PSYCHOLOGICAL SCIENCE

A JOURNAL OF THE ASSOCIATION FOR PSYCHOLOGICAL SCIENCE

Psychological Science

RESEARCH, THEORY, & APPLICATION IN PSYCHOLOGY AND RELATED SCIENCES

Research Article

Sociochemosensory and Emotional Functions

Behavioral Evidence for Shared Mechanisms

Wen Zhou and Denise Chen

Rice University

ABSTRACT—***Olfaction and emotion are distinctively different systems. Nevertheless, there are reasons to suspect that they influence each other on the social level. Functionally, olfactory chemosensory communication is used by a wide range of animals to convey individual and group identity, as well as attraction or repulsion. Anatomically, the olfactory brain overlaps with the socioemotional brain, and is believed to have contributed to the evolution of the latter. Little is known about how the functional and anatomical links are manifested in behavior, however. Using human olfaction as a model, we demonstrate that chemosensory recognition of individuals—one of the most ubiquitous forms of social communication—is interconnected with both the cognitive and the visual processing of emotion. Our results provide the first behavioral evidence for mechanisms being shared by a sensory system and emotion.***

Human communication is often considered to be dominated by vision. Still, there is evidence that social chemosensory signals also play an important role. Natural sweat secreted from the human body has been shown to convey individual identity (Weisfeld, Czilli, Phillips, Gall, & Lichtman, 2003), familiarity (Lundström, Boyle, Zatorre, & Jones-Gotman, 2008; Olsson, Barnard, & Turri, 2006; Weisfeld et al., 2003), and genetic relatedness (Porter, 1998), in addition to signaling reproductive state (Stern & McClintock, 1998) and affect (Chen & Haviland-Jones, 2000; Chen, Katdare, & Lucas, 2006; Pause, Ohrt, Prehn, & Ferstl, 2004; Zhou & Chen, 2008, 2009). Such chemosensory signals are believed to have privileged access to emotion because of the evolutionary affinity and anatomical overlap between olfaction and emotion. Being phylogenetically the oldest sense, chemosensation was evolutionarily advantaged to assume the role of socioemotional communication (Gloor, 1997), and it is believed to have contributed to the evolution of the socioemotional brain (Barton, 2006; Gloor, 1997).

Chemosensory signals are ubiquitously used in the animal kingdom to convey individual and group identity, as well as attraction or repulsion (Wyatt, 2003). The olfactory pathways underlying sociochemosensory processing consist of the amygdala, the hypothalamus, and the medial and lateral orbitofrontal cortex (Neville & Haberly, 2004). All of these are structures well known to participate in processing emotions and biological functions with important social implications (Dolan, 2002). Accordingly, accumulating empirical evidence indicates that olfaction influences hedonic experience (Bensafi, Tsutsui, Khan, Levenson, & Sobel, 2004; Jacob & McClintock, 2000; Li, Moallem, Paller, & Gottfried, 2007) and vice versa (Chen & Dalton, 2005; Li, Howard, Parrish, & Gottfried, 2008). Yet the functional relatedness of olfaction and emotion has not been investigated by a direct comparison of the processing of sociochemosensory and emotional information. Because considerable individual variation has been observed in both sociochemosensory (Chen & Haviland-Jones, 2000; Olsson et al., 2006) and socioemotional (Lane, Quinlan, Schwartz, Walker, & Zeitlin, 1990) processing, we assessed their relationship by testing whether the individual variance in sociochemosensory recognition can be mapped onto the variance in socioemotional perception.

Given that individual recognition is one of the most ubiquitous forms of social communication, we employed olfactory identification of familiar individuals as an index of sociochemosensory skills (competency). Body odors of female roommates were used as the target sociochemosignals. Possible confounds, including subjects' olfactory threshold and ability to name common smells, as well as the intensity and pleasantness of the olfactory stimuli, were also assessed. Following standard practice, we assessed subjects' socioemotional skills

Address correspondence to Denise Chen, Department of Psychology MS-25, Rice University, 6100 Main St., Houston, TX 77005, e-mail: xdchen@rice.edu.

by measuring their cognitive and perceptual awareness of other individuals' emotions.

