

# Entangled chemosensory emotion and identity: Familiarity enhances detection of chemosensorily encoded emotion

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Biologically significant, natural human body odors convey emotion and identity—two qualities shown to build on dissociated modules in face and voice perceptions. To what extent such segregation applies to chemosensory processing of body odors has hardly been studied. The current study probes this issue by recruiting heterosexual couples, who are genetically independent yet sexually and emotionally engaged to one another, as both odor donors and odor judges, and comparing their sensitivities to the chemosensory emotional cues from their partner vs. those from opposite-sex strangers. We demonstrate that familiarity subconsciously sharpens one's sensitivity to chemosensory emotional cues, which increases as a function of the time couples have spent together. Nevertheless, the specific chemosensory identity and emotional content remain undelineated and inaccessible to verbal awareness. Our findings reveal a different pattern from those of face and voice perceptions and provide insights into the mechanisms and interplays of chemosensory emotion and identity processings.

**Keywords:** Chemosensory emotion; Identity; Familiarity; Heterosexual couples.

## INTRODUCTION

Human emotion manifests itself in facial expressions, tones of voice, touch, and body odors (Chen & Haviland-Jones, 2000; Chen, Katdare, & Lucas, 2006; Pause, Ohrt, Prehn, & Ferstl, 2004; Zhou & Chen, 2008, 2009): a conglomerate of secretions from the sebaceous, eccrine, and apocrine glands that respond to emotion (Labows & Preti, 1992). Whereas facial, vocal, and tactile emotions are explicit, salient, and readily recognizable (Hertenstein, Keltner, App, Bulleit, & Jaskolka, 2006; Wallbott & Scherer, 1986), chemosensory emotional cues are subtle, rarely noticeable, and tend to operate at a subconscious level (Prehn, Ohrt, Sojka, Ferstl, & Pause, 2006; Zhou & Chen, 2008, 2009). It is thus not surprising that people are generally poor at

discerning among different chemosensory emotional cues (Chen & Haviland-Jones, 2000).

Reminiscent of faces and voices, natural body odors also carry biological salience (Chaix, Cao, & Donnelly, 2008; Chen & Haviland-Jones, 1999; Herz & Inzlicht, 2002; Jacob, McClintock, Zelano, & Ober, 2002; Ober et al., 1997; Porter & Winberg, 1999) and convey identity (the invariant aspects of body odors, including familiarity) (Lundström, Boyle, Zatorre, & Jones-Gotman, 2008; Porter & Moore, 1981; Russell, 1976; Wallace, 1977; Weisfeld, Czilli, Phillips, Gall, & Lichtman, 2003) with their genetic uniqueness (Nicolaidis, 1974; Porter, Cernoch, & Balogh, 1985) in addition to signaling emotion. Systematic studies centering on facial emotion and identity perceptions have concluded that the two build on largely dissociable

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systems (Bruce & Young, 1986; Calder & Young, 2005; Haxby, Hoffman, & Gobbini, 2000). In particular, it has been shown that familiarity, an important aspect of identity, does not affect one's ability to perceive facial expression and vice versa (Bruce, 1986; Calder, Young, Keane, & Dean, 2000; Campbell, Brooks, de Haan, & Roberts, 1996; Young, McWeeny, Hay, & Ellis, 1986). A similar model with segregated modules for vocal emotion and identity perceptions has also been proposed based on neuroimaging studies on human voices (Belin, Fecteau, & Bedard, 2004). To date, the relationship between chemosensory emotion and identity processing remains unknown. The present study probes this issue by examining whether the perception of chemosensory emotional cues, albeit subtle, is facilitated by familiarity.

We recruited 20 heterosexual couples. Each served as both sweat donor and odor recipient. Sweat was collected when the subjects underwent different emotional states (happiness, fear, sexual arousal), as well as when they felt neutral. The detection and identification of the chemosensory emotional (happy, fearful, or sexually aroused) cues for one's partner were compared with those for opposite-sex strangers. Possible confounding variables including general olfactory sensitivity and olfactory naming ability were also assessed.

