Chemosignaling Emotions:

What a Smell can Tell

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Overdracht van emoties via geur:

Wat geuren kunnen zeggen

(met een samenvatting in het Nederlands)

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The human body is the best picture of the human soul

—Ludwig Wittgenstein

(Philosophical Investigations Part II, 1953, p. 178)

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Chapter 1

Introduction & Overview

Background

The animal kingdom is filled with species that use scents as a means to communicate with their conspecifics. Among the species that rely on odors for communication are invertebrates such as sea anemones and honeybees and classes of vertebrates, including fish (e.g., minnows, yellow bullheads) and mammals (e.g., rats, mice) (e.g., Todd, Atema, & Bardach, 1967; Mugford & Nowell, 1970; Leon & Moltz, 1973; Howe & Sheikh, 1975; Agosta, 1992). In these cases, the odors are called *pheromones*, a blend of the Greek *pherein* (to carry or transfer) and *hormōn* (to excite or stimulate). More specifically, pheromones are defined as "substances which are secreted to the outside by an individual and received by a second individual of the same species, in which they release a specific reaction" (Karlson & Lüscher, 1959).

Although pheromones are typically associated with sexual behavior, some organisms such as rodents produce pheromones when they are threatened (e.g., Valenta & Rigby, 1968). Rodents exposed to alarm pheromones were shown to display effects ranging from suppressed immune reactions (Cocke, Moynihan, Cohen, Grota, & Ader, 1993), to vigilant behavior (e.g., Mackay-Sim & Laing, 1980; also see, Mackay-Sim & Laing, 1981, for effects in the opposite direction—i.e., deactivation), and stress-induced hyperthermia (i.e., increased body temperature) (Kikusui, Takigami, Takeuchi, & Mori, 2001).

From the moment the pheromone concept had been coined (Karlson & Lüscher, 1959), researchers documented the existence and workings of these species-specific scents in non-human animals. This changed after 12 years when humans were for the first time associated with pheromones in a demonstration of what has been labeled the "McClintock-effect" (McClintock, 1971). McClintock (1971) found that the menstrual cycles of women living together in dormitories synchronized over time (i.e., the difference in menstrual cycle onset dates decreased); this McClintock-effect was attributed to pheromones (also see Stern & McClintock, 1998). However, over the years the McClintock-effect could not be replicated (e.g., Wilson, Kiefhaber, & Gravel, 1991; Ziomkiewicz, 2006; Yang & Schank, 2006) and received criticism on methodological, statistical, and theoretical grounds (e.g., Wilson, 1992; Strassmann, 1997, 1999; Yang & Schank, 2006). The chapter on menstrual synchrony could well be considered closed in the light of these criticisms and the existence of human pheromones remained controversial.

According to a leading researcher in the field of olfaction, the existence of human pheromones is a myth (Doty, 2010). Before body odor compounds can be classified as

pheromones, the following criteria have to be met (Beauchamp, Doty, Moulton, & Mugford, 1976): (1) species-specificity; (2) well-defined behavioral or endocrinological function; (3) large degree of genetic programming; (4) only one, or at most, a few compounds; (5) uniqueness of the compound(s) in producing the behavioral or endocrinological response (also see Doty, 2010). What is problematic is that most odors, such as human body odor, consist of multiple volatile organic compounds (e.g., Gallagher et al., 2008). The responses to these compounds may also fail to match the predicted effects (e.g., Bronson, 1976) and highly variable reactions suggest that odor perception is largely experience-based. In brief, body odors cannot be considered pheromones, since they do not function as simple "keys" that "unlock" preprogrammed behavior.

Additional evidence for the unlikelihood of pheromone communication in humans comes from the fact that we lack the sensory apparatus to detect pheromones. Many vertebrate species for whom pheromones are a (primary) means of motivating behavior have a functional vomeronasal organ (VNO) (Witt & Wozniak, 2006). Humans, too, have a VNO, but it does not function as a sensory organ (Trotier et al., 2000); the human VNO has no receptor cells (Boehm & Gasser, 1993). Similar to the appendix and tail bone, the VNO is a vestigial structure (Boehm, Roos, & Gasser, 1994). Even if humans communicate by means of pheromone-related substances, this type of communication should be mediated by the main olfactory epithelium (Wysocki & Preti, 2004).

Although human pheromone communication was supposed to be non-existent in humans (e.g., Doty, 2010), the strong link between odors and emotions left the door open for research on what has been called *emotional chemosignaling*[1]. Both emotional *and* olfactory information are primarily processed in some of the relatively more primitive regions of the brain (e.g., amygdala, entorhinal cortex, striatum, orbitofrontal cortex, hypothalamus, and hippocampus) (Gottfried, 2006). Because of this "limbic overlap", odors can become rapidly associated with emotional experience (Herz & Engen, 1996). Not surprisingly, the sense of smell is often conceived of as the "most emotional sense" (Chrea et al., 2009). The strong link between odors and emotions leaves open the possibility that certain odors can elicit emotions in receivers without having to fulfill the earlier mentioned criteria of a pheromone.

Chemosignaling emotions

[1]Chemosignals are defined here as (a set of) odoriferous molecular volatiles that emanated from the skin of a *sender*. Chemosignals could potentially be registered by a *receiver* via the olfactory epithelium in the nose (i.e., chemical sense).

Although criticism may be directed at the application of the pheromone concept to humans, it were these "species-specific scents" that inspired early research on emotional chemosignaling. The first empirical test of olfactory communication of emotions in humans was performed by Chen and Haviland-Jones (2000). Their rationale was the following: since rodents could distinguish between stressed and non-stressed conspecifics on the basis of their odor, so may humans. They sampled armpit odor on absorbent compresses from donors who were induced to be in a neutral, fearful, or happy mood. In the next stage, a group of unrelated participants were asked to select the body odor that was produced during instances of fear and happiness. Similar to rodents, the group of "receivers" performed above chance in selecting the body odor of people when they were fearful; they could even pick out the body odor of happy individuals (Chen & Haviland-Jones, 2000). This was the first demonstration of olfactory "communication" in humans.

After this pioneering study, a further 13 studies on emotional chemosignaling appeared until 2012. Different research groups examined whether exposure to the body odor of fearful individuals led to similar fearful reactions in receivers (e.g., Ackerl, Atzmueller, & Grammer, 2002; Prehn, Ohrt, Sojka, Ferstl, & Pause, 2006; Zhou & Chen, 2009; Mujica-Parodi et al., 2009; Albrecht et al., 2011). In brief[2], these studies have shown that compared to control conditions in which receivers were exposed to sport sweat, unused absorbent compresses, and/or sweat sampled during neutral conditions, fear sweat recipients showed higher state anxiety levels (Albrecht et al., 2011), increased startle reflexes (Prehn et al., 2006), and more activity in brain regions related to fear (Mujica-Parodi et al., 2009). Hence, based on these data humans appear to have the capacity to communicate fear from a sender to a receiver by means of chemosignals.

Problems

Three main problems can be identified with regard to the reported research on emotional chemosignaling. First, the evidence that has been documented in favor of emotional chemosignaling is indirect and/or unsystematic. Second, the lack of an adequate theoretical framework resulted in operational definitions that were too inclusive. Third, the boundary conditions of the phenomenon have not been examined.

1. Evidence

[2]For an extensive review of the chemosignaling literature, see Chapter 8.

Even though evidence for emotional chemosignaling was derived from multiple sources, the independent studies could not provide systematic and in some cases direct evidence to support the claim that receivers took over the fearful state of the sender. For instance, indirect evidence for "olfactory communication of emotions" was obtained by using odor discrimination tasks and by asking participants to label the odors with emotion terms (Ackerl et al., 2002). Other researchers provided pieces of evidence by measuring startle reflexes (e.g., Prehn et al., 2006), cautious and risky behavior (Chen, Katdare, & Lucas, 2006; Haegler et al., 2010), interpretations of ambiguous facial expressions (e.g., Zhou & Chen, 2009), and (vigilant) brain activity (via electroencephalography, EEG; e.g., Pause, Lübke, Laudien, & Ferstl, 2010) in areas related to fear (via functional magnetic resonance imaging, fMRI (e.g., Mujica-Parodi et al., 2009). Given that the evidence provided by the independent studies has not been systematic, alternative explanations of the research findings are likely. That is, rather than uniformly pointing into the direction of fear, the measures that were used (e.g., increased startle reflexes) could be related to any negative emotion (e.g., Lang, 1995). What is necessary to rule out alternative explanations is direct, systematic evidence for fear chemosignaling.

2. Theoretical framework

To date, research on emotional chemosignaling relied on a direct extension of animal logic to humans, which invites thinking of chemosignals as pheromones. Following this line of reasoning, exposure to "fearomones" would lead to invariant reactions of fear in recipients regardless of context. However, this assumed invariance does not fit with the actual research findings. For example, receivers exposed to fear sweat displayed cautious behavior in one study (Chen et al., 2006) and risky behavior in another (Haegler et al., 2010). Interpreting both cases as instances of fear simply because the person who donated the body odor was in a fearful state—and assuming there *should* be correspondence between the state of the "fearomone" producer and receiver—shows that the operational definition of fear is too broad. The main problem with this is that inclusive definitions reduce the falsifiability of the researched phenomenon.

3. Boundary conditions

Moreover, thinking about chemosignals in terms of pheromones does not engage researchers in (thoroughly) examining the mechanisms underlying the phenomenon. By adopting a pheromone-perspective on emotional chemosignaling, one would assume that odor Y produced during state Y would always induce state Y in a receiver. Hence, there

would be a certain invariant regularity that would always hold. Other than repeatedly demonstrating with different measures that state Y was indeed elicited by odor Y, this perspective would not invite conducting further research on this topic. As a consequence, the boundary conditions of emotional chemosignaling have not been researched. For instance, does auditory and visual information, or do different contexts override the information that is seemingly contained by the chemosignal? These questions have not been addressed in the current literature, inviting possible misinterpretations of fear chemosignals as following pheromone-like regularities.

Conclusion

The problems that were mentioned in this section suggest that knowledge about emotional chemosignaling is incomplete and its understanding potentially flawed. Incomplete knowledge and flawed understanding form two ingredients of a *research problem* (Booth, Colomb, & Williams, 2008). Gaining a better understanding of the phenomenon at hand is what solves a research problem (Booth et al., 2008) and this is what constitutes the purpose of this dissertation.

Purpose

The current dissertation includes a set of studies that were aimed to resolve the aforementioned problems. The overall purpose was to gain a better understanding of emotional chemosignaling by: (1) obtaining direct and systematic evidence; (2) having a theoretical framework that leads to falsifiable predictions; (3) exploring the boundary conditions of emotional chemosignaling in humans.

To this end, an embodied social communication framework is introduced. In fact, the idea of social communication (of emotions) is not new and was even mentioned in the first empirical demonstration of this subject (Chen & Haviland-Jones, 2000). Social communication was mentioned as one of the three functions of the sense of smell in humans (Stevenson, 2010), even though humans are unlikely to communicate by means of *pheromones* in the strict sense of the word (Doty, 2010).

In my view, body odors cannot be viewed similarly as pheromones, since the reactions of receivers do not always in every situation correspond to the state of the sender. I leave open the possibility that body odors acquired signaling value by having been paired with information from other modalities, such as vision and hearing. The key aspect, here, is that I treat emotional chemosignaling as a rather dynamic—perhaps communicative—process that can be influenced by the context. Obviously, communication occurs through the use of

multiple modalities and the auditory and visual modality are considered to be more important than the sense of smell. These potential boundary conditions should be taken into account when researching this phenomenon.

In brief, the novelty of this research does not stem from the idea of social communication, but rather from the experimental approach that was taken (see Thesis Outline section) and how communication is defined. If olfactory communication of emotions by means of chemosignals exists, then chemosignaling must follow the general principles of communication. The common denominator to any successful communication is the recruitment of joint processes in a sender and the receiver that put any two (or more) individuals on the same footing (e.g., Semin, 2007). In this case, chemosignals would serve as the medium that facilitates correspondence between a sender and a receiver. For further details about this theory, the interested reader is directed to Chapter 2 and 3.

Thesis outline

General overview

In the current dissertation, I examine whether emotional chemosignals follow the general principles that are derived from a social communication model. Chapter 2 provides proof of principle whether chemosignals fit within an embodied social communication model, and in Chapters 3 to 7 the boundary conditions of chemosignaling are explored. A more specific overview of each chapter is given in the Chapter overview section.

Manipulations

Each study consists of a body odor sampling phase and a phase in which a group of receivers is exposed to the different body odors. In the receiver phase, both the experimenter and the participant are unaware of the emotional condition; participants do not even know a priori that they are exposed to body odor. Body odor is sampled while participants watch film clips (Chapter 3-6) or have to prepare for a speech (Chapter 7). Body odors are sampled via absorbent compresses and presented to receivers in small vials. Please see the empirical chapters for additional methodological detail. During exposure to a particular body odor, receivers usually perform a task (e.g., visual search task) and multiple measures are taken.

Measures

The manipulation of the emotional state was explicit in the case of “senders”, but not for “receivers”. That is, senders could consciously reflect on the experimental manipulation (e.g., horror movies) and the feelings that were induced by the manipulation (e.g., fear). The

state of senders was thus assessed with explicit self-reports—in some cases combined with objective measures (i.e., heart rate, skin conductance level). Because odors and their effects on experience can be hard to put into words (Lorig, 1999), implicit measures that do not draw on linguistic processing (e.g., facial electromyography, EMG) were considered to be the most appropriate and reliable indicators of the affective state of "receivers". Data from multiple variables are combined to avoid interpretative looseness that would be present in single measure studies. Notably, the measures used for receivers do not exactly correspond to the measures used for senders, because the reproduction of the state of the sender by a receiver is never *complete*, it is always partial.

Experimental design

With regard to both senders and receivers, a within-subjects experimental design is chosen for the following reasons. First, the effects induced by chemosignals can be very subtle and are more likely to be observed when a participant serves as its own control. In a similar vein, responses to odors can be highly individual and within-subjects designs would counteract the error variance associated with these individual differences. Second, within-subject designs have more power and require fewer participants. As a consequence, resources such as time and money are saved. Potential carry-over effects are canceled out by counterbalancing experimental conditions and fatigue effects are not likely, given the relatively short exposure time.

Chapter overview

The next section gives a brief overview of the content of each following chapter.

Chapter 2 is essentially a theoretical chapter. The chapter begins with the assertion that humans use multiple senses to navigate the social world. Among these senses, the sense of smell is underestimated and this chapter is aimed to partly redress this imbalance, as evidence available to date suggests that body odors contain social information that can be registered by the sense of smell, which is more important than traditionally thought.

The experiment reported in **Chapter 3** was conducted to provide proof of principle for olfactory communication of emotions. The research question was: Is there such thing as olfactory communication of emotions, in the sense that emotional chemosignals elicit joint processes in a sender and a receiver? From an embodied social communication framework, the hypothesis was derived that chemosignals produced during a distinctive negative emotional state would elicit similar processes in senders and receivers. While receivers were exposed to body odor obtained from senders, multi-level correspondence was determined by

facial EMG, the degree of sensory acquisition/rejection, and visual search task performance. This study demonstrates that exposure to fear chemosignals elicited a fearful facial expression and *sensory acquisition* processes (increased sniff magnitude and more effective eye scanning in the visual search task). Body odor that was sampled during another (i.e., "opposite") negative emotion condition, disgust, induced a disgusted facial expression and signs of *sensory rejection* (decreased sniff magnitude, detection sensitivity, and impoverished eye scanning in the visual search task). Since the effects obtained in the disgust condition could have been driven by the unpleasantness of the stimulus and since previous research almost exclusively documented on fear chemosignaling, the next step following this proof of principle study was to examine the boundary conditions of fear chemosignaling.

To grasp the workings of fear chemosignals, it is essential to identify the extent to which multiple sensory modalities cooperate to make sense of the world and whether the effects otherwise induced by chemosignals can be overridden by input from other—more dominant—senses. Strikingly, fear chemosignaling has never been examined as a communicative medium in combination with input stemming from modalities traditionally associated with communication, namely vision and hearing. Investigating the potential boundaries of effective chemosignaling requires a comparison of the effectiveness of olfactory and audiovisual media to answer the question: Will effects induced by fear chemosignals be overridden by audiovisual information? The experiment reported in **Chapter 4** indicates that olfactory information was not overridden by audiovisual information. Fearful facial expression emerged in receivers regardless of whether fear was communicated through the olfactory or audiovisual modality.

Before the study reported in **Chapter 5** was conducted, what had remained unknown is whether there are sex differences in chemosignal-mediated communication. Specifically, an answer was sought to the question: Are there gender differences in the manner in which individuals respond to fear chemosignals? Because women generally have a better sense of smell and greater sensitivity to emotional signals (see Chapter 5), it was hypothesized that compared to males and relative to a neutral body odor control condition, female participants would emulate the fearful state of the fear chemosignal producer. The results indicate that only female participants took over the fearful state of the sender, as was measured by facial EMG. Hence, this study revealed a boundary condition for effective chemosignaling by reporting behavioral evidence of sexual asymmetry in fear chemosignal reception.

Another boundary condition that was examined in this dissertation is whether chemosignals are also involved in the transmission of positive states. Chemosignals are a

known medium for transferring negative emotional states such as fear from a sender to a receiver; yet, does the communicative potential of chemosignals extend to (high arousal) positive affective states? Positive emotions are important for overall well-being and yet relatively neglected in research on chemosignaling, arguably due to the stronger survival benefits linked with negative emotions. The research reported in **Chapter 6** reveals that according to facial EMG responses and participants' perceptual processing style, exposure to body odor collected from senders in a happy state induced responses indicative of happiness in receivers. These findings suggest that not only negative affect, but also a positive state (happiness) can be transferred by means of body odors.

The results that were reported in Chapter 3 to 6 suggest that—at least in the case of fear which is supported by most evidence—chemosignals have a distinctive biochemical signature that can be produced relatively rapidly, driven by a physiological mechanism that had remained unexplored in previous research. **Chapter 7** describes an experiment that was conducted to answer the question: What is the psychophysiological mechanism that drives fear chemosignal production? Since the apocrine sweat glands in the armpit allegedly responsible for chemosignal production contain adrenalin receptors, the release of adrenalin through activation of the rapid stress response system (i.e., the sympathetic-adrenal medullary system) was expected to drive the release of "fear chemosignals", rather than activation of the slower stress response system (i.e., hypothalamus-pituitary-adrenal axis). Body odor was sampled in this study while eight participants prepared for a speech. Participants had higher heart rates and produced more armpit sweat in the fast stress condition, compared to baseline and the slow stress condition. Exposure to sweat from participants in the fast stress condition induced in receivers a fearful facial expression (facial EMG) and vigilant behavior (i.e., faster classification of emotional facial expressions). This chapter shows that activation of the fight/flight mechanism under conditions of threat is sufficient to produce the typical fear chemosignals.

The last chapter of this dissertation, **Chapter 8**, constitutes a general discussion of the chemosignaling literature, including the empirical studies that make up this dissertation. In Chapter 8 I attempt to find relations between previously reported chemosignaling studies and provide a plausible basis for human chemosignaling. In this review, a situated perspective was taken that reframes the social implications of human odors, places the sense of smell in a broader context, and explains for instance individual variation in responses to body odors. What contrasts chemosignals with pheromones is that the effects typically induced by chemosignals could have been acquired by individuals through the systematic extraction of

natural relations between certain odors and situations in which they typically occur. The situation may not only play a role during the formation of associations with odors, but also in the process of re-enacting previously stored odor experiences. The situation has remained a neglected facet in rapidly accumulating chemosignaling research. The general discussion ends with the outline of ideas for future research.

This sums up the brief overview of the content discussed in each chapter. Since each chapter in this dissertation—barring the present introductory chapter and the final discussion chapter—has been published in a scientific journal, the chapters can be read independently. As such, some overlap between the chapters exists; yet, each chapter provides a unique piece to the puzzle of emotional chemosignaling.

Rationale, significance, and implications

In short, the main rationale for conducting the current research is to increase the understanding of emotional chemosignaling. The current research shows that the sense of smell can play a more significant role in human life than what had been thought decades ago. Furthermore, the findings obtained in this dissertation can have implications for disorders such as social phobia and prepare the ground for obtaining additional biochemical evidence for chemosignaling.

The present dissertation assesses the communicative function of emotional chemosignaling and its boundary conditions, thereby increasing the understanding of this remarkable phenomenon by examining *if*, *how*, and *when* exposure to emotional chemosignals results in emotional contagion. Problems in previously reported chemosignaling studies are tackled by taking a systematic approach to obtain direct evidence for emotional chemosignaling, using well-controlled within-subjects designs. The research reported here is inspired by an embodied social communication perspective, which provides us with a set of falsifiable predictions.

The sense of smell still has not received the attention it arguably deserves. One reason could be that given the complexity of odor mixtures and variable human reactions to odors, olfaction can be a challenging and complex research area (Hudson & Distel, 2002). Second, olfaction was historically considered to be “extremely rudimentary” in humans, in which the sense of smell was considered to play an “insignificant role” (Grinker, 1943, p. 337, as cited in Gottfried, 2006). The theory goes that human evolution was characterized by the increased dominance of vision and the reduced significance of the olfactory receptor repertoire, since humans lifted their noses from the ground by adopting a bipedal stance (see Shepherd, 2004).

However, the assumption that a declining number of functional olfactory receptor genes is causally linked to olfactory ability was recently challenged. Like rats and dogs, humans were shown capable of tracking a scent through a field (Porter et al., 2006). Still, problems may arise when having to name even the most common odors (see Lorig, 1999). Nevertheless, the human sense of smell is not as manifestly inferior to that of certain other species.

Odors may even play a role in (the acquisition and maintenance of) certain clinical disorders such as social phobia. Previous research has shown that non-clinically socially anxious individuals—determined by questionnaires—have a threat-related processing bias for fear chemosignals (Pause, Adolph, Prehn-Kristensen, & Ferstl, 2009; Pause et al., 2010). Specifically, socially anxious individuals showed stronger startle reflexes (Pause et al., 2009) and recruited more neural resources (Pause et al., 2010) in the presence of body odor sampled from fearful individuals. High scorers on social anxiety are at risk of developing social phobia, which is the 4th most common mental health condition; it can be found at some point during the life of about 1 in every 8 individuals (Kessler et al., 2005). Further down the line, social phobia is a risk factor for the development of depressive symptoms and substance abuse (see Pause et al., 2010). Understanding fear chemosignaling and gaining further insight into the boundary conditions are important with regard to the treatment of social phobia, since body odors can play a role in the acquisition and maintenance of the symptoms that make up this very common health problem.

The findings that are reported in this dissertation may not only have clinical implications but can also prepare the ground for the next stage of research regarding the biological "fingerprint" of chemosignals produced as a function of different (emotional) states. Biochemical assessments of the odoriferous volatiles present in body odor can be performed with the expensive gas-chromatography mass-spectrometry technique. Although finding biochemical evidence for chemosignaling (of emotions) is outside the scope of this dissertation, the reported findings will give an indication about the fruitfulness of such a pursuit.

Chapter 2

The chemical bases of human sociality

This chapter is based on:

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The chemical bases of human sociality

Communication is the foundation of sociality and is made possible by a diverse set of media. Research on human communication has primarily focused on auditory and visual modalities. Here, we discuss the role of the olfactory modality as an important medium of human communication and highlight the significance of interpersonal chemosignaling in the context of emerging research that investigates the adaptive effects of human chemosignals on cognitive-affective processes (e.g., Zhou & Chen, 2009).

As a social species, human beings rely on communication. Not surprisingly, there is considerable research on the subject. Notably, this research has relied predominantly on investigations of acoustic (e.g., language, speech, prosody) and visual (e.g., facial expressions, body posture, gestures) aspects of human communication (Semin, 2007). However, as the glue that binds members of any social species, human communication is multimodal (Semin, 2007). Of the different modalities of human communication, a sorely neglected one is the olfactory modality. This contribution is designed to bring to the fore the role of the olfactory modality as an important medium of human communication and highlight the significance of interpersonal chemosignaling amid emerging research investigating the adaptive effects of human chemosignals on cognitive–affective processes (for an extensive review, see Chapter 8 of this dissertation; also see Lundström & Olsson, 2010; Pause, 2012).

For any social species, group living is coterminus with communication and an indispensible requirement for any successful communication is to attain a common basis (Semin, 2007). This is achieved by a medium shared by two agents, namely a medium that furnishes the means by which a sender and a receiver are put on the same footing in the pursuit of adaptive goals. Across diverse social species, one finds that the modalities serving as a medium for communication vary considerably, from visual to gestural, chemical, mechanical, or even electrical as in the case of electrical fish (Semin, 2007). In the case of humans, multiple telereceptive senses (e.g., vision, audition, and olfaction) are used to navigate the social world and communicate with conspecifics (Aglioti & Pazzaglia, 2011). Humans have the inherent capacity of interacting multimodally, of which communicating via the olfactory modality, namely by means of the medium chemosignals, is an emerging research field.

Although the idea of chemical communication has been present in some form or another since the ancient Greeks, it was only in 1959 that chemical communication between

animals was identified (Karlson, & Lüscher, 1959; Wyatt, 2009). The interest in human chemosignaling was further delayed because the specialized sensory system of animals (the vomeronasal organ) for pheromonal communication appears to be a vestigial organ in humans (Trotier et al., 2000). As it turns out, the lack of a functional vomeronasal organ in humans seems to be of little significance for the functional role of the olfactory system in human chemosignaling (e.g., Wysocki & Preti, 2004; Witt & Wozniak, 2006).

The sense of smell involves the conversion of the molecular information of an odorant into an odor sensation through the activation of a series of biochemical and electrophysiological processes (for more details, the interested reader is directed to Rawson & Yee, 2006). Chemicals are arguably evolutionarily the original stimuli for the adaptive regulation of action (Dusenbery, 1992).

The detection of human body odor by the olfactory faculty has been shown to be involved in the signaling and reception of a range of socially significant information such as gender, age, individuality, and personality (for an extensive overview, see Chapter 8 of this dissertation; also see Lundström & Olsson, 2010; Stevenson, 2010; Pause, 2012). As some have argued (Stevenson, 2010), social communication is one of the three functions of the human sense of smell. Social information can arguably be derived from human odors (i.e., chemosignals) by receptors in the olfactory epithelium (e.g., Witt & Wozniak, 2006; Wysocki & Preti, 2004). The research to date suggests that the neural processing of chemosignals, due to skin-gland excretions and bacterial activity, is different from “non-social” control odors (Lundström & Olsson, 2010). The neural processes activated by chemosignals appear to resemble the processing of social signals from visual or auditory modalities (Lundström & Olsson, 2010; Pause, 2012). In the case of chemosignals, communication usually takes place without verbal awareness (e.g., de Groot, Smeets, Kaldewaij, Duijndam, & Semin, 2012).

Aside from carrying categorical social information (e.g., gender, age, individuality), chemosignals may also transfer more dynamic information about transient emotional states such as fear from a sender to a receiver, as evidence to date suggests. For instance, humans could identify the body odor collected from the same individuals during fearful and happy states (Chen & Haviland-Jones, 2000). Furthermore, people have been shown to disambiguate ambiguous facial expressions as displaying the emotion (i.e., fear) under which the chemosignal was produced (Zhou & Chen, 2009). Chemosignals have not only been related to body odors, but have also been associated with tears. One study showed that chemosignals embedded in female tears reduced the sexual appeal of female faces to men, as well as men's self-rated sexual arousal and their testosterone levels (Gelstein et al., 2011). In

short, chemosignals—whether embedded in tears or body odors—have been shown to mediate a set of distinctive and systematic diagnostic inferences and those produced under emotional conditions shape numerous social cognitive inferences without verbal awareness.

The question of how these social cognitive processes shape inferences requires a model of the state that is entered by the recipient of the donor's odor. A recent study has shown that the body odor recipient (partially) reproduced the emotional state the donor was in while producing the body odor (de Groot et al., 2012). This study has revealed that odors obtained from donors during an experimentally induced state of fear (versus disgust) lead receivers of these odors to vicariously activate the acquisition (fearful expression – opening the eyes, increased nasal inspiratory volume, perceptual enhancement, *inter alia*) patterns of that emotional state (Susskind et al., 2008). These findings suggest that the recipient reproduced the emotional state of the donor through a simulation process. This simulation process is direct and automatic and escapes verbal access, leading the recipient to achieve a non-propositional coupling with a donor thereby vicariously reconstituting the other's emotion by giving rise to a shared bodily state.

Obviously, the research to date on the processes induced by human body odors was conducted in settings where the effects of odors alone were examined under highly controlled experimental conditions, suggesting invariance across situations. However, in realistic settings emotional chemosignals would not act in a decontextualized manner. Cognition, emotion, and action emerge in interdependence with the features of the social and physical context (Smith & Semin, 2004, 2007). Whether chemical communication is invariant or subject to contextual variations is therefore an important open inquiry. Another important issue that remains open within the context of multimodal communication is the relative contribution of the olfactory modality in relation to other modalities that are traditionally involved in communication, such as vision and hearing (Figure 1). Specifically, information from one modality is usually dealt with against a background of input from other modalities and these different modalities could on occasions produce incongruent messages. Because alternative modalities can be weighed and ranked according to the likelihood of providing significant information, the olfactory modality could occasionally be the sense that sets the stage for interpreting information from other modalities. It is in such situations that chemosignals are expected to establish symmetry between donor and recipient. A further critical issue is the systematic investigation of the neural processes and brain regions activated by human body odors. Are the neural processes associated with the production of emotion induced by human body odor in the donor's brain coupled to the neural processes in

the recipient's brain via volatile transmission (Semin & Cacioppo, 2009; Gallese, Keysers, & Rizzolatti, 2004; Hasson, Ghazanfar, Galantucci, Garrod, & Keysers, 2012)? These are some of the questions that future research needs to address for an improved appreciation of the human capacity to communicate via chemosignals.