METHOD

Participants

We recruited only women because of their overall superior sense of smell (Brand & Millot, 2001), particularly their superior olfactory ability to recognize familiar individuals (Olsson et al., 2006), and their greater sensitivity to emotional signals (Broday & Hall, 2000). Twenty-two pairs of female roommates, about 20 years old (*SEM* = 0.18, range = 18–22), participated in the study, serving as both sweat donors and judges. They had spent an average of 12.82 months as roommates at the time of the study (*SEM* = 1.23 months, range = 3–36 months). Seventy percent of the subjects (31 out of 44) were not on hormone contraceptives. Hormone contraceptives did not influence either the qualities of the body odors produced (as indexed by the ability of judges to discriminate the odors), $t(42) = 1.00$, $p = .32$, or subjects' olfactory ability to identify their roommate, $t(42) = -0.51$, $p = .6$. Subjects were not menstruating at the time of participation.

Materials and Procedure

Preparation of Sociochemosensory Stimuli

Starting 2 days prior to the experiment until after it was over, subjects refrained from using deodorant, antiperspirant, or scented products, and used scent-free shampoo, conditioner, soap, and lotion provided by the experimenter. They were also instructed to wash their bedding with the scent-free detergent provided by the experimenter. Each subject was given an unused T-shirt inside two sealed plastic bags. Each was also instructed that on the night of the sweat-sample collection, she should take a shower before bed, avoid having sex, and sleep in the T-shirt continuously for a minimum of 7 hr. Donors reported having worn their shirts continuously for an average of 8.71 hr (*SEM* = 1.45). Each shirt was placed in two sealed plastic bags and returned the same day that it was taken off (*SEM* = 0.07 day). The shirts were then kept in a freezer at −20 °C until testing. The shirts were defrosted to room temperature at least 30 min before the roommate-identification test.

Assessment of Sociochemosensory Competency

Subjects were tested individually across two separate trials in a double-blind procedure. They were presented, one at a time, with a set of three shirts that were identical in appearance. They were then asked to pick the one that smelled most like their roommate and verbally rated their level of confidence in their identification using a 7-point scale (1 = *not at all confident*, 7 = *extremely confident*). No feedback was provided. Each shirt was labeled with random letters by an individual not involved in the study. Neither the experimenters nor the subjects knew who had provided each shirt. After identifying the shirt worn by the roommate, subjects were presented with the same set of three shirts and asked to pick the one that smelled the most pleasant. They were then presented with the remaining two shirts and asked to pick the more pleasant of the two. Intensity was assessed separately in the same fashion. The same procedure (identification, pleasantness rating, intensity rating) was then repeated in the second trial.

General Olfactory Threshold and Naming

Threshold for phenyl ethyl alcohol (PEA; diluted in propylene glycol in binary dilution steps) was assessed with Sniffin' Sticks (Burghart Medical Technology, Wedel, Germany), using a triple-forced-choice ascending staircase with reversal (Hummel, Sekinger, Wolf, Pauli, & Kobal, 1997). Subjects were presented with three sticks—one containing the target smell and the other two the diluent—and asked to identify the target. They were presented with a lower concentration if they made two consecutively correct identifications, and a higher concentration immediately after they made a single error. Threshold was calculated as the average concentration from the last four reversals.

Olfactory naming was assessed using the Smell Identification Test (SIT, formerly UPSIT; Sensonics Inc., Hadden Heights, NJ)—a 40-item multiple-choice test that assesses ability to name common household smells.

Assessment of Emotional Competency

To assess cognitive emotional competency, we used the Levels of Emotional Awareness Scale (LEAS; Lane et al., 1990), a self-report measure of emotional differentiation and complexity. Subjects indicated how a person other than themselves would feel in 20 different scenarios (e.g., getting lost in a foreign country). A response received the lowest score (0) if no emotional word was mentioned and the highest score (4) if the subject mentioned two or more complex emotions that differed in meaning (e.g., frustration and sympathy). Responses were coded independently by two coders according to the LEAS scoring manual and glossary (Lane, 1991). Intercoder agreement was perfect. The highest possible score was 80.