## METHOD

### Participants

Twenty heterosexual couples (mean age = 27.65 years,  $SEM = 0.77$ ) took part in the study, which was approved by the Rice University Institutional Review Board. All gave written informed consents for participation. They had spent 1 to 7 years together with their partner and were unrelated to the other subjects. All were healthy nonsmokers with normal olfactory sensitivity [mean threshold for phenyl ethyl alcohol (PEA) = 0.0023%,  $SEM$  in binary dilution steps = 0.36] and olfactory naming ability [mean score on Smell Identification Test (SIT) = 36.56,  $SEM = 0.48$ ]. All females were not on hormonal contraceptives at the time of the study.

### Materials and procedure

Threshold of PEA, diluted in propylene glycol in binary dilution steps and stored in 280 ml glass bottles, was assessed using a triple-forced-choice ascending staircase with reversal design (Deems et al., 1991;

Doty, Gregor, & Settle, 1986; Hummel, Sekinger, Wolf, Pauli, & Kobal, 1997). Olfactory naming was assessed using the SIT (Sensonics, Hadden Heights, NJ)—a 40-item multiple-choice test that assesses one's ability to name common household smells. The main study consisted of two phases: sweat collection and sweat judgment.

#### *Phase I: Sweat collection*

Participants refrained from using deodorant/antiperspirant/scented products, and used scent-free shampoo/conditioner/soap/lotion provided by the experimenter from two days prior to the sweat collection sessions until the end of the sessions. They washed their sheets with scent-free detergent provided by the experimenter, kept a diet diary, and avoided odorous food such as garlic, onion, asparagus, and spices.

Each participant went through sweat-collection sessions held at the same time of day on three consecutive days (one session per day). On the day of each session, they wore next to their skin a new T-shirt (provided by the experimenter), to prevent odor contamination by their regular clothes. During each session, they kept a 4 × 4 inch pad (Kendall; rayon-polyester blend for maximum absorbance) under each armpit while they watched each of four 20-min video segments intended to produce the emotions of happiness (slapstick comedies), fear (horror movies), and sexual arousal (sexual intercourse between heterosexual couples), as well as a neutral state (educational documentaries), respectively. Different videos were shown in each session. During the videos, heart rate and skin conductance were recorded using Biopac MP150 (BIOPAC Systems, Goleta, CA). Electrocardiogram signals were recorded using disposable snap electrodes attached to the right collarbone and the left and right (ground) rib cage. Skin conductance was recorded using 8 mm diameter Ag/AgCl electrodes filled with isotonic electrode paste and attached bipolarly to the palmar area of the nondominant hand. The order in which the videos were presented was counterbalanced. Each video was preceded by a 5 min segment of the same emotional content, which served as an emotional transition. New pads were used for each video.

After watching each video, the participants rated how angry, fearful, happy, neutral, sad, and sexually aroused they felt during the video, using a 100 mm visual analog scale. Based on the mood ratings, we selected from each participant the pads worn during the 20 min videos that elicited the highest levels of the target emotions (happiness, fear, sexual arousal, and neutrality, respectively), which were used in the later

sweat judgments. Further analyses pertaining to mood induction were based on these selected videos/sweat samples. Valid heart rate data were recorded from 30 participants (19 males, 11 females); valid skin conductance data were recorded from 20 participants (14 males, 6 females).

Once collected, sweat pads were stored in separate 20 ml polypropylene jars, coded by an individual not involved in the study, and kept at  $-80^{\circ}\text{C}$  until subsequent testing. A total of 40 sets of jars were used in the Phase II sweat judgments, each from one of the couples. Each set contained four jars with happy, fearful, sexual, and neutral sweat pads, respectively, from the same donor.