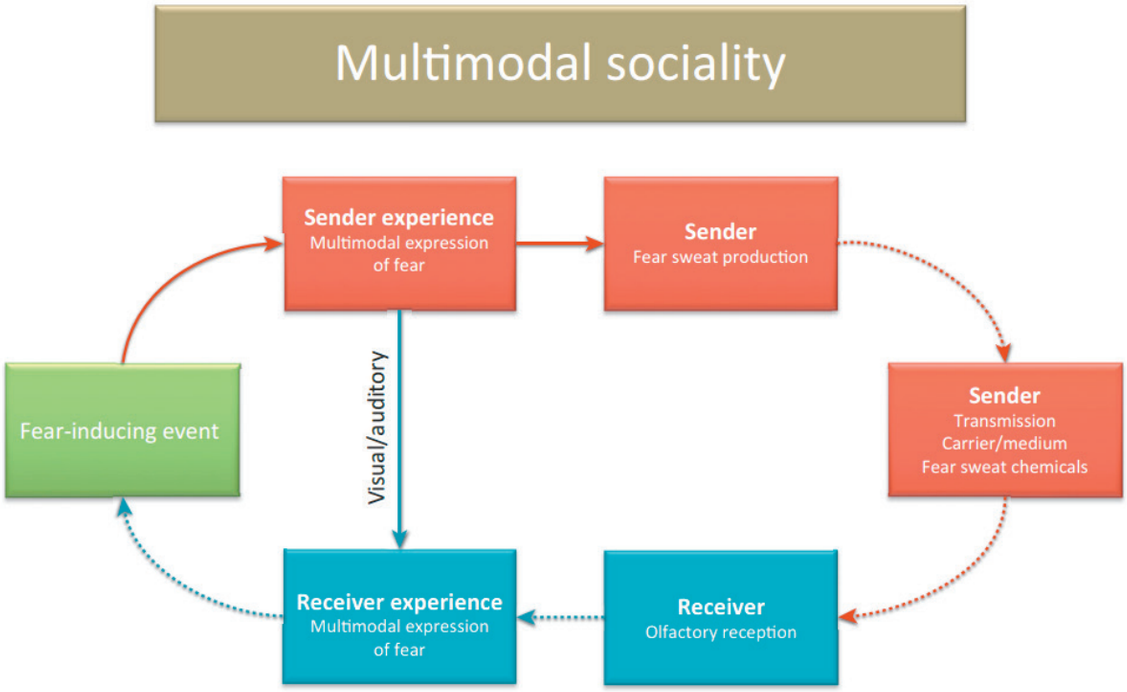

Figure 1. A fear-inducing event induces an emotional state in the "sender" that is communicated to the "receiver" via multiple modalities. In olfactory communication, the recipient reproduces the emotional state of the sender (donor) through the process of simulation. This simulation process is direct and automatic and escapes verbal access, leading the receiver to achieve a non-propositional coupling with a sender thereby vicariously reconstituting the other's emotion by giving rise to a shared bodily state.

Chapter 3

Chemosignals' communicative potential: Sender-receiver synchrony via axillary odors produced during negative emotional states

This chapter is based on:

de Groot, J. H. B., Smeets, M. A. M., Kaldewaij, A., Duijndam, M. J. A., & Semin, G. R. (2012). Chemosignals communicate human emotions. *Psychological Science*, *23*, 1417–1424. doi: 10.1177/0956797612445317

Abstract

Can humans communicate emotional states via chemical signals? In the experiment reported here, we addressed this question by examining the function of chemosignals in a framework furnished by embodied social communication theory. Following this theory, we hypothesized that the processes a sender experiences during distinctive emotional states are transmitted to receivers by means of the chemicals that the sender produces, thus establishing a multilevel correspondence between sender and receiver. In a double-blind experiment, we examined facial reactions, sensory-regulation processes, and visual search in response to chemosignals. We demonstrated that fear chemosignals generated a fearful facial expression and sensory acquisition (increased sniff magnitude and eye scanning) while disgust chemosignals evoked a disgusted facial expression and sensory rejection (decreased sniff magnitude, target-detection sensitivity, and eye scanning). These findings underline the neglected social relevance of chemosignals in regulating communicative correspondence outside of conscious access.

Introduction

Chemical signals play an important role in affecting intraspecies behavioral responses. These types of effects are not unique to animals, as they have also been reported in humans (Wysocki & Preti, 2004). The extent to which chemosignals[1] (Doty, 2010) serve a communicative function has remained unclear, mainly because hypotheses concerning the social aspect of human emotional chemosignaling have not been tested. In the experiment reported here, we investigated whether the inhalation of chemosignals emitted by another person during an emotional state induced the same state in the inhaler. Specifically, we examined whether a receiver reproduces not only the facial expression, but also the concomitant sensory-regulation processes (i.e., sniffing behavior, target-detection sensitivity, and gazing behavior) associated with the emotional states involved in the production of the chemosignals. Our findings revealed that chemosignals have a uniform and distinctive communicative impact.

Chemosignal detection was traditionally believed to require a fully functioning vomeronasal organ, allegedly absent in most humans (Wyatt, 2003). A more recent perspective is that the main olfactory system may be actively involved in chemosignal communication in both animals and humans (Tirindelli, Dibattista, Pifferi, & Menini, 2009). Moreover, evidence has been identified that supports the so-called signaling effects (e.g., Kaitz, Good, Rokem, & Eidelman, 1987) and modulating effects (e.g., Zhou & Chen, 2009) of chemical emissions in humans. To date, interest has focused primarily on the neural and behavioral consequences of chemosignaling. Of special relevance is recent research examining the effects of fear chemosignals, from which two conclusions can be drawn. First, compared with control conditions (e.g., in which donors generated sweat while playing sports), conditions in which subjects were exposed to sweat excreted by donors experiencing fear caused enhanced vigilance and caution among those subjects (Ackerl, Atzmueller, & Grammer, 2002; Albrecht et al., 2011; Chen & Haviland-Jones, 2000; Chen, Katdare, & Lucas, 2006; Haegler et al., 2010; Pause, Adolph, Prehn-Kristensen, & Ferstl, 2009; Pause, Ohrt, Prehn, & Ferstl, 2004; Prehn, Ohrt, Sojka, Ferstl, & Pause, 2006; Zernecke et al., 2011; Zhou & Chen, 2009). Second, these effects have been shown to occur outside conscious awareness (Lundström, Boyle, Zatorre, & Jones-Gotman, 2008; Mujica-Parodi et al., 2009;

[1]We prefer not to use the term *pheromone*, as the concept of pheromones is controversial and fraught with problems (Doty, 2010), partly because of widely varying and very strict definitions of what constitutes a pheromone. We instead use the term *chemosignal*, which according to Doty (2010, p. 186) is less problematic when discussing communication.

Sobel et al., 1999). In sum, these studies have clearly documented the psychological and neural consequences of fear chemosignals.

It is important to note that the social relevance of these recent developments has not been realized, presumably because the research focus has primarily been on the functional implications of chemosignals (e.g., whether fear sweat biases other people to recognize fear in ambiguous facial expressions). In contrast, the core concern in current research was the social communicative function of chemosignals. The theoretical framework we advance here suggests that chemicals in bodily secretions recruit joint processes in sender and receiver by means of which correspondence is established. This communication perspective (Semin, 2000, 2007) invites thinking about emotional chemosignaling as a process entailing partial synchronization between sender and receiver; such synchronization is probably a contributor to what has been termed *emotional contagion* (Hatfield, Cacioppo, & Rapson, 1993). What emotional contagion entails is that the affective, behavioral, and perceptual processes observed in a receiver are a partial reproduction of the state of the sender.

The specific chemosignals we investigated here are produced by emotional states of fear and disgust. Obviously, the facial expressions associated with these emotions serve a communicative function. They are also functional, because the adaptive features of facial expressions enhance survival values for the person expressing the emotion (Susskind et al., 2008). Emotional contagion optimizes chances of survival by linking individuals multimodally: Fear signals warn about environmental danger (Susskind et al., 2008), and, likewise, disgust signals tell the receiver to avoid noxious chemical stimulation (Susskind et al., 2008). Thus, fear is associated with *sensory acquisition*, disgust with *sensory rejection*. This type of sensory regulation has been shown to be initiated by artificially induced facial expressions (Susskind et al., 2008). By taking on a fearful expression (i.e., opening the eyes), subjects' nasal inspiratory volume is increased, perception is enhanced, and eye movements during target localization are accelerated (Susskind et al., 2008). The opposite action pattern was observed after expressing disgust (i.e., eyebrow lowering and nose wrinkling; Susskind et al., 2008).

Relying on this work, we advance the hypothesis that inhaling an emotional chemosignal is sufficient to induce the same consequences in a receiver as were experienced by the chemosignal's producer. Hence, chemosignals were expected to cause a receiver's facial expression to correspond with the emotional expression of the sender, and also to instigate the adaptive function of such an expression, which modulates perceptual, affective, and behavioral processes.

This general hypothesis was tested in a double-blind experiment using a within-subjects design. Participants were exposed to sweat sampled from donors in specific emotional states (i.e., fear and disgust) or to unused absorbent compresses (control condition). We expected that emotional contagion through fear chemosignals would generate a fearful facial expression (i.e., *medial frontalis* muscle activity) in a receiver, which would induce sensory acquisition reflected in an increased sniff magnitude, heightened target-detection sensitivity, and enhanced eye scanning. Emotional contagion through disgust chemosignals was hypothesized to generate a disgusted facial expression (i.e., *levator labii* muscle activity) in a receiver. This, in turn, would induce sensory rejection expressed by a reduced sniff magnitude, dampened target-detection sensitivity, and reduced eye scanning behavior. Our results were unique in that they underlined a remarkable human capability, namely that chemicals excreted by one individual have social relevance because they induce the very same somatic states in another.

Method

All studies were approved by the Utrecht University institutional review board, Utrecht, the Netherlands. We used male senders and female receivers to test our hypothesis that social communication can be chemically mediated. We used this approach because males produce stronger signals, and females are more receptive to these signals (Wysocki et al., 2009).

Part 1: Senders (donors)

Sample collection

Ten heterosexual males (M = 22.90 years, SD = 1.66 years) were paid €20 each to donate sweat. Emotions were induced by having the donors watch videos in two sessions separated by 1 week. In one session, they watched fear-evoking videos, and in the other session, they watched disgust-evoking videos; the order of sessions was counterbalanced. Donors followed a strict protocol to avoid sweat contamination. For 2 days prior to the donation, odorous food, alcohol, smoking, and excessive exercise were prohibited. Donors used scent-free personal-care products and detergents provided by the experimenter.

After applying sterile absorbent compresses (Cutisorb, BSN Medical, Hamburg, Germany) under their armpits, we seated donors individually in a room in which the temperature was 23 °C. Heart rate and skin conductance were assessed while donors watched 25-min videos that were pilot-tested for effectiveness. Fear-evoking videos (modeled after

Zhou & Chen, 2009) contained horror scenes (e.g., from *The Shining*; Rottenberg, Ray, & Gross, 2007), whereas MTV's Jackass was used to induce disgust (de Jong, van Overveld, & Peters, 2011). Before and after the videos, donors completed Spielberger's State-Trait Anxiety Inventory (van der Ploeg, Defares, & Spielberger, 1980) and rated their emotions on 7-point Likert scales. Afterward, sweat pads were removed and stored at –22 °C. The same temperature was used to store unused absorbent compresses, which in our view constitute optimal control stimuli because other nonemotional bodily secretions (e.g., sweat from playing sports) can potentially contain other chemosignals. Freezing sweat does not affect pleasantness, intensity, attractiveness, and masculinity ratings (Lenochova, Roberts, & Havliček, 2009).

Part 2: Receivers

Participants and design

Thirty-six right-handed females (M = 21.33 years, SD = 2.11 years) with a normal sense of smell (mean smell threshold = 11.26 binary dilution steps [3.25×10^{-3}% phenethyl alcohol], SD = 2.27) were paid €8 for their participation. Participants provided written informed consent prior to the experiment. The experiment had a double-blind 3 (odor condition: fear, disgust, control) × 2 (visual search task: easy, difficult) within-subjects design. The order of the odor condition was counterbalanced.

Measures, materials, and procedure

Because male experimenters have been shown to increase female participants' mood (Jacob, Hayreh, & McClintock, 2001), which would introduce bias into our results, only females served as experimenters. Both experimenters and participants were blind to stimulus content and experimental condition, because vials were coded with three-digit codes. Experimenters did not disclose the nature of the study and were instructed to display only neutral expressions.

Sweat pads from donors were cut into eight even pieces. Half of the pads came from the armpit on one side of the body, and the other half of the pads came from the opposite armpit. The odor stimuli were defrosted 30 min prior to the experiment; each participant received a fresh container that held four pads from four different donors. Olfactory threshold was assessed prior to the experiment with Sniffin' Sticks (Burghart Instruments, Wedel, Germany; see Hummel, Sekinger, Wolf, Pauli, & Kobal, 1997, for details). In addition,

participants' ability to discriminate odors was determined by a forced-choice triangle test (see Meilgaard, Civille, & Carr, 1991, for details).

Participants were seated in individual cubicles. Each testing cubicle had a ventilation system (refreshment rate = 5 cycles/hr) that cleaned the air between sessions. An unobtrusive nasal-pressure-monitoring cannula (15805-2-FT, Sleep Sense, Tel Aviv, Israel) was inserted 0.5 cm into the nostrils and connected to a DC pressure transducer (SLP14385, Sleep Sense, Tel Aviv, Israel) to measure sniffing. Electromyographic (EMG) electrodes were applied next. Facial-muscle activity was measured on the left side of the face (Dimberg & Petterson, 2000) using bipolar placements of Ag-AgCl surface electrodes to measure fear (indexed by *medial frontalis* muscle activity) and disgust (indexed by *levator labii* muscle activity; Fridlund & Cacioppo, 1986). Each participant's head was stabilized in a chin rest.

Participants had to complete an automated eye tracking calibration procedure provided by Tobii Studio software (Tobii Technology AB, Danderyd, Sweden). Eye movements were recorded using an infrared stereo camera at a 120 Hz sampling rate. Then, a vial (2 cm deep) containing the chemosensory stimulus was clipped 2 cm below the subject's nose to the chin rest, which kept the stimulus at a constant distance from subjects' noses. All vials were presented in a predetermined counterbalanced order. Participants wore nose clips to prevent preliminary sniffs. The nose clip was removed just before the start of the visual search task, at which time a marker was placed in the online registration of physiological data to mark the session's start.

The subsequent visual search task was run using the Presentation program (Neurobehavioral Systems, Albany, CA). This task was adapted from Müller-Plath and Pollmann (2003). All items in the display were equidistantly placed with 30° angular distance on an imaginary circle with a diameter of 8° of visual angle. The target was more than barely perceptible but less than clearly visible, as it varied only in shape from the distractors (width-to-height ratio = 0.83 vs. 1.00, respectively).

At the beginning of each trial, participants were instructed to look at the fixation cross in the center of the screen. Visual stimuli appeared after 1 s. Participants pressed a key to indicate whether a target was present or absent among 4 distractors (the easy version of the task) and 10 distractors (the difficult version of the task). Response keys were counterbalanced across participants. Ten practice trials had to be completed with ≥ 90% accuracy. The actual task consisted of two counterbalanced blocks (easy and difficult) of 48 trials per odor exposure condition (fear, disgust, control), with an intertrial time of 1 s.

Following the task, participants completed tests and questionnaires. Pleasantness and intensity of each odor stimulus were rated on 7-point Likert scales. A funneled postexperimental debriefing (Bargh & Chartrand, 2000) revealed that participants were unaware of the purpose of the study and the source of the compounds.

Results

Part 1: Senders

On the basis of physiological assessments, we determined that emotion induction in donors was successful. Paired *t* tests[2] revealed that donors had higher heart rates in the fear condition than in the disgust condition, $t(9) = 3.17$, $p = .011$, $d = 1.42$, but skin-conductance levels did not differ significantly, $t(9) = 2.02$, $p = .074$ (also see supplemental analyses and Tabel 1 in Appendix A).

Part 2: Receivers

We tested the social communicative function of chemosignals first by examining whether chemosignals were sufficient to induce the same facial-muscle configuration in the receiver that the sender made when producing the chemosignal[3]. A 3 (odor condition: fear, disgust, control) × 2 (facial muscle: *medial frontalis*, *levator labii*) × 5 (time after exposure: baseline, 0–1 s, 1–2 s, 2–3 s, 3–4 s) repeated measures analysis of variance (ANOVA) yielded a significant three-way interaction, $F(8, 280) = 4.74$, $p = .004$, $\eta^2 = .06$.

Next, separate ANOVAs were conducted per odor condition for facial-muscle activity induced shortly after exposure (Epoch 1: 0–4 s) and during the complete exposure time (Epoch 2: 0–420 s). An increase in *medial frontalis* activity (Figure 1A) from baseline reflected the distinctive facial-muscle signature of fear that was activated—Epoch 1: $F(4, 108) = 8.76$, $p < .001$, $\eta^2 = .02$—and maintained—Epoch 2: $F(1, 27) = 6.89$, $p = .014$, $\eta^2 = .02$—after fear chemosignal exposure. Likewise, exposure to disgust chemosignals caused *levator labii* muscles (Figure 1B) to be activated, $F(4, 116) = 15.36$, $p < .001$, $\eta^2 = .02$, and maintained, $F(1, 29) = 15.44$, $p < .001$, $\eta^2 = .01$. Moreover, fear chemosignals generated an expression of fear and not disgust, $F(4, 108) = 3.82$, $p = .006$, $\eta^2 = .01$, disgust chemosignals

[2]The alpha criterion was set at .05. When necessary, Bonferroni correction was applied.
[3]The effects reported in this section cannot have been due to significantly differing pleasantness and intensity ratings of chemosensory stimuli by receivers (cf. Supplemental Analyses and Table 2 in Appendix A), as these indicators of hedonic valence and arousal were included in the analyses as covariates in which they proved to be nonsignificant. Furthermore, in analyses of the EMG data, Greenhouse-Geisser correction for sphericity violation did not affect the interpretation of the results.

induced a facial configuration of disgust rather than fear, $F(4, 112) = 6.32$, $p < .001$, $\eta^2 = .01$, and neither fear, $F(4, 100) = 2.04$, $p = .095$, nor disgust, $F(4, 104) = 1.69$, $p = .159$, were evoked in the control condition (see supplemental analyses in Appendix A). Chemosignals thus served as a medium for communication. Mere inhalation was sufficient to induce a facial expression in receivers that reflected the emotion experienced by senders while they produced the chemosignal.

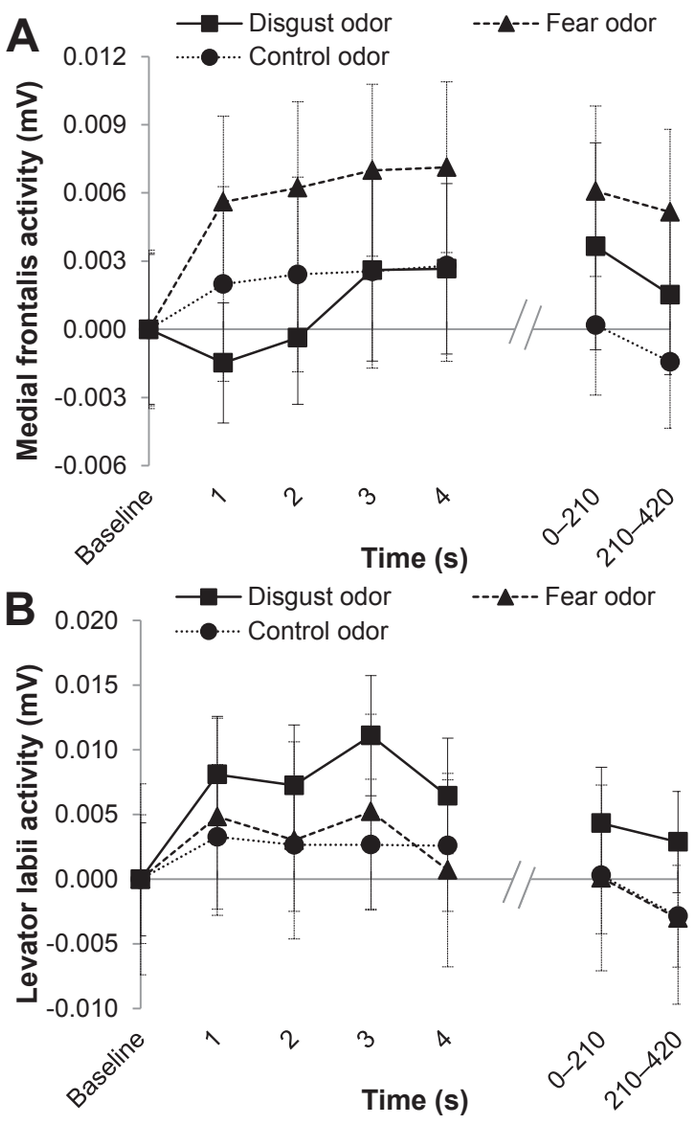

Figure 1. Mean (A) *medial frontalis* and (B) *levator labii* muscle activity as a function of time and odor condition (fear, disgust, control). Results are shown for baseline (0), Epoch 1 (0-4 s), and Epoch 2 (0-420 s). Error bars indicate ± 1 SEM.

Next, we examined whether chemosignal-induced facial expressions modulated sniffing behavior (also see supplemental analyses in Appendix A). Whereas the first sniff was expected to be reflexively elicited and exploratory, the subsequent sniff was modulated in

magnitude (Mainland & Sobel, 2006), consistent with the communicated emotion. We analyzed 10 sniffs to meaningfully chart the unfolding of sniffing magnitude over time. A 3 (odor condition: fear, disgust, control) × 10 (sniff number: 1–10) repeated measures ANOVA revealed significant changes in sniff magnitude over time as a function of the olfactory stimulus, $F(18, 540) = 3.24$, $p < .001$, $\eta^2 = .05$ (Figure 2). A further examination of the first two sniffs revealed a significant interaction between odor condition and sniff number, $F(2, 60) = 9.13$, $p < .001$, $\eta^2 = .11$, an effect that was not observed from the third sniff onward, $F(14, 420) = 1.18$, $p = .287$.

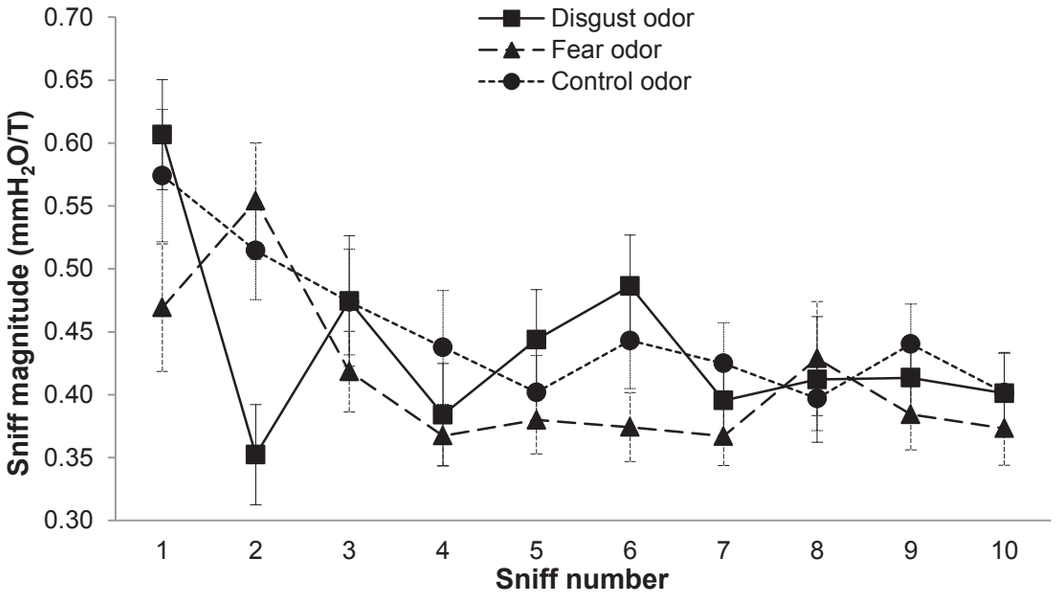

Figure 2. Mean sniff magnitude (nasal air pressure in mm H_2O over time) on the first 10 sniffs after presentation of different odors (fear, disgust, control). Error bars indicate ± 1 SEM.

Follow-up paired *t* tests on the first two sniffs indicated that the magnitude of the first sniff was lower for fear than for disgust, $t(32) = -2.87$, $p = .021$, whereas the magnitude of the second sniff was lower for disgust than for fear, $t(32) = -3.83$, $p = .003$. Exposure to emotional chemosignals thus modulated sensory-regulation processes temporarily, after which adaptation seemed to have taken place. Figure 2 shows that sniff magnitude gradually decreased after nose clips were removed in the control condition. A cyclic pattern of air intake emerged after emotional chemosignal exposure, in which each substantial reduction in sniff magnitude seems to be compensated for in the subsequent sniff. The reversed systematicity in air intake observed in the fear and disgust conditions arguably occurred as a function of the type of chemosignal received. By temporarily increasing the sniff magnitude

in the fear condition, a larger number of chemical compounds could potentially reach the olfactory epithelium (i.e., sensory acquisition). The opposite pattern (i.e., sensory rejection) was observed after exposure to disgust chemosignals, which presumably served a protective function.

Next, we examined whether changes in facial-muscle activity induced by chemosignals altered perception in the visual search task (also see supplemental analyses in Appendix A). A 3 (odor condition: fear, disgust, control) × 2 (task: easy, difficult) repeated measures ANOVA demonstrated that detection sensitivity (d'; Macmillan & Creelman, 2005) was significantly lower on the difficult task than on the easy task, $F(1, 35) = 19.04$, $p < .001$, $\eta^2 = .07$, and varied significantly among odor conditions, $F(2, 70) = 5.37$, $p = .007$, $\eta^2 = .03$. However, the interaction between odor condition and task was not significant: $F(2, 70) = 2.82$, $p = .066$. As predicted, a post hoc ANOVA revealed that detection sensitivity was lower in the disgust-odor condition than in the control condition ($p = .001$), but sensitivity was not affected by task difficulty in the disgust-odor condition, $t(35) = 1.72$, $p = .282$. In the fear-sweat condition, differences in detection sensitivity between the easy and difficult tasks were not significantly different from such differences in the disgust-odor and control condition ($F < 1$; Figure 3A). Follow-up analyses on difference scores, however, indicated that detection sensitivity decreased from the easy to the difficult task in the fear-sweat condition in comparison with the other odor conditions—control: $t(35) = 2.56$, $p = .015$; disgust odor: $t(35) = 1.82$, $p = .049$.Taken together, these data suggest that perceptual benefits from a fear state may interact with task difficulty.

In addition to detection sensitivity, response bias (β) also varied as a function of task type, $F(1, 35) = 12.25$, $p = .001$, $\eta^2 = .07$. Response bias is an individual's decision rule and is quantified as the ratio between the likelihood of responding that the target is absent versus that the target is present; higher levels indicating a more conservative response tendency. As Figure 3B shows, response bias increased markedly in the fear-sweat condition when the task became difficult, $t(35) = 3.62$, $p < .001$. Thus, fear chemosignals induced caution on the difficult part of the search task.

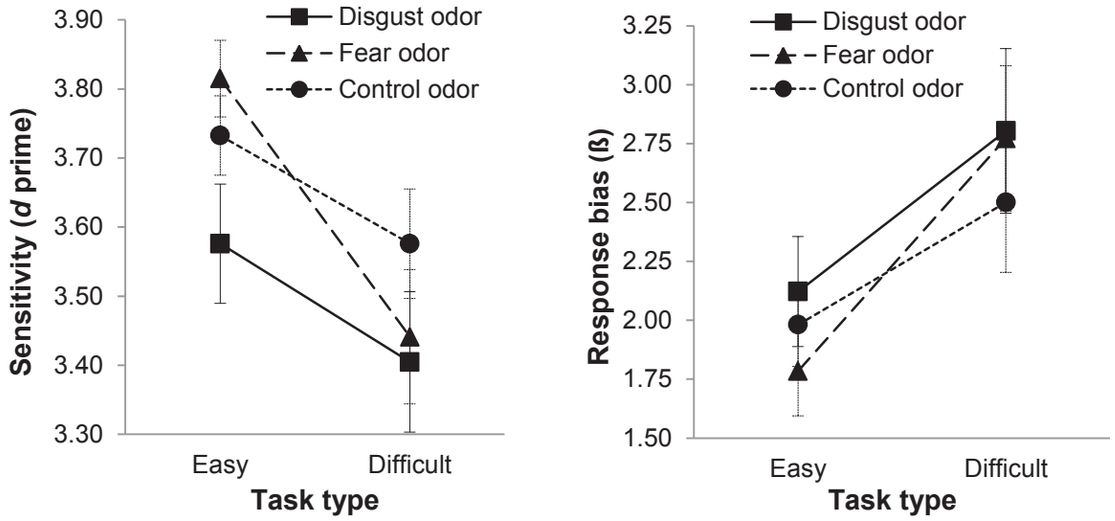

Figure 3. Mean (A) detection sensitivity (*d* prime) and (B) response bias (β) as a function of visual search task type (easy, difficult) and odor exposure (fear, disgust, control). Error bars indicate ± 1 SEM.

Exposure to disgust chemosignals reduced detection sensitivity (sensory rejection) under all circumstances. In the fear-sweat condition, however, detection sensitivity was higher (sensory acquisition) when targets were easily detectible, whereas it was lower when targets were embedded in excessive distractors. These combined results suggest that perceptual benefits associated with fear are limited to easy target-distractor configurations.