For our measure of perceptual emotional competency, we asked subjects to identify basic facial emotions. Subjects viewed 20 facial images (10 male and 10 female), selected from the Pictures of Facial Affect (Ekman & Friesen, 1976), that depicted five prototypical emotions: fear, sadness, anger, disgust, and happiness. Each image was displayed for 250 ms. Following each display, subjects provided a single verbal label for the emotion. An exact or close match to the original emotional label (e.g., "scared" instead of "fearful") was coded as correct. The proportion of facial emotions identified correctly was calculated by summing the correct responses and dividing them by the total number of images.

Experimental Procedure

Subjects were told that they were participating in a study on olfactory and visual information processing. No reference to roommate identification was made. Each subject participated in two sessions held on separate days. In Session 1, they performed the olfactory-threshold and naming tests and completed the measures of emotional awareness and facial emotion recognition. In Session 2, held at the same time of day as Session 1, they performed the roommate-identification task. Subjects were blindfolded during all olfactory tasks.

RESULTS AND DISCUSSION

Performance on the roommate-identification task reflects endogenous variance in sociochemosensory recognition and cannot be due to exogenous environmental factors. Performance on this task did not correlate with the length of time subjects had lived with their roommate ($r = .045$, $p = .77$). In addition, accuracy of roommate identification was not positively correlated within pairs of roommates ($r = -.41$, $p = .06$), a finding that rules out shared environment and familiarity as contributing factors. Chemosensory recognition seems to have been implicit, as accuracy did not correlate with subjective level of confidence ($r = .14$, $p = .37$). The cognitive and perceptual measures of awareness of other individuals' emotions reflect different aspects of socioemotional processing (Vuilleumier, Armony, Driver, & Dolan, 2003) and did not correlate significantly with each other ($r = .21$, $p = .17$).

To assess the relationship between sociochemosensory recognition and socioemotional perception, we adopted two approaches. First, we asked whether subjects who were good at chemosensory roommate identification also scored high on emotional measures, that is, whether chemosensory identification maps onto emotional competency. Second, we asked the converse question—whether subjects who scored high on emotional measures also performed well on the roommate-identification task, that is, whether emotional competency also maps onto chemosensory roommate identification.

To assess whether variance in performance on the roommate-identification task mapped onto variance in emotional processing, we first classified the subjects into three groups based on the total number of times each subject correctly identified her roommate by smell (correct neither time: $n = 21$; correct once: $n = 10$; correct both times: $n = 13$). Because chance accuracy was 33%, subjects who were correct neither time (0%) and some of the subjects who were correct once (50%) were merely guessing. One-way analyses of variance (ANOVAs) and Kruskal-Wallis tests were conducted to examine whether PEA and SIT scores, as well as intensity and pleasantness rankings of the roommate's odor, differed among the three groups of subjects. The three groups of subjects differed marginally in PEA threshold, $F(2, 40) = 2.55$, $p = .091$, a measure of general olfactory sensitivity. They did not differ in general olfactory naming as assessed by the SIT, $F(2, 41) = 1.33$, $p = .28$. Nor did they differ in the intensity rankings of the roommate's odor, $\chi^2(2, N = 41) = 1.68$, $p = .43$, or the pleasantness rankings of the roommate's odor, $\chi^2(2, N = 41) = 3.90$, $p = .14$.

We then analyzed emotional awareness and proportion of correct facial emotion identifications in separate univariate ANOVAS with number of correct roommate identifications (0, 1, 2) as the independent variable. We included PEA threshold as a covariate in these analyses. Sociochemosensory recognition of the roommate was positively related to subjects' levels of emotional awareness, as assessed by LEAS scores, $F(2, 39) = 7.91$, $p = .001$, $\eta_p^2 = .29$ (Fig. 1a). Subjects who identified their roommate both times scored higher in awareness of other people's emotions ($M = 67.44$, $SEM = 2.30$) than those who identified their roommate one time ($M = 57.53$, $SEM = 2.43$), $p = .015$, or neither time ($M = 56.07$, $SEM = 1.72$), $p = .001$ (ps Bonferroni-corrected). Likewise, sociochemosensory recognition of the roommate was positively related to identification of facial emotions, $F(2, 39) = 4.34$, $p = .02$, $\eta_p^2 = .18$ (Fig. 1b). Women who identified their roommate by smell both times ($M = .61$, $SEM = .037$) were more accurate at identifying facial emotional expressions than those who did not identify their roommate on either trial (M = .49, $SEM = .028$), $p = .036$, and those who identified their roommate once ($M = .59$, $SEM = .039$) were marginally more accurate at identifying facial emotional expressions than those who did not identify their roommate on either trial, $p = .10$ (Bonferroni-corrected). General olfactory sensitivity had no significant bearing on either cognitive awareness of other people's emotions ($p = .57$) or perceptual identification of facial emotions ($p = .14$).

