Does Human Body Odor Represent a Significant and Rewarding Social Signal to Individuals High in Social Openness?

Katrin T. Lübke1, Ilona Croy2, Matthias Hoenen1, Johannes Gerber3, Bettina M. Pause1, Thomas Hummel2

1 Department of Experimental Psychology, University of Düsseldorf, Düsseldorf, Germany, 2 Department of Otorhinolaryngology, University of Dresden Medical School, Dresden, Germany, 3 Department of Neuroradiology, University of Dresden Medical School, Dresden, Germany

Abstract

Across a wide variety of domains, experts differ from novices in their response to stimuli linked to their respective field of expertise. It is currently unknown whether similar patterns can be observed with regard to social expertise. The current study therefore focuses on social openness, a central social skill necessary to initiate social contact. Human body odors were used as social cues, as they inherently signal the presence of another human being. Using functional MRI, hemodynamic brain responses to body odors of women reporting a high (n = 14) or a low (n = 12) level of social openness were compared. Greater activation within the inferior frontal gyrus and the caudate nucleus was observed in high socially open individuals compared to individuals low in social openness. With the inferior frontal gyrus being a crucial part of the human mirror neuron system, and the caudate nucleus being implicated in social reward, it is discussed whether human body odor might constitute more of a significant and rewarding social signal to individuals high in social openness compared to individuals low in social openness process.

Introduction

Across a wide variety of domains, experts differ from novices in their response to stimuli linked to their respective field of expertise. These differences, apparent in overt behavior, are correlated with differential central nervous processing patterns in experts versus novices. For example, when presented with expertise linked stimuli, athletes show stronger activation within task related brain areas compared to novices [1–3]. Similar results have been reported when comparing chess masters to chess novices [4], or professional musicians to musical lay persons [5]. Similar differences between “experts” and “novices” can be expected within the domain of social skills. However, whenever social expertise is reported to affect responses to social stimuli, “normal” control groups are compared to individuals featuring social deficits, such as patients suffering from schizophrenia, or autism spectrum disorders [6]. How social expertise affects brain activation in response to social stimuli when otherwise normal individuals with social skills below average are compared to social experts is currently unknown.

Social expertise, or social competence, can be defined as being able to correctly identify and interpret social and emotional information, being highly sensitive to socio-emotional information, being able to memorize social information, and being able to manage social and emotional situations (for an overview see [7]). Importantly, in order to establish social contacts, being socially open is a central skill for socially competent people. Following Kanning’s model of social skills, “social openness” (German “Offensivität”, [8]) is characterized by being outgoing and sociable, but also being assertive, decisive, and able to negotiate social conflicts without intentionally causing them. Individuals who describe themselves as high in social openness display a pervasive drive and the necessary skills to initiate and maintain social contact. So far, imaging studies have linked both empathy and social reward sensitivity to brain areas subserving the perception and integration of social information [9–11], as well as the processing of social reward [10,11]. Kaplan and Jacoboni [9] interpreted their findings as suggesting a close link between social competence and mirror neuron system activity. Moreover, similar to social openness, social reward sensitivity, as examined in [10] and [11], reflects the individual disposition to social relationships.

Human body odor represents a ubiquitous and ancient social signal, linked to the domain of social expertise. Humans permanently produce and perceive body odor, and its social and emotional content cannot be manipulated (for reviews on human chemosensory communication see [12–15]). It inherently signals the presence of another individual, and has been shown to carry a diversity of social information, ranging from individual identity [16,17] to transiently experienced affect [18–20]. Social expertise seemingly affects responses to chemosensory social stimuli, as social anxiety modulates the central nervous processing of human body odors [21,22] as well as motor behavior in the context of human body odors [23]. Social anxiety itself is tightly linked to...
deficits in social skills [24], causing deficits in social interaction performance [25,26]. Emotionally highly competent individuals, on the other hand, presumably also tending to be socially skilled, outperform less emotionally adept individuals in identifying familiar persons by their body odor [27].