We examined eye-scanning behavior to corroborate the connection between detection sensitivity and the visual system. Eye scanning is facilitated by fear, as widely opening the eyes increases the visual field (Susskind et al., 2008). Two 3 (odor condition: fear, disgust, control) × 2 (task: easy, difficult) repeated measures ANOVAs revealed significant differences in the number of target fixations, $F(2, 70) = 4.43$, $p = .016$, $\eta^2 = .03$, and fixation durations, $F(2, 70) = 4.45$, $p = .015$, $\eta^2 = .03$, among odor conditions. Compared with the control condition, chemosignals in the fear-sweat condition induced sensory acquisition, as evidenced by fewer target fixations ($p = .014$) and faster target and distractor fixations ($p = .011$; also see Table 3 in Appendix A). Sensory rejection was evidenced by avoidance behavior rather than a decrease in scanning speed and effectiveness. A facial-muscle expression of disgust (i.e., raising the cheek) restricted the lower visual field, which is already limited during neutral viewing conditions (Susskind et al., 2008). Exposure to disgust chemosignals specifically resulted in fewer overall fixations on visual stimuli, $F(2, 70) = 5.40$, $p = .007$, $\eta^2 = .02$, than did fear chemosignals ($p = .025$) and no chemosignals ($p = .024$). In sum, fear chemosignals induced sensory acquisition, causing subjects to adopt a

quick scan strategy of the entire visual field, whereas disgust chemosignals induced sensory rejection, causing subjects to decrease the number of fixations.

Discussion

The current study's main aim was to seek evidence for the human capability to communicate emotions via chemicals embedded in bodily secretions. Our results directly supported this hypothesis. Chemosignals induced emotional contagion (Hatfield et al., 1993), as was evidenced by receivers' distinctive facial-muscle configurations, which changed in line with the specific emotion experienced by a sender while secreting the chemosignal. Specifically, exposure to fear chemosignals generated a facial configuration of fear (i.e., *medial frontalis* activity) and not of disgust (i.e., *levator labii* activity). In contrast, exposure to disgust chemosignals resulted in a facial configuration of disgust rather than of fear. Moreover, fear chemosignals induced sensory acquisition in receivers. Conversely, disgust initiated sensory rejection. These consequences occurred outside of receiver awareness and showed no relationship to receivers' judgments of the pleasantness and intensity of chemosensory stimuli. These results can be considered unique in that they reveal a remarkable human capability, namely that chemosignals of fear and disgust establish correspondence between a sender and a receiver.

In the current research, we introduced an embodied social-communication model (Semin, 2000, 2007) derived from the argument that communication can be achieved only when a receiver emulates the bodily state of the sender. The present study supports the core contention of this model and reveals that chemosignals have a socially significant function because they constitute a medium by which two individuals can be emotionally synchronized in a multimodal fashion (i.e., facial mimicry, sensory-regulation processes). Synchrony specifically entails the production of partial parity or correspondence, which occurs after a chemosignal receiver produces an internal representation of the emotional state communicated by a sender. Exposure to sweat from donors awaiting an examination, for instance, automatically activated a neural circuit (i.e., insula, cingulate cortex, precuneus) in a receiver that mapped the sender's state (Prehn-Kristensen et al., 2009). What we propose is that chemosignals induce emotional contagion by recruiting joint states and processes in sender and receiver.

The current data suggest that fear and disgust are not only distinctive emotions in the way they are reflected in facial expressions and behavior, but also that they are distinctive with respect to the biomarker profile deposited onto the skin while individuals—in this case,

sweat donors—are experiencing these respective emotions. Questions regarding the composition of the "emotional chemosignal fingerprints" of fear and disgust as well as the exact mechanisms involved in sensing the chemosignals have largely remained unanswered. Nevertheless, chemical analyses of stress-related odors revealed that male signals were stronger than female signals, whereas females displayed greater sensitivity to these signals than males did (Wysocki et al., 2009). The present results show strong evidence that different emotions can be communicated from males to females by chemical signals. One limitation of the current study, however, is that we cannot rule out the fact that the greater unpleasantness and higher intensity of disgust sweat is what actually drove receivers to emulate the state of the sender.

The current findings are contrary to the commonly accepted assumption that human communication runs exclusively via language or visual channels. Neuronal networks responsible for body-odor processing are remarkably similar to those of auditory and visual processing (cf. Lundström et al., 2008); like emotional visual stimuli, body odors receive increased attention and differential processing (e.g., amygdala and insular cortex) than do nonbody odors (Lundström et al., 2008). The difference, however, is that chemosignals embedded in bodily secretions contribute to a close-distance emotional message. Although its ecological validity has to be substantiated, our research suggests that emotional chemosignals can be potential contributors to emotional contagion in situations involving dense crowds. Moreover, although bodily secretions may be consciously registered because of their inherent stimulus intensity, chemosignal recipients could not discriminate between different chemosensory stimuli and were unable to access the processes induced by these chemosignals. The present research thus demonstrated that humans have the capability to communicate emotional states via chemosignals and constitutes an invitation to investigate the communicative function of other chemosignals produced under other emotional states, such as happiness or anger.

Chapter 4

I can see, hear, and smell your fear: Comparing olfactory and audiovisual media in fear communication

This chapter is based on:

de Groot, J. H. B., Semin, G. R., & Smeets, M. A. M. (2014a). I can see, hear, and smell your fear: Comparing olfactory and audiovisual media in fear communication. *Journal of Experimental Psychology: General*, *143*, 825–834. doi: 10.1037/a0033731

Abstract

Recent evidence suggests that humans can become fearful after exposure to olfactory fear signals; yet, these studies have reported the effects of fear chemosignals without examining emotion-relevant input from traditional communication modalities (i.e., vision, audition). The question that we pursued here was therefore: How significant is an olfactory fear signal in the broader context of audiovisual input that either confirms or contradicts olfactory information? To test this, we manipulated olfactory (fear, neutral) and audiovisual (fear, neutral) information and demonstrated that olfactory fear signals were as potent as audiovisual fear signals in eliciting a fearful facial expression. Irrespective of confirmatory or contradictory audiovisual information, olfactory fear signals produced by senders induced fear in receivers outside of conscious access. These findings run counter to traditional views that emotions are communicated exclusively via visual and linguistic channels.

Introduction

Communication constitutes the glue that binds the social species. Communication has its unique specialization for each species with distinctive types of dedicated media (Semin, 2007). Some social species like humans use multiple modalities (vision, audition, olfaction, gustation, touch) to adaptively interact with their world (Aglioti & Pazzaglia, 2011). These modalities are often deployed simultaneously by both senders and receivers to create coherent percepts (Partan & Marler, 1999). Imagine witnessing an individual experiencing fear. Your visual and auditory senses would record this person's fearful facial expression and hear the tremble in their voice. This example illustrates the traditional view that vision and audition are the primary sensory channels involved in communication. The current contribution aims to redress the apparent imbalance created by this view and places olfaction, a neglected medium, as an integral part of the multimodal communication. A number of studies have reported the fear-inducing effects of olfactory fear signals upon judgments and inferences when these signals were presented in a unimodal and decontextualized manner. These results are not informative about whether the effects of fear chemosignals translate across different contexts that involve input from other senses. Thus, we examined the question: How significant is an olfactory fear signal in the context of audiovisual input that can be either confirmatory or contradictory with the olfactory information?

When it comes to communicating socially significant states such as fear, the detection of this particular emotion can be improved by the use of multiple communication channels. If the same emotional state is communicated through multiple channels (e.g., visual, auditory, and olfactory), then one can speak of multiple redundant signals (Partan & Marler, 1999, 2005), or backup signals. The advantage of backup signals is that the signals are better protected against environmental noise interfering with the different modalities (e.g., darkness, loudness, odor masking) and both senders and receivers share this benefit. The basic idea is that individual components of a multimodal signal can be replaced or removed without necessarily impacting the efficacy of the signal (Partan & Marler, 2005).

Arguably, the efficacy of the multimodal signal is not impeded by removal of its unimodal components because of the high interconnectedness between populations of neurons in modality-specific sensory-motor and affective systems (Niedenthal, 2007). That is, neural activation in one system can cascade to the full activation pattern thereby creating a partial multimodal reenactment of, for instance, the emotional experience (Barsalou, Niedenthal, Barbey, & Ruppert, 2003). This simulation process is direct and automatic,

escapes verbal access and leads the receiver to achieve a coupling with the sender that gives rise to a shared bodily state (Semin & de Groot, 2013). Following this line of reasoning, an integrated multimodal experience of fear may be elicited by the olfactory modality in itself, regardless of confirmatory or conflicting audiovisual information.

When each modality (i.e., visual, acoustic, and olfactory) is examined separately, psychophysiological evidence indicates that fear induces *emotional contagion* (Hatfield, Rapson, Cacioppo, 1993). Emotional contagion may emerge across different communicative media, as was demonstrated when individuals exposed to emotionally laden faces, bodies, and voices showed similar facial expressions (e.g., Magnée, Stekelenburg, Kemner & de Gelder, 2007). Facial expressions may unfold automatically and independently from visual information, driven by the activation of emotion-specific affect programs (Magnée et al., 2007). Relatedly, the modality specific human capability to chemically communicate fear from a sender to a receiver was revealed outside the context of multimodal communication. Individuals exposed to sweat produced by fearful individuals demonstrated a fearful facial expression (de Groot, Smeets, Kaldewaij, Duijndam, & Semin, 2012). This result supported an embodied social communication model (e.g., Semin, 2000, 2007), from which facial expressions were argued to contain a "self-serving" function. Lifting the eyebrows increased visual field size and instigated sensory vigilance processes (Susskind et al., 2008). Through this framework, important findings such as the neural and behavioral consequences of fear sweat could be interpreted (Albrecht et al., 2011; Chen, Katdare, & Lucas, 2006; Haegler et al., 2010; Mujica-Parodi et al., 2009; Pause, Adolph, Prehn-Kristensen, & Ferstl, 2009; Pause, Ohrt, Prehn, & Ferstl, 2004; Prehn, Ohrt, Sojka, Ferstl, & Pause, 2006; Prehn-Kristensen et al., 2009; Zernecke et al., 2011; Zhou & Chen, 2009). In sum, humans can communicate fear from a sender to a receiver by means of each modality (i.e., vision, audition, and olfaction) separately and emotional contagion of fear can be reflected, inter alia, by a receiver's fearful facial expression.

Studies using combined input from the olfactory and visual modality have not focused on the communication of socially significant information (e.g., fear) within a multimodal framework. As a consequence, it has remained unclear whether reactions evoked by chemically communicated fear can be overridden by conflicting information from the audiovisual modalities, for instance as in the case of a film of a person in a bright and summery meadow while the olfactory fear signal is present. Do humans rely more on vision than on small sets of chemicals that trigger pre-defined behavioral responses (Doty, 2010)? Although visual cues can override olfactory information within a decision-making context

(e.g., Morrot, Brochet, & Dubourdieu, 2001), visual perception can also be modulated by olfactory information. Males inhaling androgen (vs. estrogen) compounds perceived gender-ambiguous faces as more masculine (Kovács et al., 2004) and females exposed to fear sweat classified ambiguous facial expressions as fearful (Zhou & Chen, 2009). In sum, what may determine the leading influence of one modality over the other(s) is whether one particular modality contains socially significant information.

The first of the two complementary avenues that have to be considered in how people process multimodal information is the relative weighting between different modalities that are activated. For instance, is it the case that more weight is assigned to visual input compared to input from other sensory facilities such as olfaction? Moreover, what is the relation between the different modalities and how would this relation shape the intensity of multimodal responses? Before information from each modality can be weighed, however, the relative salience of the contextual cues is also critical in determining the modalities that are activated, namely, the relative contextual saliences of the modalities that 'capture' attention. This constitutes the second avenue. Obviously, these two avenues operate in tandem and the distinction made here is an analytic one.

Sensory processing in general could be tuned to the selection of socially significant information in situ (Lakatos et al., 2009), and the modality that contains the most salient information may set the stage for interpreting information stemming from other modalities (Lakatos et al., 2009). Specifically, more weight could be assigned to the modality that contains the most valuable (e.g., threat-relevant) information. When the same threat-relevant information is mapped onto multiple modalities, then the most common cases are shown to lead to response enhancement manifested in an increase in response intensity that exceeds the unimodal responses (Stein & Stanford, 2008). When multimodal information converges, another option is the occurrence of response equivalence reflected by mere summation of the intensity of the unimodal responses (e.g., Partan & Marler, 2005). From this perspective, one may expect that fear contagion is increased when fear chemosignals are combined with confirmatory audiovisual information in a multimodal communication context and this increase may take any shape from response equivalence to response enhancement. Moreover, when olfactory and audiovisual information is contradictory with regard to the presence of threat, fear contagion would emerge regardless of the communicative medium as the modality containing threat-relevant information would receive more weight.

Before information from each modality is weighed, eventually resulting in the multimodal expression of a "state", the contextual cues in the situation may determine which

information initially captures attention. According to the situated perspective (Griffiths & Scarantino, 2005; Semin & Smith 2013; Smith & Semin 2004), emotional expressions are the result of the diverse information sources present in an environmental context. Thus, whereas the response of an organism is multimodal, contextual cues may activate different modalities with messages that differ and thus lead to contradictory information between modalities. For instance, the olfactory modality may be activated with a fear message, whereas the audiovisual modality may be activated with a safety message. That is, different aspects of the context dynamically shape emotions, and vice versa (Griffiths & Scarantino, 2005). That particular responses were only elicited under particular contextual influences was evidenced by at least two studies on human body odor perception. In one, sex-specific body odor compounds increased sexual arousal only after participants watched a sexually arousing film (Bensafi, Brown, Kahn, Levenson, & Sobel, 2004). In another, mood increased only when females were exposed to male body odor compounds in the presence of a male experimenter (Jacob, Hayreh, & McClintock, 2001). While these studies used non-emotional body odors, the prediction that follows from the situated context model is that fear chemosignals are dynamically coupled in the situated context with different signals (e.g., threat, safety) that are activated via different modalities.

Because research on fear chemosignals has only proceeded in a unimodal, decontextualized manner without examining emotion-relevant input from other modalities, it has remained an open question to what extent fear chemosignals would produce fear when placed in a context with different modalities signaling convergent or divergent information. The current research investigates responsiveness to fear chemosignals (vs. control sweat sampled in a nonthreatening environment) in the context of confirmatory and contradictory audiovisual information. Fear contagion in receivers is specifically examined through the emergence of a fearful facial expression over time evidenced by increased facial electromyographic (EMG) activity over the *medial frontalis* (lifting the eyebrows: fear) and *corrugator supercilii* (knitting the eyebrows: negative affect) muscles.

First, we predict that both fear chemosignals and audiovisual threat signals follow the typical properties of multiple redundant signals in the sense that a fear message from each of the modalities should elicit fear contagion independently from the other. Moreover, a situated context model suggests that the context can induce different signals across different modalities and these signals can be convergent or divergent. We predicted increased fear contagion when information from multiple modalities is *convergent* with regard to the presence of fear. This can either be response equivalence (i.e., the fear response is equal to

what can be expected based on the combined contribution of each separate modality: no moderation effect) or response enhancement (i.e., the fear response is larger than what can be expected based on the combined contribution of each separate modality: moderation effect). Importantly, when information from multiple modalities is *divergent*, two different prediction paths with the same result would follow from a situated context model. When fear sweat is presented within a nonthreatening audiovisual context, the expected response is fear contagion due to the salience of the fear stimulus. For the same reason, we expect the emergence of fear contagion when control sweat is presented within the context of audiovisual input indicating threat. That is, fear is adaptively more significant in whichever modality it is processed. These combined predictions allow for the interpretation that fear chemosignals serve as communication signals within the broader context of multimodal communication.

Method

All studies were approved by the Utrecht University Institutional Review Board, Utrecht, the Netherlands.

Part 1: Senders

Participants and design

8 Heterosexual Caucasian males (M_{age} = 22.38, SD = 2.33) donated sweat while they watched 30-min fear and neutral videos in two counterbalanced sessions separated by a week's interval. Consistent with previous research (e.g., de Groot et al., 2012; Zhou & Chen, 2009), only males were recruited as sweat donors because of their larger apocrine sweat glands (Sergeant, 2010).

Materials, measures, and procedure

We excluded individuals who smoked, were ill, used medication, or were diagnosed with a psychological disorder. The donors who passed these criteria were informed about the experimental procedures and restrictions that had to be in place at least 3 days before the first donation. To avoid sweat contamination, donors had to follow a strict regimen starting two days before the actual donation: alcohol use, smoking, sexual activity, consumption of odorous food (e.g., onions, garlic, and asparagus), and excessive exercise was prohibited. After informed consent was obtained, donors collected scent-free products (shampoo, soap, and deodorant), two t-shirts in zip-locked plastic bags, and a diet diary. If the diet diary revealed more than one violation per donor per donation session, the donor had to be

excluded. Prior to coming into the lab, donors had to unpack and wear the sealed t-shirt to prevent odor contamination from their clothes.

In the lab, donors first completed the Dutch State Anxiety Inventory (van der Ploeg, Defares, & Spielberger, 1980). Next, they rinsed and dried their armpits with water and paper towels. Hypoallergenic tape was used to attach one sterile absorbent compress (Cutisorb, BSN medical GmbH & Co KG, Hamburg, Germany) under each armpit. During this process, the experimenter wore nitrile gloves to avoid bacterial contamination. Donors put on a new t-shirt and a sweater, after which they were instructed to perform a computer task and complete questionnaires. They were seated individually in a cubicle (temperature: 23 ˚C).

We manipulated emotional state by varying video presentation. Per session, participants watched either the 30-min fear video or the neutral video. Using the original English-spoken clips, the fear video consisted of 9 clips that reliably induced fear (Schaefer, Nils, Sanchez, & Philippot, 2011; database codes: 7, 16, 28, 32, 38, 46, 50, 55, 66). The neutral video consisted of parts from a BBC documentary about Yellowstone National Park, because wildlife documentaries were shown to elicit a pleasant, relaxing form of neutrality rather than plain neutrality, which could result in negative feeling states such as boredom or irritation (Rottenberg, Ray, & Gross, 2007).

Directly after the video, donors again filled in the State Anxiety Inventory and rated their feelings on seven-point Likert scales (1: “not at all”; 7: “very much”). Finally, sweat pads were removed and stored per donor, per condition, per armpit in vials at -22 ºC. Stimulus freezing would not affect pleasantness and intensity ratings (Lenochova, Roberts, & Havlicek, 2009). After completion of the second donation, donors were debriefed, thanked, and paid €35.

Part 2: Receivers

Participants and design

Informed consent was obtained from thirty right-handed female Caucasian undergraduates (M_{age} = 20.47, *SD* = 2.42). Consistent with previous research (e.g., de Groot et al., 2012; Zhou & Chen, 2009), only females were recruited as chemosignal recipients because of their documented superior sense of smell (Brand & Millot, 2001) and sensitivity to emotional signals (Brody & Hall, 2000). All participants were assessed by means of a standardized psychophysical test of olfactory function (Sniffin’ Sticks, Burghart Instruments, Wedel, Germany) and were observed to have a normal sense of smell (smell threshold: *M* = 12.47 binary dilution steps: 1.41×10^{-3}% phenethyl alcohol, *SD* = 3.15; Hummel, Sekinger,

Wolf, Pauli, & Kobal, 1997). Participants had passed the pre-experimental screening that excluded left-handers, smokers, and individuals that suffered from a psychological disorder, respiratory disease, illness, cold or allergy. Participants enrolled in a counterbalanced 2 x 2 within-subjects design, with olfactory input (2 levels: fear, neutral) and audiovisual input (2 levels: fear, neutral) as main independent variables.

Independent variables

Olfactory information. Olfactory input was manipulated by randomly presenting individuals with fear sweat and neutral sweat. Both participants and the experimenter were unaware of the nature of the chemical stimulus (fear sweat, neutral sweat) that was presented, as each vial was marked by a three-digit code devised by a researcher that was not involved in the experiment. Before the experiment started, sweat pads were prepared for presentation. For this purpose, each sweat pad (100 cm²) was cut into eight pieces (12.5 cm²). To reduce effects of inter-individual variability in sweat secretion, each vial presented to participants contained four pad parts. Each pad part (size: 12.5 cm²) came from a different donor and stemmed from either the left (two parts) or right (two parts) armpit.

Audiovisual information. Audiovisual input was manipulated by presenting a number of pilot-tested video clips. These clips depicted social situations that would communicate either safety or danger to a witnessing participant. In the neutral condition, clips of a woman having a conversation with a man were displayed. In the fear condition, clips depicted a woman (victim) that was assaulted by a man (perpetrator). This role-division was created for female participants to empathize with the same-sex character. From 72 pilot-tested clips (duration: ≥ 30 s ≤ 120 s), we selected the 12 most threatening ($M = .59$, $SD = .29$) and 12 least threatening clips ($M = .32$, $SD = .28$). This selection was based on the proportion of ambiguous Chinese symbols displayed directly after the clips (further details below) that individuals identified as threatening (vs. not-threatening).

For exploratory reasons, we created a subcategory for the fear-inducing and not fear-inducing clips by varying the man's group-membership as being either ingroup (Caucasian) or outgroup (African American). Importantly, a pilot-test revealed that Chinese symbol ratings did not vary between ingroup and outgroup clips (neutral, ingroup: $M = .32$, $SD = .26$; neutral, outgroup: $M = .31$, $SD = .30$; fear, ingroup: $M = .60$, $SD = .28$; fear, outgroup: $M = .58$, $SD = .22$). Hence, any effects of group-membership in the actual experiment (see Appendix B) could be attributed to the chemical signal.

Measures and materials

Handedness scale. The Handedness scale was included to corroborate the right-handedness of the sample and to control for possible handedness-related differences in facial EMG activity. On a 10-item questionnaire (van Strien, 1992; Cronbach's $\alpha = .98$), participants indicated which hand(s) they use to perform a range of activities. The current sample was right-handed ($M = 8.97$, $SD = 1.38$).

Facial electromyography. Facial EMG activity was recorded bipolarly with sintered Ag/AgCl electrodes that were applied to the left side of the face—that is, the side most strongly involved in spontaneous affective reactions in right-handed participants (Dimberg & Petterson, 2000). Electrodes filled with hypoallergenic conductive gel (Lectron II, Newark, NJ) were applied to the *medial frontalis* (to measure fear) and *corrugator supercilii* (to measure general negative affect) following Fridlund and Cacioppo's (1986) guidelines. The reference electrode was placed on the middle of the forehead. EMG signals were recorded with Biolab Acquisition Software (Version 3.0.10) and filtered online with a .5 Hz low cutoff filter and 200 Hz high cutoff filter. The EMG signal was rectified and smoothed with a 20 Hz low pass filter with a time constant of 100 ms.

Chinese symbol task. Stimulus presentation was controlled by a computer (19-in. screen: FlexScan S1932, 1280 x 1024 screen resolution) running Presentation software (Version 16.4). This software was used to run the Chinese symbol task, which measures implicit affect through dichotomous ratings of briefly presented Chinese symbols—adapted from Payne and colleagues (Payne, Cheng, Govorun, & Stewart, 2005). Each Chinese symbol was unique and stemmed from a pilot-tested database (http://www.unc.edu/~bkpayne/materials.htm). The proportion of Chinese symbols identified as threatening served as a manipulation check.

Filler items. A series of three randomly selected neutral items from the International Affective Picture System (Lang, Bradley, & Cuthbert, 2008; database codes: 6150, 7002, 7025, 7035, 7100, 7217) served as filler items in the main experiment.

Odor ratings. In randomized order, participants evaluated the pleasantness and intensity of the olfactory stimuli they were exposed to during the experiment on 7-point Likert scales (1 = "not at all"; 7 = "very much").

Odor discrimination test. A duo-trio task was used to assess participants' ability to discriminate fear sweat from neutral sweat. On two trials, participants smelled the reference

odor (either fear sweat or neutral sweat) and indicated whether it corresponded to either one of two odors (neutral sweat, fear sweat). Each vial was presented in a predetermined counterbalanced order. With the minimum number of 20 ($N = 30$) to accept the hypothesis that participants could discriminate the two odors (O'Mahony, 1986; $n = 3–0$, $\alpha = 5$, $\pi = ⅓$), participants neither could identify fear sweat (correct / total responses: 13/60), nor neutral sweat (correct / total responses: 19/60).

Smell threshold test. Threshold for phenethyl alcohol (PEA) was assessed with Sniffin' Sticks (Burghart Instruments, Wedel, Germany), using a triple-forced choice staircase method (Hummel et al., 1997). While blindfolded, participants were presented with three markers—one contained the target smell, two the diluents—and asked to identify the target. Markers were randomly presented ~2 cm below participants' nostrils for two seconds. Markers were presented in ascending concentrations ($1.22x10^{-4}$% - 4%, with 1:2 binary dilution steps) until participants made two consecutively correct identifications, after which they were presented with a lower concentration (first reversal). If participants erred, they were again presented with a higher concentration (second reversal). Smell threshold was calculated by taking the mean of the final four (of seven) reversal points.

Awareness check. Funneled post-experimental debriefing (Bargh & Chartrand, 2000) revealed that six participants identified the olfactory stimulus as "sweat"; yet, when probed for suspicion regarding the study purpose, no participant correctly guessed the hypothesis.

Procedure

The main experiment was carried out by a female experimenter, as the presence of a male experimenter could increase female participants' mood (Jacob et al., 2001). Olfactory stimuli were defrosted 30 min prior to exposure, and each participant received a new vial.

After entering the lab, all participants provided written informed consent. They were instructed that physiological measures would be applied to their face, after which they had to perform a computer task and complete a series of tests. Participants were seated. The skin on the middle and left side of their forehead was cleaned with alcohol and abrasive lotion (Lemon Prep, Mavidon, Lake Worth, FL). In the short break that followed, participants filled in a handedness questionnaire, after which the cleaning routine was repeated to further reduce the impedance of the EMG signal. Next, EMG electrodes were applied. The impedance of EMG electrodes was checked with an impedance measure. In the rare cases that impedances exceeded 30 kΩ, an online check of the EMG signal was performed by the experimenter to determine whether the signal was reliably discernible from noise. For this purpose,

participants had to lift (*medial frontalis*) and knit (*corrugator supercilii*) their brows. All electrodes were correctly placed and electrode replacement was unnecessary.

Participants were seated in individual cubicles on an adjustable chair with their heads placed in a chin rest. This chin rest both stabilized participants' heads and contained the vial that was located 2 cm below their noses. Before the vial containing either fear sweat or neutral sweat (presented randomly) was opened, they watched a 4-min relaxing baseline video (beach sunset with acoustic guitar soundtrack) and became familiar with the Chinese symbol task through 8 practice trials. Participants' job was to judge the visual pleasantness of each Chinese symbol. They were instructed to press a key labeled "threatening" if they judged the Chinese symbol to be more threatening than average and a key labeled "not threatening" if they judged it to be less threatening than average. Response keys were counterbalanced across participants. Participants were told that they should ignore the clip when making judgments about the Chinese characters. They were furthermore instructed to respond quickly.

After this practice round, the vial containing the sweat pad was opened; the moment of exposure could be identified with the video capture embedded in EMG analysis software. Participants were presented with 12 clips targeting the audiovisual modalities that were fear inducing (six clips) and not fear inducing (six clips). These 12 clips depicted either ingroup members or outgroup members (per group: three fear inducing and three not fear inducing). Three randomly presented clips constituted a block; each randomly presented block was separated from another block by three neutral filler items (duration: 3 s). Within each block, each clip was preceded by a fixation cross (1.5 s) and followed by a Chinese symbol (100 ms) and mask consisting of black and white noise. This mask disappeared as soon as the participant responded. Per clip, participants judged four symbols. After the presentation of 4 blocks (total: 12 clips), participants took a short break (~15 s) during which time the vial containing the odor was switched. The experiment continued with 4 randomized blocks of 12 new clips as soon as the newly placed vial was opened.

Participants finished when all 24 clips had been displayed. The experimenter removed the electrodes. Next, participants were asked to rate the presented olfactory stimuli on pleasantness and intensity, discriminate between those odors in a duo-trio task, and perform an olfactory threshold test. Finally, they were debriefed and paid €12.

Statistical analysis

Sample size (N = 30) was determined by a priori power analysis (G*Power 3.1; Faul, Erdfelder, Lang, & Buchner, 2007) for within-subjects analysis of variance (ANOVA; d = .27, power = .80, α = .05). Effect size d was converted (Cohen, 1988) from the effect sizes (η^2 = .018) obtained in previous research with regard to the impact of fear sweat on facial muscle activity (de Groot et al., 2012). For all statistical analyses, the manner of handling the data was determined a priori. For all variables, outliers were identified as values that surpassed ±3 SD of the mean (Z > ±2.33). When outliers were revealed for a particular variable, these values were altered to be one unit (microvolt for EMG, percent for symbols) above the next extreme score on that variable (Field, 2009). This sequence was twice repeated. The percentage of outliers was reduced from ~4% to virtually 0%. Hence, outliers did not drive the current study's results. Second, missing values due to measurement error were handled by means of stochastic regression imputation (i.e., deterministic regression imputation with an added random error component). For Participants 2 and 4, the proportion of Chinese symbols identified as (not-) threatening was missing due to an error in the program. In addition, the video capture of Participant 14 failed due to technical difficulties. Because the video capture was embedded in EMG analysis software and this combined interface would determine the exact time point at which the participant was exposed to the olfactory stimulus, EMG data was considered missing for Participant 14, and regression imputation was applied.

Results

Part 1: Senders

The experiment consisted of two stages. The first stage served to collect sweat from "senders" to which "receivers" would be exposed in the second stage. Sweat was sampled while eight donors watched videos that induced fear or a pleasant-neutral state. Emotion induction was effective (see also Appendix B). In the fear condition, participants reported greater fear than in the neutral condition, Z = 2.53, p = .011, r = .89, whereas more calmness was reported in the neutral condition compared to the fear condition, Z = 2.55, p = .011, r = .90. As expected, a repeated measures ANOVA on state anxiety levels with factors emotion induction (fear, neutral) and time (pre-induction, post-induction) revealed a significant interaction between emotion induction and time, $F(1,7) = 7.01$, p = .033, η_p^2 = .50 (see Figure 1). Follow-up paired t-tests indicated that there were no significant differences in state anxiety prior to emotion induction, $t(7) = .17$, p = .871. As predicted, significantly differing levels of state anxiety were encountered after emotion induction, $t(7) = 2.47$, p = .043, d = 1.38, with higher levels in the fear condition compared to the neutral condition.

