

Original Article

You Smell Dangerous: Communicating Fight Responses Through Human Chemosignals of Aggression

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Accepted 14 September 2015.

Abstract

The ability to detect conspecifics that represent a potential harm for an individual represents a high survival benefit. Humans communicate socially relevant information using all sensory modalities, including the chemosensory systems. In study 1, we investigated whether the body odor of a stranger with the intention to harm serves as a chemosignal of aggression. Sixteen healthy male participants donated their body odor while engaging in a boxing session characterized by aggression-induction methods (chemosignal of aggression) and while performing an ergometer session (exercise chemosignal). Self-reports on aggression-related physical activity, motivation to harm and angry emotions selectively increased after aggression induction. In study 2, we examined whether receivers smelling such chemosignals experience emotional contagion (e.g., anger) or emotional reciprocity (e.g., anxiety). The aggression and exercise chemosignals were therefore presented to 22 healthy normosmic participants in a double-blind, randomized exposure during which affective/cognitive processing was examined (i.e., emotion recognition task, emotional stroop task). Behavioral results indicate that chemosignals of aggression induce an affective/cognitive modulation compatible with an anxiety reaction in the recipients. These findings are discussed in light of mechanisms of emotional reciprocity as a way to convey not only affective but also motivational information via chemosensory signals in humans.

Key words: approach motivation, olfaction, social chemosignals, threat

Introduction

The study of communication via chemosignals among humans is progressively gaining foothold in olfactory research and has been extensively explored on a variety of rather stable features that identify the individual: health status (Olsson et al. 2014), gender assignment (Penn et al. 2007; Mitro et al. 2012), kin recognition and fertility assessment (Grammer et al. 2005; Gildersleeve et al. 2012). A subdivision of chemosignal research focuses on the transmission of less stable information, such as transitory emotional states. Emotions

communicated via chemosignals are mostly negative: Besides sadness (Gelstein et al. 2011) and disgust (de Groot et al. 2012), most widely, anxiety- and fear-related chemosignals have been studied (although evidence of chemosignals of positive affect has been suggested; Chen and Haviland-Jones 2000; de Groot et al. 2015). Such stress-related chemosignals are collected from donors in highly distressing situations like university examinations (Pause et al. 2004), life threatening environments as high rope courses (Albrecht et al. 2011) or first-time sky-diving experiences (Mujica-Parodi et al. 2009).

The stress-related chemosensory message embedded in the donors' body odor affects a wide range of a receiver's psychological processes such as social judgment, emotion recognition, decision making, attention (e.g., Chen et al. 2006; Dalton et al. 2013; Haegler et al. 2010; Zernecke et al. 2011; Zhou and Chen 2009) as well as endophenotypes of behavior investigated via neuroimaging (e.g., Mujica-Parodi et al. 2009; Rubin et al. 2012). From an evolutionary point of view, this type of social communication grants the unique survival benefit of fast detecting that a sender is (or recently was) in a distressing situation and is prompting the receiver to be alerted, because such potentially distressing situation might be proximal. This line of reasoning could be extended from situations to people. In fact, individuals themselves can be a source of threat, for instance when they manifest the intention to harm and engage in a fight. Therefore, detecting the presence of aggressive individuals constitutes an important additional survival benefit.

A fight response is an acute psychobehavioral stress response characterizing the motivational and behavioral state of an individual (Cannon 1932). It is related to an approaching behavioral tendency and a motivation to harm (e.g., Hortensius et al. 2012; although not exclusively; Zimmer et al. 2008), feelings of hostility (i.e., anger) and cognitively mediated by angry rumination (Denson et al. 2011). Internal and external factors, as theorized by the general aggression model (Anderson and Bushman 2002), were shown to increase the likelihood of implementing a fight response, namely negative intelligence feedback, endangered self-esteem, the need to defend one's goods, and the experience of lack of fairness and temporary reduction of self-control as a consequence of high attentional demands (i.e., Bettencourt and Miller 1996; Lobbestael et al. 2008; Denson et al. 2011; Smith et al. 2014). Overall, these correlates and mediators of aggressive behavior help clarifying how a fight response, based on a motivation to act aggressively, is discriminable from purely physically challenging situations (e.g., exercise) and other types of stress responses, such as those related to anxiety responses (Kenemy and Shestyuk 2008).

The cardinal role of the olfactory system in signaling to conspecifics an intention to harm via chemicals has been intensively studied in rodents. Territorial aggression is communicated via pheromones in the urine of male mice and results in inter-male attacks toward an intruder (Tirindelli et al. 2009). Critically, the experimental deactivation of the main and vomeronasal olfactory system in rodents inhibits such aggression. In humans, direct evidence of chemosignals related to aggressive behavior has been scant (Schloesser et al. 2011). The topic has been marginally explored through research on competitive situations and trait dominance and is suggesting that transient aggressive states can manifest in volatile components of body odors. In a study by Adolph et al. (2010), male participants donated body odor samples during a competitive sport situation and yielded different reactions depending on the level of social anxiety of the recipients. Nonetheless, they failed to observe increase in competitor's anger ratings or approach motivation. Sorokowska (2013) provides the first evidence for body odor differences in association with dominance, a personality trait related to aggression (Buss and Craik 1981). Adult participants succeeded in identifying a donor's high trait dominance when rating the donor's body odor samples.