The current study was designed to examine effects of social expertise, precisely social openness, on hemodynamic brain responses to social stimuli, using human body odor as the most basic social stimulus. Comparable to studies in other fields of expertise, an experimental approach comparing highly socially open individuals (“social experts”) with individuals low in social openness (“social novices”) was chosen. Effects of social openness are expected to be most prominent within brain areas involved in social information and reward processing: When presented with human body odor, highly socially open individuals should show stronger hemodynamic responses in these brain regions than individuals low in social openness.

**Materials and Methods**

**Ethics statement**

Participants gave written informed consent and were paid for their participation. The current study, including the sweat sampling procedure, was carried out in accordance with the Declaration of Helsinki and was approved by the University of Dresden Medical Faculty Ethics Review Board.

**Participants**

Twenty-six right-handed women (mean age: 23.0 years, SD = 2.2, range 18–27) of European descent participated in the current study. Only women were recruited due to their overall greater olfactory abilities compared to men [28], and especially due to their higher sensitivity regarding chemosensory social cues [21,29,30]. None of these women reported a history of chronic medication, of neurological, psychiatric, major endocrine or immunological disease, or using drugs. Their body-mass-index ranged from 19.3 to 26.0 kg/m² (M = 22.5, SD = 1.9), and all of them were non-smokers. Female donors reported having a regular menstrual cycle and denied use of hormonal contraception.

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). Male as well as female donors shaved their armpits one day prior to the odor donation. For collecting the axillary odors, one cotton pad was fixed in each of the donor’s armpits. The axillary odors were sampled during sleep over the course of one night (sampling duration: M = 8.5 h, SD = 1.0 h). All donors gave written informed consent and were paid for their donation. None of the odor donors acted as a participant within the current study.

Following the completion of collection, cotton pads carrying the sweat samples were chopped and pooled with respect to the donor’s sex, then divided into small portions of 0.6 g cotton pad and stored at −20°C. Additionally, samples of pure, unused cotton pads were treated the exact same way to provide for baseline measurements within the fMRI sessions.

**Stimulus Presentation**

Participants underwent four scanning sessions in total. In two of these sessions they were presented with male body odors, while in the other two they were presented with female body odors. The order of the scanning sessions was counterbalanced across groups. A self-constructed olfactometer delivered odor pulses embedded in a constant flow of humidified, odorless air in order to avoid any mechanical stimulation. The odors were presented biphassically and intranasally (inner diameter of the Teflon tubing: 4 mm), with a total airflow of 2 liter per minute. Further, the odors were delivered non-synchronously to breathing, as participants performed the velopharyngeal closure technique [33]. The body odors (during ON blocks) as well as the odor-free, pure cotton pads (during OFF blocks) were presented for a period of 1 second with an interstimulus interval of 2 seconds (see Fig. 1).
Participants were not cued for stimulus presentation, and were not asked to perform any detection or other cognitive tasks. Following each session, however, participants were asked to rate the odor’s intensity (0 = not perceivable; 10 = extremely intense) and hedonic quality (*-5 = extremely unpleasant; 5 = extremely pleasant).

**fMRI Protocol**

A 1.5 T scanner (SONATA-MR, Siemens, Erlangen, Germany) was used for fMRI data acquisition. For functional data 96 volumes per session were acquired by means of a 33 axial-slice matrix 2D SE/EP sequence. Scan parameters included a 192 x 192 mm² field of view, a TR of 2500 ms, a TE of 40 ms, a 64 x 64 matrix, a 90° flip angle, a slice thickness of 3 mm, and a voxel size of 3 x 3 x 3.75 mm³. Additionally, T1-weighted images were acquired using a 3D IR/GR sequence (TR: 2180 ms/TE: 3.39 ms) to localize activated areas. Eight dummy scans were conducted at the beginning of each session to allow the magnetization to reach magnetic equilibrium. Utilizing a block design, in each session the participants received 8 scans during the 22 s ON blocks and 8 scans during the 22 s OFF blocks (see Fig. 1). ON and OFF blocks were repeated 6 times in alternation. Each session lasted 4:40 minutes.