### *Phase II: Sweat judgment*

The 20 couples were randomly assigned to one of two groups which differed in the sweat samples judged by the couples. That is, participants judged the sweat samples obtained from their partner as well as each of the nine individuals of the opposite sex within their group. The order of the sets was randomized across the participants. During the experiment, the experimenter sat behind a screen to eliminate possible influence of irrelevant visual cues on the participants' judgments. Both the participants and the experimenters were blind to the identities and the emotional contents of the sweat samples.

The judgment of each set began with an emotion detection task, in which the participants were presented with three jars, each fitted with a pair of Teflon nose-pieces. They were asked to take a single inhalation through the pair of nose-pieces attached to each jar, exhale through the mouth, and select the smell that was different from the other two. Two of the jars contained a neutral sweat pad (unknown to the participants, the same jar containing neutral sweat was presented twice); one contained an emotional (happy, fearful, or sexually aroused) sweat pad. The task was repeated twice for each of the emotions for a total of six trials in a randomized manner, with a 30 s break between the trials. After that, the participants were presented with all four jars (with happy, fearful, sexual, and neutral sweat, respectively) and rank-ordered them by their intensity and pleasantness, respectively. In addition, they were asked to identify from the four jars the one containing smells from people when they experienced a particular emotion (happiness, fear, or sexual arousal). This was also repeated twice for each emotion, for a total of six trials in a randomized manner. Lastly, the participants rated on a seven-point Likert scale how similar the set

of sweat samples smelled like his/her partner (1 = not at all, 7 = very much so).

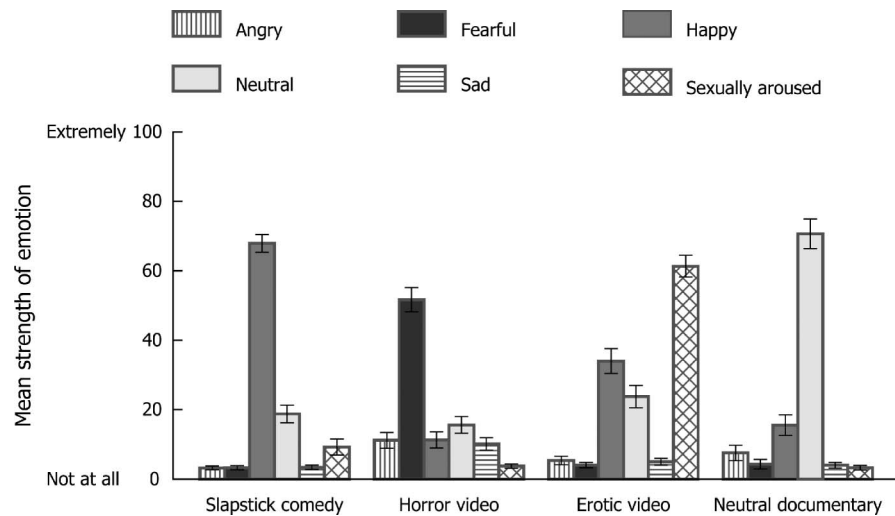
## **Analyses**

The effect of familiarity on the detection of chemosensory emotional cues (emotion detection task) was assessed using repeated-measures ANOVA, with familiarity (partner vs. opposite-sex stranger) and emotion (three levels: happiness, fear, sexual arousal) as the within-subject factors, gender as the between subject factor, and olfactory sensitivity (threshold for PEA) and olfactory naming ability (SIT score) as the covariates. The same procedures were applied to examine the effect of familiarity on the identification of the emotional contents of the sweat samples. Likewise, to test whether the participants rated partners and opposite-sex strangers differently on how similar the sweat samples smelled like their partner, familiarity (partner vs. opposite-sex stranger) was set as the within-subject factor, gender as the between-subjects factor, and olfactory sensitivity and olfactory naming ability were used as covariates. Wilcoxon signed-ranks tests were performed to assess whether the intensity and pleasantness of the sweat samples were ranked differently for partner and opposite-sex strangers. In addition, to quantify the effect of familiarity, a partial correlation analysis was performed between the accuracies of chemosensory emotional detection for partners (emotion detection test, averaged across the three emotions) and the years the couples had spent together, controlling for their actual ages.