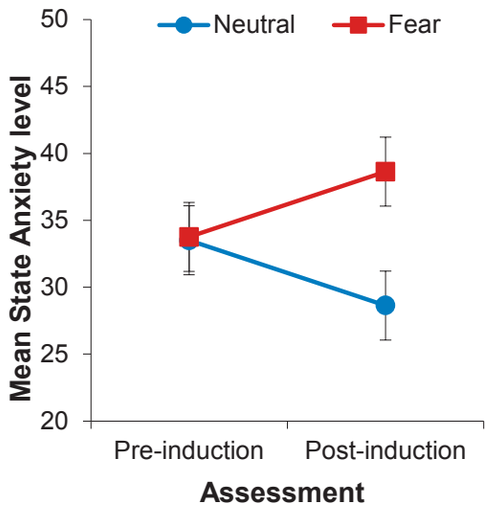

Figure 1. Mean state anxiety levels before and after emotion induction (fear, neutral) in senders (donors). Error bars represent 68% confidence intervals based on the mean square error of the interaction between emotion induction and time—that is, all have the same size (see Loftus & Masson, 1994, for formulas to calculate confidence intervals; see Estes, 1997, for a recommendation of using 68% confidence intervals for these type of analyses).

Part 2: Receivers

Next, all samples were frozen and thawed before presentation to receivers. In the second stage, 30 receivers enrolled in a double-blind, within-subjects experiment. Four main conditions were created by manipulating olfactory information (fear vs. neutral) and audiovisual information (fear vs. neutral). Receivers were randomly exposed to fear and neutral sweat while they watched several randomly presented clips that displayed a man assaulting (fear inducing) and interacting with (not fear inducing) a woman.

Because emotional contagion of fear is reflected by facial expressions that reproduce the emotion of the sender, we measured facial electromyographic (EMG) activity over receivers' *medial frontalis* (brow raise) and *corrugator supercilii* (brow knit) muscle. When combined, significantly elevated *medial frontalis* and *corrugator supercilii* activity would reflect a negative affective fear expression (Fridlund & Cacioppo, 1986).

Our first prediction was that fear contagion could be induced by separate fear messages carried by the olfactory and audiovisual modalities. Separate analyses were conducted to examine how facial muscle activity would unfold over time as a function of either olfactory or audiovisual input. The effect of olfactory input (fear sweat, neutral sweat) on facial EMG activity was charted shortly after odor exposure for three reasons: first, to reveal the independent effect of olfactory information before clips containing audiovisual

information were presented (> 5 s); second, to demonstrate the fear-inducing effects of fear sweat in a time period that could contain at least two sniffs (duration typical sniff: ~1.6 s; see Mainland & Sobel, 2006), from which the second was shown to be effectively modulated according to the experienced emotion (de Groot et al., 2012); and third, to replicate and extend previous findings (de Groot et al., 2012). The current results indeed constituted a replication (*medial frontalis*) and extension (*corrugator supercilii*) of earlier work, as only during exposure to fear sweat, *medial frontalis*, $F(24,696) = 2.67$, $p < .001$, $\eta_p^2 = .08$, and *corrugator supercilii* activity, $F(24,696) = 2.29$, $p < .001$, $\eta_p^2 = .07$, increased as a function of time (see Figure 2). Hence, a facial expression of fear emerged in receivers after having sampled fear-inducing olfactory information.

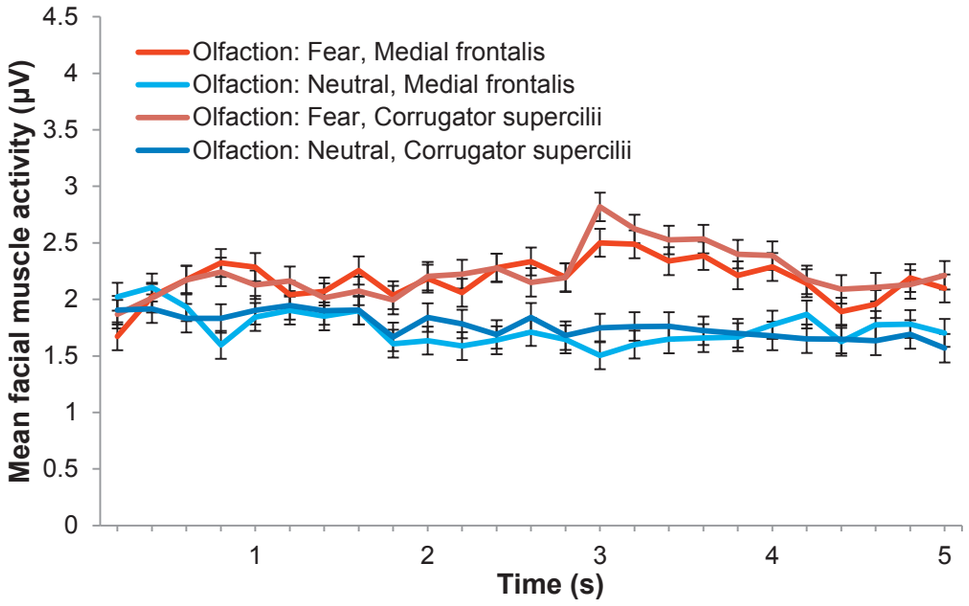

Figure 2. Mean impact of the olfactory "message" (fear, neutral) on *medial frontalis* and *corrugator supercilii* activity over time. Error bars indicate 68% confidence intervals based on the mean square error of the interaction between odor and time.

While olfactory information was copresent, participants witnessed randomly presented audiovisual information that was fear inducing and not fear inducing. Next, we charted the independent effects of audiovisual information on facial EMG activity over time by collapsing the levels of olfactory input. As predicted, participants displayed greater fear: *medial frontalis* activity, $F(29,841) = 2.36$, $p < .001$, $\eta_p^2 = .08$; *corrugator supercilii* activity, $F(29,841) = 2.85$, $p < .001$, $\eta_p^2 = .09$, over time when presented with fear-inducing clips (see Figure 3). These combined findings indicate that threat-relevant information can be communicated from a sender to a receiver by means of both olfactory and audiovisual

information. Olfactory fear signals seemingly served as communication signals within a multimodal communication context; yet, this conclusion cannot be drawn before facial EMG activity is examined when olfactory and audiovisual input are combined to create divergent or convergent information. Will fear that is communicated via the olfactory modality be dampened by audiovisual information that indicates the absence of threat?

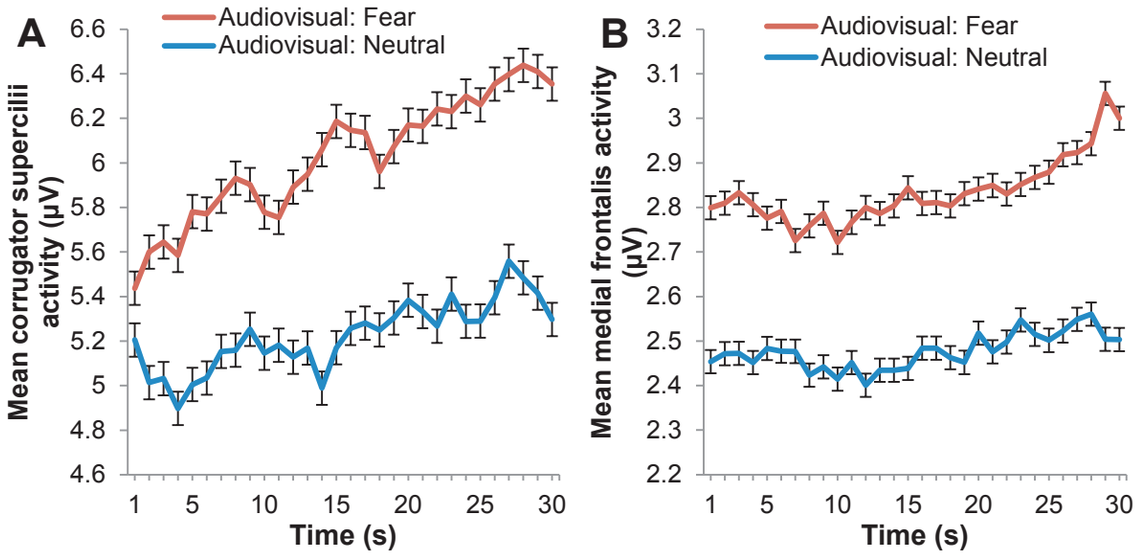

Figure 3. Mean impact of the audiovisual message (fear, neutral)—averaged over all clips—on *corrugator supercilii* (A) and *medial frontalis* (B) muscle activity over time. Error bars indicate 68% confidence intervals based on the mean square error of the interaction between audiovisual information and time.

When different modalities produce *divergent* messages with regard to the presence of danger, fear arguably constitutes the most significant signal in whichever modality it is processed. When fear sweat is presented within a nonthreatening audiovisual context, the expected response is fear contagion due to the salience of the fear stimulus. For the same reason, we expect the emergence of fear contagion when neutral sweat is presented within the context of audiovisual input that indicates threat. Indeed, irrespective of contradicting information from the other modalities, analyses of variance on facial EMG activity averaged over exposure time (~12 min) revealed that fear contagion resulted from the exposure to fear sweat: *medial frontalis*, $F(1,29) = 9.06$, $p = .005$, $\eta_p^2 = .24$; *corrugator supercilii* (trend), $F(1,29) = 3.78$, $p = .062$, $\eta_p^2 = .12$; and fear-inducing clips: *medial frontalis*, $F(1,29) = 4.33$, $p = .046$, $\eta_p^2 = .13$; *corrugator supercilii*, $F(1,29) = 10.08$, $p = .004$, $\eta_p^2 = .26$). Furthermore, planned paired t-tests (see Appendix B) indicated no significant difference between the conditions in which either olfactory or audiovisual fear messages were combined with

divergent audiovisual and olfactory information (see Figure 4). Hence, olfactory fear signals were at least as equivalent as audiovisual fear signals in inducing fear.

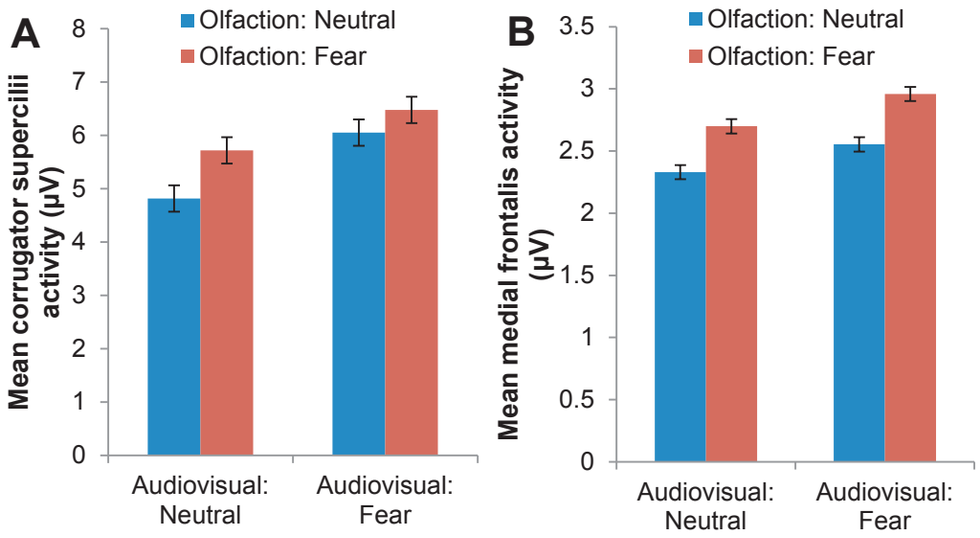

Figure 4. Mean impact of the olfactory and audiovisual message (fear, neutral) on *corrugator supercilii* (A) and *medial frontalis* (B) activity. Error bars reflect 68% confidence intervals.

When information from multiple modalities is *convergent* with regard to the presence of fear, increased fear contagion was predicted that could take any form from what is labeled equivalence (i.e., addition of the unique modality fear responses) to response enhancement (i.e., superadditivity of the unique modality fear responses). An ANOVA on facial EMG activity with factors olfactory information (fear, neutral) and audiovisual information (fear, neutral) provided the first support for response equivalence, because the interaction between audiovisual information and olfactory information did not reach significance: *medial frontalis*, $F(1,29) = .10$, $p = .75$; *corrugator supercilii*, $F(1,29) = .95$, $p = .34$). Second, planned paired t-tests (see Appendix B) demonstrated lowest levels of *medial frontalis* and *corrugator supercilii* activity when neutral olfactory information was presented together with neutral audiovisual information, whereas highest levels (i.e., mere *summation* of the unique modality fear responses) emerged when fear-inducing olfactory information was presented together with fear-inducing audiovisual information (Figure 4); the incongruent conditions falling in-between. In sum, olfactory and audiovisual fear signals communicated fear independently from one another. When olfactory and audiovisual information was combined and was divergent with regard to the presence of threat, fear contagion was observed, arguably due to the salience of the fear signal. Moreover, when olfactory and audiovisual

information was confirmatory on the presence of danger, fear responses were increased to reflect the combined contribution of the separate modalities.

To examine whether the effects reported here were caused by consciously accessible characteristics of the olfactory stimuli, we compared participants' pleasantness and intensity ratings of fear sweat (pleasantness: $M = 3.23$, $SD = 1.28$; intensity: $M = 3.90$, $SD = 1.40$) and neutral sweat (pleasantness: $M = 3.40$, $SD = 1.04$; intensity: $M = 3.80$, $SD = 1.40$), but no significant differences emerged: pleasantness, $t(29) = -.56$, $p = .582$; intensity: $t(29) = .34$, $p = .739$. Participants were furthermore unable to discriminate fear sweat from neutral sweat in an odor discrimination task. Because sensitivity for odors may vary with fluctuations in sex hormones during the menstrual cycle (Jacob et al., 2001), menstrual cycle was added as a covariate to all analyses, but proved to be a nonsignificant contributor in all cases. Funneled debriefing indicated that six participants correctly identified the olfactory stimulus as sweat; yet, rerunning all analyses without these individuals did not eliminate the significant impact of the olfactory fear stimulus on facial muscle activity. Essentially, receivers emulated the fearful state of the sender and this occurred without participants' awareness of the process.

Discussion

In this study our aim was to ask how influential fear chemosignals would be in the broader context of audiovisual input that was either confirmatory (threat) or contradictory (no threat) with the olfactory information. The main finding was that fear chemosignals served as communication signals within the broader context of multimodal communication and generally induced fear contagion, evidenced by increased facial EMG activity over the *medial frontalis* (fear) and *corrugator supercilii* (negative affect) muscles. The conclusion that fear chemosignals served as communication signals within a multimodal context was derived from three findings. First, both fear chemosignals and audiovisual threat signals elicited fear independently from the other modality. Second, when information from multiple modalities was *convergent* with regard to the presence of threat, increased fear contagion was observed in the form of response equivalence (i.e., summation of the intensity of the unique olfactory and audiovisual fear responses). Third, when information from multiple modalities was *divergent* with regard to the presence of threat, instead of audiovisual dominance, we observed fear contagion regardless of whether the threat signal was transmitted by the olfactory or audiovisual modalities. Hence, fear was adaptively more significant in whichever modality it was processed. Because olfactory fear signals were as potent as audiovisual fear

signals in inducing fear, the combined findings argue against the commonly accepted view that human communication of emotions runs exclusively via linguistic or visual channels.

The relative salience of the contextual cues may be critical in determining the activation of the different modalities within a multimodal communication context (Griffiths & Scarantino, 2005; Semin & Smith 2013; Smith & Semin 2004). Sensory processing may in that sense be tuned to the selection of socially significant stimuli in the environment (Li, Howard, Parrish, & Gottfried, 2008), and more weight could be assigned to the modality containing the most valuable (e.g., threat-relevant) information. Because the fear-inducing effects of fear chemosignals were not dampened by copresent audiovisual input that indicated the absence of threat, the current results confront the assumption that audiovisual input generally receives more weight than olfactory information. Moreover, the modality carrying the threat message may in turn have biased individuals to interpret information from modalities signaling divergent information in an emotion-congruent manner (cf. Zhou & Chen, 2009). In sum, contextual cues may determine which modality initially captures attention, after which the modality that carries socially significant information receives more weight and sets the stage to interpret *divergent* input from other modalities in a congruent manner.

When information from multiple modalities was instead *convergent* on the presence of threat, the relation between the olfactory and audiovisual modalities was such that the increased intensity of the multimodal fear response corresponded to summation of the individual olfactory and audiovisually induced fear responses, labeled response equivalence (cf. Partan & Marler, 1999, 2005). We observed response equivalence rather than response enhancement (Partan & Marler, 2005; Stein & Stanford, 2008), because the latter would have been reflected by the presence of a moderation effect, namely superaddition of the separate fear responses. In fact, the occurrence of either response equivalence or response enhancement may be determined by the distance of the respective modalities relative to the individual (Stein & Stanford, 2008). Because stimulus distance was kept constant in the current study, future research could focus on how multisensory integration is impacted by audiovisual and olfactory fear signals presented at different distances from the individual. Obviously, humans rely on successful integration of multiple signals to function adequately (Schaal & Durand, 2012), and the current study demonstrated that combined audiovisual and olfactory fear input leads to a fear response that has the combined intensity of the fear responses instigated by the separate modalities.

The current study revealed the separable fear-inducing capacity of the audiovisual and olfactory modalities, as each modality was as potent as the other, and each modality induced fear independently from the other. Because fear chemosignals elicited a fearful facial expression irrespective of the audiovisual input that was copresent in the environment, our findings support the statement that facial expressions can unfold independently from visual input and may be driven by the activation of emotion-specific affect programs (e.g., Magnée et al., 2007). The person assuming a fearful facial expression may benefit from this expression, because raising the eyebrows and upper eyelids increases a person's visual field size and instigates sensory vigilance processes (Susskind et al., 2008). Essentially, the fearful facial expression that emerges in a receiver after exposure to threat signals may contribute to what has been labeled emotional contagion (Hatfield et al., 1993). Although bodily feedback of this kind is argued by some (Cannon, 1927) to be too slow and undifferentiated to represent an emotional experience, facial expressions can in fact support subtle distinctions in emotional states (Niedenthal, 2007). Thus, facial expressions cannot simply be conceived of as nonaffective automatic motor reactions (Moody, McIntosh, Mann, & Weisser, 2007). Moreover, fear input arguably triggered in a receiver modality-specific brain systems that are capable of processing a number of states in a fast, refined, and flexible manner (Niedenthal, 2007), which may have further contributed to emotional contagion. Although emotional contagion was demonstrated when fear chemosignals produced by a sender induced a fearful facial expression in a receiver (de Groot et al., 2012), the current contribution provided the first evidence that fear chemosignals induce fear contagion in the broader context of multimodal communication regardless of whether the information from other modalities is contradictory or confirmatory.

Although fear responses could result from threat signals transmitted by each modality separately (e.g., de Groot et al., 2012; Magnée et al., 2007), more commonly threat signals are communicated by a combination of multiple modalities, and this often leads to increased fear responses (Partan & Marler, 2005). The benefit of threat messages being communicated through multiple modalities is that the message is better protected against environmental noise impacting the different modalities, which increases the chance that the message comes across (Partan & Marler, 2005). Because the efficacy of the fear signal was not hampered by the removal of individual components (i.e., audiovisual fear signals) of the multimodal signal (cf. Partan & Marler, 2005), the results of the current study suggest that fear chemosignals may serve as backup signals within a broader multimodal communication context. This finding establishes the independent position of the olfactory modality as one of multiple

modalities that are equally capable of transmitting fear from male senders to female receivers and raises the question whether the same principle applies to different gender constellations of senders and receivers and to other adaptively and socially significant emotional states such as anger.

In summary, although a number of studies demonstrated the fear-inducing properties of fear chemosignals (Albrecht et al., 2011; Chen et al., 2006; Haegler et al., 2010; Mujica-Parodi et al., 2009, 2004; Prehn et al., 2006; Prehn-Kristensen et al., 2009; Zernecke et al., 2011; Zhou & Chen, 2009), these olfactory threat signals had only been presented in a unimodal and decontextualized manner without examining emotion-relevant input from other modalities. A hitherto unanswered question was therefore how significant an olfactory threat signal would be in the broader context of audiovisual input that was either confirmatory or contradictory with the olfactory input. The current study revealed that fear chemosignals constitute a particular class of fear signals that induce fear irrespective of the input from modalities that are traditionally regarded as more relevant for communication (i.e., vision, audition). This finding requires a revision of our view regarding the relative contribution of chemical signals and may necessitate the inclusion of the olfactory modality into traditional communication models that have relied exclusively on language and visual information.

Chapter 5

Chemical communication of fear: A case of male-female asymmetry

This chapter is based on:

de Groot, J. H. B., Semin, G. R., & Smeets, M. A. M. (2014b). Chemical communication of fear: A case of male-female asymmetry. *Journal of Experimental Psychology: General, 143*, 1515–1525. doi: 10.1037/a0035950

Abstract

Previous research has documented sex differences in nonverbal communication. What has remained unknown is whether similar sex differences would exist with regard to olfactory communication via chemosignals, a relatively neglected nonverbal medium. Because women generally have a better sense of smell and greater sensitivity to emotional signals, we hypothesized that compared with male participants and relative to a neutral control condition, female participants would emulate the fearful state of the sender producing the chemosignals. Facial electromyography was used in a double-blind experiment to measure in the receiver a partial reproduction of the state of the sender, controlling for the moderating influence of the sex of the sender and receiver. The results indicated that only female participants emulated the fearful state of the sender. The present study revealed a boundary condition for effective chemosignaling by reporting behavioral evidence of sexual asymmetry in olfactory communication via chemosignals.

Introduction

Differences between the sexes span the gamut from genes to behavior (Cahill, 2006; Hyde, 2014). Although genes that are found on the sex chromosomes influence sexually dimorphic brain development (Arnold, 2004), the behavior displayed by males and females can be remarkably similar (Cahill, 2006; Hyde, 2014). Similarity is particularly important in a communication context, since having common ground is the base of any efficient communication and that implies similarity of perspectives. Nevertheless, sex differences have been reported with regard to nonverbal communication, for instance, as women judged the emotional meaning of nonverbal cues with greater accuracy than men (e.g., Hall, Carter, & Horgan, 2000). In a similar vein, the research we report concerns a relatively neglected modality carrying nonverbal information, namely the olfactory modality, and in particular we examine sexual asymmetry in the chemical signaling and reception of fear.

In the course of the last decade, chemosignaling has become established as a medium to transfer social information from one individual to another such as the emotional state of fear (e.g., Zhou & Chen, 2009; Mujica-Parodi et al., 2009; de Groot, Smeets, Kaldewaij, Duijndam, & Semin, 2012; Adolph, Meister, & Pause, 2013; de Groot, Semin, Smeets, 2014a). General interest in emotion-specific effects induced by fear chemosignals may have rendered research on sex differences in the chemical communication of fear less prominent (but see Radulescu & Mujica-Parodi, 2013). This however is the focus of the current contribution, namely sexual asymmetry in fear chemosignaling. Do fear chemosignals produced by male and female senders induce a similar partial reproduction of the state of the sender in male and female receivers?

Communication occurs when an individual (sender) signals *information* to another individual (receiver) and this can occur with or without explicit communicative intent (Semin, 2007). Whereas such *information* can be about (relatively) static features such as sex and age, we are concerned with the transmission of dynamic information about a person's internal state. The transfer of dynamic information takes place by means of diverse modalities (e.g., visual, auditory, olfactory) and their respective manifestations (e.g., facial expressions, prosody, chemosignals) (Semin & de Groot, 2013). These modalities serve the purpose of establishing in a receiver a partial affective, behavioral, perceptual, and neural reproduction of the state of the sender (Semin, 2007). This partial reproduction can occur automatically, outside of conscious access, and contributes to what we call *synchronization*—the recruitment of joint affective, behavioral, perceptual, and neural processes. Synchronization

can be regarded as the common base that is necessary for any successful communication (Semin, 2007).

Evidence for the emergence of a partial reproduction has been mainly reported for visual and acoustic signals (Semin, 2007). The establishment of a partial reproduction via olfactory signals may be impeded by sex differences in olfactory capabilities. Women of different ethnic and cultural backgrounds were documented to generally outperform men on olfactory tests that involve odor detection, discrimination, identification, memory, and processing (for reviews, see Doty & Cameron, 2009; Stevenson, 2010; Sergeant, 2010). Similar, yet more limited, evidence has been obtained for body odors (e.g., Chen & Haviland-Jones, 2000; Ackerl, Atzmueller, & Grammer, 2002; Wysocki et al., 2009). Essentially, these combined findings seem to indicate that the olfactory system is sexually dimorphic.

Sexual asymmetry in chemical communication may be based on sex differences in brain areas related to assessing the emotional meaning of odors rather than areas responsible for odor perception. Before an odor is perceived, odorants have to reach odorant receptors (OR) in the nose (olfactory epithelium), after which OR activity is transduced by olfactory receptor neurons (ORN); ORNs directly project to the olfactory bulb in the cortex, the location where odors are perceived (e.g., Zelano & Sobel, 2005). Notably, when participants were exposed to socially meaningful odors, no sex differences in olfactory bulb activity were observed (Radulescu & Mujica-Parodi, 2013). Thus, sexual asymmetry in chemical communication is more likely to arise from differences in brain areas regulating emotions rather than perception.

The neuroanatomy of the olfactory system allows for a strong link between odors and emotions. The olfactory bulb is connected to brain regions that assess the emotional quality of odors within one (amygdala) or a few (hippocampus, orbitofrontal cortex) synapses (Zelano & Sobel, 2005). Evidence for a sexually dimorphic olfactory network comes from women having a larger concentration of grey matter in these brain areas (Garcia-Falgueras et al., 2006). The greater biological significance of olfactory signals for women was substantiated by a sex-specific increase in right amygdala activity after exposure to fear-related olfactory signals (Radulescu & Mujica-Parodi, 2013). Women seem to be endowed with an olfactory system that is specifically tailored toward detecting emotional information, as they showed more difficulty than men in overcoming increased attention elicited by survival-related signals in a cross-adaptation paradigm (Wysocki et al., 2009). Besides the distinctive neural make-up of their emotional olfactory system, women have more grey matter in brain regions that are essential for understanding and imitating (social) action

(Cheng et al., 2009). Based on this combined evidence, we expect the presence of sexual asymmetry in fear chemosignal reception, with women showing stronger signs of a partial reproduction of fear following exposure to fear chemosignals compared to men.

Before fear chemosignals can be sampled by a receiver with a sniff (Mainland & Sobel, 2006), they have to be produced by a sender. The likely candidates for fear chemosignal production are the apocrine sweat glands (Pause, 2004, 2012), not to be confused with the eccrine glands used for evaporative cooling (Sergeant, 2010). Apocrine glands are abundantly present in the armpit region, contain adrenergic receptors, and were shown to release sweat once activated by the sympathetic nervous system (see Harker, 2013). Compared to women, men on average have less yet slightly larger and more active apocrine glands (Sergeant, 2010). The complex armpit odor of men was furthermore more difficult to conceal from receivers in a cross-adaptation paradigm and this effect was observed regardless of stimulus intensity (Wysocki et al., 2009). Since current evidence regarding sexual asymmetry in chemosignal production is rather limited, we only make the tentative prediction that compared to female fear sweat, male fear sweat would induce increased fear in receivers.

Sexual asymmetry has not been the focal object of attention in research on fear chemosignaling (but see Radulescu & Mujica-Parodi, 2013), arguably because any sex differences were considered to be subordinate to emotion-specific effects induced by olfactory fear signals. Most studies on fear chemosignaling relied on male sweat samples and presented these to either male (Zernecke et al., 2011) or female participants (Zhou & Chen, 2009; Albrecht et al., 2011; de Groot et al., 2012, 2014a). Other studies used a mix of male and female senders and receivers (Chen, Katdare, & Lucas, 2006; Haegler et al., 2010; Mujica-Parodi et al., 2009; Pause, Adolph, Prehn-Kristensen, & Ferstl, 2009; Prehn, Ohrt, Sojka, Ferstl, & Pause, 2006; Prehn-Kristensen et al., 2009). The few studies that did examine sex differences focused on the recipients of chemosignals and showed that women were better than men in identifying the emotional state of donors on the basis of their body odor (Chen & Haviland-Jones, 2000). Furthermore, sweat sampled from both sexes awaiting an oral examination elicited an effect of emotional priming that was only apparent in women (Pause, Ohrt, Prehn, & Ferstl, 2004) and recruited in men much weaker brain activity as was evidenced by event-related potentials (Pause, Lübke, Laudien, & Ferstl, 2010).

To disentangle the specific influence of both the sex of the sender and the sex of the receiver on chemical communication, sexual asymmetry in fear chemosignaling has to be examined via an experiment that includes male and female senders as well as male and female receivers.

Recently, a neuroimaging study shed light on the issue by providing neural evidence for sex differences in fear sweat processing (Radulescu & Mujica-Parodi, 2013). Male fear sweat produced a strong response in the left and right amygdala of both men and women, whereas women in particular showed stronger activity in the right amygdala in response to female fear sweat (Radulescu & Mujica-Parodi, 2013). These findings were acknowledged by the authors to provide a starting point for studying sex differences in olfactory processing, given the study's small sample size and lack of power.

Using a well-powered double-blind experiment, the question we pursued was framed from a communication perspective and was aimed at providing the first affective and behavioral evidence for sexual asymmetry in fear chemosignaling: Does fear sweat produced by men and women induce a similar partial behavioral and affective reproduction of fear in male and female receivers?