**fMRI Data Analysis**

Preprocessing and statistical analysis were performed using the statistical parametric mapping software package (SPM8, Wellcome Trust Centre for Neuroimaging, London; www.fil.ion.ucl.ac.uk/spm) implemented in Matlab R2010b (Math Works Inc., Natick, MA; USA). Head motions across time were corrected by realigning all scans to the first volume. Participants’ T1-weighted images were co-registered to the corresponding mean EPI images and subsequently normalized to Montreal Neurological Institute (MNI) standard space using the segmentation procedure. EPI images were then normalized using the parameters written during segmentation of co-registered T1-weighted images and spatially smoothed using an isotropic Gaussian kernel at 6 mm full width at half maximum.

The responses to male and female body odors were combined for analyses, as the current literature does not provide data that would allow for specific sex-related hypotheses. Both body odors were presented during scanning in order to prevent any bias that might result from processing of same-sex vs. other-sex body odors. However, the odors were not combined during scanning to avoid creating an artificial chemosignal.

In order to identify the effects of the body odor presentation, first level linear contrast images were entered into a general linear model, applying a canonical hemodynamic response function. Statistical parametrical maps were generated for each participant. The parameters written during realignment were entered as

---

Table 1. Distribution of “Openness” standard scores across included and excluded participants.

| Participants     | “Openness” standard score | n | M ± SD “Openness” standard score |
|------------------|---------------------------|---|---------------------------------|
| Excluded Participants | 92                        | 3 | 101.47 ± 5.32                  |
|                  | 95                        | 5 |                                 |
|                  | 96                        | 2 |                                 |
|                  | 97                        | 2 |                                 |
|                  | 98                        | 3 |                                 |
|                  | 101                       | 9 |                                 |
|                  | 103                       | 4 |                                 |
|                  | 106                       | 8 |                                 |
|                  | 109                       | 7 |                                 |
| “Low Level of Openness” | 78                       | 1 | 86.33 ± 3.73                   |
|                  | 83                        | 3 |                                 |
|                  | 86                        | 1 |                                 |
|                  | 89                        | 7 |                                 |
| “High Level of Openness” | 112                      | 10 | 113.86 ± 3.09               |
|                  | 118                       | 3 |                                 |
|                  | 120                       | 1 |                                 |

---

doi:10.1371/journal.pone.0094314.t001

---

Figure 1. Schematic time course of a scanning session. The participants underwent 4 scanning sessions in succession. Each session consisted of 6 ON-blocks (with presentation of body odor) and 6 OFF-blocks (with presentation of odor-free, pure cotton pad), resulting in a total of 12 blocks. During each block, the stimuli were presented for a period of 1 s with an interstimulus interval of 2 s. Each block had a duration of 22 s, during which 8 scans were conducted.

doi:10.1371/journal.pone.0094314.g001
Results

The hemodynamic brain response to the body odors presented indeed varied with social openness. Comparing the parameter estimates of the first level ON-OFF-contrasts in HO versus LO participants showed greater activation within the right inferior frontal gyrus (peak located at x = 40/y = 38/z = 0; t = 5.26; cluster size 37, see Fig. 2), and within the right caudate nucleus (peak located at x = 16/y = 22/z = 14; t = 4.28; cluster size 33, see Fig. 2) in HO compared to LO participants. The reverse (LO vs. HO) contrast did not yield any suprathreshold activation. Further, significant linear relationships between individual beta values and social openness scores were observed: Social openness scores were highly positively correlated with both peak activation within the right inferior frontal gyrus ($r = 0.715$, $p < 0.001$, see Fig. 3, left paragraph) and the right caudate nucleus ($r = 0.685$, $p < 0.001$, see Fig. 3, right paragraph).

Contrasting the perception of body odors (ON) with the perception of pure cotton pad (OFF) across all participants, using the specified masks, significant activation within the fusiform cortex, the anterior and posterior cingulate cortex and the insular cortex was evident (see Table 2, Fig. 4). The reverse contrast did not yield any suprathreshold activation.