We then adopted a standard bootstrapping procedure (Davison & Hinkley, 1997) that could more clearly demonstrate the distinct distribution of emotional competency in each group. From the original data set for each group (correct neither time, correct once, and correct both times), a bootstrapped data set with the same sample size (21, 10, and 13, respectively) was nonparametrically resampled with replacement (i.e., a participant could be selected more than once). The mean cognitive and perceptual emotional competencies of these bootstrapped samples were then calculated. The same procedure was repeated 1,000 times to estimate the population mean and variation for each group. As illustrated in Figure 1c, which highlights the central tendency of each group, the bootstrapped sample means for cognitive awareness of other people's emotions were higher for subjects who correctly identified the roommate in both trials than for subjects who correctly identified the roommate in one or neither trial. Similarly, the bootstrapped sample means for accuracy of facial emotion identification were lower for subjects who failed the roommate-identification task twice than for subjects who were correct once or both times. Overall, above-chance performance (correct choice from among three options on two out of two trials) in the chemosensory task was clearly linked with superior emotional competencies.

We next examined whether variance in emotional competency mapped onto variance in chemosensory identification. Separate

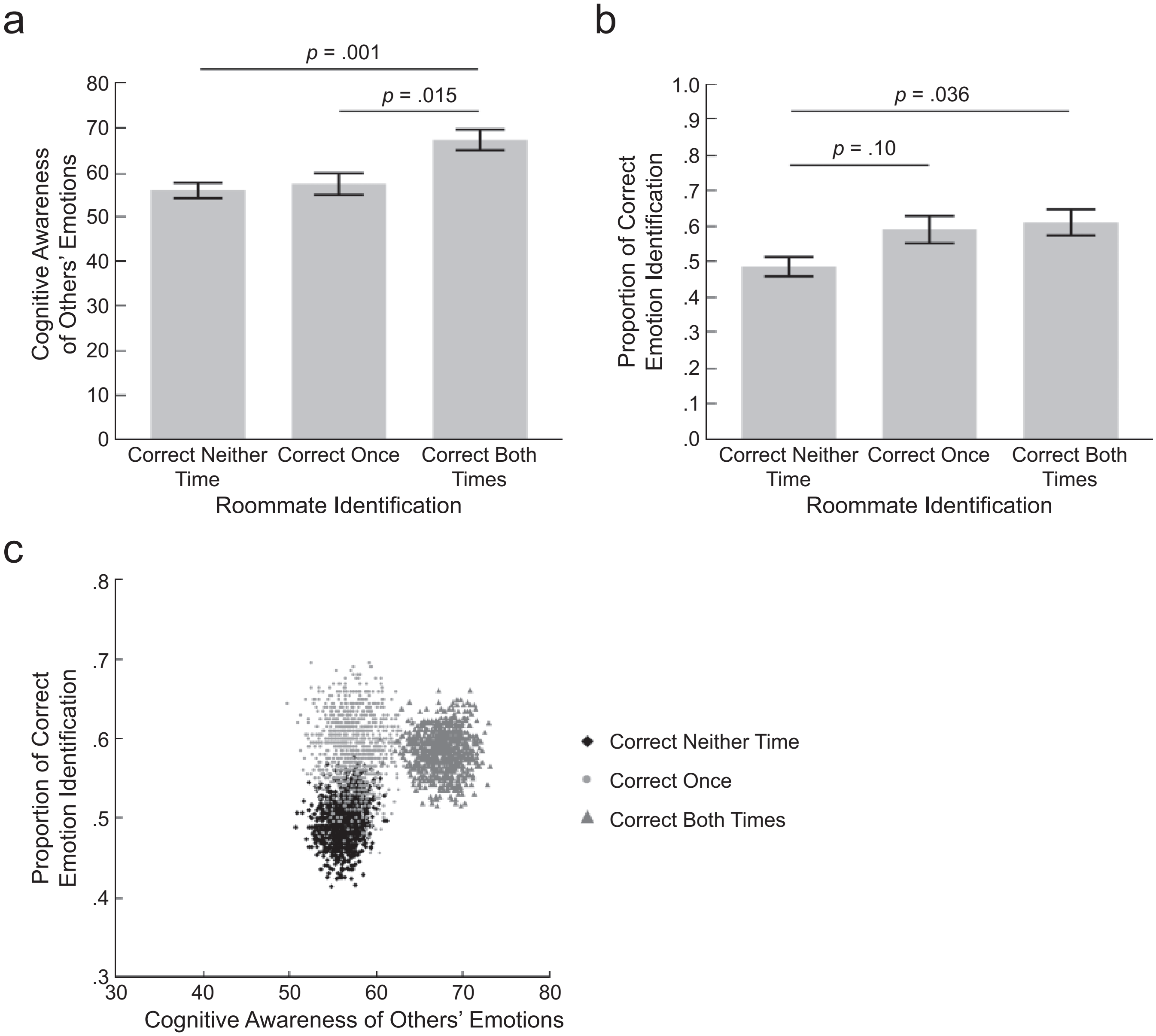