The main objective of the current contribution was to determine whether men and women would show a differential partial reproduction of the state of the sender. For this purpose, we used a reliable and sensitive measure of a partial (affective and behavioral) reproduction by measuring participants' facial expressions with facial electromyography (EMG). Previous research indicated the emergence of a fearful facial expression (*medial frontalis* activity) in women following exposure to male fear chemosignals (de Groot et al., 2012, 2014a); this fearful facial expression was shown to have adaptive consequences for female receivers by eliciting a host of sensory acquisition processes related to fear, including (temporarily) increased sniffing behavior, enhanced perceptual sensitivity, and effective eye scanning (de Groot et al., 2012). Increased *medial frontalis* activity *alone* could be misidentified as surprise (e.g., Hess & Fischer, 2013) and to limit the likelihood of emotion misidentification, we additionally measured a general indicator of negative affect, *corrugator supercilii* activity, and determined that increased activity of both muscles would indicate the presence of specific negative affect namely fear (cf. de Groot et al., 2014a). Finally, facial EMG activity constitutes a sensitive indicator of a partial affective and behavioral reproduction and any systematic sex differences in facial muscle patterns induced by (male and female) fear chemosignals would be an indicator of sexual asymmetry in the chemical signaling of fear.

By controlling for the sex of the sender and the receiver, the current experimental set-up allowed for the exploration of sex differences in chemosignal perception and production. We explored whether receivers show stronger activity on the *medial frontalis* and *corrugator supercilii* muscle in response to fear chemosignals produced by men compared to women.

More importantly, we predicted that—compared to men—women would show a partial (behavioral and affective) reproduction of fear following exposure to fear chemosignals relative to the neutral condition, evidenced by *medial frontalis* and *corrugator supercilii* activity.

Method

All studies were approved by the Utrecht University Institutional Review Board, Utrecht, the Netherlands.

Part 1: Senders

Participants and design

Twenty-six participants ("senders"; 13 men: M_{age} = 22.85, *SD* = 2.91; 13 women: *M* = 21.20, *SD* = 2.66) provided written informed consent to donate sweat in two sessions (fear, neutral) separated by a week's interval. All participants were heterosexual, healthy, non-smokers who refrained from medication and had no psychological disorder. All women were required to use oral contraceptives at the time of testing to prevent ovulation, which would introduce a potential confound in the current design, as previous research indicated that odors stemming from ovulating women were rated as more attractive by men (Kuukasjärvi et al., 2004).

Materials, measures, and procedure

Donors followed a strict regimen to avoid sweat contamination starting two days before the donation session. Alcohol use, sexual activity, odorous food consumption (e.g., garlic, onions, and asparagus), and excessive exercise were prohibited. Donors were provided with scent-free hygiene products to use in the pre-donation period and they filled in a diet diary to monitor food intake. On the donation day, donors wore a pre-washed t-shirt stored in a zip-locked plastic bag to prevent odor contamination from their clothes.

After entering the lab, donors rinsed and dried their armpits with water and paper towels. The experimenter used hypoallergenic tape to attach a 10x10 cm sterile absorbent compress (Cutisorb, BSN medical GmbH & Co KG, Hamburg, Germany) under each armpit while wearing latex gloves to avoid bacterial contamination. Donors put on a new t-shirt and sweater before entering a separate room (23 °C) in which the experiment was run.

Per session, participants watched either the 30-min fear video or the neutral video. Using the original English-spoken clips, the fear video consisted of 9 clips that were demonstrated to induce fear (Schaefer, Nils, Sanchez, & Philippot, 2011; database codes: 7,

16, 28, 32, 38, 46, 50, 55, 66). The neutral video consisted of parts from a BBC documentary about Yellowstone National Park, as wildlife documentaries were shown to elicit a relaxing form of neutrality as opposed to plain neutrality, which could cause boredom or irritation (Rottenberg, Ray, & Gross, 2007).

Prior to watching the videos, participants completed 8 practice trials of the Chinese Symbol Task (CST) (Payne, Cheng, Govorun, & Stewart, 2005), which implicitly measures misattributed affect induced by the videos to seemingly unrelated Chinese symbols. Donors were instructed to press a key labeled (un)pleasant if they judged the Chinese symbol to be more (un)pleasant than the average Chinese symbol. Participants were told to ignore any preceding information when making a judgment. Each symbol, presented for 100 ms, was followed by a black and white noise mask during which a response was recorded. Response keys were counterbalanced across participants. Directly after the emotion induction procedure, donors completed 9 trials of the CST and evaluated their feelings on 7-point Likert scales. Next, sweat pads were removed, weighed, and stored separately in vials at -22 °C. Stimulus freezing does not affect the pleasantness and intensity of sweat stimuli (Lenochova, Roberts, & Havlíček, 2009). After the second session, donors were debriefed and received €30.

Part 2: Receivers

Participants and design

Informed consent was obtained from 52 participants ("receivers"; 26 men: M_{age} = 23.71, SD = 5.44; 26 women: M = 21.00, SD = 2.02). Participants had passed the pre-experimental screening that excluded left-handers, smokers, and individuals who had suffered from a psychological disorder, respiratory disease, illness, cold or allergy. All participants were assessed by means of a standardized psychophysical test of olfactory function (Sniffin' Sticks, Burghart Instruments, Wedel, Germany). The smell threshold of women (M = 9.72 binary dilution steps: 5.26×10^{-2}% phenethyl alcohol (PEA), SD = 3.61) did not differ from that of men (M = 10.14: 4.78×10^{-2}% PEA, SD = 2.97) ($t(49) = .46$, $p = .65$) (Hummel, Sekinger, Wolf, Pauli, & Kobal, 1997). Participants enrolled in a counterbalanced 2 x 2 x 2 mixed design with receiver sex (2 levels: male, female) as between-subjects factor and olfactory input (2 levels: fear, neutral) and sender sex (2 levels: male, female) as within-subjects factors.

Stimulus composition

Olfactory input was manipulated by randomly presenting individuals with fear sweat and neutral sweat. Sweat pads obtained from donors had to be prepared for presentation to receivers. For this purpose, each sweat pad (100 cm²) was cut into eight pieces (12.5 cm²). Each vial presented to participants contained four pad parts. To reduce effects of inter-individual variability in sweat production, each pad part (size: 12.5 cm²) came from a different donor and stemmed from either the left (two parts) or right (two parts) armpit in a pre-determined randomized order. Each participant was exposed to the same combination of pad parts across sweat conditions. Both participant and experimenter were unaware of the experimental condition, as each vial was marked by a three-digit code representing the sweat condition by a researcher other than the experimenter.

Our secondary target was to conceptually replicate previous results (de Groot et al., 2014a) in which facial EMG activity was measured following exposure to both olfactory information (fear, neutral) and audiovisual information (fear, neutral). To this end, audiovisual input was manipulated by presenting a number of pilot-tested video clips. These clips depicted social situations that would signal either safety or danger to a witnessing participant. In the neutral condition, clips of a woman having a conversation with a man were displayed. In the fear condition, clips depicted a woman (victim) that was assaulted by a man (perpetrator). From 72 pilot-tested clips (duration: ≥ 30 s ≤ 120 s), we selected the 12 most threatening ($M = .59$, $SD = .29$) and 12 least threatening clips ($M = .32$, $SD = .28$). This selection was based on the proportion of ambiguous Chinese symbols displayed directly after the clips (further details below) that individuals identified as threatening (vs. not-threatening). Video presentation was controlled by Presentation software (Version 16.4) installed on a personal computer (19-inch screen: FlexScan S1932, 1280 x 1024 screen resolution).

Measures and materials

Handedness scale. The Handedness scale was included to corroborate the right-handedness of the sample and to control for possible handedness-related differences in facial electromyographic (EMG) activity. On a 10-item questionnaire (van Strien, 1992; Cronbach's $\alpha = .98$), participants indicated which hand(s) they use to perform a range of activities. The current sample was right-handed (men: $M = 9.73$, $SD = .66$; women: $M = 9.77$, $SD = .43$).

Facial electromyography. Facial EMG activity was recorded bipolarly with sintered Ag/AgCl electrodes that were applied to the left side of the face—that is, the side most strongly involved in spontaneous affective reactions in right-handed participants (Dimberg & Petterson, 2000). Electrodes filled with hypo-allergenic conductive gel (Lectron II, Newark,

NJ) were applied to the *medial frontalis* and *corrugator supercilii* muscles following general guidelines (Fridlund & Cacioppo, 1986). The reference electrode was placed on the middle of the forehead. EMG signals were recorded with Biolab Acquisition Software (Version 3.0.10) and filtered online with a .5 Hz low cutoff filter and 200 Hz high cutoff filter. The EMG signal was rectified and smoothed with a 20 Hz low pass filter with a time constant of 100 ms.

Filler items. A series of three randomly selected neutral items from the International Affective Picture System (Lang, Bradley, & Cuthbert, 2008; database codes: 6150, 7002, 7025, 7035, 7100, 7217) served as filler items in the main experiment.

Sweat ratings. In randomized order, participants evaluated the sweat stimuli they were exposed to (male fear, male neutral, female fear, female neutral) with regard to their pleasantness and intensity on 7-point Likert scales (1 = "very unpleasant/weak"; 4 = "neither unpleasant/weak, nor pleasant/strong"; 7 = "very pleasant/strong").

Sweat discrimination test. To assess participants' ability to discriminate sweat, the 2-Alternative Forced-Choice Reminder (2-AFCR) task was used (Van Hout, Hautus, & Lee, 2011). On four trials, participants indicated which of two odor stimuli (presented second or third) corresponded to the reminder (R) odor stimulus (presented first). Comparisons were made between odors obtained from the conditions: fast stress (R) and slow stress (trial 1, 2), baseline (R) and slow stress (trial 3), and baseline (R) and fast stress (trial 4). Comparison stimuli were presented in a pre-determined counterbalanced order.

Smell threshold test. Participants' smell threshold was assessed with Sniffin' Sticks (Burghart Instruments, Wedel, Germany), using a triple-forced choice staircase method (Hummel et al., 1997). While blindfolded, participants were presented with three markers in a row and asked to identify the single marker that contained the target smell (phenethyl alcohol). Each marker was randomly presented (2 s), about 2 cm below participants' nostrils. The concentration of the odor in the target marker was increased each time ($1.22x10^{-4}$%-4%, with 1:2 binary dilution steps) until participants made two consecutively correct identifications, after which they were presented with a lower concentration (first reversal). If participants erred, they were again presented with a higher concentration (second reversal). The smell threshold was calculated by taking the mean of the final four (out of seven) reversal points.

Awareness check. Funneled post-experimental debriefing (Bargh & Chartrand, 2000) revealed that only 4 male participants and 1 female participant identified the olfactory stimulus as "sweat". When probed for suspicion regarding the study purpose, no participant correctly guessed the hypothesis.

Procedure

Because the presence of a male experimenter was shown to increase female participants' mood (Jacob, Hayreh, & McClintock, 2001) and to prevent a potential confound the sex of the experimenter was identical to the sex of the participant. Sweat stimuli were defrosted 30 min prior to exposure and each participant received a new vial.

After entering the lab, all participants provided written informed consent. They were instructed that physiological measures would be applied to their face, after which they had to perform a computer task and complete a series of tests. Participants were seated. The skin on the middle and left side of their forehead was cleaned with alcohol and abrasive lotion (Lemon Prep, Mavidon, Lake Worth, FL). In the short break that followed, participants filled in a handedness questionnaire, after which the cleaning routine was repeated to further reduce the impedance of the EMG signal. Next, EMG electrodes were applied. The impedance of EMG electrodes was checked with an impedance measure. In the rare cases that impedances exceeded 30 kΩ, an online check of the EMG signal was performed by the experimenter to determine whether the signal was reliably discernible from noise. To this end, participants had to lift (*medial frontalis*) and knit (*corrugator supercilii*) their brows. Electrode replacement was unnecessary.

Participants were seated in individual cubicles on an adjustable chair with their heads placed in a chin rest. This chin rest both stabilized participants' heads and supported the vial that was located 2 cm below their noses. Before the vial that contained the sweat stimulus was opened, participants watched a 4-min relaxing baseline video displaying a beach sunset with acoustic guitar soundtrack.

In a pre-determined counterbalanced order, participants were exposed to each of 4 sweat stimuli (male fear sweat, male neutral sweat, female fear sweat, female neutral sweat). Participants wore a nose clip to prevent preliminary sniffs. The nose clip was removed directly after the vial had been opened. The video capture embedded in EMG analysis software would reveal the exact moment of sweat exposure. As soon as the vial was opened, participants looked at a fixation cross that was presented in the middle of the screen for 5 seconds.

Next, per sweat exposure condition, participants were presented with 6 clips that were fear inducing (3 clips) and not fear-inducing (3 clips). Three randomly presented clips constituted a block and each randomly presented block was separated from another block by three neutral filler items (duration: 3 s). After two blocks, participants took a short break (~15 s) and the vial containing the sweat stimulus was switched. The above-mentioned sequence was repeated for the second, third, and fourth vial.

Participants finished when 24 clips had been displayed. The experimenter removed the electrodes. Next, participants were asked to rate the presented sweat stimuli on pleasantness and intensity, discriminate between sweat stimuli, and perform a smell threshold test. Finally, they were debriefed and paid €12.

Statistical analysis

Sample size ($N = 52$) was determined by a priori power analysis (G*Power 3.1; Faul, Erdfelder, Lang, & Buchner, 2007) for analysis of variance, $f = .26$, power = .80, $\alpha = .05$. Effect size f was converted (Cohen, 1988) from the lowest effect size, $\eta^2 = .06$, obtained in recent research examining the impact of fear sweat on *medial frontalis* and *corrugator supercilii* activity (de Groot et al., 2014a). The manner of handling the data was determined a priori. For all variables, outliers were identified with the most robust scale measure in the presence of outliers, by means of values that surpassed 3 median absolute deviation (MAD) units (Leys, Ley, Klein, Bernard, & Licata, 2013). When outliers were revealed for a particular variable, these values were altered to be one unit (microvolt for EMG) above the next extreme score on that variable (Field, 2009). Second, missing values due to measurement error were handled by means of stochastic regression imputation (i.e., deterministic regression imputation with an added random error component). For two female participants, the video capture indicated that the sweat stimulus was not properly presented to participants in four sweat exposure conditions; hence, EMG data was considered missing in these cases and regression imputation was applied. To reduce inter- and intra-participant variability in EMG responses, EMG data analysis was based on baseline corrected facial muscle activity. Because participants wore a nose clip that would bias the pre-exposure baseline, the a priori selected baseline constituted a time interval (600 ms) after nose clip removal that would be prior to any odorant-related response, since a typical first sniff starts after ~400 ms (Sela & Sobel, 2010) and—arguably because of ligand binding processes at the level of the olfactory receptors—the first odor-related brain potential emerges after ~300 ms (Pause, Hellmann, Göder, Aldenhoff, & Ferstl, 2008).

Results

Part 1: Senders (donors)

The effectiveness of the emotion induction (fear, neutral) procedure in the donor phase was verified by separate analyses of three parameters: sweat production, implicit affect misattribution scores, and self-reported feeling states. Relative to the neutral condition, increased sweat production, negative affect, more intense feelings of fear, and less intense feelings of calmness and neutrality were expected to result from the fear condition.

First, an ANOVA on sweat production revealed that participants produced more sweat as a function of the emotion induction condition, $F(1,24) = 6.58$, $p = .017$, $\eta^2 = .06$. Male (female) sweat production was a factor 3.83 (3.62) higher in the fear condition compared to the neutral condition. Sweat production varied neither as a function of the sex of the participant, $F < 1$, nor as a combined function of participant sex and the emotion induction condition, $F < 1$. Hence, quantity differences in sweat production emerged as a function of the affective state of the donor (Figure 1A).

To further explore this assumption, we examined the transfer of affect induced by the fear and neutral video clips to seemingly unrelated Chinese symbols. As predicted, participants rated a greater proportion of symbols as pleasant in the neutral compared to the fear condition, $F(1,24) = 7.86$, $p = .01$, $\eta^2 = .13$, as was revealed by an ANOVA (Figure 1B). The response pattern of men (fear: $M = .49$, $SD = .19$; neutral: $M = .67$, $SD = .18$) did not differ from that of women (fear: $M = .44$, $SD = .23$; neutral: $M = .55$, $SD = .17$), $F(1,24) = 2.34$, $p = .14$. Again, there was no evidence for an interaction between participant sex and the emotion induction condition, $F < 1$.

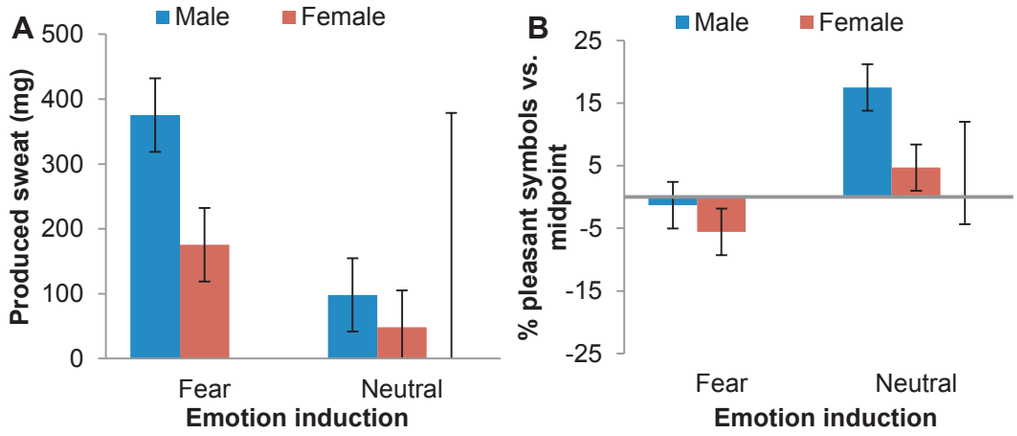

Figure 1. Mean produced sweat and implicit affect misattribution score as a function of the between-subjects (sender sex: male, female) and within-subjects (emotion induction: fear, neutral) factor. (A) Relative increase in sweat pad weight (mg) pre to post emotion induction procedure. (B) Percentage of symbols judged as pleasant (vs. unpleasant) relative to the midpoint. Within-subjects error bars indicate 68% confidence intervals; between-subjects error bar (far right) reflects the 95% confidence interval (calculations based on Loftus & Masson, 1994; interval based on recommendations by Estes, 1997).

Next, a Wilcoxon-signed ranks test was used to examine the extent to which target feeling states (fear, neutral, calmness) were impacted by the emotion induction condition. As predicted, participants reported more fear in the fear condition, $Z = 4.40$, $p < .001$, $r = .86$, and more calmness, $Z = 3.88$, $p < .001$, $r = .76$, and neutral feelings, $Z = 2.66$, $p < .001$, $r = .52$, in the neutral condition (Figure 2). Compared to the fear condition, participants in the neutral condition experienced more amusement, $Z = 2.94$, $p = .003$, more happiness, $Z = 4.17$, $p < .001$, less disgust, $Z = -4.41$, $p < .001$, less sadness, $Z = -3.12$, $p = .002$, less anger, $Z = -4.06$, $p < .001$, and less surprise, $Z = -2.87$, $p = .004$. When comparing the intensities of each feeling state per emotion induction condition, however, fear was ranked as the most intense feeling state in the fear condition (comparisons: $p < .021$, barring disgust: $p = .08$; surprise: $p = .12$), whereas calmness was ranked as the most intense feeling state in the neutral condition (all comparisons: $p < .020$). Moreover, as a within-subjects ANCOVA controlling for other negative emotional states (sadness, disgust, anger) indicated that fear was rated as significantly more intense in the fear condition (log-transformed: $M = .69$; $SD = .19$) compared to the neutral condition ($M = .03$, $SD = .09$), $F(1,19) = 7.59$, $p = .013$, there is a high likelihood that fear rather than general negative affect was induced in the fear condition. Subsequently, a Mann-Whitney U test was performed to examine sex differences in self-reported feeling states per emotion induction condition. Whereas women reported more intense neutral feelings in the neutral condition than men, $U = 45.50$, $p = .041$, men reported less intense fear, $U = 44.50$, $p = .034$, and more calmness, $U = 38.00$, $p = .013$, in the fear condition compared to women (all other comparisons: $p > .05$).

Despite sex differences in the reporting of fear (cf. Pierce & Kirkpatrick, 1992; Pickersgill & Arrindell, 1994), the combined findings indicate that the emotion induction procedure was effective for both males and females by eliciting a relaxing, pleasant state of neutrality in the neutral condition and a predominantly fearful state relative to other highly rated negative emotions in the fear-condition.

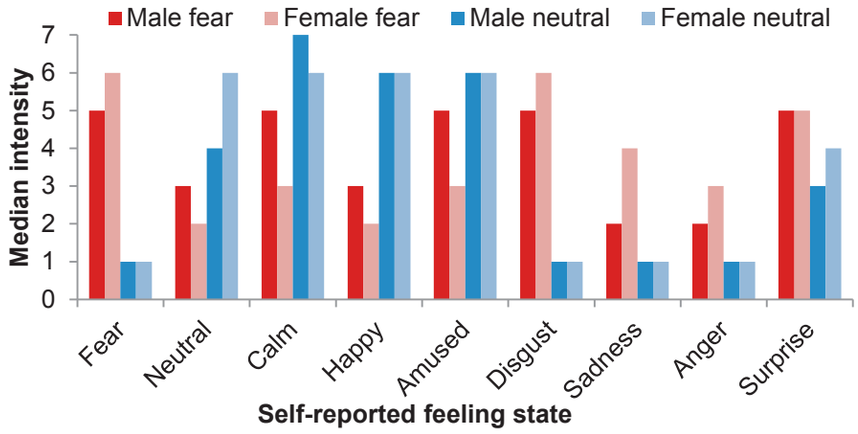

Figure 2. Median self-reported feeling state intensity on 7-point Likert scale (1 = "not at all"; 7 = "very much") as a function of the between-subjects factor (sender sex: male, female) and within-subjects factor (emotion induction: fear, neutral).

Part 2: Receivers

Fifty-two receivers were exposed to both fear and neutral sweat produced by male and female senders in a double-blind manner, while facial EMG activity was being measured. A first examination of sex differences with regard to mean facial muscle activity revealed no significant differences, *medial frontalis*, $F < 1$; *corrugator supercilii*, $F < 1$. Next, we explored sexual asymmetry with regard to chemosignal production and—more importantly—chemosignal perception by examining within-between interaction effects. Below, we report only the effects that were significant for both the *medial frontalis* and *corrugator supercilii* muscles (but see Appendix C, for additional results), since combined activation of these facial muscles was determined to imply the presence of specific negative affect, namely fear, with a low likelihood of emotion misidentification.

A four-way analysis of variance was carried out on mean facial muscle activity (*medial frontalis*, *corrugator supercilii*) with receiver sex (male, female) as between-subjects factor and sender sex (male, female), emotion (fear, neutral), and time (0-4 s) as within-subjects factors. This analysis revealed a significant three-way interaction between sender sex, time, and receiver sex, *medial frontalis*, $F(4,200) = 2.70$, $p = .032$; *corrugator supercilii*, $F(4,200) = 2.97$, $p = .021$, and another three-way interaction between emotion, time, and receiver sex, *medial frontalis*, $F(4,200) = 6.00$, $p < .001$; *corrugator supercilii*, $F(4,200) = 5.97$, $p < .001$. Next, we examined the significant two-way interactions. A distinctive facial muscle activity pattern emerged as a combined function of receiver sex and time, *medial frontalis*, $F(4,200) = 6.61$, $p < .001$; *corrugator supercilii*, $F(4,200)$ 5.39, $p < .001$, receiver

sex and emotion, *medial frontalis*, $F(1,50) = 9.98$, $p = .003$; *corrugator supercilii*, $F(1,50) = 9.73$, $p = .003$, and receiver sex and sender sex, *medial frontalis*, $F(1,50) = 5.57$, $p = .022$; *corrugator supercilii*, $F(1,50) = 6.67$, $p = .013$.

Because receiver sex constituted the common element in all significant two-way interactions, we conducted a three-way ANOVA on mean facial muscle activity (*medial frontalis*, *corrugator supercilii*) for male and female receivers separately with sender sex (male, female), emotion (fear, neutral), and time (0-4 s) as within-subjects factors. Male receivers showed a different facial muscle activity pattern over time, *medial frontalis*, $F(4,100) = 17.11$, $p < .001$; *corrugator supercilii*, $F(4,100) = 28.63$, $p < .001$, compared to female receivers, *medial frontalis*, $F(4,100) = 2.39$, $p = .056$; *corrugator supercilii*, $F(4,100) = 4.09$, $p = .004$. More importantly, female receivers showed significantly stronger facial muscle activity following exposure to fear sweat, *medial frontalis*, $F(1,25) = 9.08$, $p = .006$, $\eta^2 = .12$; *corrugator supercilii*, $F(1,25) = 6.36$, $p = .018$, $\eta^2 = .06$, regardless of the sex of the sender, *medial frontalis*, $F < 1$; *corrugator supercilii*, $F(1,25) = 3.25$, $p = .084$. For male receivers, the pattern was reversed (Figure 3). Men did not show emotion-differentiation in their facial muscle response to fear and neutral sweat, *medial frontalis*, $F < 1$; *corrugator supercilii*, $F(1,25) = 4.79$, $p = .038$ (reverse direction); yet, they did demonstrate increased facial muscle activity following exposure to sweat obtained from females as opposed to males, *medial frontalis*, $F(1,25) = 10.36$, $p = .004$, $\eta^2 = .09$; *corrugator supercilii*, $F(1,25) = 7.13$, $p = .013$, $\eta^2 = .06$. In sum, the hypothesis that female receivers are more sensitive than male receivers to emotional information embedded in sweat was supported.

With regard to chemosignal production, the exploratory hypothesis that participants would show a stronger facial expression indicative of fear following exposure to male fear sweat as opposed to female fear sweat was not supported. Instead, mixed evidence was obtained from a single factor (sender sex: male, female) ANOVA. Whereas *medial frontalis* (male receivers: $F(1,25) = 5.70$, $p = .025$; female receivers: $F(1,25) = 5.75$, $p = .024$) activity was higher following exposure to female fear sweat, *corrugator supercilii* (male receivers: $F(1,25) = 5.08$, $p = .033$; female receivers: $F(1,25) = 8.23$, $p = .008$) activity was increased following exposure to male fear sweat. In sum, whereas sexual asymmetry in chemosignal production was not observed in the current study, in line with our prediction, we did document evidence for sexual asymmetry in chemosignal reception.

The effects reported here emerged irrespective of the pleasantness and intensity of the sweat stimuli (see Appendix C). Furthermore, the removal of five participants who could identify the olfactory stimulus as sweat did not change the interpretation of the results.

Funneled post-experimental debriefing indicated that participants were unaware of (i.e., they could not verbalize) the influence of the olfactory stimulus on their behavior.

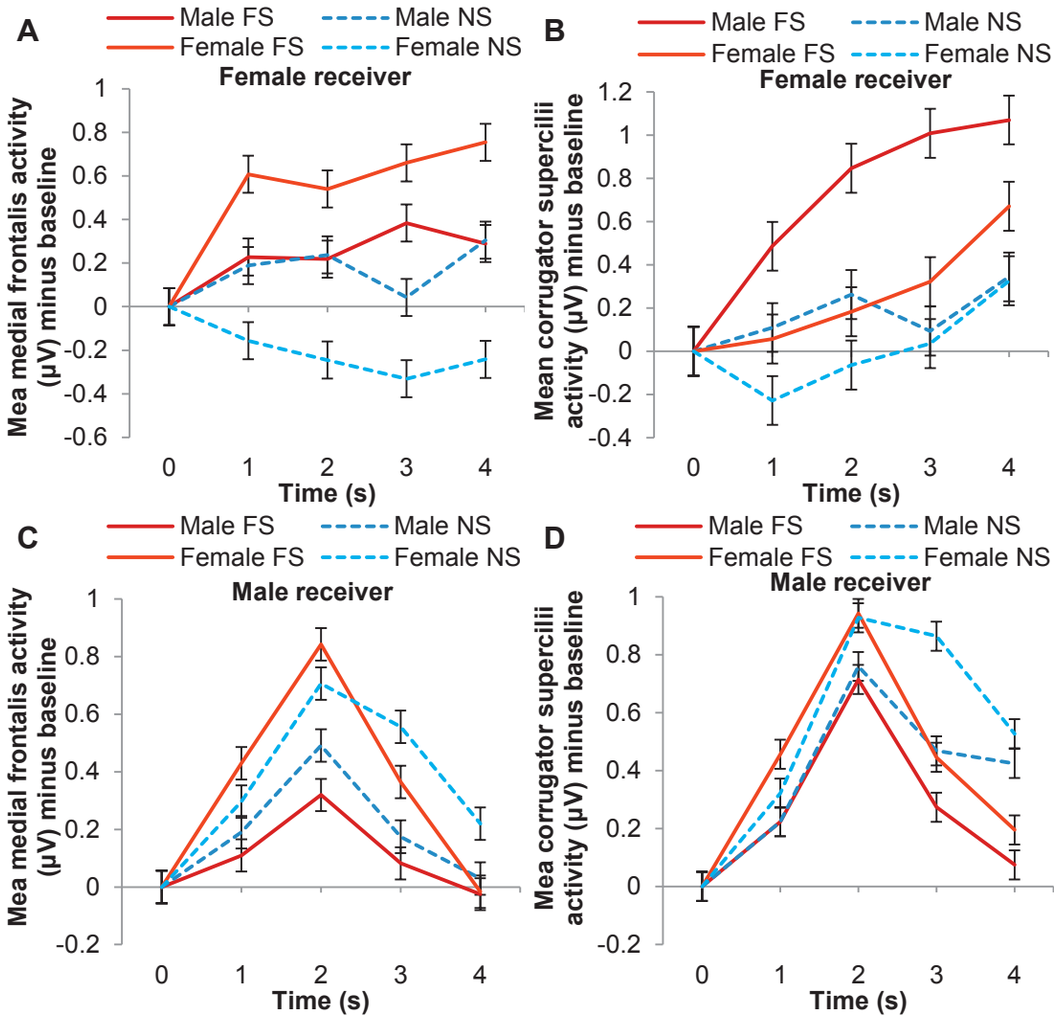

Figure 3. Mean facial muscle activity as a function of the between-subjects factor receiver sex (male, female), and within-subjects factors: sender sex (male, female), emotion (fear, neutral), and time (0-4 s). FS = fear sweat. NS = neutral sweat. (A) Mean increase in female receivers' baseline subtracted *medial frontalis* activity (microvolt) over time. (B) Mean increase in female receivers' baseline subtracted *corrugator supercilii* activity (microvolt) over time. (C) Mean increase in male receivers' baseline subtracted *medial frontalis* activity (microvolt) over time. (D) Mean increase in male receivers' baseline subtracted *corrugator supercilii* activity (microvolt) over time. Error bars reflect the 68% confidence interval based on the mean square error of the three-way interaction (Loftus & Masson, 1994; Estes, 1997).