However, how humans react to the chemosignals of an unfamiliar person involved in an overt or covert fight response has yet to be fully uncovered. Chemosignals of unknown individuals can be used to discriminate whether individuals perpetrated harmful versus nonharmful acts (Alho et al. 2015). Also, at the neural level, the odor

of unknown/potentially harmful individuals selectively increases the activation of brain areas involved in the fear network (i.e., amygdala and insula) and it remains inactive when smelling the odor of known/friendly individuals (Lundström et al. 2008). But which are the behavioral options of receivers smelling the chemosignal of individuals engaging in aggressive behaviors? Two possible options are imaginable. In emotional contagion, smelling the chemosignal of an individual engaging in a fight response would automatically trigger the mirroring of this emotional state in the receiver, who would experience anger and aggression (Hatfield et al. 1994). In emotional reciprocity, the emotional tone of the olfactory communication would not only be mirrored (anger), but complemented, in the reaction of the receiver (anxiety; e.g., for other types of social interactions, see Sartori et al. 2013). With specific reference to olfactory communication of threat, the reaction in a receiver can be represented by a stress-related response compatible with anxiety.

Investigating—what we could call for the sake of brevity—*chemosignals of aggression*, determined by a stressful situation whose behavioral response is a fight one—would allow us not only to investigate whether danger-related motivational states and behavioral intentions other than withdraw can be conveyed via human chemosignals, but it would also allow us to take the field of stress-related chemosensory research a step forward by investigating the type of emotional communication such chemosignals stimulate in recipients.

In Study 1 (chemosignal sampling), we induced an aggressive response in body odor donors. We hypothesized that their subjective experience will be characterized by differences in emotional, motivational, and cognitive aspects while donating chemosignals of aggression compared with exercise chemosignals, only sharing with the former the physical activity component. In detail, we expected a selective increase (via self-ratings) of anger and a motivation to harm in the aggression condition as compared with the exercise condition.

In Study 2 (exposure to chemosignals), we expected that aggression chemosignals elicit emotional reciprocity (i.e., anxiety-related focus) in extension to pure emotional contagion (i.e., aggression-related focus). In detail, we hypothesized that recipients are differentially affected by the exposure to chemosignals of aggression compared with exercise chemosignals and no odor while performing perceptual (i.e., odor recognition and rating), affective (i.e., mood self-report, emotional recognition task) and cognitive tasks (i.e., emotional stroop test). We expected cognitive/affective processing impairments of anxiety-related content to be associated with aggression, but not with exercise or control chemosignals.

Study 1—Chemosignal sampling

Materials and methods

All participants provided written informed consent to participate in the study and were explicitly informed that they could drop out of the study anytime, without any consequences or additional explanations. The research protocol was approved by the ethics committee of Uniklinik RWTH Aachen and is compatible with the Declaration of Helsinki.

Participants

Sixteen out of 22 recruited healthy male heterosexual nonsmokers ($M = 25.38$ years; $SD = 3.82$) donated chemosignals. Participants gave written consent in complying to behavioral and food restrictions standardly used in studies for body odor donation (Lenochova et al. 2009; Albrecht et al. 2011). They engaged in a washout phase of two days

during which they restrained from consumption of odor-intense spices (e.g., curry, asparagus, onions, garlic), coffee and the use of body scents, visits to saunas or public pools prior to the experiment. An a priori sample size was estimated via power analysis (G*Power, Version 3; Faul et al. 2007) and yielded a total sample size of $n = 18$ participants entering an estimated effect size $f = 0.4$ for F -tests (ANOVA with repeated measures) and an error probability of $\alpha = 0.05$.

Donation procedure

Upon arrival, participants signed informed consent and filled out aggression-related personality questionnaires, such as the aggression questionnaire (AQ; Buss and Perry 1992) and the reactive-proactive aggression questionnaire (RPQ; Raine et al. 2006). Participants then showered with fragrance-free body wash and dressed with a prepared t-shirt with sewn cotton pads placed under their armpits. In a within-subject design, they first donated body odor in a physically challenging exercise condition (ergometer workout of two sessions lasting 3 min each). Upon completion of this first part, they were asked to shower again, get changed and then they donated their body odors in a physically challenging aggression condition. All experimental sessions were performed between noon and 2 PM. In order to minimize experimenter's effects, only female experimenters were present during the experimental session and only one experimenter was in charge of the aggression induction manipulation and the debriefing at the end of the experiment whereas the other was involved in the donation procedure. At baseline and after each donation condition (exercise and aggression chemosignals), the participants conducted a series of self-ratings, based on items taken from the state aggression version of the STAXI questionnaire (Spielberger 1999) and from a series of items taken from Denson et al. (2011). Given the lack of standardized self-reports separating the behavioral, motivational, and emotional constituents of aggression, we a priori subgrouped items as to reflect judgments on: angry feelings (emotional, e.g., angry, furious, annoyed), readiness to aggress (motivational, e.g., harmful, hurtful, hostile, violent) and pure physical activity (behavioral, e.g., active, strong, exhausting). To account for the other negative emotions co-occurring during aggression (Kuppens et al. 2003), the assessment of factors related to anxiety (i.e., nervous, stressed), cognitive load and resource depletion (i.e., exhausted) and frustration (i.e., disappointed) were included. The exercise and aggression conditions were similarly constructed (Figure 1). They both involved a mental calculation task (two session of 20 equations each), physical activity (two session of 3 min each) and subjective ratings. Overall each condition took approximately 20 min. The exercise condition was designed to produce a donation in a cognitively neutral and nondemanding but physically challenging situation, in the absence of a fight response. Participants started with a computerized mental calculation task without time constraint. They were asked to solve mental arithmetic equations, containing five various difficulty

levels and received a computerized and bogus feedback of average performance. They then all performed a training on the same hand ergometer (100 W; Ergosana) in a neutral environmental stimulation (i.e., in an exercise room, facing a window to a clear inner court). Furthermore, they completed the self-rating before and after the training, as described earlier.