Discussion

This study aimed to compare brain responses to human chemosensory social signals of individuals describing themselves as high in social openness (HO) with the brain responses of individuals describing themselves as low in social openness (LO). Consistent with the hypotheses, HO participants display stronger activation than LO participants in brain regions known to be involved in social perception (inferior frontal gyrus) and within the reward system (caudate nucleus). These results suggest that HO individuals perceive human body odors as subjectively important social signals associated with positive experience more readily than LO individuals. This effect, however, seems not to extend to conscious evaluation, as HO and LO individuals do not differ in their judgments of the body odors’ qualitative features.

The inferior frontal gyrus has been shown to be involved in social perception, as it is activated when viewing (emotional) faces (for a review see [39,40]), during implicit facial judgments [41] or when observing positive and negative social encounters [42]. Moreover, activity within the inferior frontal gyrus is found to be positively correlated with the level of trait empathy [43], and individuals with an empathizing rather than systemizing cognitive style show pronounced activity within the inferior frontal gyrus during a face-based mind reading task [44]. Empathy seems to be crucial for social interaction. It can be regarded as having a concept about how another individual feels, being able to take another one’s perspective and, in some instances, displaying a corresponding response [45]. Hence, the concept of empathy is closely related to social openness and other social competencies. In general, the inferior frontal gyrus is discussed as a crucial part of the human mirror neuron system [46,47]. Accordingly, in HO individuals compared to LO individuals, body odors more readily activate components of a system thought to mediate the perception and recognition of actions and emotions, which is pivotal for social cognitive functioning.

The current study is the first to report activation within the reward system in response to human chemosensory social signals (for a recent meta-analysis of basal ganglia functions see [48]). HO compared to LO individuals display a stronger hemodynamic response to body odors within the caudate nucleus. Both activation within the ventral striatum (nucleus accumbens) and the dorsal striatum (caudate nucleus, putamen) have been reported consistently in positive social interaction, indicating that reward processing and social interaction share common neural substrates [49,50]. It has even been demonstrated that the individual disposition to social openness is positively associated with the gray matter density within the striatum [10]. Considering social perception and behavior, the caudate nucleus is discussed as a

![Figure 2. Activation in response to body odors in HO vs. LO participants. HO participants show activation within the right inferior frontal cortex and within the right caudate nucleus (k≥20; p<0.001). For visualization a normalized template provided by SPM 8 software (single_subj_T1.nii) was used. doi:10.1371/journal.pone.0094314.g002](Image 58x123 to 298x274)
neuronal correlate of trust [51,52] and thus to be implemented in a neuronal network that positively reinforces reciprocal altruism and cooperation [53,54]. Moreover, it has been shown to be involved in the anticipation of positive (social) encounters in the near future [55]. Interestingly, recent research showed that socially isolated individuals show less activity within the reward system in response to people than to objects, while non-lonely individuals show the opposite response pattern [56]. The authors concluded that socially isolated individuals are less rewarded by social stimuli than non-lonely individuals, mirroring the results of the current study. Here, the social signal of human body odor seems more rewarding to individuals high in social openness, than to individuals low in social openness.

Both neural responses within the inferior frontal gyrus, and neural responses within the caudate nucleus increase in strength with rising social openness scores. These results suggest that the differences between HO and LO individuals might be driven by a linear relationship between social expertise and brain responses to social odors. However, the design underlying the current study applied a two-group approach, comparing participants either belonging to the 15.8% highest ranking or to the 15.8% lowest ranking individuals in social openness within the population. Individuals showing intermediate levels of social expertise were excluded from participation, similar to other studies comparing "experts" and "novices" (e.g. [1,2,4,5]). While promising, conclusions based on the results of the correlational analyses appear somewhat limited due to "missing data" within the medium range

Table 2. Significant peaks for body odor perception across all participants (n = 26) in areas reported to be involved in body odor processing.