## **RESULTS**

### **Mood induction**

The participants reported experiencing mostly the target emotions of happiness, fear, sexual arousal, as well as neutrality, respectively, during the sweat collections (Figure 1). Their autonomic responses mirrored their subjective reports. As compared with watching neutral documentaries, the participants showed higher skin conductance and increased heart rate during horror [ $t(19) = 2.69, p = .015$  for skin conductance;  $t(29) = 2.27, p = .031$  for heart rate] and erotic videos [ $t(19) = 2.59, p = .018$  for skin conductance;  $t(29) = 2.10, p = .044$  for heart rate, but not during slapstick comedies [ $t(19) = 0.22, p = .83$  for skin conductance];  $t(29) = 0.23, p = .82$  for heart rate.



**Figure 1.** Mean strength of self-reported emotions on a 100 mm visual analog scale while the participants watched happy, fearful, erotic, and neutral video segments, respectively. Error bars represent standard errors of the mean.

### Familiarity enhances chemosensory emotion detection

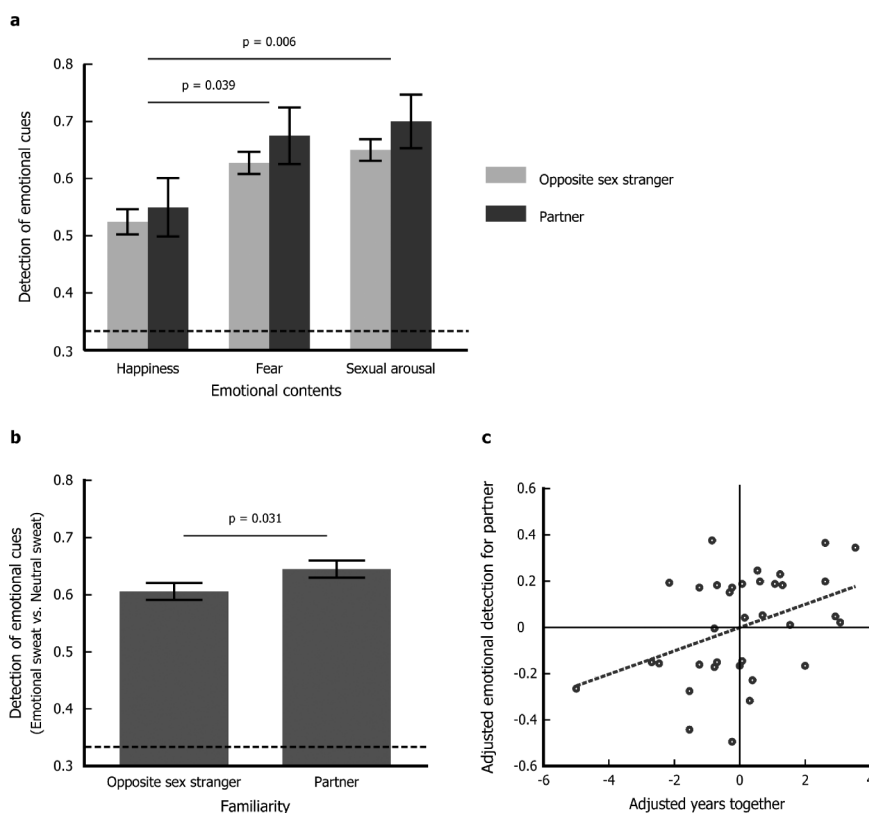
Overall, the participants were significantly above chance level in distinguishing emotional sweat from neutral sweat for both partners (mean accuracy = 0.55, 0.68, 0.70, for happy, fearful, and sexually aroused sweat, respectively, vs. chance = 0.33,  $p$  values < .01, Bonferroni corrected) and opposite-sex strangers (mean accuracy = 0.52, 0.63, 0.65, for happy, fearful, and sexually aroused sweat, respectively, vs. chance = 0.33,  $p$  values < .01, Bonferroni corrected) (Figure 2a), with no significant difference between males and females,  $F(1, 35) = 0.75$ ,  $p = .39$ . There was a marginally significant main effect of emotion,  $F(2, 70) = 2.59$ ,  $p = .082$ . Pairwise comparisons showed that the participants were less accurate at differentiating happy sweat from neutral sweat, as compared with differentiating fearful sweat or sexual sweat from neutral sweat ( $p = .039$  and  $.006$ , respectively, Bonferroni corrected, Figure 2a). Regardless of the gender [no significant interaction with familiarity,  $F(1, 35) = 0.22$ ,  $p = .64$ ], and the emotional contents (happiness, fear, or sexual arousal) [no significant interaction with familiarity,  $F(2, 70) = 1.83$ ,  $p = .17$ ], the participants were more accurate at detecting the chemosensory emotional cues from their partner as compared to those from opposite-sex strangers [ $F(1, 35) = 5.04$ ,  $p = .031$ , partial eta squared = .13, Figure 2b]. Importantly, further analysis revealed a significant positive correlation between the number of years one had spent together with their partner and their accuracies in the olfactory