In the aggression condition, participants started with a computerized mental calculation task that had to be accomplished under severe time pressure. They received a computerized and bogus feedback of performance below average and negative social feedback. Then, behavioral fight responses were stimulated by prompting participants to act aggressively (Smith et al. 2014): The participants were asked to hit a punching bag repeatedly while exposed to implicit aggression-related objects in the testing environment (see Supplementary Material for further information). Furthermore, the participants again rated their emotional, motivational and behavioral state and donated aggression chemosignals. In a funneled debriefing conversation with the experimenter to check for study compliance, participants were asked if they observed irregularities during testing, any thoughts about their performance feedback and if there were remarkable objects in the testing environment. The data collection stopping rule was adapted according to the sample size estimation and the drop out of participants ($n = 6$).

Body odor handling

The collected chemosensory samples were then prepared for their application in Study 2 (exposure to chemosignals). The cotton pads were cut in four pieces (approximately 2 cm²), put in separate resealable storage bags, labeled and stored at -80 °C until application. In order to rule out interindividual differences in body odor of the donors, the pads of four different donors constituted an application odor sample, thereby creating a super-donor (Mitro et al. 2012). No condition-based donor pools, as in other experimental set ups (Dalton et al. 2013), were used to make sure that the same donors were chosen for both chemosensory conditions (exercise and aggression chemosignals). The no odor sample constituted of four odorless pad pieces that had undergone the same treatment in terms of cutting and freezing. To avoid contamination, it was made sure that there was no skin contact between the cotton sample and neither the experimenter nor the participant during the handling of the cotton pad.

Data analysis

Data was analyzed using SPSS (Version 20). Descriptive analyses followed by repeated-measures ANOVAs were conducted. Violations of sphericity were adjusted via Greenhouse-Geisser correction. Planned and post hoc comparisons via t -tests were Bonferroni corrected for multiple comparisons. Effect sizes were calculated for F -tests (η_p^2 partial Eta²)

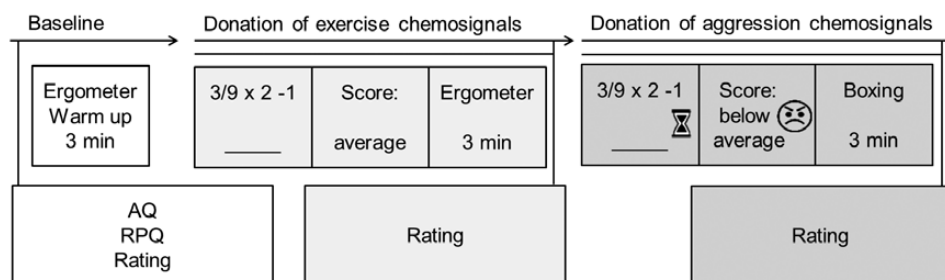


Figure 1. Experimental stages of the chemosignal donation procedure. During exercise and aggression condition, the 3 experimental manipulation factors (mental calculation task, feedback, and physical activity) were conducted twice. Note: During the aggression chemosignal donation, cognitive load was induced via time pressure. Participants received negative computerized and social feedback and were given time to ruminate.

and *t*-tests (Cohen's *d*). No gender differences were found for odor- and task-related measures and the data was therefore collapsed into an overall sample. To reveal the effect of personal traits on both, donation and application measures, correlational analyses were performed.

Results

In order to evaluate whether the provocation techniques were effective in inducing in the donors a fight response with aggression correlates, results of the evaluation of self-ratings (i.e., emotion, motivation, and physical activity) and associated convergent validity measures (i.e., frustration, resource depletion, trait aggression) are reported.

Induction techniques promoted a fight response with aggression constituents in donors

A repeated-measures 3×3 ANOVA was calculated to assess whether self-reports regarding dimensions referring to different constituents of a fight response (angry emotions, motivation to harm, and physical activity) change across the sampling conditions (baseline, exercise, and aggression chemosignals). Significant main effects of the sampling condition, $F(1, 17) = 21.33$, $P = 0.001$, $\eta_p^2 = 0.587$, and of the constituents, $F(1, 18) = 82.61$, $P < 0.001$, $\eta_p^2 = 0.846$, as well as a significant interaction between these factors, $F(2, 35) = 6.10$, $P = 0.004$, $\eta_p^2 = 0.288$, (Figure 2) were found. As an increase in self-ratings was expected, we conducted planned comparisons (one-tailed and Bonferroni adjusted) of the constituents of aggression across the sampling conditions. During the aggression condition, both an increase in anger, $M_{\text{aggression}} - M_{\text{exercise}} = 16.04$, $SE = 3.37$; $t(15) = 4.754$, $P = 0.001$, Cohen's $d = 0.80$, and motivational ratings, $M_{\text{aggression}} - M_{\text{exercise}} = 17.05$, $SE = 5.56$; $t(15) = 3.065$, $P = 0.024$, Cohen's $d = 0.82$, was observed but not in physical activity, $M_{\text{aggression}} - M_{\text{exercise}} = 6.12$, $SE = 2.71$; $t(15) = 2.26$, $P = 0.118$. Physical activity specifically increased from the baseline ($M = 48.50$ [SD = 17.17]) to the exercise condition ($M = 71.28$ [SD = 13.15]), $M_{\text{exercise}} - M_{\text{baseline}} = 22.77$, $SE = 4.15$; $t(15) = 5.487$, $P < 0.001$, Cohen's $d = 1.45$, whereas angry feelings and motivation to harm were not found to be increased, all $P > 0.302$.