Discussion

The object of the current research was to examine sexual asymmetry in human chemosignaling of fear. The current results indicate the presence of sexual asymmetry in chemosignal reception. That is, following exposure to fear sweat compared to neutral sweat, women demonstrated a facial expression indicative of negative affect, namely fear, whereas men did not show an emotion-differentiated response to the different types of sweat. Rather, men showed a distinctive peak in *medial frontalis* and *corrugator supercilii* after exposure to female sweat, regardless of the emotional content. Notably, the sweat of a sender may contain two types of information, one that is transient (i.e., emotional state; cf. de Groot et al., 2012, 2014a), whereas the other is static (i.e., the sex of the participant; cf. Penn et al., 2007). The facial expression assumed by receivers arguably contributed to sensory acquisition processes (Susskind et al., 2008), such as enhanced eye scanning and perceptual sensitivity (de Groot et al., 2012). By means of these processes, the facial expression may facilitate the sexes to take in information that is particularly relevant to them, with men showing stronger reactions to sex-related information, whereas women demonstrated a distinct response to survival-related information. One speculative evolutionary argument as to why women developed a greater sensitivity to (survival-related) olfactory information compared to men is that women—possessing less physical strength than men—have developed a compensatory mechanism to detect danger in the environment through a more sensitive sensory system (Brand & Millot, 2001). Nevertheless, to our knowledge, this is the first demonstration of a distinctive behavioral pattern of the sexes following exposure to chemosignals, raising the question whether these mechanisms are evolutionarily preserved, learned, or a combination thereof.

The results of the current study dovetail with previous research showing that women are more sensitive to emotional signals in general (e.g., Brody & Hall, 2000) and olfactory signals in particular (e.g., Brand & Millot, 2001; Chen & Haviland-Jones, 2000; Ackerl et al., 2002). Arguably, the specific neural make-up of the female olfactory system renders it more sensitive to emotional information and is a likely contributor to sex differences in emotional chemosignal reception. Exposure to olfactory fear signals was demonstrated to instigate increased right amygdala activity in women compared to men (Radulescu & Mujica-Parodi, 2013). Women not only have more grey matter in emotion-related parts of the olfactory system (Garcia-Falgueras et al., 2006), but also in regions that are essential for understanding and imitating social action (Cheng et al., 2009) and both these factors may contribute to establishing a common base between individuals. The current research reveals the boundary

conditions of effective fear signaling, since women, and not men, displayed a partial affective and behavioral reproduction of the chemically communicated fearful state of the sender.

The psychological state of receivers was derived from facial EMG activity over the *medial frontalis* and *corrugator supercilii* muscle. There are two limitations to this inference. First, increased *medial frontalis* and *corrugator supercilii* activity could be tied to the experience of fear (e.g., van Boxtel, 2010; Kret, Stekelenburg, Roelofs, & de Gelder, 2013, but see Hess & Fischer, 2013). However, this statement bears with it the implicit assumption that facial muscle activity could reflect discrete emotional states (e.g., Ekman, 1999). An alternative perspective suggests that emotions are rooted in *core affect* that is characterized by valence and arousal (e.g., Barrett, 2009a; Wilson-Mendenhall, Barrett, & Barsalou, 2013) and classifying a particular facial configuration as "fear" may fail to match the actual experience of the receiver (Barrett, 2009). Second, physiological outcome variables (e.g., facial EMG) may not have a one-to-one relation with psychological constructs (e.g., fear) in the sense that other constructs (e.g., negative affect) could have resulted in a similar outcome (Cacioppo & Tassinary, 1990). Hence, when the results obtained in the current research are examined in isolation, caution is required with regard to the interpretation that receivers experienced discrete fear. Nevertheless, for the following reason we presume that receivers were more likely to experience fear rather than general negative affect. Previous research using a similar paradigm (de Groot et al., 2012) provided multi-faceted evidence for the presence of fear by measuring not only facial EMG activity, but also sensory acquisition processes particularly related to fear (Susskind et al., 2008). These processes ranged from increased nasal aperture and more efficient eye scanning to enhanced perceptual sensitivity under easy task conditions (de Groot et al., 2012). Note that these findings do not challenge the assumption of core affect (i.e., high arousal, negative valence), as they provided mainly more detailed information about a person's state by demonstrating action-tendencies that would be particularly adaptive when threat is present. In sum, to increase the likelihood that the inferred psychological construct is above all fear, future research would benefit from adopting a similar multi-outcome approach.

In another vein, the sex-specific responses to fear sweat observed here ostensibly question the view of an evolutionary preserved pheromone-like one-to-one relation between produced fear sweat and perceiver fear (cf. Doty, 2010). This does not preclude fear sweat from having certain invariant properties across senders, as sex-specific responses are seemingly dependent on receivers. The fear-inducing effects of fear sweat may become apparent in female receivers only because females—generally having a better sense of smell

and greater sensitivity to emotional signals—are better equipped to combine emotion-related olfactory, audiovisual, and contextual information through associative learning (cf. Li, Howard, Parrish, & Gottfried, 2008). Learning may occur in olfactory mediated social communication as, although males did not show a partial reproduction of the fearful state of the sender in the current study, males' detectability of the emotional state of the sender was shown to be enhanced by increased familiarity with body odors (Zhou & Chen, 2011). The exact role of learning in chemosignaling in addition to evolutionary preserved mechanisms will be important to uncover in future research.

An additional open issue is whether the self, the other, or both the self and other are the *functional referent* of the olfactory fear signal. The apocrine glands are responsible for chemosignal production (Pause 2004, 2012) and what is known about apocrine glands is that they contain adrenergic receptors (Lindsay, Holmes, Corbett, Harker, & Bovell, 2008) and release sweat as a function of sympathetic activity (Shelley & Hurley, 1953; Robertshaw, 1977; Wilke, Martin, Terstegen, & Biel, 2007). Whether sympathetic activity can be considered as a more proximal mechanism than fear for the production of what is labeled "fear sweat" is still unknown. Notably, fear sweat production is not under voluntary control and was theorized to intensify the fear experience of the fear sweat producer by means of a positive feedback loop (Harker, 2013). Intensified fear may in turn lead to increased sweat production, but whether increased sweat production implies that both the self and the other are functional referents of olfactory signals is unknown, given the lack of empirical evidence. Based on the current research and previous findings (de Groot et al., 2012, 2014a), it is however safe to assume that *at least* others—by becoming fearful following fear chemosignal exposure—serve as a functional referent. Empirical studies should determine the exact referents of olfactory signals by examining whether fear chemosignals impact not only other individuals, but also the self, and if fear chemosignals impact the self, how that would in turn impact the other.

In sum, what was evidenced in the current research is that both males and females are capable of producing fear sweat that elicited a partial affective and behavioral reproduction of negative affect, namely fear, in female rather than in male receivers. Hence, female receivers were capable of establishing synchrony as they emulated the state that was experienced by the senders. By investigating the boundary conditions of effective fear chemosignaling, the approach adopted in the current research enabled us to move away from a pheromone-like view that fear chemosignals induce undifferentiated responses in receivers. Uncovering the

role of learning would further our knowledge about chemically mediated social communication—an asymmetric human capability that requires further in-depth exploration.

Chapter 6

Chemosignaling positive affect

This chapter is based on:

de Groot, J. H. B., Smeets, M. A. M., Rowson, M. J., Bulsing, P. J., Blonk, C. G., Wilkinson, J. E., & Semin, G. R. (2015). A sniff of happiness. *Psychological Science.* Advance online publication. doi: 10.1177/0956797614566318

Abstract

The transfer of happiness between individuals through mimicry induced by vision and hearing is well known, but the communication of happiness through the sense of smell via chemosignals has received little attention and the evidence is inconclusive. As chemosignals are a known medium for transferring negative emotions from a sender to a receiver, we examined whether chemosignals are also involved in the transmission of positive emotions. Positive emotions are important for overall well-being and yet relatively neglected in research on chemosignaling, arguably due to the stronger survival benefits linked with negative emotions. We observed that exposure to body odor collected from "senders" in a happy state induced a facial expression and perceptual processing style indicative of happiness in "receivers". Our findings suggest that not only negative affect, but also a positive state (happiness) can be transferred by means of odors.

Introduction

The pursuit of happiness is not an individual enterprise. As a social species, humans communicate happiness by smiling, cheering, or hugging someone, using the respective modalities of vision, hearing, and touch. However, what has received little attention and what is inconclusive in current evidence is whether there is an olfactory transfer of happiness, namely by odors produced by the body – also referred to as *chemosignaling*.

Chemosignals have been shown to convey social information, ranging from static features such as genetic relatedness (Jacob, McClintock, Zelano, & Ober, 2002) and sex (Penn et al., 2007) to emotional states (e.g., de Groot, Smeets, Kaldewaij, Duijndam, & Semin, 2012; Prehn, Ohrt, Sojka, Ferstl, & Pause, 2006; Mujica-Parodi et al., 2009; Zhou & Chen, 2009). The literature on emotional chemosignaling has focused almost exclusively on negative emotions, of which fear has received most attention. Can a positive state be communicated from a sender to a receiver? Specifically, can odors produced by a happy "sender" elicit behavioral, perceptual, and affective processes in a "receiver" that partially reflect the state of the sender?

Communication in the context of chemosignaling entails the transfer of information from a sender to a receiver, without the requirement of communicative intent (Semin & de Groot, 2013). Transmission of dynamic information such as emotional states can occur by means of diverse modalities (e.g., visual, auditory, olfactory) through their respective manifestations (e.g., facial expressions, vocal intonation, chemosignals) (Semin, 2007; Semin & de Groot, 2013). These modalities, individually or in combination, serve the purpose of establishing in a receiver a partial affective, behavioral, perceptual, and neural reproduction of the state of the sender (Semin, 2007). The word *partial* is used explicitly to denote that the receiver does not reproduce an exact copy the state of the sender. A partial reproduction of a state can occur automatically, outside of conscious access, and contributes to what we call *synchronization*: the common base required for any successful communication (Semin, 2007).

A well-known case of synchronization is the demonstration that macaque monkeys' *mirror neurons* discharge both when the monkey is engaged in a particular action as well as when the monkey observes another monkey engaging in the same action (e.g., Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). For humans, the range of actions supporting synchronization (for an overview, see Chartrand & van Baaren, 2009) include mimicry of facial expressions, language, behavior, and emotions (Hatfield, Cacioppo, & Rapson, 1993).

Evidence for synchronization has been limited mostly to the visual and acoustic domain (Semin, 2007); yet, recent research revealed the human capability to mirror another person's sniffing behavior (Arzi, Shedlesky, Secundo, & Sobel, 2014). Body odors were long neglected as a potentially shared medium in humans (but see Wilson, 1992, for a critical review of McClintock's menstrual synchrony research, first published in 1971). This changed only recently when researchers started to explore the role of chemosignals in transferring emotions (Chen & Haviland-Jones, 2000).

Humans appear to have the necessary make-up to engage in emotional chemosignaling. Apocrine sweat glands in the armpit containing adrenalin-receptors produce sweat as a function of adrenergic activity (Harker, 2013). Notably, the production of adrenalin is not limited to negative states (see Levi, 1965); arousing states on opposing ends of the valence dimension (e.g., fear, happiness) (Russell & Barrett, 1999) could lead to the release of different (quantities of) odor compounds. As a consequence, individuals may have extracted statistical regularities from the environment resulting in the formation of associations between the odor and the emotional state with which it usually co-occurs. For instance, androstadienone is associated mainly, but not always, with positive mood effects, which occur primarily in females when concentrations are high (Havlíček, Murray, Saxton, & Roberts, 2010). Humans can detect chemosignals via the main olfactory epithelium in the nose (Wysocki & Preti, 2004), as the vomeronasal organ used by animals to detect pheromones is not functional in humans (e.g., Trotier et al., 2000). By re-activating previously stored emotion-specific representations of the odor, chemosignals can serve as a medium establishing synchrony between individuals.

While robust evidence for emotional contagion via chemosignals has been reported for fear (e.g., de Groot, Semin, & Smeets, 2014a; de Groot et al., 2012; Mujica-Parodi et al., 2009; Zhou & Chen, 2009) similar effects for positive affect-related chemosignals were only examined in three studies, where happiness served mainly as a control condition for fear. In a pioneering study by Chen and Haviland-Jones (2000), female participants were shown to identify above chance "the odor of people when they were happy" from fear odor and control odor (unused sweat pads) (for a replication, see Zhou & Chen, 2011). However, although participants exposed to fear odor more often identified the most ambiguous expression (i.e., morphed halfway between happy and fear) as fearful, similar evidence was not obtained for the happy condition (Zhou & Chen, 2009). Moreover, participants were marginally less accurate at discriminating happy sweat from neutral sweat compared with differentiating fear

sweat from neutral sweat (Zhou & Chen, 2011). Arguably, happiness does not carry as much "evolutionary salience" as fear (Zhou & Chen, 2009, p. 181) and received no further attention in the chemosignaling literature. Hence, the evidence has remained inconclusive as to whether humans produce chemosignals of happiness. Moreover, if they do produce happiness chemosignals then one requires multi-faceted (behavioral, affective, and perceptual) evidence to verify whether the state of the receiver actually constitutes a simulacrum of the state of the sender.

Examining whether the state induced in receivers approximates the receivers' state requires careful attention to how one ascertains such potential correspondence. Odors and the effects they elicit are hard to verbalize (Lorig, 1999). Therefore, implicit measures were considered to be more reliable indicators of the affective state of receivers rather than self-report measures. Among the measures that would represent a behavioral, affective, and perceptual simulacrum of the state of the sender were facial expressions, mood states, and global-local processing. First, electromyographic (EMG) activity of the *zygomaticus major* and *orbicularis oculi* facial muscle would reflect happiness ("Duchenne smile"; Ekman, Friesen, & Hager, 2002), whereas the eyebrow lifting *medial frontalis* muscle would increase sensory intake, an adaptive response in fearful situations (Ekman et al., 2002; Susskind et al., 2008; cf. de Groot et al., 2012; but see Hess & Fischer, 2013, for a critique on measuring discrete emotions via facial EMG). Furthermore, from the myriad of tests that tap implicit affect and perceptual processing style, two options were selected, because they had received strong support for affect-specific modulation of task performance, namely an implicit affect misattribution task (Payne, Cheng, Govorun, & Stewart, 2005) and global-local processing tasks (see Gasper & Clore, 2002). Whereas happiness broadens the attentional scope, highly arousing negative states such as fear narrow attention (e.g., Fredrickson, 2001).

The present research examined whether sweat produced by individuals induced to be happy would modulate the facial expression (behavior), mood state (affect), and global-local processing style (perception) of receivers reflecting the sender's state. This hypothesis was tested in a within-subjects experiment that included both fear and neutral states as control conditions. The research was divided into a sweat sampling (sender) and sweat exposure (receiver) phase. In the receiver phase, exposure to sweat obtained from happy individuals was expected to elicit a Duchenne smile, positive mood, and global processing style, whereas exposure to sweat obtained from fearful individuals was expected to induce a fearful facial expression, negative mood, and more local processing style.

Method

All studies received clearance from the medical ethical committee (METC-WU), Wageningen, the Netherlands.

Part 1: Sweat sample collection ("senders")

Participants and design

12 Males (M_{age} = 22.42, *SD* = 3.80) provided written informed consent to donate sweat in three consecutive sessions (fear, happy, neutral), each separated by a week's interval. Participants were heterosexual, non-smoking (≤ 6 months) Caucasian males (18-35 years) that refrained from medication and had no psychological disorder. Only males were recruited because they have larger and more active apocrine sweat glands (cf. procedure Zhou & Chen, 2009). Only heterosexuals were included because females have been shown to evaluate homosexual male sweat differently (Martins et al., 2005).

Materials and measures

State induction. The material selected for the fear condition consisted of the original version of 9 English language clips (Schaefer, Nils, Sanchez, & Philippot, 2011; film database codes: 7, 16, 28, 32, 38, 46, 50, 55, 66). These were the same clips used to induce fear in previous experiments (de Groot, Semin & Smeets, 2014b; de Groot et al., 2014a). Happy and neutral clips were selected based on a pilot-test (N = 30). Analysis of the clips that were eventually selected revealed that participants reported significantly more happiness (happy: M = 6.05, SD = 1.12) in the happy condition than in the neutral condition (happy: 3.75, SD = 1.66), $t(28) = 7.45$, $p < .001$, Cohen's d = 2.72. Furthermore, participants in the neutral condition felt significantly more neutral (M = 4.38, SD = 1.41) than participants in the happy condition (M = 3.72, SD = 1.53), $t(28) = 2.67$, $p = .013$, $d = .97$. The happy condition contained the film clip 'Bear Necessities' from Jungle Book (4.29 min), Kurt Kuenne's short movie Validation (16.23), the opera scene from The Intouchables (2.12), and an elaborate televised prank on Mobistar (10.43). The neutral condition contained 9 scenes. The first scene (8.00) was a first person view of a car and boat traveling through the Dutch countryside. The second scene, an excerpt from "Rail away", displayed a train traveling through the Alps (13.26). Scene 3 (2.04) and 4 (2.27) were American weather forecasts, whereas old Dutch weather forecasts completed the neutral condition: scene 5 (1.11), 6 (1.04), 7 (1.06), 8 (1.02), and 9 (1.22). The total duration of the clips was about 30 minutes.

Sweat production. Sweat was sampled with a 10 x 10 cm sterile absorbent pad (Cutisorb, BSN medical GmbH & Co KG, Hamburg, Germany) and weighed on a portable LT-TP500 scale with .01 g precision. Sweat production was determined by subtracting the weight of the pad before the emotion induction from the post-induction weight.

Chinese symbol task. The Chinese symbol task (CST) implicitly measures the misattribution of affect to seemingly unrelated affectively neutral Chinese symbols (Payne et al., 2005). Each Chinese symbol was unique and stemmed from a pilot-tested database (http://www.unc.edu/~bkpayne/materials.htm).

Self-report. Participants rated to what extent they felt angry, fearful, happy, sad, disgusted, neutral, surprised, calm, and amused on 7-point Likert scales, ranging from 1 "not at all" to 7 "very much". Combinations of these states were averaged to create an indicator of low arousal (neutral, sad, calm), high arousal (angry, fearful, happy, disgusted, surprised, amused), positive affect (happy, calm, amused), and negative affect (angry, fearful, sad, disgusted).

Procedure

Participants followed a strict regimen to avoid sweat contamination starting two days before the donation session. Alcohol use, sexual activity, odorous food consumption (e.g., garlic, onions), and excessive exercise were prohibited. Donors ("senders") shaved their armpits two days before each donation session. They were provided with scent-free hygiene products to use in the pre-donation period and filled in a diet diary to monitor food intake. On the donation day, donors wore a pre-washed t-shirt stored in a zip-locked plastic bag to prevent odor contamination from their clothes.

After entering the lab, donors rinsed and dried their armpits with water and paper towels. The experimenter used hypoallergenic tape to attach an absorbent pad under each armpit while wearing latex gloves to avoid bacterial contamination. Donors put on a t-shirt and sweater before entering a separate dim-lit room (23 °C) in which the experiment was run (see Figure 1).

Participants first completed 4 practice trials of the CST. Each Chinese symbol was presented for 100 ms and was immediately followed by a black and white noise mask. Participants were instructed to press a key labeled (un)pleasant if they judged the Chinese symbol to be more (un)pleasant than the average Chinese symbol. Response keys were counterbalanced across participants. Next, participants watched a series of video clips (30 min) that were selected to induce a specific state (fear, happy, or neutral). By presenting clips

in rank order from least to most intense, donors were expected to experience a gradual buildup of emotional experience. To further maximize the effectiveness of the emotion induction procedure, donors were seated individually in the fear and neutral condition, whereas they were placed together with two other donors in the happy condition.

Directly after the state induction, donors completed 9 trials of the CST. Participants were told to ignore any preceding (visual) information when making their judgment. Subsequently, they rated their feelings on 7-point Likert scales. Next, sweat pads were removed, weighed, and stored separately in vials at -22 °C. After the third session, donors were debriefed and received €50.

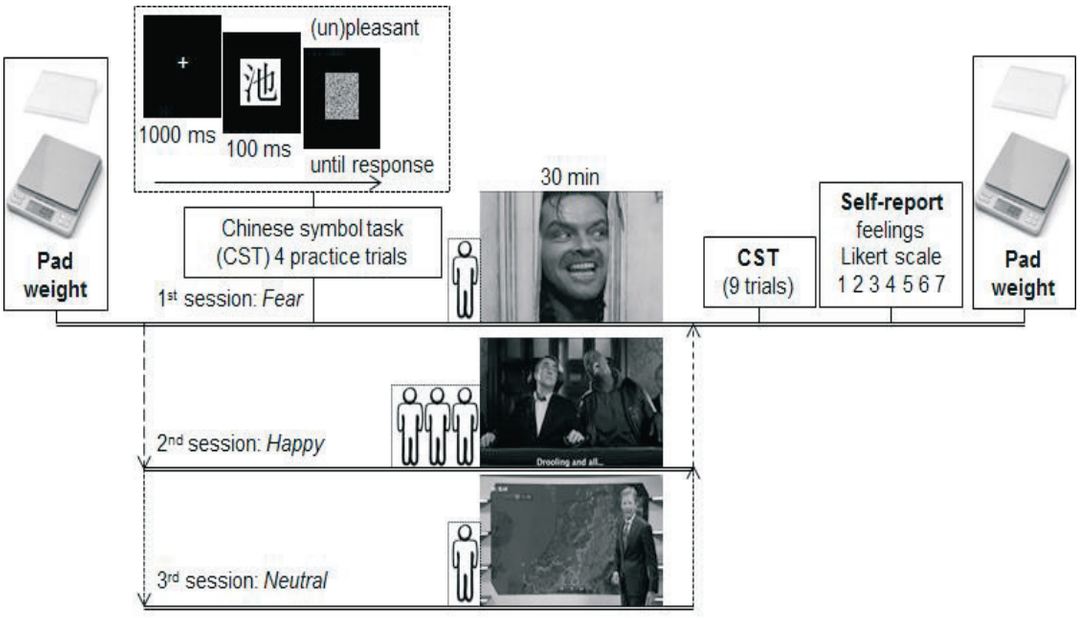

Figure 1. Schematic overview Experiment Part 1. Manipulated variable (emotional state: happy, fear, neutral) in italics, measured variables (sweat pad weight, Chinese Symbol Task scores, and explicit affect ratings) in boldface.

Statistical analysis

All data were checked for assumptions regarding normality and checked for outliers. With regard to the CST, the results of the fear condition were not included in the analysis, as the symbol ratings of 7 participants were missing due to a logging error in the program. Since self-report data was not normally distributed, a non-parametric Friedman's Test was performed. The materials from 3 of 12 donors were not used in the main experiment, as these individuals had violated multiple aspects of the protocol. The sender sample size ($N = 9$) was small, yet sufficient to provide material for the receiver experiment ($N = 35$), as each sender provided a 200-cm² pad (100-cm² from the left and 100-cm² from the right armpit); similar to

previous studies (e.g., de Groot et al., 2012), receivers were presented with a 50-cm² pad that was pooled over four senders to reduce inter-individual variation in sweat production.

Part 2: Odor exposure ("receivers")

Participants and design

Written informed consent was obtained from 36 female Caucasian undergraduates (18-35 years) (M_{age} = 20.59, *SD* = 1.85). Participants had passed the pre-experimental screening that excluded left-handers, smokers (≤ 6 months), and individuals that had participated in a similar odor experiment, suffered from a psychological disorder, respiratory disease, illness, cold or allergy. Only females were recruited as chemosignal recipients as they generally have a better sense of smell and greater sensitivity to emotional signals (cf. procedure Zhou & Chen, 2009). Indeed, gender differences were reported in emotional chemosignal reception; compared to males, only female recipients displayed behavioral consequences of fear following exposure to fear chemosignals (de Groot et al., 2014b). Furthermore, only heterosexual females were recruited because of demonstrated differences in the evaluation of male sweat as a function of female sexual orientation (Martins et al., 2005).

The olfactory threshold of participants was assessed by means of a standardized psychophysical test of olfactory function ("Sniffin' Sticks", Burghart Instruments, Wedel, Germany) indicating that participants had a normal sense of smell (smell threshold: *M* = 11.79 binary dilution steps: 2.26×10^{-3}% phenethyl alcohol, *SD* = 2.72; Hummel, Sekinger, Wolf, Pauli, & Kobal, 1997). They enrolled in a double-blind counterbalanced within-subjects design, with sweat type (3 levels: happy, fear, neutral) as single factor.

Measures and materials

Stimulus composition. Sweat pads obtained from donors were prepared for presentation to receivers as follows: first, each sweat pad (10 x 10 cm) was cut into eight equal pad parts. Four different pad parts were placed in the vial that was presented to receivers: to reduce effects of inter-individual variability in sweat production, each pad part (size: 12.5 cm²) came from a different donor and stemmed from either the left (two parts) or right (two parts) armpit in a pre-determined randomized order. Each participant was exposed to the same combination of pad parts across sweat conditions. Vials containing either sweat from happy, fearful, and neutral individuals were presented in a counterbalanced manner using a fully randomized Latin Square design. Both participant and experimenter were

unaware of the experimental condition, as each vial was marked by a three-digit code representing the sweat condition by a researcher other than the experimenter. Three of the twelve donors appeared not to have (fully) complied with the armpit shaving procedure and their samples were therefore not used in the main study.

Facial electromyography. EMG electrodes measure subtle differences in facial muscle activity as a function of the experienced emotion induced by sweat. Sintered Ag/AgCl electrodes were bipolarly applied to the left side of the face—the side most strongly involved in spontaneous affective reactions in right-handed participants (see Dimberg & Petterson, 2000, as detailed in e.g., de Groot et al., 2012). EMG signals were recorded with Biolab Acquisition Software (Version 3.0.10) and filtered online with a low cutoff (.5 Hz) and high cutoff (200 Hz) filter. The EMG signal was rectified and smoothed with a 20 Hz low pass filter with a time constant of 100 ms.

Kimchi-Palmer task. In this task (Kimchi & Palmer, 1982), participants were presented with a reference figure (e.g., a square consisting of triangles) above two adjacent comparison figures that contained either the local (e.g., a triangle made of triangles) or global (e.g., a square made of squares) elements of the reference figure. The local (global) comparison figures were presented randomly on the left and right. In 32 trials, participants had to decide which of two comparison figures was similar to the target figure by pressing one of two response keys. Response keys were counterbalanced across participants.

Navon task. In this non-geometrical equivalent of the Kimchi-Palmer task, participants were presented with relatively large letters (global elements) that were made up of smaller letters (local elements) (cf. Navon, 1977, for the original version). Each trial consisted of a reference figure (e.g., H made out of Z's) placed above two adjacent comparison figures containing either the local (e.g., T made out of *Z*'s) or global (e.g., *H* made out of F's) elements of the reference figure. The local and global comparison figures were presented randomly on each side of the screen. In a total of 32 trials participants judged which comparison figure was most similar to the reference figure. A relatively greater selection of global comparison figures reflects a predominantly global processing mode.

Dummy task. Because the Kimchi-Palmer and (adapted) Navon task could only be administered once and because no directional hypothesis was postulated for the neutral condition, participants in this condition performed a dummy task in which they classified

numbers ranging from -16 to 16 as either negative (i.e., having a minus symbol) or positive. The task consisted of 32 trials. Response keys were counterbalanced across participants.

Chinese symbol task. Identical to Experiment Part 1.

Handedness scale. The Handedness scale was included to ascertain the right-handedness of the sample and to control for possible handedness-related differences in facial electromyographic (EMG) activity. On 10 items (van Strien, 1992; Cronbach's $\alpha = .98$) participants indicated which hand(s) they use to perform a range of activities. The current sample was right-handed ($M = 9.17$, $SD = 1.95$).

Sweat ratings. In randomized order, participants evaluated the pleasantness and intensity of the sweat stimuli (happy, fear, neutral) they were exposed to during the experiment on 7-point Likert scales (1 = "not at all"; 7 = "very much").

Sweat discrimination test. To assess participants' ability to discriminate between sweat obtained from happy, fearful, and neutral individuals, participants performed the 2-Alternative Forced-Choice Reminder (2-AFCR) task (Van Hout, Hautus, & Lee, 2011). On four trials, participants indicated which of two sweat stimuli (presented second or third) corresponded to the reference (i.e., reminder) (R) sweat stimulus (presented first). Trial 1 and 2 contained a comparison between fear (R) and neutral, trial 3 between happy (R) and neutral, and trial 4 between happy (R) and fear. Comparison stimuli were presented in a predetermined counterbalanced order.