| MNI coordinates | X  | Y  | Z  |
|-----------------|----|----|----|
| Fusiform Cortex | 21 | 4.36 | -30 | -10 | -30 |
|                 | 35 | 4.12 | 40  | -68 | -20  |
| Anterior Cingulate Cortex | 461 | 5.43* | 0   | 38  | 22   |
|                 |    | 5.14* | -2  | 22  | 20   |
|                 |    | 4.08* | 0   | 50  | -2   |
| Posterior Cingulate Cortex | 155 | 5.38* | 8   | -38 | 8    |
|                 |    | 4.51* | 2   | -42 | 28   |
|                 |    | 3.90* | 2   | -44 | 14   |
| Insula          | 35 | 5.18* | 46  | 16  | -10  |
|                 | 31 | 3.71* | 40  | 14  | -16  |
|                 | 31 | 4.32* | -44 | 14  | -8   |

Notes: significant primary peaks of activation in the small volume corrected areas are presented (cluster level k≥20, p<0.001); positive x-values denote right-sided activation, negative x-values denote left-sided activation;
*: peak activation is significant if family-wise error (FWE) correction is applied (p<0.05).
of social expertise. The issue of a potential linear relationship between social expertise and brain responses to social odors thus needs to be addressed within upcoming research.

Across all participants, the presentation of body odors activated the fusiform cortex, the cingulate cortex, and the insular cortex. These areas are discussed as being part of specialized neuronal networks involved in the processing of chemosensory social signals, strongly overlapping with areas implicated in the processing of other socioemotional information [12,14]. The pattern of activation observed within the current study strongly suggests that the utilized body odors were processed as social signals. The statistical criterion for significant contrasts was set at a rather liberal level (p < 0.001, uncorrected) within the current study. While this threshold is not uncommon in olfactory fMRI experiments: KTL IC. Analyzed the data: KTL IC. Contributed reagents/ materials/analysis tools: JG TH BMP MH. Wrote the paper: KTL.

Acknowledgments
The authors would like to thank Friederike Barthels for her help in collecting the body odor samples, and Sabine Schlösser for helping during language editing.

Author Contributions
Conceived and designed the experiments: KTL BMP TH. Performed the experiments: KTL IC. Analyzed the data: KTL IC. Contributed reagents/materials/analysis tools: JG TH BMP MH. Wrote the paper: KTL.

References
1. Kim J, Lee HM, Kim WJ, Park HJ, Kim SW, et al. (2008) Neural correlates of pre-performance routines in expert and novice archers. Neurosci Lett 445: 236–241.
2. Wei GX, Luo J (2010) Sport expert’s motor imagery: Functional imaging of professional motor skills and simple motor skills. Brain Res 1341: 52–62.
3. Wright MJ, Bishop DT, Jackson RC, Abernethy B (2011) Cortical fMRI activation to opponents’ body kinematics in sport-related anticipation: Expert–novice differences with normal and point-light video. Neurosci Lett 500: 216–221.
4. Duan X, Liao W, Liang D, Qiu L, Gao Q, et al. (2012) Large-scale brain networks in board game experts: insights from a domain-related task and task-free resting state. PLoS ONE 7: e52532. doi: 32510.31371/ journal.pone.0052532.
5. Horneg K, Muller C, Herrnberger B, Sim EJ, Spitzer M, et al. (2011) Neuroplasticity of semantic representations for musical instruments in professional musicians. Neuroimage 56: 1714–1725.
6. Sugranyes G, Kyriakopoulos M, Corrigall R, Taylor E, Frangou S (2011) Autism spectrum disorders and schizophrenia: Meta-analysis of the neural correlates of social cognition. PLoS ONE 6: e25322. doi: 25310.21371/journal.pone.0025322.
7. Suß H-M, Weis S, Seidel K (2005) Soziale Kompetenzen. In: Weber H, Rammsayer T, editors. Handbuch der Persönlichkeitpsychologie und Differentialen Psychologie. Göttingen: Hogrefe. pp. 350–362.
8. Kanning UP (2009) ISK. Göttingen: Hogrefe.
9. Kaplan JT, Lacoboni M (2006) Getting a grip on other minds: Mirror neurons, intention understanding, and cognitive empathy. Soc Neurosci 1: 173–183.
10. Lebrunet M, Barnes A, Miettunen J, Peltonen L, Ridler K, et al. (2009) The brain structural disposition to social interaction. Eur J Neurosci 29: 2247–2252.
11. Cohen MX, Schoone-Bake JC, Elger CE, Weber B (2009) Connectivity-based segregation of the human striatum predicts personality characteristics. Nat Neurosci 12: 32–34.
12. Lundström JN, Olsson MJ (2010) Functional neuronal processing of human body odors. Vitam Horm 83: 1–23.
13. Pause BM (2004) Are androgen steroids acting as pheromones in humans? Physiol Behav 83: 21–29.
14. Pause BM (2012) Processing of body odor signals by the human brain. Chemosens Percept 5: 55–63.
15. Wyatt TD (2004) On the scent of human attraction: Human pheromones? Pheromones and Animal Behaviour. Cambridge: Cambridge University Press. pp. 270–301.
16. Porter RH (1999) Offaction and human kin recognition. Genetica 104: 259–263.