Motivation to harm was selectively heightened during aggression chemosignal sampling, whereas increase in physical activity characterized both aggression and exercise chemosignals sampling

Repeated-measures ANOVAs investigated the self-rating of physical activity and motivation to harm across sampling conditions

(baseline, exercise condition, and aggression condition). A significant main effect of sampling condition was found for both the ratings of physical activity $F(2, 30) = 28.653$, $P < 0.001$, $\eta_p^2 = 0.656$ and motivation to harm, $F(1, 17) = 9.602$, $P = 0.005$, $\eta_p^2 = 0.390$. Motivation to harm, instead, was significantly heightened in the aggression condition, $M = 33.38$, $SD = 25.73$, as compared with both exercise (+17.05%), $M = 16.38$, $SD = 14.23$, and baseline condition (+21.13%), $M = 12.25$, $SD = 12.29$ (Figure 2).

Self-ratings of anger-related items increased during the aggression chemosignals sampling

In total, 15 items constituted the category of emotional items, including angry feelings and negative emotions. To investigate which of the items increased in self-rating during the experiment, a repeated-measures 3×15 ANOVA inspected the variation of each of the anger-items in the course of sampling conditions (baseline, exercise chemosignals, and aggression chemosignals). Significant main effects of sampling condition, $F(1, 17) = 12.63$, $P = 0.002$, $\eta_p^2 = 0.457$, and item, $F(5, 78) = 11.27$, $P < 0.001$, $\eta_p^2 = 0.429$, as well as a significant interaction between these factors, $F(28, 420) = 3.51$, $P < 0.001$, $\eta_p^2 = 0.190$, emerged. Post hoc pairwise comparisons (one-tailed, Bonferroni corrected *t*-tests) revealed that eight out of 15 angry emotional items were significantly higher only after the aggression condition compared with the exercise condition (i.e., angry, outraged, irritable, vexed, disappointed, annoyed; all $P < 0.030$).

Low-hostility donors were as aggressive as high-hostility donors only during the induction of aggression

To investigate the convergent validity of the self-ratings of anger feelings with aggression personality measures, a two-step cluster analysis separated the donors in two groups of low ($n = 8$, $M = 14.31$, $SD = 3.24$) and high scorers ($n = 8$, $M = 23.12$, $SD = 2.47$) on the basis of the AQ hostility scale. A 2×3 mixed ANOVA with sampling condition (baseline, exercise, and aggression condition) as a within-subjects factor and level of hostility (high vs. low) as a between-subject factor was conducted. A significant main effect of sampling condition, $F(1, 15) = 11.95$, $P = 0.003$, $\eta_p^2 = 0.461$, as well as of hostility group, $F(1, 14) = 9.86$, $P = 0.007$, $\eta_p^2 = 0.413$, were established. As expected, paired comparisons revealed higher hostility ratings for high versus low scorers at baseline, $M_{\text{high}} - M_{\text{low}} = 21.08$, $SD = 6.96$, $t(14) = 3.131$, $P = 0.007$, Cohen's $d = 1.57$, and during exercise condition, $M_{\text{high}} - M_{\text{low}} = 17.31$, $SD = 6.96$, $t(14) = 3.131$, $P = 0.007$,

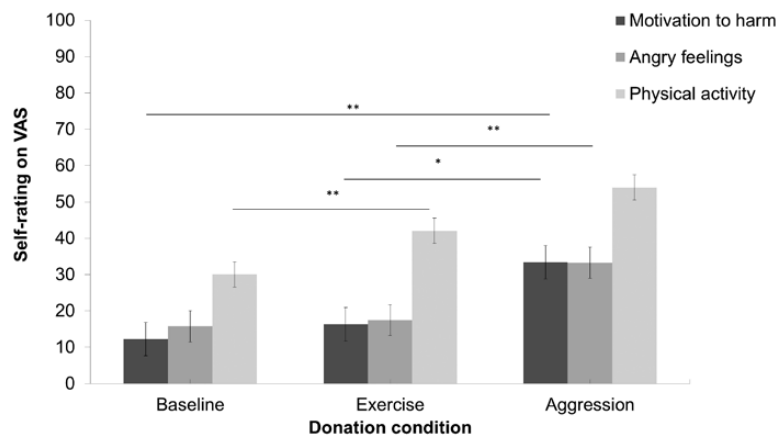


Figure 2. Mean values (with standard error bars) of the donors' self-rating of the constituents of aggression (angry feelings, physical activity, and motivation to harm) in relation to the chemosensory donation conditions. Significant (Bonferroni corrected) differences are labeled by asterisks, ** for $P < 0.05$ and * for $P < 0.001$ ($N = 16$, $df = 15$).