Smell threshold test. Participants' smell threshold was assessed with Sniffin' Sticks (Burghart Instruments, Wedel, Germany), using a triple-forced choice staircase method (Hummel et al., 1997). While blindfolded, participants were presented with three markers in a row and asked to identify the single marker that contained the target smell (phenethyl alcohol). Each of the markers was randomly presented (2 s), about 2 cm below participants' nostrils. The concentration of the odor in the target marker was increased each time (1.22×10^{-4}%-4%, with 1:2 binary dilution steps) until participants made two consecutively correct identifications, after which they were presented with a lower concentration (first reversal). If participants erred, they were again presented with a higher concentration (second reversal). The smell threshold was calculated by taking the mean of the final four (out of seven) reversal points.

Awareness check. Funneled post-experimental debriefing revealed that seven participants identified the olfactory stimulus as "sweat"; yet, when probed for suspicion regarding the study's purpose, none of the participants identified the hypothesis.

Procedure

Sweat stimuli were thawed ~30 min before presentation to receivers and each receiver was presented with a new vial. The experimenters were female, because in body odor-related experiments male experimenters were shown to increase positive mood in females (see Jacob, Hayreh, & McClintock, 2001).

After entering the lab, all participants received the instruction that physiological measures would be applied to their face, after which they had to perform computer tasks and a series of sensory tests (see Figure 2). Before EMG electrodes were applied, the skin below these sites was cleaned with alcohol and abrasive lotion (Lemon Prep, Mavidon, Lake Worth, FL). Participants then completed a handedness questionnaire, after which the cleaning routine was repeated. Following Fridlund & Cacioppo's (1986) guidelines, electrodes filled with hypoallergenic conductive gel (Lectron II, Newark, NJ) were applied to the middle of the forehead (reference electrode) and to the *medial frontalis* (forehead), *orbicularis oculi* (below the eye), and *zygomaticus major* (cheek) muscle. The signal impedance of each electrode was checked; in the rare cases that values > 30 kΩ were encountered, the experimenter performed an online check to verify that the EMG signal was reliably discernible from noise. Electrode replacement was unnecessary in all cases.

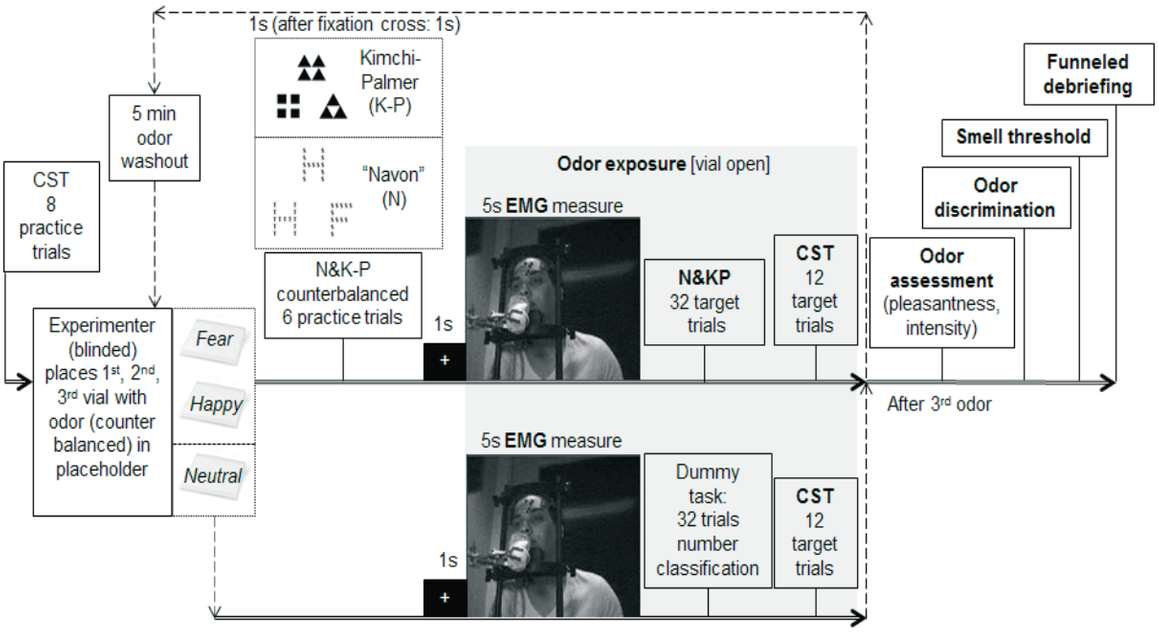

Figure 2. Schematic overview Experiment Part 2. Manipulated variables (odor exposure: happy, fear, neutral) in italics, measured variables in boldface. CST = Chinese symbol task.

Participants were seated individually on an adjustable chair with their heads placed in a head-stabilizing chin rest. The chin rest functioned as placeholder for the vial (2 cm below a participant's nose) that contained the randomly presented sweat stimulus (happy, fear, neutral). Before the vial was opened, participants watched a 4-min relaxing baseline video and practiced the CST (8 trials). Stimulus presentation was controlled by Presentation software (Version 16.4) and run on a personal computer (19-in. screen: FlexScan S1932, 1280 x 1024 screen resolution).

Next, participants were exposed to one of three sweat stimuli (happy, fear, neutral). Participants wore nose clips to prevent preliminary sniffs. The nose clip was removed directly after the vial had been opened. The video capture embedded in EMG analysis software would reveal the near exact moment of nose clip removal.

During the opening of the vial, participants looked at a fixation cross that was presented in the middle of the screen for 5 seconds. They subsequently faced 32 trials (picture display: 1 s, inter-stimulus interval: 1.5 s) of a specific computer task. To assess global-local processing style, participants performed the Navon and Kimchi-Palmer tasks that were each allocated to either the happy or fear condition in a counterbalanced manner across participants. Since both tasks are non-repeatable within participants due to possible learning effects, each receiver undertook the Navon and Kimchi-Palmer task only once. In the neutral condition, a dummy task was performed. The Navon, Kimchi-Palmer and dummy task were directly followed by an assessment of implicit affect through dichotomous ratings (pleasant vs. unpleasant) of 12 Chinese ideographs in the CST.

After completing the third assessment of implicit affect in the CST, the experimenter carefully removed the electrodes from the face of the participant. Participants rated the previously presented sweat stimuli on pleasantness and intensity, performed a sweat discrimination task, and smell threshold test, before they were debriefed and paid €12.

Statistical analysis

The primary analysis of the receiver data concerned traces of EMG movement obtained from each of three facial muscles (*medial frontalis*, *orbicularis oculi*, *zygomaticus major*) of each receiver ($N = 35$; 1 participant was excluded because of prior participation) as a function of the sweat exposure condition (happy, fear, neutral). Whenever artifacts were present across all three muscles (i.e., in 17 out of 105 cases), artifacts were removed pre-

unblinding with Mindware software (Version 2.5). Unblinding occurred after all decisions regarding data handling and statistical procedures were made.

Although facial EMG recordings provided a continuous data stream, our interest was focused on the first 5 seconds post-exposure, a time period that was summarized by averaging across 200 ms time windows. Two reasons can be provided why we charted the effect of sweat from happy individuals on facial EMG activity for this time window: (1) to reveal the independent effect of sweat from happy individuals on facial muscle activity prior to the global-local processing task; and (2) to demonstrate the effects of sweat from happy individuals in a time period that would contain at least two sniffs (Sela & Sobel, 2010), from which the second sniff was shown to be effectively modulated according to the experienced emotion (e.g., de Groot et al., 2012, 2014a).

Given that the variation in EMG data was positively skewed, a log transformation was applied to all means. Four EMG parameters (maximum, standard deviation, mean response, time to maximum) were derived from each individual profile.

Prior to any type of sweat exposure, a baseline measure of EMG activity was recorded. However, agreement was reached pre-unblinding that these baseline measures could not be used for analysis purposes. The baseline was recorded prior to nose clip application and removal and the variability introduced by the clip removal eradicated the baseline score's value for its stated purpose.

Before unblinding, we considered three alternative approaches to standardizing the data to counteract the effects of confounding factors. Approach I was to consider no correction of post-exposure EMG data, that is to ignore any baseline effect. Approach II involved a correction to a baseline estimated from the first 600 ms post-exposure. Since a typical first sniff in humans occurs around 600 ms (Sela & Sobel, 2010), facial EMG responses recorded during the first 600 ms were more likely to reflect an orientation response rather than an odor-based reaction. Although we cannot exclude the possibility that participants already registered the odor during this short interval, the worst case scenario would be that the test was in fact *less* sensitive by including an "early reaction" to the odor in our baseline measurement.

Approach III involved a correction based on an estimate of the order effect obtained from all data across all receivers and sweat exposure conditions. Although this latter approach may account for order-based variation in EMG data, any baseline variation above and beyond order-based variation would not be addressed. Nevertheless, the blind decision was to pursue all three approaches and the results were compared. Because the difference

between approaches I and III proved negligible and since no evidence of order effects was observed, only Approach I (no baseline correction) and II (600 ms baseline correction) are reported in this paper.

To account in part for the considerable participant-to-participant variation in facial muscle activity profiles, each of four EMG parameters was mean-centered around zero per participant across conditions such that parameters were interpretable as relatively high/low per participant, thus accounting for a degree of this participant-to-participant variability. So, for example, Time To Peak response recorded as 1000 ms, 2000 ms, 3000 ms for subject X in response to the three conditions would be recoded as -1000, 0, 1000 respectively. Initially, in each case, a stepwise procedure identified the best discriminating subset of parameters. Discriminant analysis was then conducted in an attempt to differentiate between facial muscle activity patterns, with distinct analyses comparing happy vs. neutral and fear vs. neutral. The happy vs. fear comparison was conducted after unblinding (post hoc), as we were primarily interested in determining whether the happy response could be discriminated from neutral next to seeking additional evidence for fear chemosignaling (vs. neutral) using a different and more optimal statistical model than analysis of variance. However, based on the results that were obtained for senders and receivers, the possibility was left open that receivers failed to show valence- or emotion-differentiated EMG responses between the happy and fear condition. Hence, a third comparison—that is, between fear and happy—was carried out to complement the initial happy vs. neutral and fear vs. neutral comparison.

The adequacy of the identified models was assessed via leave-one-out cross-validation (LOO-CV). This approach results in an unbiased estimate of the adequacy of the model by sequentially omitting each participant's response, and subsequently repeating the discriminant analysis process to verify the classification accuracy of the omitted case. The robustness of our discriminant rules under the cross-validation assessment technique should offer reassurance that the one odor repetition per participant was not inadequate and that the model is not driven by an influential subset of observations. The strength of the findings was underlined with a binomial test. The binomial test compared to chance the proportion of "receivers" for whom facial EMG patterns were correctly classified. Parallel discriminant analyses were conducted on baseline corrected (BC) and not baseline corrected (NBC) data. Although the BC method was both theoretically more justifiable and—in terms of cross-validation classification rate—mathematically superior, the results of both methods are reported.

Even though general linear modeling has been used in previous research to demonstrate EMG response differences as a function of sweat sampled under different conditions (de Groot et al., 2012, 2014a, 2014b), the current research adopted a discriminant analysis method—a decision that was taken before data collection. The current study is an exploratory exercise and we are at the stage of making observations, not claims, regarding the hypotheses. By deliberate selection of models and endpoints in this complex multi-dimensional problem it might be possible to present an unduly favorable subset of outcomes by adopting a general linear model approach. Discriminant analysis does not pre-suppose a well-defined model and endpoint.

The parameters provided along with discriminant analysis should be interpreted as follows. For the NBC method, all numbers are expressed relative to mean per subject (i.e., standardized). For example, a figure of .12 implies that the parameter in question was, on average, .12 (units) higher than was typical for subjects across all conditions. For the BC method, mean figures are standardized mean differences from baseline. The hypothetical numbers depicted in Table 1 signify that those classified into the Fear group exhibit an average difference in *medial frontalis* activity (from baseline) that is .12 units on the log scale greater than the average of this value across all conditions. It follows that on the original (unlogged) scale, average *medial frontalis* activity of the reactions classified as Fear is: $e^{.12}$ = 1.13 times (i.e., 13%) higher than the average similar figure across all conditions. Similarly, average *medial frontalis* activity classified as Neutral is $e^{-.08}$ = .92 times (i.e., 8%) lower than the average similar figure across all conditions. In the Results sections, means and standard errors are enclosed for illustrative purposes, since unlike what is the case for analysis of variance, means cannot be directly related to a *p*-value.

Table 1

Baseline corrected discriminant analysis

Classified Into	N	*Medial frontalis* activity (log mV)
Fear	35	.12
Neutral	35	-.08

Note. Hypothetical data for illustrative purposes.

Generalized linear models based on logistic regression were used to assess secondary outcomes: the proportion of pleasant (vs. unpleasant) responses in the CST and the proportion of global (vs. local) responses in the Navon and Kimchi-Palmer task. In these analyses,

"participant" was treated as a random effect, while condition, task, the condition by task interaction, and order of application were entered as fixed effects. Prior to unblinding, the absence of evidence for a difference between the Navon and Kimchi-Palmer task across opposite-valenced odor conditions (happy, fear) was verified by assessing the (coded) task by sweat exposure condition interaction, which proved to be not significant (see Results). Hence, whilst not ruling out the possibility of a difference between the Navon and Kimchi-Palmer task, this result indicated that both tasks assessed the same response and thus it was valid to combine the results ($N = 35$) yielded by the Navon and Kimchi-Palmer task into a more powerful within-subject analysis.

Results

Part 1: Sweat sample collection ("senders")

The first experimental stage consisted of sampling body odor from senders during different states (happy, fear, neutral) to be presented to receivers in the main experiment. The small sample size should be taken into account when interpreting the results reported for senders.

Since mean temperature did not significantly differ between the happy ($M = 23.16$°C, $SD = .18$°C), fear ($M = 23.22$, $SD = .16$), and neutral ($M = 23.22$, $SD = .27$) condition, $F(2,16) = .37$, $p = .70$, any differences in sweat production could be ascribed to physiological changes that accompanied the induced state. The effectiveness of the state induction procedure was determined by conducting analyses on implicit (affect projected on Chinese symbols), explicit (self-report), and objective (sweat production) measures.

With regard to the implicit affect measure, a repeated measures ANOVA on the proportion of Chinese symbols rated as pleasant showed no evidence of a significant difference between the happy ($M = .57$, $SD = .21$) and neutral ($M = .60$, $SD = .29$) condition, $F < 1$. This was contrary to the prediction that participants in the happy condition were expected to rate more symbols as pleasant compared to the neutral condition. To obtain evidence for this prediction on this subtle mood manipulation check, a larger sample size may be required.

Non-parametric analysis of the explicit measures did reveal significant differences in self-reported feelings as a function of the induced state (see Figure 3). A Friedman's test showed significant differences across conditions (happy, fear, neutral) in reported happiness, χ^2 (2, $N = 9$) = 12.77, $p = .002$, fear, χ^2 (2, $N = 9$) = 16.76, $p < .001$, and a non-significant trend for neutral feelings, χ^2 (2, $N = 9$) = 5.03, $p = .081$. The planned follow-up Wilcoxon

signed-rank test indicated that participants reported more fear in the fear condition compared to the happy condition, $Z = 2.70$, $p = .007$, $r = .55$, and neutral condition, $Z = 2.72$, $p = .007$, $r = .54$ (happy-neutral comparison, $Z = .44$, $p = .66$). More happiness was reported in the happy condition than in the fear condition, $Z = 2.69$, $p = .007$, $r = .55$, and neutral condition, $Z = 2.54$, $p = .011$, $r = .53$ (fear-neutral comparison, $Z = .87$, $p = .39$). Finally, neutral ratings were higher in the neutral condition relative to the happy condition, $Z = 2.23$, $p = .026$, $r = .50$, and fear condition (non-significant trend), $Z = 1.72$, $p = .086$ (happy-fear, $Z = -1.00$, $p = .32$). Whereas there were no differences in self-reported anger: χ^2 (2, $N = 9$) = 2.00, $p = .37$, surprise: χ^2 (2, $N = 9$) = 1.03, $p = .60$, and sadness: χ^2 (2, $N = 9$) = .33, $p = .85$, differences across conditions were observed for self-reported amusement, χ^2 (2, $N = 9$) = 12.74, $p = .002$, calmness, χ^2 (2, $N = 9$) = 7.28, $p = .026$, and disgust, χ^2 (2, $N = 9$) = 15.93, $p < .001$. The pattern of disgust is consistent with donor findings in studies inducing fear by means of video clips, which repeatedly show high disgust ratings (de Groot et al., 2014a, 2014b).

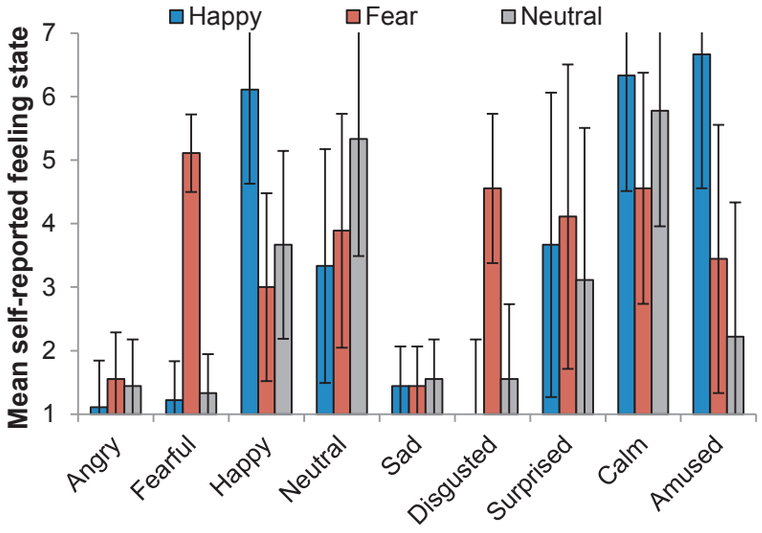

Figure 3. Mean intensity of self-reported feeling state (1 = "not at all; 7 = "very much") by senders as a function of the induced state (happy, fear, neutral). Error bars represent 95% within-subjects confidence intervals based on the mean square error of each main effect.

An analysis of core affect dimensions (low arousal, high arousal, negative affect, and positive affect) furnishes a complementary understanding. A repeated measures ANOVA on combined high arousal items (angry, fearful, happy, disgusted, surprised, amused) indicated a significant difference between conditions (happy, fear, neutral), $F(2,16) = 10.25$, $p = .001$, $\eta^2 = .42$. Compared to the neutral condition, participants scored higher on the high arousal items in the happy condition, $t(8) = 3.31$, $p = .011$, and fear condition, $t(8) = 3.94$, $p = .004$, as was

demonstrated by follow-up paired t-tests (see Figure 4). High arousal items did not reveal a difference between the fear and happy condition, $t(8) = 1.34$, $p = .22$, and low arousal items (neutral, sad, calm) did not reveal condition main effect, $F(2,16) = 2.51$, $p = .113$. However, significant effects were observed for positive affect items (happy, calm, amused), $F(2,16) = 16.31$, $p < .001$, $\eta^2 = .60$, and negative affect items (angry, fearful, sad, disgusted), $F(2,16) = 25.97$, $p < .001$, $\eta^2 = .63$. Participants in the fear condition scored higher on negative affect items compared to the happy condition, $t(8) = 8.31$, $p < .001$, and neutral condition, $t(8) = 4.70$, $p = .002$, whereas participants in the happy condition scored higher on positive affect items compared to the fear condition, $t(8) = 6.72$, $p < .001$, and neutral condition, $t(8) = 4.58$, $p = .002$. Other comparisons were not significant.

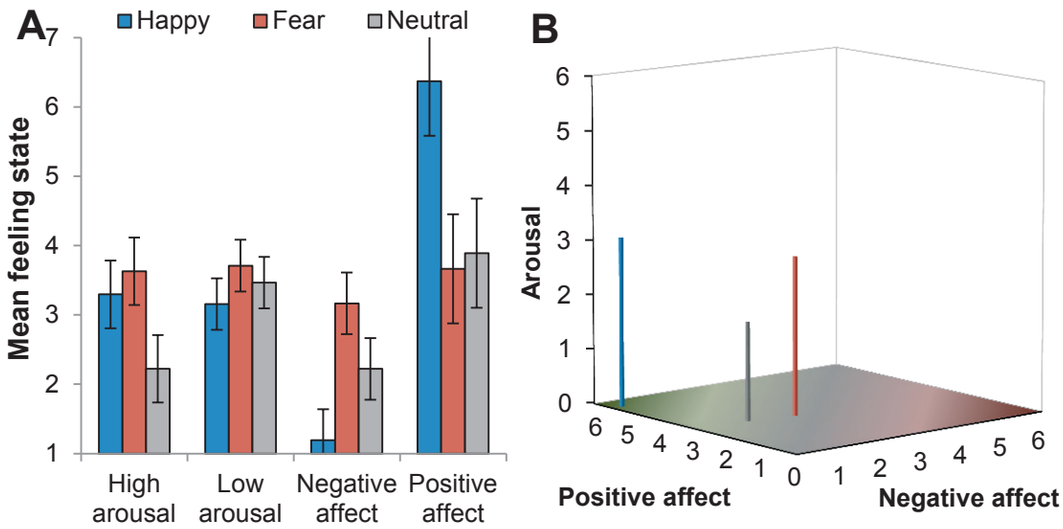

Figure 4. Experience of senders transformed into dimensions of core affect. (A) Mean self-reported feeling states divided into four categories (high arousal, low arousal, negative affect, positive affect). Error bars represent 95% within-subjects confidence intervals based on the mean square error of each main effect. (B) Affect items represented in three-dimensional space, with one dimension for positive affect (score range 0-6 corresponds to 1-7 Likert scores), one for negative affect, and one for arousal (low arousal item scores subtracted from high arousal item scores, with 3 constituting the "midpoint"). The blue bar represents that happy condition, whereas the red and grey bars represent the fear and neutral condition, respectively.

Third, a repeated measures ANOVA on sweat production with the induced state (happy, fear, neutral) as single factor revealed a significant main effect, $F(2,16) = 3.98$, $p = .04$, $\eta^2 = .16$. Follow-up paired t-tests indicated two non-significant trends (see Figure 5).

Relative to the neutral condition (M = 26.10 mg, SD = 43.86 mg), people produced more armpit sweat in both the happy condition (M = 177.8, SD = 207.85), $t(8) = 2.28$, $p = .052$, and fear condition (M = 149.40, SD = 170.30), $t(8) = 2.21$, $p = .058$. Notably, sweat production did not differ significantly between the happy and fear condition, $t(8) = .59$, $p = .569$.

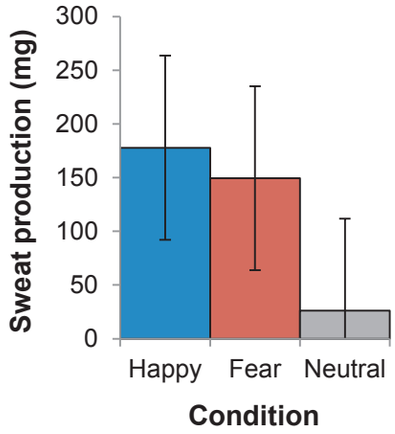

Figure 5. Mean sweat production (milligram) on 10 x 10 cm pad as a function of the induced state (happy, fear, neutral). Error bars represent 95% within-subjects confidence intervals based on the mean square error of the main effect.

In sum, the combined results suggest that predominantly positive affect was elicited in the happy condition and predominantly negative affect was induced in the fear condition. Given that the current experimental context involved an explicit manipulation of feeling state by means of videos, the senders could further label their experience as "happy" in the happy condition, "fearful" (but also disgusted) in the fear condition, and "neutral" (but also calm) in the neutral condition.

Part 2: Odor exposure ("receivers")

The preserved (frozen) sweat samples were thawed before being presented to a new group of participants (receivers: N = 35) in the main experiment. The first step was to test whether there was evidence of *correspondence* between the state of the receiver and the state of the sender. Receivers exposed to sweat obtained from happy (vs. fearful) senders were expected to show a facial EMG response that would partially reflect the happy (vs. fearful) state of the sender during sweat production.

According to leave-one-out cross-validation (LOO-CV), the identified models based on facial EMG activity patterns could adequately distinguish between the happy, fear, and neutral conditions (Table 2). The strength of the findings was underlined with a binomial test. Regardless of the application of baseline correction, receivers demonstrated significantly

different patterns of facial muscle activity following exposure to sweat obtained from senders induced to be in a happy state, compared to the fear condition and neutral condition (Table 3).

Table 2

Cross-validation outcomes for baseline correction and no baseline correction model

Method	**F → F**	**F → N**	**N → F**	**N → N**	**% incorrect**
BC	23	12	15	20	39% (27/70)
NBC	22	13	13	22	37% (26/70)
Method	**H → H**	**H → N**	**N → H**	**N → N**	**% incorrect**
BC	29	6	9	26	21% (15/70)
NBC	21	14	10	25	34% (24/70)
Method	**H → H**	**F → H**	**H → F**	**F → F**	**% incorrect**
BC	26	8	9	27	24% (17/70)
NBC	25	14	10	21	34% (24/70)

Note. BC: Baseline correction; NBC: No baseline correction. Besides the percentage of incorrect classifications (far right), the numbers reflect the amount of observations (from total: 35) of the sweat condition specified before the arrow symbol (F: Fear, N: Neutral, H: happy) that were classified into the sweat condition specified after the arrow symbol.

Table 3

Discriminant analysis

Comparison	**Method**	**LOO-CV**	***p***
Happy vs. Neutral	Baseline correction	22/35	<.001
	No Baseline correction	17/35	.002
Fear vs. Neutral	Baseline correction	16/35	.006
	No Baseline correction	12/35	.14
Happy vs. Fear	Baseline correction	21/35	<.001
	No Baseline correction	19/35	<.001

Note. The numbers under LOO-CV (leave-one-out cross-validation) indicate the number of receivers divided by the total number of receivers with both conditions correctly classified by the method. Under H_0 implying no relationship between response and treatment, only one in four receivers should be categorized completely correctly: *p* represents the *p*-value of the binomial test (H_0: proportion correct classifications = 25% vs. H_A: proportion correct classifications > 25%).

Evidence for a behavioral simulacrum of happiness following exposure to sweat obtained from senders induced to be in a happy state would be reflected by the emergence of a Duchenne smile (i.e., combined activation of the *orbicularis oculi* and *zygomaticus major* muscle). Discriminant analysis determined to what extent facial muscle activity patterns in the happy condition were different from the neutral condition (Table 1-6 in Appendix D display a complete list of means and standard errors of each facial EMG parameter classified into the discriminant model). The identified NBC method revealed that relative to the neutral condition the happy condition was characterized by a rapid peak in *orbicularis oculi* activity and delayed peak in *zygomaticus major* activity. Furthermore, the identified BC method indicated that happiness was characterized by a high peak and lower variation in *orbicularis oculi* activity next to high *zygomaticus major* activity. Further inspection of mean facial muscle activity revealed patterns consistent with our hypothesis for the BC method (see Figure 6), with high activity in the *zygomaticus major* (M_{log} = .14; corresponding to 15% higher than the average similar figure across all conditions, SE_{log} = .04) and *orbicularis oculi* (M_{log} = .10; corresponding to 11% higher than the average similar figure across conditions, SE_{log} = .03) muscles reflecting the presence of a Duchenne smile in the happy condition, compared to the neutral condition (*zygomaticus*: M_{log} = -.19; 17% lower, SE_{log} = .04; *orbicularis*: M_{log} = -.13; 12% lower, SE_{log} = .05).

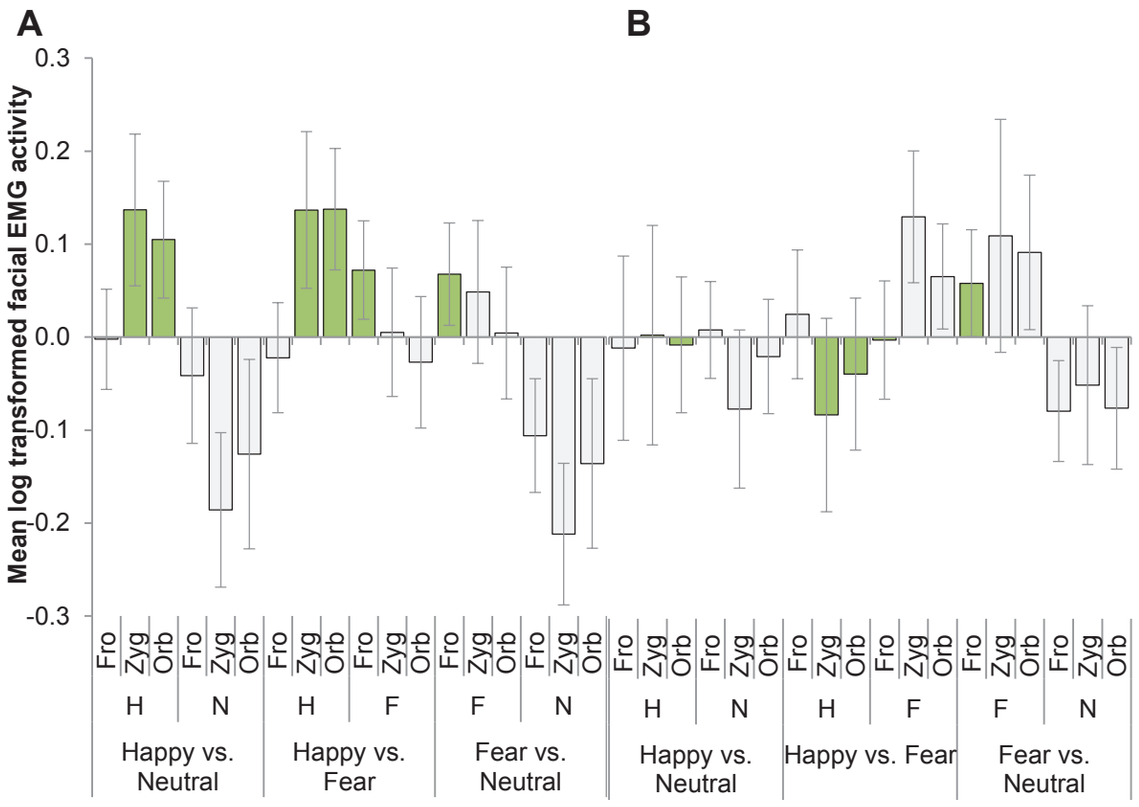

Figure 6. Mean log transformed facial muscle activity–one of the facial EMG parameters classified into sweat condition (happy, fear, neutral) by discriminant analysis. The green bars reflect facial muscle activity predicted to be elevated. Fro: *medial frontalis*; Zyg: *zygomaticus major*; Orb: *orbicularis oculi*. H: Happy, F: Fear, N: Neutral. (A) Baseline corrected data; (B) Baseline uncorrected data. Error bars represent 95% confidence intervals calculated per muscle per condition.