Fig. 1. Emotional competency as a function of accuracy on the chemosensory identification task. Subjects were divided into three groups on the basis of whether they identified their roommate's odor twice, once, or on neither trial. The bar graphs show how the three groups compared in (a) mean cognitive awareness of other people's emotions and (b) mean accuracy in identifying facial expressions of emotion. Error bars represent standard errors of the mean. The scatter plot (c) presents the results of a bootstrap procedure that estimated mean cognitive awareness of other people's emotions and mean accuracy in facial emotion identification for each group of subjects (1,000 bootstrapped samples). Potential group differences in phenyl ethyl alcohol (PEA) threshold were statistically equated in calculating the means in (a) and (b).

independent-sample t tests and Mann-Whitney U tests were conducted to examine whether PEA and SIT scores, as well as intensity and pleasantness rankings of the roommate's odor, differed between subjects with high versus low LEAS scores (defined by a median split), as well as subjects with high versus low accuracy in facial emotion identification (again defined by a median split). We then performed two independent-sample t tests to examine the effect of LEAS group (high score vs. low score) and facial-emotion-identification group (high accuracy vs. low accuracy) on roommate-identification performance (number of correct roommate identifications).

When we used a median split on LEAS scores to classify subjects according to their level of emotional awareness of other individuals, the two groups (high LEAS vs. low LEAS) did not differ in PEA threshold, $t(41) = -1.26$, $p = .21$; general olfactory naming on the SIT, $t(42) = -0.27$, $p = .79$; intensity rankings of the roommate's odor, Mann-Whitney $U = 176$, $n_1 = 19$, $n_2 = 22$, $p = .36$; or pleasantness rankings of the

