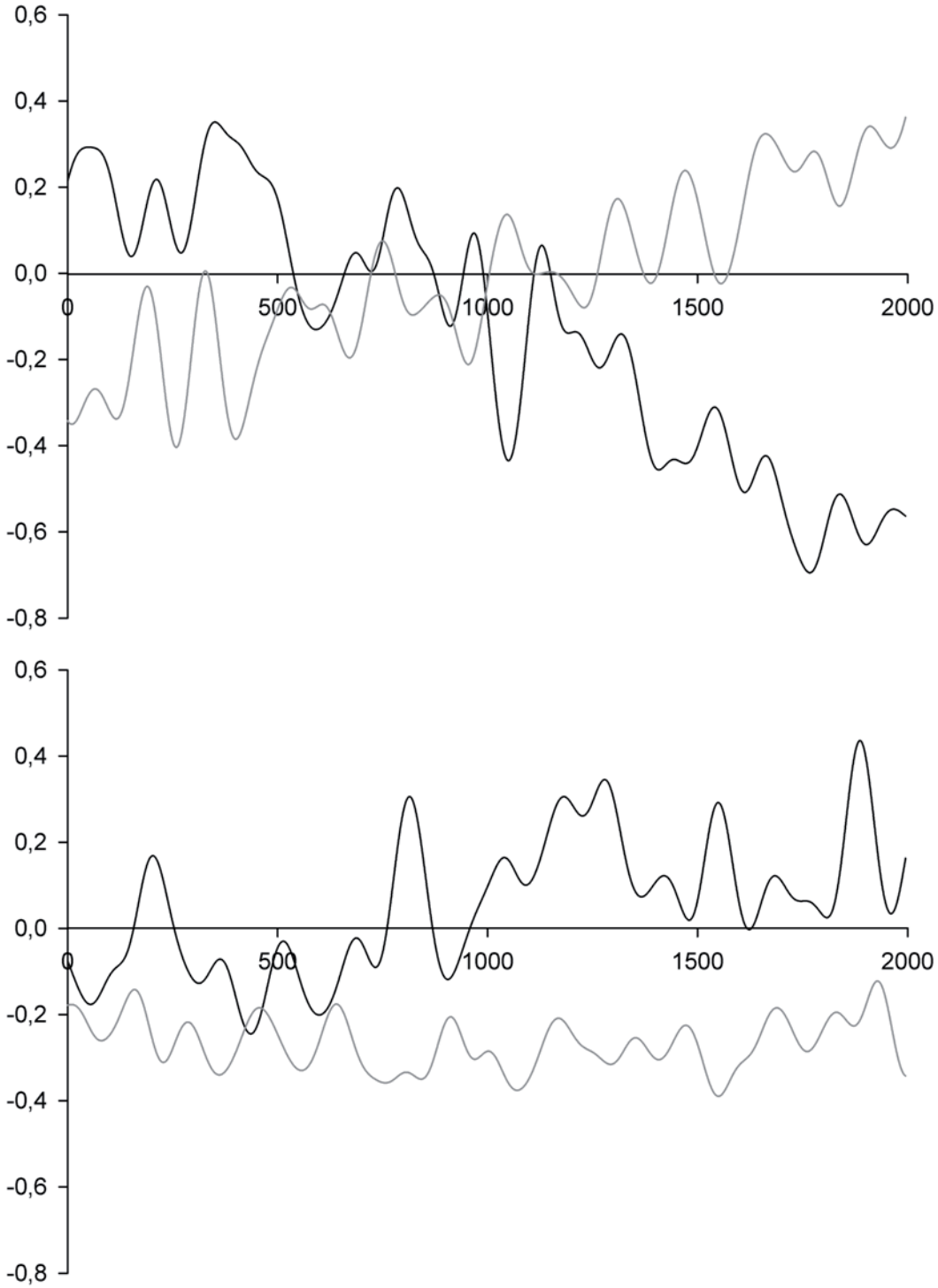
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Fig. 1