detection of their partner's chemosensory emotional cues [ $r(37) = .42$ ,  $p = .008$ , Figure 2c], controlling for their actual age, which covaried with the number of years they had spent together with their partner,  $r(40) = .525$ ,  $p = .001$ .

The superior chemosensory emotional detection for partners cannot be because some donors' emotional sweat samples were perceptually more distinctive than others, as each donor served as the partner for one of the sweat judges, and as an opposite-sex stranger for the other nine judges (see Method). In addition, the rankings of the happy, fearful, sexually aroused, and neutral sweat pads were not significantly different between partner and opposite-sex strangers on either intensity ( $p$  values > .26) or pleasantness ( $p$  values > .32).

### Familiarity and chemosensory emotional identification

When asked to identify the jars containing happy, fearful, or sexually aroused sweat, the participants were mostly at chance for both partner (mean accuracy = 0.24, 0.24, 0.20 for happiness, fear, and sexual arousal, respectively, vs. chance = 0.25) and opposite-sex strangers (mean accuracy = 0.24, 0.27, 0.29 for happiness, fear, and sexual arousal, respectively, vs. chance = 0.25), with no significant difference between males and females,  $F(1, 35) = 2.34$ ,  $p = .14$ , or among the emotions,  $F(2, 70) = 0.42$ ,  $p = .66$ , or between partner and opposite-sex strangers,  $F(1, 35) = 0.26$ ,  $p = .61$ . Thus the participants were verbally



**Figure 2.** Familiarity sharpens chemosensory emotional detection. (a) Regardless of gender, the participants were significantly above chance level in distinguishing emotional sweat from neutral sweat for both partners and opposite-sex strangers, with lower accuracy in differentiating happy sweat from neutral sweat as compared with differentiating fearful sweat or sexual sweat from neutral sweat. (b) The participants were better at differentiating between emotional (happy, fearful, or sexually aroused) and neutral sweat samples for partners than for opposite-sex strangers. Since there is no significant interaction between gender and familiarity, or emotion and familiarity (see Results), the detection accuracies are collapsed across the emotions for male and female judges, controlling for olfactory threshold and olfactory naming ability. In both (a) and (b), the dashed line represents chance level (0.33) and error bars represent standard errors of the mean, adjusted for individual differences. (c) The detection of partner's chemosensory emotional cues (averaged across the three emotions of happiness, fear, and sexual arousal) improved with the number of years the couples had spent together, adjusting for their actual ages. Each circle represents a participant. The dashed line shows the linear fit of the circles.

unaware of the emotional contents of the sweat samples from both their partner and opposite-sex strangers.