Cohen's $d = 2.41$. In the aggression condition, the difference in self-ratings of angry feelings between high and low hostility scorer, did not reach statistical significance, $M_{\text{high}} - M_{\text{low}} = 21.6$, $SD = 10.46$, $t(14) = 2.064$, $P = 0.058$, Cohen's $d = 1.03$.

Aggression induction increased ratings of negative emotions co-occurring during aggression

As a manipulation check, it was evaluated how the self-ratings of items reflecting the experimental induction of frustration, cognitive load (resource depletion) and negative emotions (i.e., stressed, nervous, disappointed, under pressure) changed across olfactory sampling conditions. Paired t -tests (one-tailed and Bonferonni-corrected) exhibited a mean increase in the self-rating of negative emotions co-occurring during aggression from exercise to aggression condition, $M_{\text{exercise}} = 26.06$, $SD = 14.94$ versus $M_{\text{aggression}} = 42.59$, $SD = 20.46$; $t(15) = 6.51$, $P < 0.001$, Cohen's $d = 1.63$, but not for the comparison baseline, $M_{\text{baseline}} = 25.67$, $SD = 17.46$, versus exercise condition, $t(15) = 0.100$, $P = 0.922$.

Donors felt angrier and performed poorer when donating chemosignals of aggression

Participants performed two mental calculation tasks: one with medium feedback without time pressure in the exercise condition and one with negative feedback and with time pressure in the exercise condition. To investigate, whether a poorer calculation score would go along with angry emotions (i.e., resource depletion), the mental arithmetic scores, and the angry emotions were compared between the two sampling conditions (exercise condition and aggression condition). A one-way repeated-measures ANOVA was used to establish significant main effects of sampling condition, $F(1, 15) = 9.02$, $P = 0.009$, $\eta_p^2 = 0.376$, and aggression dimension condition (calculation score and anger rating), $F(1, 15) = 9.17$, $P = 0.008$, $\eta_p^2 = 0.379$. Importantly, a significant interaction between the participants' cognitive load (mental arithmetic score) and anger ratings in the two sampling conditions is found, $F(1, 15) = 38.32$, $P < 0.001$, $\eta_p^2 = 0.720$. Specifically, participants displayed a lower mental arithmetic performance during the aggression induction, $M = 12.09$; $SD = 2.3$, compared with the exercise condition, $M = 18.43$; $SD = 1.25$; paired t -test: $t(15) = 10.55$, $P < 0.001$, Cohen's $d = 2.64$. This effect interacts with an increasing anger rating within the exercise in comparison to the aggression condition. In sum, low anger ratings are associated with a high mental arithmetic performance whereas high anger ratings are associated with low mental arithmetic performance, hypothetically due to a high cognitive load and a depletion of resources for anger control.

Discussion

The results of the donation study exhibit that the constituents of aggression (the psychobehavioral fight response) were enhanced in the aggression donation condition. Importantly, the motivation to harm selectively increased along with the involvement in aggressive behaviors and angry feelings, and it is not triggered by a general increase in physical activity. Via self-ratings, the participants confirmed their involvement in emotional, motivational, and physical behaviors specifically linked to the fight response, unaffected during pure physical activity. Interestingly, trait aggression (hostility) group differences persisted at baseline and exercise condition but were not maintained during the aggression condition and therefore providing evidence that the trait and state aggression of participants approach due to the aggression induction. In summary, the donation

study contributed to the field of the chemosensory transmission of psychobehavioral tendencies among humans.

After differentiation of the sender's emotional, motivational, and physical constituents of a fight response from pure physical activity, the obtained chemosensory samples were, in Study 2, applied to a different population to investigate their affective and cognitive effect on recipients.

Study 2—Exposure to chemosignals

Materials and methods

Participants

Healthy normosmic heterosexual male ($N = 10$) and female ($N = 12$) participants ($M = 29.27$ years; $SD = 9.62$) took part in the body odor application session. Sample size and data-collection stopping rule was determined based on sample sizes in other chemosensory research studies (Ackerl et al. 2002; Pause et al. 2004; Zernecke et al. 2011). Female participants did not use hormonal contraception and were invited for the study in the luteal phase of their menstrual cycle. Normal olfactory functioning was ensured by means of the MONEX-40 (Freiherr et al. 2012; $M = 31.14$, $SD = 2.68$; range = 27–38). Participants were included when they stated to be healthy (no past or acute neurological, psychiatric, or chronic illnesses). As a general indicator of cognitive functionality, we only included participants whose years of education and academic degree were comparable. Additionally, to rule out interindividual differences in attention and processing speed, a d2 vigilance task (Brickenkamp and Zillmer 1998) was conducted. Aggression (AQ, RPQ) and anxiety-related personality questionnaires (the trait sub-part of the German version of the State Trait Anxiety Inventory; STAI; Laux et al. 1981) were assessed. In a period of 24 h prior to testing, the participants restrained from alcoholic and caffeinated drinks as well as scented shower gels, deodorants or body lotions. They were screened for compliance to the behavioral restrictions before the experimental procedure started. The testing room was the same for all participants, lightly dimmed and highly ventilated. It included an office table and chair, laptop, and mouse and no other distractive stimulations or references with exercise or aggression.