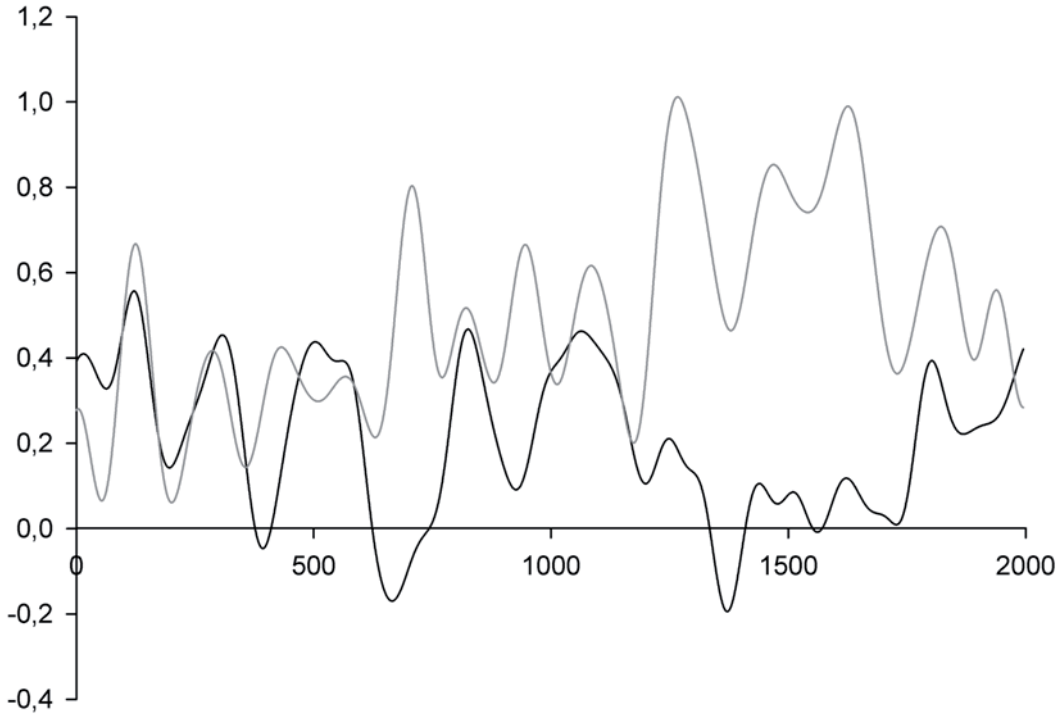

Fig. 2

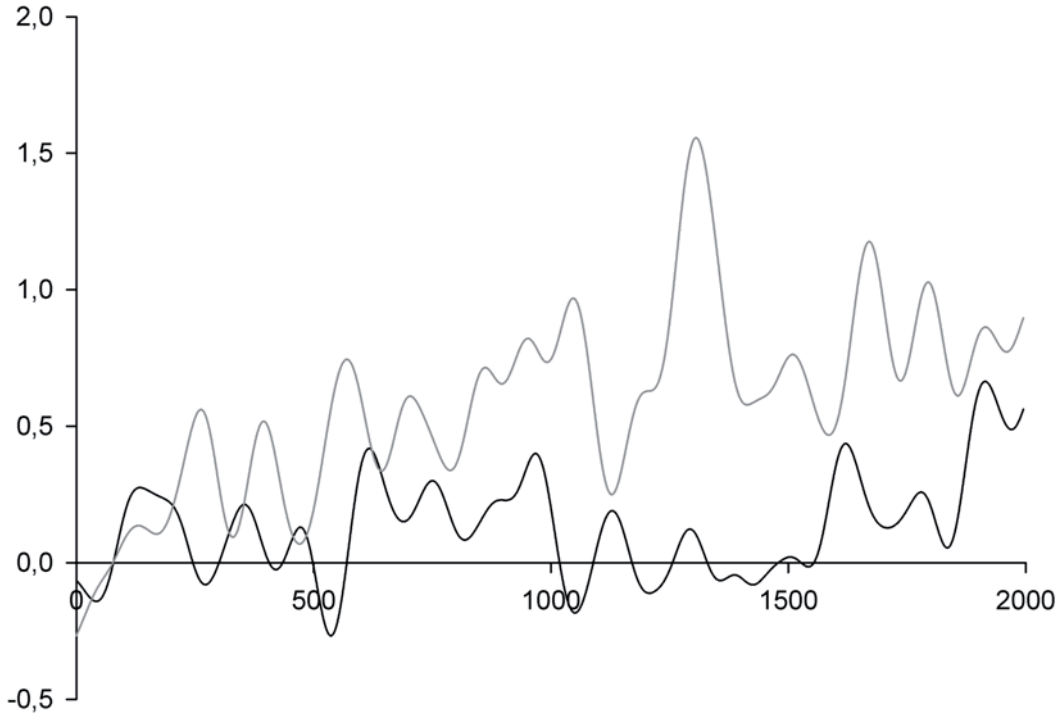

Fig. 3

General information concerning the original research article:

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Erklärung

Die hier vorgelegte Dissertation habe ich eigenständig und ohne unerlaubte Hilfsmittel angefertigt. Die Dissertation wurde in vorliegender oder in ähnlicher Form bei keiner anderen Institution eingereicht. Ich habe bisher keine erfolglosen Promotionsversuche unternommen.

Katrin Lübke