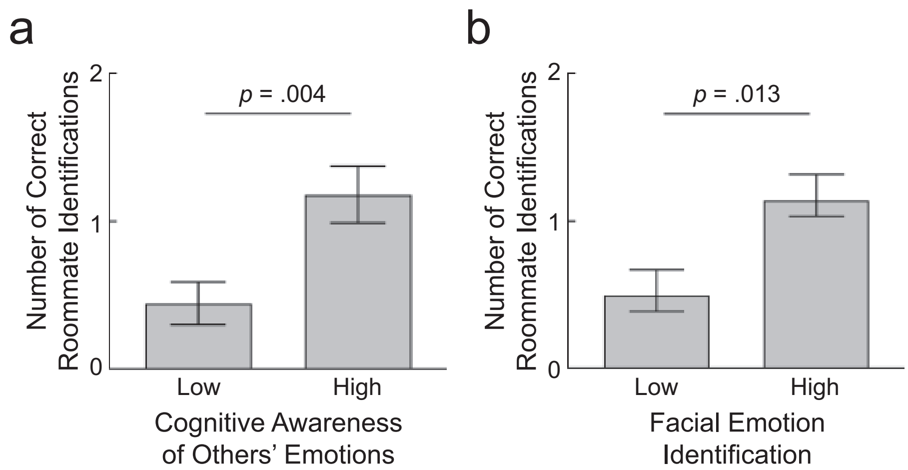

Fig. 2. Accuracy in chemosensory roommate identification as a function of emotional competency: mean number of correct identifications for (a) subjects high and low in cognitive awareness of other people's emotions and (b) subjects with high and low accuracy in identifying facial expressions of emotion. For each measure of emotional competency, subjects were categorized by a median split. Error bars represent standard errors of the mean.

roommate's odor, Mann-Whitney $U = 198$, $n_1 = 19$, $n_2 = 22$, $p = .76$. Subjects in the high-LEAS group were significantly better at chemosensory roommate identification ($M = 1.18$, $SEM = 0.19$) than those in the low-LEAS group ($M = 0.45$, $SEM = 0.14$), $t(42) = 3.02$, $p = .004$, Cohen's $d = 0.93$ (Fig. 2a).

Likewise, when we used a median split to classify subjects according to their accuracy in facial emotion identification, the two groups (high accuracy vs. low accuracy) did not differ in PEA threshold, $t(41) = 0.42$, $p = .68$; general olfactory naming on the SIT, $t(42) = -1.28$, $p = .21$; intensity rankings of the roommate's odor, Mann-Whitney $U = 150.5$, $n_1 = 20$, $n_2 = 21$, $p = .10$; or pleasantness rankings of the roommate's odor, Mann-Whitney $U = 184.5$, $n_1 = 20$, $n_2 = 21$, $p = .48$. Subjects with high accuracy in facial emotion identification were better at chemosensory roommate identification ($M = 1.14$, $SEM = 0.18$) than those with lower accuracy in facial emotion identification ($M = 0.50$, $SEM = 0.17$), $t(42) = 2.58$, $p = .013$, Cohen's $d = 0.80$ (Fig. 2b).

Finally, we also conducted a linear regression analysis with roommate-identification performance (times correct) as the dependent variable and LEAS score and accuracy of facial emotion identification as the independent variables. Taken together, the cognitive and perceptual measures of awareness of other individuals' emotions explained 32% of the variance in performance on the chemosensory-roommate identification task, $R^2 = .32$, $F(2, 41) = 9.63$, $p < .001$.

Neuroanatomically, feeling empathetic activates limbic and paralimbic structures including the anterior cingulate cortex and the anterior insula (de Vignemont & Singer, 2006), whereas processing facial emotions involves the amygdala (Vuilleumier et al., 2003), anterior cingulate cortex (Bush, Luu, & Posner, 2000), anterior insula (Wicker et al., 2003), and orbitofrontal cortex (Blair, Morris, Frith, Perrett, & Dolan, 1999). Most of these structures also participate in processing smells, including socially significant smells (Gottfried, 2006; Jacob, Kinnunen, Metz, Cooper, & McClintock, 2001; Lundström et al., 2008; Savic, 2001). Our results show that such functional anatomical relatedness is also manifested at the behavioral level: Sociochemosensory recognition reflects cognitive and perceptual awareness of other individuals' emotions, which in turn reflects performance in sociochemosensory recognition. The close connection between sociochemosensation and emotion observed here is consistent with a privileged connection between social communication and emotion (Britton et al., 2006; Darwin, 1872/1965). In normal subjects, threshold for nonsocial smells correlates with the volume of olfactory bulbs (Turetsky et al., 2000), but not with the volume of the perirhinal cortex, entorhinal cortex, or temporopolar cortex (Turetsky, Moberg, Roalf, Arnold, & Gur, 2003). We speculate that the threshold for the nonsocial PEA involves lower levels of sensory and emotional processing, and therefore does not correlate with emotional sophistication. By contrast, identifying familiar individuals by smell may evoke greater socioemotional meanings and therefore recruit structures more widely involved in emotion.