Exposure procedure

In a within-subject design, all participants were sequentially and continuously exposed to one of three randomized chemosensory condition blocks (no odor, exercise, and aggression chemosignals; mean duration of odor exposure ($M = 26.56$ min; $SD = 4.67$; $M_{\text{no odor}} = 25.71$; $M_{\text{exercise}} = 27.23$; $M_{\text{aggression}} = 26.73$) during the duration of the experiment (Albrecht et al. 2011). At each chemosensory condition, a cellulose filter mask with the four quadrants was placed under the participants' noses and attached with a rubber band around their heads. The participants were asked to inhale normally through their nose. In order to avoid carry-over effects, a washout phase of 15 min between chemosensory conditions was included. To ensure a double-blinded application, participants and the experimenter applied the samples in cotton masks under the participants noses coded with A, B, and C. Participants were blind for the purpose of the study and the origin of the samples. The experimenter was blind to the affiliation of the coded letters to the donation conditions. In each chemosensory condition, participants performed olfactory ratings of intensity, pleasantness, and familiarity of the odor and performed computerized versions of an emotional face recognition paradigm first and an emotional stroop task (Williams et al. 1996) second

(E-Prime 2.0; Psychology Software Tools, Inc.) although the odor conditions were applied in a randomized order. The emotional face recognition contained standardized pictures of male and female faces in angry, sad, happy, and neutral facial expressions (Karolinska Directed Emotional Faces; Lundqvist and Litton 1998). Faces were shown in different angles: frontal (0°), half-sided (45°), and sided (90°) in a total of 80 trials. Emotion recognition time and correct identification (forced choice between fearful, angry, happy, and neutral) were measured. Three parallel versions were programmed in order to randomize button presses and individuals representing target faces across the odor conditions. During the emotional stroop task, participants had to assign the font color (blue, green, yellow, and red) of emotional words matching the emotional connotations happy, neutral, angry, or fearful. They completed each emotional block of words two times within one experimental block of 12 words. As a last task, three-alternative forced choice discrimination test of the neutral, exercise, and aggression chemosignals was conducted. Participants indicated blindly among three samples (two distractors vs. one target sample) the 1 sample smelling differently with three repetitions of all target and distractor combinations (four discriminations per odor condition and 12 discriminations in total). Data analysis was the same as for Study 1. Chi-square tests (χ^2) were performed to investigate odor discrimination differences between the chemosensory conditions.

Results

Participants' judgments on olfactory features and induced mood did not differ between aggression and exercise chemosignals

Assessment of perceptual odor differences (intensity and pleasantness) as well as induced mood was conducted by means of three separate repeated-measures ANOVAs on self-report ratings with chemosensory condition (no odor, exercise, and aggression chemosignals) as a within-subject factor. Across chemosensory conditions, there were neither intensity nor mood judgment differences for happiness, anxiety, anger, sadness, or frustration, all $P > 0.069$. However, pleasantness ratings significantly differed, $F(2, 20) = 5.43$, $P = 0.013$, $\eta_p^2 = 0.352$: Specifically, aggression chemosignals were rated as less pleasant only in comparison with no odor pads, $M_{\text{aggression}} = 42.21$; SD = 25.47, versus $M_{\text{no odor}} = 68.91$; SD = 17.25; $t(10) = 3.66$, $P = 0.012$, Cohen's $d = 1.10$, but not with exercise pads, $M_{\text{exercise}} = 53.73$; SD = 27.88; $t(10) = 1.82$, $P = 0.264$. In the three-alternative forced-choice discrimination test (chance level = 33%), participants correctly discriminated the target odor in $M = 39.76\%$ (SD = 17.98) of the comparisons which not differed from chance level, one sample t -test: $t(21) = 1.679$, $P = 0.108$. No discrimination differences were found comparing aggression chemosignals, $M_{\text{aggression}} = 40.91\%$; SD = 29.42, with no odor pads, $M_{\text{no odor}} = 31.81$, SD = 24.62; $\chi^2(16, N = 22) = 9.53$, $P = 0.657$, and with exercise pads, $M_{\text{exercise}} = 46.59$, SD = 28.12; $\chi^2(16, N = 22) = 25.20$, $P = 0.060$.

Chemosignals of aggression induced complementary emotional responses in receivers

Reaction times (RT) of the correct responses to the emotional face recognition task were evaluated with a repeated-measures ANOVA including chemosensory condition (no odor, exercise, and aggression), target emotion (happy, neutral, angry, and fear) and task difficulty (frontal, half-sided, and side) as within-subject factors. No significant main effect of chemosensory condition as well as no two-way or three-way interaction with the target emotions or task difficulty (all $P_s > 0.408$) emerged. However, main effects of target emotions, $F(1, 40) = 3.81$, $P = 0.032$, $\eta_p^2 = 0.153$, and task difficulty, $F(2, 42) = 9.40$,

$P < 0.001$, $\eta_p^2 = 0.321$, were ascertained. In other words, smelling the exercise or the aggression chemosignals did not significantly affect performance as compared with the no odor condition.