Social Skills Affect BOLD Response to Body Odor

Figure 4. Activation in response to the body odors across all participants (n = 26). Parameters: k = 20; p < 0.001; contrast: ON vs. OFF. For visualization, a normalized template provided by SPM 8 software (single_sub.T1.nii) was used. doi:10.1371/journal.pone.0094314.g004
21. Pause BM, Lübke K, Laudien JH, Ferstl R (2010) Intensified neuronal
20. Zhou W, Chen D (2009) Fear-related chemosignals modulate recognition of fear
19. Prehn-Kristensen A, Wiesner C, Bergmann TO, Wolff S, Jansen O, et al. (2009)
17. Mallet P, Schaal B (1998) Rating and recognition of olfactory function: an
16. Zhou W, Hou P, Zhou Y, Chen D (2011) Reduced recruitment of orbitofrontal
15. Lundstro¨m JN, Boyle JA, Zatorre RJ, Jones-Gotman M (2008) Functional
14. Focquaert F, Steven-Wheeler MS, Vanneste S, Doron KW, Platek SM (2010)
13. Cacioppo JT, Norris CJ, Decety J, Monteleone G, Nusbaum H (2009) In the eye
12. Zhou W, Chen D (2009) Sociochemosensory and emotional functions. Psychol
11. Hummel T, Sekinger B, Wolf SR, Pauli E, Kobal G (1997) Sniffin’ Sticks:
10. Pause BM, Ohrt A, Prehn A, Ferstl R (2004) Positive emotional priming of facial
9. Ashbaugh AR, Antony MM, McCabe RE, Schmidt LA, Swinson RP (2005)
8. Maldjian JA, Laurienti PJ, Kraft RA, Burdette JH (2003) An automated method
7. Maldjian JA, Laurienti PJ, Kraft RA, Burdette JH (2000) Precentral gyrus discrepancy in
6. Maldjian JA, Laurienti PJ, Kraft RA, Burdette JH (2004) Centrally gyrus discrepancy in
5. Lundstro¨m JN, Boyle JA, Zatorre RJ, Jones-Gotman M (2000) Functional
4. Hummel T, Kobal G, Grudzio H, Mackay-Sim A (2007) Normative data for the
3. Zhou W, Chen D (2008) Encoding human sexual chemosensory cues in the
2. Hummel T, Oc¸kun S, Gerber J, Huchel U, Frasnelli J (2013) Brain responses to
1. Pause BM, Lübke K, Laudien JH, Ferstl R (2010) Intensified neuronal