GENERAL DISCUSSION

Social skills are commonly believed to be interlinked with emotional skills, yet there has been little empirical evidence regarding how the two types of processing are related. Using the unique channel of olfaction, we examined the hypothesis that superior skill in identifying social chemosensory information is related to higher emotional competency. We ruled out possible confounds, including subjects' general olfactory sensitivity and olfactory naming ability, as well as the intensity and pleasantness of the target stimuli. Our results demonstrate that olfactory identification of a familiar individual is interconnected with both cognitive and emotional measures of emotional competency: Subjects who identified their roommates on the basis of olfactory cues scored higher than other subjects on both awareness of other individuals' emotions and accuracy in identifying facial expressions of emotion; at the same time, subjects who scored higher on cognitive awareness or perceptual identification of other individuals' emotions also were better able to recognize their roommates by their odor. To our knowledge, this study provides the first empirical evidence of the behavioral connection between a sensory system and emotional processing.

Individual recognition has important socioemotional ramifications. It forms the basis for bonding, mating, and cooperative behavior (Konig, 2006). The behavioral findings reported here suggest that sociochemosignals may tap into a broader network of social cognition and emotion, and that similar underlying mechanisms may regulate sociochemosensory and emotional competencies. Unlike vision and audition, olfaction and emotion reside in the same phylogenetically primitive part of the brain, the rhinencephalon. This anatomical overlap, and the concomitant evolutionary affinity, likely underlies the behavioral connection between sociochemosensation and emotion observed in this study.

Acknowledgments—This work was supported in part by National Institutes of Health Grant R03DC4956. We thank Judy Jia, Beth Leimbach, Nadia Lucas, Meghan Wilson, and Jacob Zachariah for their assistance.

REFERENCES

Barton, R.A. (2006). Olfactory evolution and behavioral ecology in primates. *American Journal of Primatology*, *68*, 545–558.

Bensafi, M., Tsutsui, T., Khan, R., Levenson, R.W., & Sobel, N. (2004). Sniffing a human sex-steroid derived compound affects mood and autonomic arousal in a dose-dependent manner. *Psychoneuroendocrinology*, *29*, 1290–1299.

Blair, R.J., Morris, J.S., Frith, C.D., Perrett, D.I., & Dolan, R.J. (1999). Dissociable neural responses to facial expressions of sadness and anger. *Brain*, *122*, 883–893.

Brand, G., & Millot, J.L. (2001). Sex differences in human olfaction: Between evidence and enigma. *Quarterly Journal of Experimental Psychology B*, *54*, 259–270.

Britton, J.C., Phan, K.L., Taylor, S.F., Welsh, R.C., Berridge, K.C., & Liberzon, I. (2006). Neural correlates of social and nonsocial emotions: An fMRI study. *NeuroImage*, *31*, 397–409.

Broday, L.R., & Hall, J.A. (2000). Gender, emotion, and expression. In M. Lewis & J.M. Haviland-Jones (Eds.), *Handbook of emotions* (2nd ed., pp. 338–349). New York: Guilford Press.

Bush, G., Luu, P., & Posner, M.I. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in Cognitive Sciences*, *4*, 215–222.

Chen, D., & Dalton, P. (2005). The effect of emotion and personality on olfactory perception. *Chemical Senses*, *30*, 345–351.

Chen, D., & Haviland-Jones, J. (2000). Human olfactory communication of emotion. *Perceptual & Motor Skills*, *91*, 771–781.

Chen, D., Katdare, A., & Lucas, N. (2006). Chemosignals of fear enhance cognitive performance in humans. *Chemical Senses*, *31*, 415–423.

Darwin, C. (1965). *The expressions of the emotions in man and animals*. Chicago: University of Chicago Press. (Original work published 1872)

Davison, A.C., & Hinkley, D.V. (1997). *Bootstrap methods and their application*. Cambridge, England: Cambridge University Press.

de Vignemont, F., & Singer, T. (2006). The empathic brain: How, when and why? *Trends in Cognitive Sciences*, *10*, 435–441.

Dolan, R.J. (2002). Emotion, cognition, and behavior. *Science*, *298*, 1191–1194.

Ekman, P., & Friesen, W. (1976). *Pictures of facial affect*. Palo Alto, CA: Consulting Psychologists Press.