Second, analyses of the correct response RT in the emotional stroop task were conducted. A 3×4 repeated-measures ANOVA with chemosensory conditions (no odor, exercise, and aggression) and four emotional word categories (i.e., anger, anxiety, neutral, and happiness) was conducted on the correct response RTs in the emotional stroop task. No significant main effects were revealed, but the interaction reached the significance level, $F(6, 126) = 2.264$, $P = 0.041$, $\eta_p^2 = 0.097$. Paired t -tests revealed exclusive impairment of the processing of anxiety-related words by aggression chemosignals, $F(2, 42) = 4.62$, $P = 0.015$, $\eta_p^2 = 0.180$. Also, a significant RT difference between exercise and aggression chemosignals in the context of anxiety-related words emerged, $t(21) = 3.07$, $P = 0.018$, Cohen's $d = 0.65$. Participants were significantly slower in the color naming competence when faced with anxiety-related words (Figure 3).

Discussion

The application study indicates that aggression chemosignals in body odors impair higher-order processing of social information, selectively compatible with an anxiety-related stress response in receivers. Given that this effect emerges only in tasks in which the cognitive load is high (emotional stroop word vs. emotional face recognition task), it can be interpreted as to reflect the stress of needing to gather further information about a potential harmful individual in the vicinity. Furthermore, as suggested by Kenemy and Shesryuk (2008), the presence of psychosocial and uncontrollable physical threats that are associated with the activation of emotional and physiological systems often elicit behavioral disengagement and withdrawal tendencies. In line with the literature on behavioral reciprocity and aggression communication in social interactions, an emotional fear response after exposure to a threat signal is plausible. This emotional reciprocity reaction is therefore extending emotional contagion in chemosensory communication.

General discussion

This research contributes to the understanding of whether communication of aggression can be first elicited and second mediated in

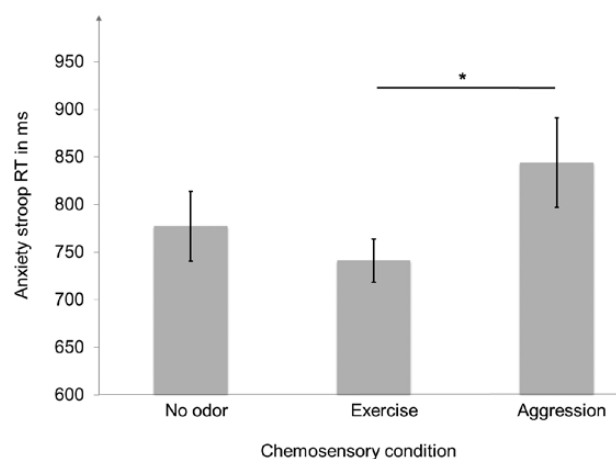


Figure 3. Mean RT values (with standard error bars) in the emotional anxiety stroop task in relation to the chemosensory conditions (no odor, exercise, and aggression chemosignals) with $P < 0.05$.

humans via chemosignals. By combining aggression research in the field of social psychology and body odors research in the field of chemosensation, a first attempt of chemosensory threat communication emitted by an unknown conspecific with the intention to harm was made. Further, chemosignals of aggression elicited a mechanism of emotional reciprocity (i.e., anxiety-related focus on cognition and emotion) in receivers.

To collect chemosignals of aggression, we induced angry feelings and an intention to harm in donors. We opted to distinguish between emotional, physical, and motivational constituents of an aggressive fight response and found that such components can be represented by chemosignals alone. In Study 1, we innovatively coupled aggression induction with body odor sampling that have already been meta-analyzed in detail to check for general validity (Lobbestael et al. 2008; Lenchova et al. 2009). In the methods used, we claim that the olfactory high-level baseline (i.e., exercise chemosignals) can be considered most adapted to reveal the effect of chemosignals on the processing of social information (Albrecht et al. 2011). Based on Pause et al. (2004), we assume that no communicative function should derive from exercise chemosignals because it mainly involves the activity of eccrine glands (watery sweat for thermoregulation) and not apocrine glands (glands producing social chemosignals) that commonly react to psychological stimuli (Schaal and Porter 1991). We acknowledge that the current study design might have compared the secretions of two different gland types. Therefore, one could expect comparison differences in the odor rating. However, exercise and aggression chemosignals, unlike no odor pads, were rated equally intense and pleasant. A closer look at the control conditions across studies reveals the use of different high-level baselines: Studies investigating the effect of anxiety-related chemosignals are comparing to chemosignals of normal body odor (Ackerl et al. 2002), joy (Zhou and Chen 2009), disgust (de Groot et al. 2012), or exercise (Rubin et al. 2012), leading to hardly comparable results among studies. Importantly, some studies have no physical activity involved in the induction phase, for example, watching videos (de Groot et al. 2012) or university examinations (Pause et al. 2004). These methodological differences in donation studies might have affected the quality and quantity of information communicated through chemosignals and therefore might be related to the diverse effects that chemosensory signals had on recipients. Chemical analyses of the chemosensory samples in olfactory emotional communication (e.g., via gas chromatography-mass spectrometry; Mujica-Parodi et al. 2009) are scarce but would constitute a suitable method to characterize and quantify chemical differences in emotional chemosignals.

Observing emotional reciprocity, an emotionally complementary response in the recipient's behavior, in Study 2 raises the question of whether this behavior can be characterized as an emotionally reciprocal stress response (e.g., a flight reaction) to the threatening chemosignal. Experiencing the need of gathering further information about the potentially harmful individual in the vicinity, the receiver adapts an anxiety-related focus in cognition and emotion. This idea is strongly supported by Lundström et al. (2008) reporting that a stranger's body odor is processed in brain areas of the fear network and by Adolph et al. (2010) reporting that competition chemosignals are differently processed depending on a recipients' degree of social anxiety.