### Chemosensory identification

When asked how similar each set was to the smell of one's partner, both male and female participants [no significant interaction with familiarity,  $F(1, 35) = 0.69$ ,  $p = .41$ ] rated their partner's sweat samples and opposite-sex strangers' sweat samples as equally similar,  $F(1, 35) = 0.32$ ,  $p = .58$ . Therefore, the participants did not explicitly know if they were smelling the sweat samples from their partner or an opposite-sex stranger, despite demonstrating superior detection of chemosensory emotional cues from their partner.

### DISCUSSION

The current study examined the relationship between chemosensory emotional perception and familiarity, a reflection of identity. In doing so, we extended the findings of some previous studies (Ackerl, Atzmueller, & Grammer, 2002; Chen & Haviland-Jones, 2000) and showed that people are capable of detecting the emotional cues carried by natural human body odors, despite not being verbally aware of the emotional contents. Smells are generally difficult to name (Lawless & Engen, 1977) and olfaction is therefore termed "the mute sense" (Ackerman, 1991). It is thus not surprising that the subjects failed to capture the subtle differences among various emotional sweat samples with emotion labels. The participants exhibited better detection for fear and sexual arousal than happiness, consistent with what has been observed

using visual cues (Jiang, Costello, Fang, Huang, & He, 2006; Pourtois, Grandjean, Sander, & Vuilleumier, 2004). It can be argued that these two emotions, being related to survival and reproduction, carry more evolutionary salience than happiness.

Critically, with the participation of couples who are intimately connected to one another—both physically and emotionally—we demonstrate that familiarity enhances the detection of chemosensory emotional cues, irrespective of the perceptual properties of the sweat samples. This is the case for both males and females and for all the three emotions tested (happiness, fear, and sexual arousal). Yet the participants could not verbalize if the sweat samples belonged to their partner or an opposite-sex stranger. In addition, there is a significant linkage between the number of years the couples had spent together and their sensitivity to the chemosensory emotional cues from their partner, after controlling for possible age-related reductions in olfactory abilities (Doty, 1989). This further shows that one's capability to detect emotional changes by chemosensory cues improves with greater familiarity. Moreover, it serves as an example of continuous subconscious perceptual learning or sensitization over an extended period of time in a naturalistic setting. Whereas identity and emotion processing rely on two dissociated systems in vision and audition (Belin et al., 2004; Bruce & Young, 1986; Calder & Young, 2005; Haxby et al., 2000) and facial familiarity is independent of facial emotion perception (Bruce, 1986; Calder et al., 2000; Campbell et al., 1996; Young et al., 1986), our findings suggest this not to be the case with body odors: Chemosensory familiarity sharpens one's sensitivity to chemosensory emotional cues, yet their identity (e.g., whether belonged to partner) and emotional content (e.g., fear) remain undelineated and inaccessible to verbal awareness. We suspect that such distinction is in part due to the fact that chemosensory processing resides in a phylogenetically ancient part of the brain, the rhinencephalon (Gottfried, 2006), which makes it likely that chemosensory identity and emotion lack well delineated cortical representations. By contrast, in the case of audition and vision, the processing of identity and emotion takes place in separate parts of the brain (Bruce & Young, 1986; Calder & Young, 2005; Haxby et al., 2000).

Though rarely the subject of attention, the chemosensory cues of natural body odors are automatically processed in the brain, which recognizes their socioemotional contents (Zhou & Chen, 2008, 2010), and distinguishes between odors from familiar individuals and strangers (Lundström et al., 2008). Future studies will further elucidate the neural correlates of the familiarity-induced sensitivity to chemosensory

emotional cues and clarify the relationships between chemosensory emotion and identity processing.

In summary, with the use of a unique group of participants, couples who are genetically independent yet sexually and emotionally related to each other, the present study demonstrates that chemosensory familiarity, itself not explicitly known to the participants, facilitates the detection of chemosensory emotional cues whereas the emotional contents remain below awareness—a pattern distinctively different from emotion and identity perceptions in vision and audition. Our findings provide new insights into the interplay of chemosensory emotion and identity processing, and add to the understanding of human chemosensory communication.