Gloor, P. (1997). *The temporal lobe and limbic system*. New York: Oxford University Press.

Gottfried, J.A. (2006). Smell: Central nervous processing. *Advances in Otorhinolaryngology*, *63*, 44–69.

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*, 39–52.

Jacob, S., Kinnunen, L.H., Metz, J., Cooper, M., & McClintock, M.K. (2001). Sustained human chemosignal unconsciously alters brain function. *NeuroReport*, *12*, 2391–2394.

Jacob, S., & McClintock, M.K. (2000). Psychological state and mood effects of steroidal chemosignals in women and men. *Hormones and Behavior*, *37*, 57–78.

Konig, B. (2006). Non-offspring nursing in mammals: General implications from a case study on house mice. In P.M. Kappeler & C.P. van Schaik (Eds.), *Cooperation in primates and humans: Mechanisms and evolution* (pp. 191–205). Berlin, Germany: Springer.

Lane, R. (1991). *LEAS scoring manual and glossary*. Tucson: University of Arizona Health Sciences Center.

Lane, R.D., Quinlan, D.M., Schwartz, G.E., Walker, P.A., & Zeitlin, S.B. (1990). The Levels of Emotional Awareness Scale: A cognitive-developmental measure of emotion. *Journal of Personality Assessment*, *55*, 124–134.

Li, W., Howard, J.D., Parrish, T.B., & Gottfried, J.A. (2008). Aversive learning enhances perceptual and cortical discrimination of indiscriminable odor cues. *Science*, *319*, 1842–1845.

Li, W., Moallem, I., Paller, K.A., & Gottfried, J.A. (2007). Subliminal smells can guide social preferences. *Psychological Science*, *18*, 1044–1049.

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*, 1466–1474.

Neville, K.R., & Haberly, L.B. (2004). Olfactory cortex. In G.M. Shepherd (Ed.), *The synaptic organization of the brain* (5th ed., pp. 415–454). New York: Oxford University Press.

Olsson, S.B., Barnard, J., & Turri, L. (2006). Olfaction and identification of unrelated individuals: Examination of the mysteries of human odor recognition. *Journal of Chemical Ecology*, *32*, 1635–1645.

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*, 797–805.

Porter, R.H. (1998). Olfaction and human kin recognition. *Genetica*, *104*, 259–263.

Savic, I. (2001). Processing of odorous signals in humans. *Brain Research Bulletin*, *54*, 307–312.

Stern, K., & McClintock, M.K. (1998). Regulation of ovulation by human pheromones. *Nature*, *392*, 177–179.

Turetsky, B.I., Moberg, P.J., Roalf, D.R., Arnold, S.E., & Gur, R.E. (2003). Decrements in volume of anterior ventromedial temporal lobe and olfactory dysfunction in schizophrenia. *Archives of General Psychiatry*, *60*, 1193–1200.

Turetsky, B.I., Moberg, P.J., Yousem, D.M., Doty, R.L., Arnold, S.E., & Gur, R.E. (2000). Reduced olfactory bulb volume in patients with schizophrenia. *American Journal of Psychiatry*, *157*, 828–830.

Vuilleumier, P., Armony, J.L., Driver, J., & Dolan, R.J. (2003). Distinct spatial frequency sensitivities for processing faces and emotional expressions. *Nature Neuroscience*, *6*, 624–631.

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*, 279–295.

Wicker, B., Keysers, C., Plailly, J., Royet, J.-P., Gallese, V., & Rizzolatti, G. (2003). Both of us disgusted in my insula: The common neural basis of seeing and feeling disgust. *Neuron*, *40*, 655–664.

Wyatt, T.D. (2003). *Pheromones and animal behavior: Communication by smell and taste*. London: Cambridge University Press.

Zhou, W., & Chen, D. (2008). Encoding human sexual chemosensory cues in the orbitofrontal and the fusiform cortices. *Journal of Neuroscience*, *28*, 14416–14421.

Zhou, W., & Chen, D. (2009). Fear-related chemosignals modulate recognition of fear in ambiguous facial expressions. *Psychological Science*, *20*, 177–183.

(Received 10/6/08; Revision accepted 1/23/09)