39. Adolphs R (2002) Recognizing emotion from facial expressions: psychological
38. Maldjian JA, Laurienti PJ, Kraft RA, Burdette JH (2003) An automated method
37. Maldjian JA, Laurienti PJ, Kraft RA, Burdette JH (2004) Centrally gyrus discrepancy in
36. Maldjian JA, Laurienti PJ, Kraft RA, Burdette JH (2000) Precentral gyrus discrepancy in
35. Lundstro¨m JN, Boyle JA, Zatorre RJ, Jones-Gotman M (2008) Functional
34. Zhou W, Chen D (2008) Encoding human sexual chemosensory cues in the
33. Kobal G (2003) Electrophysiological measurement of olfactory function. In:
32. Hummel T, Kobal G, Gudziol H, Mackay-Sim A (2007) Normative data for the
31. Hummel T, Sekinger B, Wolf SR, Pauli E, Kobal G (1997) Sniffin’ Sticks:
30. Pause BM, Ohrt A, Prehn A, Ferstl R (2004) Positive emotional priming of facial
29. Doty RL, Cameron EL (2009) Sex differences and reproductive hormone influences on human odor perception. Physiol Behav 97: 213–228.
28. Doty RL, Cameron EL (2009) Sex differences and reproductive hormone influences on human odor perception. Physiol Behav 97: 213–228.
27. Zhou W, Chen D (2009) Sociochemosensory and emotional functions. Psychol
26. Baker SR, Edelmann RJ (2002) Is social phobia related to lack of social skills? Duration of skill-related behaviours and ratings of behavioural adequacy. Br J Clin Psychol 41: 243–257.
25. Ashbaugh AR, Antony MM, McCabe RE, Schmidt LA, Swinson RP (2005)
24. Arsalidou M, Duerden EG, Taylor MJ (2012) The centre of the brain: Topographical model of motor, cognitive, affective, and somatosensory functions of the basal ganglia. Hum Brain Mapp.
23. Pause BM, Adolph D, Prehn-Kristensen A, Ferstl R (2009) Startle response to chemical anxiety signals in socially anxious individuals. Int J Psychophysiol 74: 88–92.
22. Zhou W, Hou P, Zhou Y, Chen D (2011) Reduced recruitment of orbitofrontal
cortex to human social chemosensory cues in social anxiety. Neuroimage 55: 1401–1406.
21. Pause BM, Lübke K, Laudien JH, Ferstl R (2010) Intensified neuronal
20. Zhou W, Chen D (2009) Fear-related chemosignals modulate recognition of fear
19. Prehn-Kristensen A, Wiesner C, Bergmann TO, Wolff S, Jansen O, et al. (2009)
18. Croy I, Schellong J, Gerber J, Joraschky P, Lumilli E, et al. (2010) Women with a history of childhood maltreatment exhibit more activation in association areas following non-traumatic olfactory stimuli: A fMRI study. PLoS ONE 5: e9362. doi: 936210.1371/journal.pone.0009362.
17. Mallet P, Schaal B (1998) Rating and recognition of olfactory function: an
16. Zhou W, Chen D (2009) Sociochemosensory and emotional functions. Psychol
15. Lundstro¨m JN, Boyle JA, Zatorre RJ, Jones-Gotman M (2000) Functional
14. Focquaert F, Steven-Wheeler MS, Vanneste S, Doron KW, Platek SM (2010)
13. Cacioppo JT, Norris CJ, Decety J, Monteleone G, Nusbaum H (2009) In the eye of the beholder: Individual differences in perceived social isolation predict regional brain activation to social stimuli. J Cogn Neurosci 21: 83–92.
12. Zhou W, Chen D (2009) Sociochemosensory and emotional functions. Psychol
11. Hummel T, Sekinger B, Wolf SR, Pauli E, Kobal G (1997) Sniffin’ Sticks: olfactory performance assessed by the combined testing of odor identification, odor discrimination and olfactory threshold. Chem Senses 22: 38–52.
10. Pause BM, Ohrt A, Prehn A, Ferstl R (2004) Positive emotional priming of facial affect perception in females is diminished by chemosensory anxiety signals. Chem Senses 29: 797–805.
9. Hummel T, Kobal G, Grudzio H, Mackay-Sim A (2007) Normative data for the “Sniffin’ Sticks” including tests of odor identification, odor discrimination, and olfactory thresholds: An upgrade based on a group of more than 3000 subjects. Eur Arch Otorhinolaryngol 264: 237–243.
8. Maldjian JA, Laurienti PJ, Kraft RA, Burdette JH (2003) Precentral gyrus discrepancy in electronic versions of the Talairach atlas. Neuroimage 21: 450–453.
7. Maldjian JA, Laurienti PJ, Kraft RA, Burdette JH (2000) Precentral gyrus discrepancy in electrical versions of the Talairach atlas. Neuroimage 21: 450–453.