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## REFERENCES

- Ackerl, K., Atzmueller, M., & Grammer, K. (2002). The scent of fear. *Neuroendocrinology Letters*, *23*(2), 79–84.
- Ackerman, D. (1991). *A natural history of the senses*. London: Vintage.
- Belin, P., Fecteau, S., & Bedard, C. (2004). Thinking the voice: Neural correlates of voice perception. *Trends in Cognitive Sciences*, *8*(3), 129–135.
- Bruce, V. (1986). Influences of familiarity on the processing of faces. *Perception*, *15*(4), 387–397.
- Bruce, V., & Young, A. (1986). Understanding face recognition. *British Journal of Psychology*, *77*(Pt 3), 305–327.
- Calder, A. J., & Young, A. W. (2005). Understanding the recognition of facial identity and facial expression. *Nature Reviews Neuroscience*, *6*(8), 641–651.
- Calder, A. J., Young, A. W., Keane, J., & Dean, M. (2000). Configural information in facial expression perception. *Journal of Experimental Psychology: Human Perception and Performance*, *26*(2), 527–551.
- Campbell, R., Brooks, B., de Haan, E., & Roberts, T. (1996). Dissociating face processing skills: Decision about lip-read speech, expression, and identity. *Quarterly Journal of Experimental Psychology A*, *49*(2), 295–314.
- Chaix, R., Cao, C., & Donnelly, P. (2008). Is mate choice in humans MHC-dependent? *PLoS Genetics*, *4*(9), e1000184.
- Chen, D., & Haviland-Jones, J. (1999). Rapid mood change and human odors. *Physiology and Behavior*, *68*(1–2), 241–250.
- Chen, D., & Haviland-Jones, J. (2000). Human olfactory communication of emotion. *Perceptual and Motor Skills*, *91*(3 Pt 1), 771–781.
- Chen, D., Katdare, A., & Lucas, N. (2006). Chemosignals of fear enhance cognitive performance in humans. *Chemical Senses*, *31*(5), 415–423.
- Deems, D. A., Doty, R. L., Settle, R. G., Moore-Gillon, V., Shaman, P., Mester, A. F., et al. (1991). Smell and taste disorders: A study of 750 patients from the university of