The co-occurrence and the discernibility between the emotional qualities of anger and anxiety is an important caveat in the present study. Although it has been shown that negatively valenced emotions tend to co-occur (Kuppens et al. 2003), especially anger and anxiety seem to be affected by this, as both emotions are a response to stressful situations (Deschênes et al. 2012). Accordingly, in the aggression

condition of Study 1, we acknowledge that ratings increase in items reflecting stress experience (e.g., stressed, under pressure) and anxiety and sadness (e.g., nervous, disappointed) in association with aggression and its emotional, behavioral, and motivational constituents. Accounting for the assumption that the emotional value of stress-related chemosensory samples might be discriminable, the main difference between anger and anxiety is an approach motivation tendency. Although stress and emotions with negative valence (especially anxiety) are related to withdrawal tendencies (Mansell et al. 2008), hostility is clearly distinguishable by the lack of agreeableness and prosocial tendencies (Watson and Clark 1992) and an initiation of fight responses (motivational approach tendencies) on different psychological and physiological levels (Archer 1991, 2006; Harmon-Jones 2003; Carver and Harmon-Jones 2009). A recent finding by Kashdan et al. (2015) suggests that the motivational tendencies associated with anger are distinct from other negative emotions. The authors describe five superordinate anger triggers (interpersonal triggers, psychological, and physical stress, intrapersonal demands and environmental triggers) in everyday life situations. These triggers majorly overlap with well-established laboratory frustration methods and aggression inducing factors (Lobbestael et al. 2008; Smith et al. 2014). An alternative account to discuss the chemosensory effect of aggression chemosignals is the question of whether the emotional value of the stress-related chemosensory samples is discriminable. Most importantly, this issue affects the broader field of emotional chemosignaling. First, a variety of negative emotions tends to co-occur with anger. As an example, Kuppens et al. (2003) find that frustration is inducing not only anger but also disappointment. In line with the findings of Lobbestael et al. (2008), aggression-inducing factors, such as arrogant entitlement and accountability of others for unfair situations, tend to lower an individuals' self-esteem. These are defined as specific (but not sufficient) prerequisites to differentiate anger from other negative emotional states, for instance fear or sadness. Second, often no clear distinction between the labels of stress, anxiety, and fear in human chemosignals is made. Although stress is referred to as an unspecific physiological arousal, anxiety and fear constitute feelings of unease and doom, Steimer (2002) defines anxiety as a response to unknown threat or an internal conflict (as in the generalized anxiety disorder) and fear as a feeling of unease in response to an imminent external danger (as in phobias). Stress-related chemosignals are collected in a variety of hardly comparable internally and externally threatening situations and psychobehavioral tendencies are investigated. In contrast to anger and aggression, anxiety-related emotions are in association with several different psychobehavioral tendencies (motivations to emit an approach or withdrawal reaction; Stemmler et al. 2007).

During affective/cognitive processing, our receivers engaged in an emotionally complementary response (i.e., anxiety-related focus on cognition and emotion). In contrast, chemosignals of aggression failed to influence affective processing in the emotional face recognition in the receivers. This is compatible with what has previously been shown for chemosignals of competition (Adolph et al. 2010). Also in comparison to stress-related chemosignaling, missing effects on affective processing have already been observed (e.g., Pause et al. 2004). Interestingly, only the perception of complex and ambiguous faces (e.g., Mujica-Parodi et al. 2009; Zhou and Chen 2009; Zernecke et al. 2011) was influenced by stress-related chemosignals. Although, the manipulation of task difficulty in the emotional face recognition is associated with differences in our participants' response time, no influence of aggression chemosignals was found. This is suggesting that an effect of chemosignals might be more likely to be observed in combination with ambiguity and high task

difficulty—effects that are consistent in literature but rather small in size. In both, the sampling and the exposure study, the magnitude of the empirical effects remain rather small to medium, yet in line with the effect sizes found in other chemosignals studies investigating olfactory-communicated transient emotional states (de Groot et al. 2012).

As the discernibility of negative emotions is not fully disentangled within the olfactory communication research, we aim to encourage future research to investigate an alternative dimensional approach to differentiate if chemosignals communicate distinct appetitive or aversive motivational and behavioral tendencies (i.e., in approach-avoidance paradigms) rather than basic emotions only.

To unravel the ongoing quest of aggression communication via human chemosignals, we recommend that future sampling studies compare chemosignalling of different emotional content (anxiety, stress, and anger) with inclusion of behavioral and motivational constituents of the individuals' state. To further the concept of emotional reciprocity in olfaction, the neural basis of aggression chemosignals could be compared with the neural networks involved in aggression and fear. This research might successfully investigate the olfactory threat communication among humans representing behavior with a high survival benefit and therefore of crucial importance for the individual.

Supplementary material

Supplementary material can be found at <http://www.chemse.oxfordjournals.org/>

Funding

This work was supported by a grant from the Interdisciplinary Center for Clinical Research within the Faculty of Medicine at RWTH Aachen University, Germany (531214, N4-3).

Acknowledgments

We thank Olga A. Wudarczyk, Margarete C. Ohse, and Anja Kofoet for their support during data collection and evaluation as well as for helpful comments during manuscript preparation.

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