- pennsylvania smell and taste center. *Archives of Otolaryngology: Head & Neck Surgery*, 117(5), 519–528.
- Doty, R. L. (1989). Influence of age and age-related diseases on olfactory function. *Annals of the New York Academy of Sciences*, 561, 76–86.
- Doty, R. L., Gregor, T. P., & Settle, R. G. (1986). Influence of intertrial interval and sniff-bottle volume on phenyl ethyl alcohol odor detection thresholds. *Chemical Senses*, 11(2), 259–264.
- Gottfried, J. A. (2006). Smell: Central nervous processing. *Advances in Otorhinolaryngology*, 63, 44–69.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, 4(6), 223–233.
- Hertenstein, M. J., Keltner, D., App, B., Bulleit, B. A., & Jaskolka, A. R. (2006). Touch communicates distinct emotions. *Emotion*, 6(3), 528–533.
- Herz, R. S., & Inzlicht, M. (2002). Sex differences in response to physical and social factors involved in human mate selection: The importance of smell for women. *Evolution and Human Behavior*, 23(5), 359–364.
- Hummel, T., Sekinger, B., Wolf, S. R., Pauli, E., & Kobal, G. (1997). ‘Sniffin’ sticks’: Olfactory performance assessed by the combined testing of odour identification, odor discrimination and olfactory threshold. *Chemical Senses*, 22(1), 39–52.
- Jacob, S., McClintock, M. K., Zelano, B., & Ober, C. (2002). Paternally inherited hla alleles are associated with women’s choice of male odor. *Nature Genetics*, 30(2), 175–179.
- Jiang, Y., Costello, P., Fang, F., Huang, M., & He, S. (2006). A gender- and sexual orientation-dependent spatial attentional effect of invisible images. *Proceedings of the National Academy of Sciences of the United States of America*, 103(45), 17048–17052.
- Labows, J. N., & Preti, G. (1992). Human semiochemicals. In S. Van Toller & G. H. Dodd (Eds.), *Fragrance: The psychology and biology of perfume* (pp. 69–90). New York, NY: Elsevier Science.
- Lawless, H., & Engen, T. (1977). Associations to odors: Interference, mnemonics, and verbal labeling. *Journal of Experimental Psychology: Human Learning and Memory*, 3(1), 52–59.
- Lundström, J. N., Boyle, J. A., Zatorre, R. J., & Jones-Gotman, M. (2008). Functional neuronal processing of body odors differs from that of similar common odors. *Cerebral Cortex*, 18(6), 1466–1474.
- Nicolaides, N. (1974). Skin lipids: Their biochemical uniqueness. *Science*, 186(4158), 19–26.
- Ober, C., Weitkamp, L. R., Cox, N., Dytch, H., Kostyu, D., & Elias, S. (1997). HLA and mate choice in humans. *American Journal of Human Genetics*, 61(3), 497–504.
- Pause, B. M., Ohrt, A., Prehn, A., & Ferstl, R. (2004). Positive emotional priming of facial affect perception in females is diminished by chemosensory anxiety signals. *Chemical Senses*, 29(9), 797–805.
- Porter, R. H., Cernoch, J. M., & Balogh, R. D. (1985). Odor signatures and kin recognition. *Physiology and Behavior*, 34(3), 445–448.
- Porter, R. H., & Moore, J. D. (1981). Human kin recognition by olfactory cues. *Physiology and Behavior*, 27(3), 493–495.
- Porter, R. H., & Winberg, J. (1999). Unique salience of maternal breast odors for newborn infants. *Neuroscience & Biobehavioral Reviews*, 23(3), 439–449.
- Pourtois, G., Grandjean, D., Sander, D., & Vuilleumier, P. (2004). Electrophysiological correlates of rapid spatial orienting towards fearful faces. *Cerebral Cortex*, 14(6), 619–633.
- Prehn, A., Ohrt, A., Sojka, B., Ferstl, R., & Pause, B. M. (2006). Chemosensory anxiety signals augment the startle reflex in humans. *Neuroscience Letters*, 394(2), 127–130.
- Russell, M. J. (1976). Human olfactory communication. *Nature*, 260(5551), 520–522.
- Wallace, P. (1977). Individual discrimination of humans by odor. *Physiology and Behavior*, 19(4), 577–579.
- Wallbott, H. G., & Scherer, K. R. (1986). Cues and channels in emotion recognition. *Journal of Personality and Social Psychology*, 51(4), 690–699.
- Weisfeld, G. E., Czilli, T., Phillips, K. A., Gall, J. A., & Lichtman, C. M. (2003). Possible olfaction-based mechanisms in human kin recognition and inbreeding avoidance. *Journal of Experimental Child Psychology*, 85(3), 279–295.
- Young, A. W., McWeeny, K. H., Hay, D. C., & Ellis, A. W. (1986). Matching familiar and unfamiliar faces on identity and expression. *Psychological Research*, 48(2), 63–68.
- Zhou, W., & Chen, D. (2008). Encoding human sexual chemosensory cues in the orbitofrontal and fusiform cortices. *Journal of Neuroscience*, 28(53), 14416–14421.
- Zhou, W., & Chen, D. (2009). Fear-related chemosignals modulate recognition of fear in ambiguous facial expressions. *Psychological Science*, 20(2), 177–183.
- Zhou, W., & Chen, D. (2010). *Social anxiety and reduced recruitment of orbitofrontal cortex to human social chemosensory cues*. Manuscript submitted for publication.