Next, evidence for a behavioral simulacrum of fear was derived from elevated *medial frontalis* activity (i.e., eyebrow lifting) following exposure to sweat from senders induced to be in a fearful state. The identified NBC method suggested that relative to the neutral condition, the fear condition was characterized by high variation in *medial frontalis* activity and a high peak in *orbicularis oculi* activity, whereas relatively high variation in *orbicularis oculi* activity was characteristic of the neutral condition. The identified BC method again revealed that high variation in *orbicularis oculi* activity was characteristic of the neutral condition, whereas fear was characterized by high activity in both the *zygomaticus major* (M_{log} = .05, SE_{log} = .04; vs. neutral: M_{log} = -.21, SE_{log} = .04) and *medial frontalis* (M_{log} = .07, SE_{log} = .02; vs. neutral: M_{log} = -.11, SE_{log} = .03) muscle. In sum, further inspection of mean facial muscle activity (cf. Figure 6A, BC method) indicated that besides a marked increase in *zygomaticus* activity (+5% in fear; -19% in neutral), the hypothesized increase in *medial frontalis* activity was encountered in the fear condition only (i.e., 7% higher than the average similar figure across all conditions; neutral: -10%).

The main purpose of the current research was to examine chemosignaling of happiness. However, comparing facial EMG responses classified as happy and fear to only the neutral condition leaves open the possibility that participants failed to show facial EMG responses that differed in conditions (i.e., happy and fear) representing opposite ends of the valence dimension. Hence, discriminant analysis was used to determine if facial muscle activity patterns in the happy condition were different from those patterns in the fear condition. The identified NBC method indicated that the fear condition was characterized by a high and delayed peak in *zygomaticus major* activity and greater variation in *medial frontalis* activity, whereas the happy condition was characterized by high variation in *zygomaticus major* activity, a delayed peak in *orbicularis oculi* activity, and high *medial frontalis* activity. Whereas the NBC method did not reveal emotion-differentiated facial EMG responses, the BC approach again revealed results that were consistent with our hypothesis. Whereas fear was characterized by a delayed peak in *zygomaticus major* activity and a high

peak in *medial frontalis* activity, the happy condition was characterized by a delayed peak in *orbicularis oculi* activity and high activity in both the *orbicularis oculi* (M_{log} = .14, SE_{log} = .03, vs. fear: M_{log} = -.03, SE_{log} = .03) and *zygomaticus major* (M_{log} = .14, SE_{log} = .0, vs. fear: M_{log} = .01, SE_{log} = .04) muscle. Further inspection of mean facial muscle activity (Figure 6A, BC method) indicated that consistent with our hypothesis, receivers displayed a Duchenne smile in the happy condition only (*orbicularis oculi*, happy: 15%, fear: -3%; *zygomaticus major*: happy: 15%, fear: 1%), whereas elevated *medial frontalis* activity was observed in the fear condition only (M_{log} = .07; corresponding to 9% higher than the average similar figure across all conditions, SE_{log} = .03; vs. happy, 2% lower: M_{log} = -.02, SE_{log} = .03) (Figure 1 and 2 in Appendix D consist of canonical plots showing the data that best separate the conditions in two dimensional space).

In sum, receivers were shown to emulate the state of the sender, at least behaviorally. Exposure to sweat obtained from fearful individuals induced *medial frontalis* activity, which replicates previous research (de Groot et al., 2012, 2014a, 2014b). More importantly, exposure to sweat obtained from happy individuals elicited a Duchenne smile in receivers. Hence, the current research provided the first demonstration of behavioral synchronization between sender and receiver (cf. Chen & Haviland-Jones, 2000; Zhou & Chen, 2009) realized by means of odors obtained during a positive state.

Aside from eliciting a happy facial expression, exposure to sweat from senders induced to be happy was expected to modulate perceptual processing in a manner that would partially reflect the happy state of the sender. Relative to the fear condition, receivers were expected to display a more global processing style in the happy condition. Indeed, subsequent examination of global-local responses on the Navon and Kimchi-Palmer task revealed strong evidence of a difference between the happy and fear condition, $F(1,64) = 5.54$, $p < .001$, in the expected direction (Figure 3 in Appendix D presents each individual's global-local response ratio), with a significantly greater proportion of global responses reported in the happy condition (Navon: M = 81.0%; Kimchi-Palmer: M = 71.0%) compared to the fear condition (Navon: M = 66.1%; Kimchi-Palmer: M = 57.4%). Notably, although the Navon task was significantly more likely to provoke global responses than the Kimchi-Palmer task, $F(1,63) = 3.39$, $p < .001$, the conclusion regarding the impact of sweat condition (happy, fear) on global-local processing style was not distorted because differences between sweat conditions were not task-dependent, $F < 1$. Thus, the relatively more global focus observed while receivers were being exposed to sweat obtained from senders induced to be happy was

consistent with previous research showing similar processing styles in participants under positive mood conditions (e.g., Gasper & Clore, 2002; Fredrickson, 2001).

Next to examining whether receivers emulated the happy state of the sender in terms of behavior (facial EMG) and perception (Navon, Kimchi-Palmer tasks), we analyzed whether the affective state of receivers differentially induced by the sweat condition (happy, fear, neutral) would spillover to the judgment of seemingly unrelated Chinese symbols. A greater proportion of Chinese symbols was expected to be judged as pleasant in the happy condition compared to the fear condition. However, analysis of variance revealed no evidence for the influence of sweat (happy, fear, neutral) on implicit affect, $F(2,100) = 1.09$, $p = .34$, given the proportion of symbols identified as "positive" in the happy compared to fear condition, $M_{logit} = .06$, 95% CI [-.22, .34], happy compared to neutral condition, $M_{logit} = -.14$, 95% CI [-.42, .14], and fear compared to neutral condition, $M_{logit} = -.20$, 95% CI [-.48, .08].

Near the end of the experiment, receivers rated the properties of the sweat (happy, fear, neutral) they had been exposed to. A repeated measures ANOVA found no statistically significant evidence of difference between conditions in self-reported intensity, $F(2,68) = 2.07$, $p = .134$ (happy: $M = 4.06$, $SD = 1.19$; fear: $M = 4.03$, $SD = 1.22$; neutral: $M = 3.60$, $SD = 1.09$), and pleasantness, $F(2,68) = .22$, $p = .753$ (happy: $M = 3.71$, $SD = 1.02$; fear: $M = 3.80$, $SD = 1.07$; neutral: $M = 3.86$, $SD = 1.06$). Although sweat rated as more intense was also considered to be less pleasant ($r = -.41$), facial EMG activity appeared to have emerged independently of pleasantness and intensity ratings, aside from faster *medial frontalis* peak amplitude when more intense sweat was presented ($r = -.26$) (a complete list of multivariate correlations between odor ratings and facial EMG parameters are displayed in Table 7, Figure 4, and Figure 5 in Appendix D). Furthermore, receivers could discriminate the sweat of fearful (15/35 over two tests, proportion under $H_0 = .25$, $p = .016$) and happy (24/35, proportion under $H_0 = .5$, $p = .02$) individuals from that of neutral individuals, but they could not distinguish between sweat obtained from happy and fearful individuals (correct N / total N: 17/35, proportion under $H_0 = .5$, $p = .50$), as was revealed by a binomial test on the results of the sweat discrimination task.

Discussion

The current research was designed to examine whether sweat produced by happy senders elicits a behavioral, affective, and perceptual simulacrum of happiness in receivers. Indeed, exposure to sweat from happy (vs. fearful, neutral) "senders" elicited in "receivers" a happy facial expression and more global processing style relative to fear. However, the

misattribution of happy (positive) and fearful (negative) affect to the judgment of affectively neutral Chinese symbols was not observed. Furthermore, facial muscle responses could not be related to pleasantness and intensity ratings of sweat.

Although seemingly conflicting at first, the pattern of results reported here becomes clearer when a distinction is made between measures drawing on language (i.e., sweat ratings, Chinese symbol task) versus those that are language-unrelated (i.e., facial EMG, global-local processing). The apparent disconnect between olfaction and language (Lorig, 1999) is supported by previous research reporting a similar discrepancy between EMG responses and results on the Chinese symbol task, which requires participants to select one label (e.g., pleasant) over another (i.e., unpleasant) (de Groot et al., 2014a). Concerning pleasantness ratings of sweat, the current findings dovetail with the majority of emotional chemosignaling studies (i.e., 13 out of 21) documenting no statistical differences across sweat conditions on this variable (e.g., Mujica-Parodi et al., 2009; Prehn et al., 2006; Zernecke et al., 2011). This does not imply that odor pleasantness bears no relation to EMG responses; yet, it suggests that language-based measures and language-unrelated measures tap different processes. In olfaction research, directly asking receivers what they feel—a common practice in psychology (see Baumeister, Vohs, & Funder, 2007, for a critique)—may not be optimal. Alternatively, a more successful approach would be to infer the construct of interest through within-subject designs, using implicit, non-language related measures of what can be labeled "actual behavior" (Baumeister et al., 2007).

With regard to "actual behavior", the question remains whether one can classify a state as a "discrete emotion" rather than core affect characterized by valence and arousal (Russell & Barrett, 1999). Two issues are important to this respect: first, does/do the measure(s) reflect discrete emotions or core affect?; second, did the experimental context provide consciously accessible information about the state? With regard to the first point, some researchers consider facial muscle activity indicative of discrete emotions (e.g., Ekman et al., 2002), whereas others remain skeptical as to whether one can distinguish beyond positive and negative affect (see for a review, Hess & Fischer, 2013). Because the global-local processing task and Chinese symbol task were additional measures of global affect rather than discrete states, the statement that receivers emulated the discrete state of the sender is ostensibly too strong. Notably, what may distinguish the experience of the sender and that of the receiver is the presence of an explicit experimental manipulation, allowing senders to label their experience as "fear" or "happiness", whereas the same did not hold for receivers having no (audiovisual) contextual information to explicitly label their experience.

Note that this does not contest the notion of olfactory communication, as receivers showed a simulacrum of core affect based on non-language-related measures. Hence, based on these relatively more sensitive measures, humans appear to have produced different *chemosignals* during fear (negative affect) and happiness (positive affect). The obvious next step is to test this assumption by examining the different chemical "fingerprints" responsible for eliciting positive and negative affect in receivers outside of awareness.

Although funneled debriefing indicated that receivers were unaware of the content of the vials, the presence of a nose-clip applying and removing and vial-opening experimenter may have elicited non-odor related anticipatory responses, such as those recorded over the facial muscles shortly after odor onset. Whereas the use of a double-blind within-subjects design may counteract potential confounds introduced by conspicuous odor presentation, future research needs to corroborate whether the exploratory baseline correction method reported here adequately filters out non-odor related anticipatory facial muscle responses. Presenting odors using vials is suboptimal compared to using an olfactometer (cf. Prehn et al., 2006), which delivers odors directly to the nose with a continuous airflow following the opening of a valve by a pre-programmed trigger.

Notwithstanding these limitations, the present research took the first step in resolving conflicting evidence (Chen & Haviland-Jones, 2000; Zhou & Chen, 2009, 2011) as to whether humans communicate happiness via chemosignals, by exploring whether the behavioral, affective, and perceptual processes in a receiver signify a simulacrum of the happy state of the sender. Happiness benefits the individual on multiple levels, as it restores the damaging impact of negative emotions on the cardiovascular, neuroendocrine, and immune system (Steptoe, Wardle, & Marmot, 2005) and broadens attention to inspire creative ideas (Fredrickson, 2001). Notably, humans are a social species having the capacity to *share* these positive effects, using not only the well-known modalities such as vision, hearing, and touch, but also—as this exploratory study indicates—the sense of smell.

Chapter 7

Rapid stress system drives chemical transfer of fear from sender to receiver

This chapter is based on:

de Groot, J. H. B., Smeets, M. A. M., & Semin, G. R. (2015). Rapid stress system drives chemical transfer of fear from sender to receiver. *PLoS ONE*, *10*, e0118211. doi: 10.1371/journal.pone.0118211

Abstract

Humans can register another person's fear not only with their eyes and ears, but also with their nose. Previous research has demonstrated that exposure to body odors from fearful individuals elicited implicit fear in others. The odor of fearful individuals appears to have a distinctive signature that can be produced relatively rapidly, driven by a physiological mechanism that has remained unexplored in earlier research. The apocrine sweat glands in the armpit that are responsible for chemosignal production contain receptors for adrenalin. We therefore expected that the release of adrenalin through activation of the *rapid* stress response system (i.e., the sympathetic-adrenal medullary system) is what drives the release of *fear* sweat, as opposed to activation of the slower stress response system (i.e., hypothalamus-pituitary-adrenal axis). To test this assumption, sweat was sampled while eight participants prepared for a speech. Participants had higher heart rates and produced more armpit sweat in the fast stress condition, compared to baseline and the slow stress condition. Importantly, exposure to sweat from participants in the fast stress condition induced in receivers ($N = 31$) a simulacrum of the state of the sender, evidenced by the emergence of a fearful facial expression (facial electromyography) and vigilant behavior (i.e., faster classification of emotional facial expressions).

Introduction

Accumulating evidence has indicated that humans are capable of communicating fear via the sense of smell. Neural and behavioral data showed that exposure to body odor from fearful "senders" elicited in "receivers" a state that resembled the fearful state of the sender (i.e., *simulacrum*; e.g., Mujica-Parodi et al., 2009; Zhou & Chen, 2009; de Groot, Smeets, Kaldewaij, Duijndam, & Semin, 2012; Prehn, Ohrt, Sojka, Ferstl, & Pause, 2006). Recently, a dynamic social communication framework was applied to chemosignaling research (de Groot et al., 2012; Semin & de Groot, 2013), as social communication was regarded as one of three functions of human olfaction (Stevenson, 2010). However, what previous research has not examined was the time course and physiological mechanism responsible for the release of fear chemosignals. Because apocrine sweat glands—related to chemosignal excretion (Wysocki & Preti, 2004)—are activated by adrenalin (Lindsay, Holmes, Corbett, Harker, & Bovell, 2008), we examined whether the release of so-called fear chemosignals is driven by the activation of a rapid physiological concomitant of fear, the adrenalin-releasing sympathetic-adrenal medullary (SAM) stress system. Since an empirical test of this assumption had not been forthcoming, the current research was tailored to answer the question: Is there a rapid physiological process that drives the release of a distinctive fear odor signature leading a receiver to display a simulacrum of the state of the sender?

Even though most humans nowadays live in a protected and considerably safe environment, modern societal challenges can still trigger the rather primitive response to fight or flee (Cannon, 1932). By serving to prepare an individual for action toward or away from perceived threat, the fight/flight response is an essential mechanism in the survival process of the *individual*, yet particular examples (e.g., a cry for help in a dark alley) illustrate the importance of *communicating* fear-related information to other members of the species to promote survival. From an evolutionary perspective, it can be argued that survival chances of the species were increased by using multiple (i.e., visual, acoustic, and olfactory) modalities to signal danger. Compared to olfactory signals, however, auditory and visual signals have become more important over human evolutionary history. Although auditory and visual signals can be produced *intentionally* and are quickly transferred to a receiver with the speed of sound and light, the value of rapid production and secretion of chemical markers of fear would come to the forefront when the audiovisual modalities fall short (e.g., dark environments, larger distance communication, and communication while no longer being present; Pause, 2012). At present, evidence suggests that body odors produced under

particular circumstances may still be sufficient to induce—particularly in female receivers (de Groot, Semin, & Smeets, 2014b)—a simulacrum of the state of the sender (de Groot et al., 2012, 2014a). Although fear-related odors were demonstrated numerous times to establish synchrony between sender and receiver, what has remained unknown is the (rapid) physiological mechanism that drives the production of fear chemosignals.

An answer to this question may follow from examining the physiology of the stress response. When an event is interpreted as threatening by an individual, then it elicits not only behavioral responses such as a fearful facial expression, but also physiological responses, such as in an almost instantaneous activation of the sympathetic nervous system (SNS) (McEwen, 2000). As a part of the sympathetic-adrenal medullary (SAM) system, the SNS activates the adrenal medulla, resulting in the release of adrenalin. Adrenalin exerts its short-living effects on peripheral parts of the body (Molina, 2006), for instance by activating the apocrine sweat glands in the armpit that contain (β_2 and β_3) adrenoceptors (Lindsay et al., 2008). The apocrine sweat glands differ from the eccrine sweat glands. Whereas the eccrine glands are used primarily for evaporative cooling, the apocrine glands are thought to be involved in chemosignaling (Wysocki & Preti, 2004). In sum, the release of what has been labeled fear sweat is expected to be driven by relatively rapid physiological changes that accompany a system associated with the fight/flight response, namely the SAM system.

The SAM system operates in concert with another physiological stress response system, the hypothalamus-pituitary-adrenal (HPA) axis. Both physiological stress response systems co-ordinate action to deal with threatening situations in a complex manner (Ulrich-Lai & Herman, 2009). However, what is clear is that activation of the SAM system is much more rapid (i.e., within minutes) and has short-lived effects (e.g., adrenalin circulation half-life: ~10-100 seconds) compared to HPA axis activation, which takes longer (i.e., peaks occur around 10-30 minutes after stress cessation) and effects may last for several hours (Kirschbaum & Hellhammer, 2000). Activity of the HPA axis—usually only observed under extreme circumstances—may be determined by a person's appraisal of the threatening situation and prior experience (Jones & Bright, 2001). There is no evidence to date that the main product of the HPA axis (i.e., cortisol) directly influences the most likely candidates for fear chemosignal release: the apocrine sweat glands (Harker, 2013). Hence, the relatively more rapid SAM system is presumed to activate the apocrine glands through the release of adrenalin, which drives the release of a distinctive affective signature that can be picked up by and modulate the behavior of another individual.

The odor emitted by humans as a function of fear, or rather, as a reaction to a threatening stimulus, may thus have a distinctive signature. Recent evidence provided strong biochemical support for the hypothesis that the odor produced by people who were sick was qualitatively different from a placebo condition, ostensibly refuting the argument that a person's reaction to sweat produced under particular conditions is simply based on the presence of "more of the same components" (Olsson et al., 2014). Similar to what has been demonstrated for the scent of disease (Olsson et al., 2014), a qualitatively different odor may be produced rather quickly in the case of fear, facilitated by apocrine sweat that arrives on the skin along with odorless precursor molecules. Enzymes of axillary (armpit) skin bacteria transform these precursor molecules into volatile odoriferous substances (Natsch, Derrer, Flachsmann, & Schmid, 2006) that can be sampled with a sniff. Hence, a quick and distinctive chemosensory cue may be released into sweat in the case of threat, the effect of which can be observed in a receiver who is expected to show a simulacrum of the sender's experience.

Even though fear was not experimentally induced and the establishment of a simulacrum of the experience of a sender in a receiver was not examined, one study reported evidence suggestive of qualitative differences in apocrine sweat related to stress (Wysocki et al., 2009). More specifically, intradermal injection of adrenalin stimulated the apocrine glands in the armpit to produce a rapid flux of apocrine secretion onto the skin surface (Wysocki et al., 2009) (for the procedure, see Zeng et al., 1992). This apocrine secretion, rated as stronger and as more pungent than regular armpit sweat, was more difficult to mask with other odorants (Wysocki et al., 2009). The apparent resistance to masking of stress-related apocrine sweat may illustrate the importance of the stress-related signal in transmitting information to conspecifics. However, conclusions regarding the communicative value of the signal cannot be drawn without testing whether receivers display a simulacrum of the state of the sender following exposure to sweat released as a result of experimentally induced fear.

Previous research has provided relatively consistent neural and behavioral evidence with regard to receivers exposed to sweat that was obtained from participants induced to be in a state of fear or anxious apprehension. Fear was induced by means of horror movie clips (Chen & Haviland-Jones, 2000; Chen, Katdare, & Lucas, 2006; Zhou & Chen, 2009, 2011; de Groot et al., 2012, 2014a, 2014b), participation in a high rope course (Haegler et al., 2010; Albrecht et al., 2011; Zernecke et al., 2011), and tandem skydiving (Mujica-Parodi et al., 2009; Rubin, Botanov, Hajcak, & Mujica-Parodi, 2012; Radulescu & Mujica-Parodi, 2013).

Others sampled sweat from individuals prior to an academic examination (Pause, Ohrt, Prehn, & Ferstl, 2004; Prehn et al., 2006; Pause, Adolph, Prehn-Kristensen, & Ferstl, 2009; Prehn-Kristensen et al., 2009; Pause, Lübke, Laudien, & Ferstl, 2010; Adolph, Meister, & Pause, 2013) and during the administration of the Trier Social Stress Task (Dalton, Mauté, Jaén, & Wilson, 2013; Wintermann, Donix, Joraschky, Gerber, & Petrowski, 2013). Although procedures to induce fear or anxiety differed markedly, the relatively consistent findings in receivers, ranging from amygdala activity (Mujica-Parodi et al., 2009) to the emergence of a fearful facial expression (de Groot et al., 2012, 2014a, 2014b) and vigilant behavior (de Groot et al., 2012) point to a common physiological mechanism that drives the quick release of chemosignals related to fear and anxiety.

Previous research has already shown that different stress manipulations led to increased cortisol levels (Mujica-Parodi et al., 2009; Prehn-Kristensen et al., 2009; but see Ackerl, Atzmueller, & Grammer, 2002, for nonsignificant differences), heart rate (in virtually all studies, e.g., de Groot et al., 2012; Adolph et al., 2013, but see Chen et al., 2006, for nonsignificant differences) and skin conductance levels (e.g., Zhou & Chen, 2011) compared to the neutral condition. However, the underlying physiological mechanism had not been systematically manipulated and median sweat sampling times constituted 30 minutes. As a consequence, no evidence was documented that could substantiate the claim that the production of what has been labeled fear or anxiety sweat could be produced relatively rapidly as a function of SAM activity. If indeed the SAM system would be responsible for driving the release of fear sweat, sweat sampling procedures could be reduced by many minutes, and sampling procedures could become more effective by using measures of SAM activity. Essentially, to determine whether the release of fear/anxiety sweat by so-called senders is related to SAM activity following a threatening event rather than HPA activity, indicators of fast and slow stress need to be examined in combination.

Present research

The present research examined whether the activation of the fight/flight response (i.e., SAM activity) following the introduction of a social stressor would lead to the production of a qualitatively different body odor that would induce a *simulacrum* of the sender's state in a receiver. To this end, we first introduced senders to a well-validated social stressor, the Trier Social Stress Task (TSST; Kirschbaum, Pirke, & Hellhammer, 1993). Previous research successfully used the TSST to elicit "stress sweat" (Martin et al., 2011; Schmidt-Rose et al., 2013; Biehle-Hulette et al., 2014). However, what has remained unclear has been the time

frame of stress sweat production and whether receivers would show a simulacrum of the state of the sender. To test the hypothesis that SAM activity (vs. HPA axis activity) drives the chemical transfer of fear from sender to receiver, sweat sampling was divided into a "fast stress" and "slow stress" interval. First, sweat was sampled during a relaxing baseline (10 min). Next, sweat was sampled during the "fast stress" condition; participants prepared for a speech in front of an expert audience (10 min) which would result in a quick SAM response. Finally, "slow stress" sweat was sampled at a later time interval (10 min) during which SAM activity would have waned at the expense of high HPA axis activity (i.e., the slower stress response system) (Kirschbaum & Hellhammer, 2000).

Evidence for the hypothesis that the activation of the fight/flight response (i.e., SAM activity) following the introduction of a social stressor would lead to the production of a qualitatively different body odor was derived from two sources: the sender and the receiver. Three measures were used to assess whether target states were effectively induced in senders. Heart rate (HR) is a well-established non-invasive (compared to a blood test) and non-controversial measure (compared to α-amylase) of the sympathetic nervous system component of the SAM stress response (Nater & Rohleder, 2009). The amount of armpit sweat could serve as a second indicator of SAM activity, because the adrenal medulla releases adrenalin, which activates the apocrine sweat glands in the armpit region. Third, salivary cortisol is a reliable indicator of HPA axis activity (Jones & Bright, 2001). Compared to baseline, the fast stress condition was expected to be characterized by high HR and increased axillary sweat production, whereas high cortisol levels were expected to be encountered in the slow stress condition.

What is essential is that receivers were expected to display signs of a simulacrum of the state of the sender only when they were exposed to sweat obtained from participants in the fast stress condition. Since the effects induced by odors are usually hard to verbalize (Lorig, 1999), only implicit measures of affect and behavior were included. Specifically, a simulacrum of fear was determined by (i) measuring the emergence of a fearful facial expression (i.e., increased *medial frontalis* and *corrugator supercilii* activity; cf. de Groot et al., 2012, 2014a, 2014b) and explored further by (ii) assessing whether participants displayed increased speed and/or accuracy with regard to the classification of fearful facial expressions, compared to happy, neutral, and disgusted expressions. Since previous research reported facilitated recognition of fearful facial expressions when these expressions (i.e., visual information) were paired together with fearful voices (Dolan, Morris, & de Gelder, 2001), we expected that exposure to fast stress odor would result in enhanced processing of fearful

facial expressions, compared to (other) negative affective expressions (disgust), positive affective expressions (happiness), and neutral expressions.

Method

All studies were approved by the Utrecht University Institutional Review Board, Utrecht, the Netherlands.

Part 1

Participants and design

Eight males ("senders"; M_{age} = 22.50, SD_{age} = 3.25) provided written informed consent prior to participating. In line with previous research (see e.g., Zhou & Chen, 2009; de Groot et al., 2012), we recruited only males because they have larger and more active apocrine sweat glands responsible for chemosignal production. All participants reported to be heterosexual, healthy, and non-smokers. They refrained from medication and were not diagnosed with a psychological disorder. Each participant completed three within-subjects conditions in the following order: baseline, fast stress, and slow stress.

Materials and measures

Personality. The Dutch version (Sanderman, Arrindell, Ranchor, Eysenck, & Eysenck, 1995) of the Eysenck Personality Questionnaire-Revised Short Scale (EPQ-RSS; Eysenck & Eysenck, 1991) was administered to measure psychoticism, neuroticism, extraversion, and social desirability. The EPQ-RSS consists of 48 yes/no items. Senders' scores on the subscales (12 items each) fell in the typical range (neuroticism: M = 3.75, SD = 2.82; psychoticism: M = 3.62, SD = 2.00; extraversion: M = 7.88, SD = 2.95; social desirability: M = 3.50, SD = 2.73).

Sweat pad weight. Sweat was sampled from each axilla (armpit) on a 10 x 10 cm sterile absorbent compress (Cutisorb, BSN medical GmbH & Co KG, Hamburg, Germany) and weighed on a TP 500 pocket scale with .01 gram precision. Sweat was sampled during 10 minutes (baseline, fast stress, slow stress). A 10 minute sweat sampling interval is likely to be sufficient as axillary stress sweat production could be as high as 32 mg/min (unpublished data, as cited in Biehle-Hulette et al., 2014) and previous research showed that receivers displayed a simulacrum of fear after exposure to "fear sweat" that weighed ~200-300 mg (de Groot et al., 2014b).

Heart rate. Heart rate was recorded with a photoplethysmograph (PPG) transducer (TSD200C, BIOPAC Systems, Inc., CA, USA) attached to the right ear lobe. Operating with a pulse plethysmogram amplifier (PPG100C), the TSD200C consists of a matched infrared emitter (wavelength: 860 nm ± 60 nm) and photo diode detector, which transmits changes in infrared reflectance resulting from varying blood flow.

Cortisol. Salivary cortisol was sampled while participants gently chewed on a cotton swab that was contained in a transparent plastic test tube (Salivette, Sarstedt, Newton, North Carolina). Cortisol measurement would not be affected by salivary flow rate (Vining & McGinley, 1987).

Procedure

Donors followed a strict regimen to avoid sweat contamination starting two days before the sweat donation session. Alcohol use, sexual activity, odorous food consumption (e.g., garlic, onions, and asparagus), and excessive exercise were prohibited. Donors were provided with scent-free hygiene products to use in the pre-donation period. They filled in a diet diary to monitor food intake. On the donation day, donors wore a pre-washed t-shirt stored in a zip-locked plastic bag to prevent odor contamination from their clothes. From one hour before the experiment, participants were not allowed to eat food with high sugar or acidity, or take in high doses of caffeine, as this could compromise the cortisol level assay.

The actual experiment took 70 min and was carried out in the afternoon (13:00–17:00), as cortisol levels would show less variation during these hours (Kirschbaum & Hellhammer, 2000). Sweat was sampled during 10 min on three occasions (Figure 1): baseline, fast stress (SAM activity), and slow stress (HPA activity). The first sweat sampling session was preceded by a 20 min wildlife documentary (BBC's "Yellowstone, Autumn") that was used to induce a pleasant-neutral *baseline* feeling state (Rottenberg, Ray, & Gross, 2007; cf. de Groot et al., 2014a, 2014b). The documentary started as soon as participants had gently chewed on a Salivette for one min. The documentary—divided into six parts—was shown during the non-sweat sampling intervals (Figure 1) and both during the baseline condition and slow stress condition. During the fast stress condition, participants performed the anticipatory stage of the (adapted) Trier Social Stress Task (Kirschbaum et al., 1993); they received a pre-recorded verbal instruction to prepare for an application as research assistant in front of a panel of scientists.

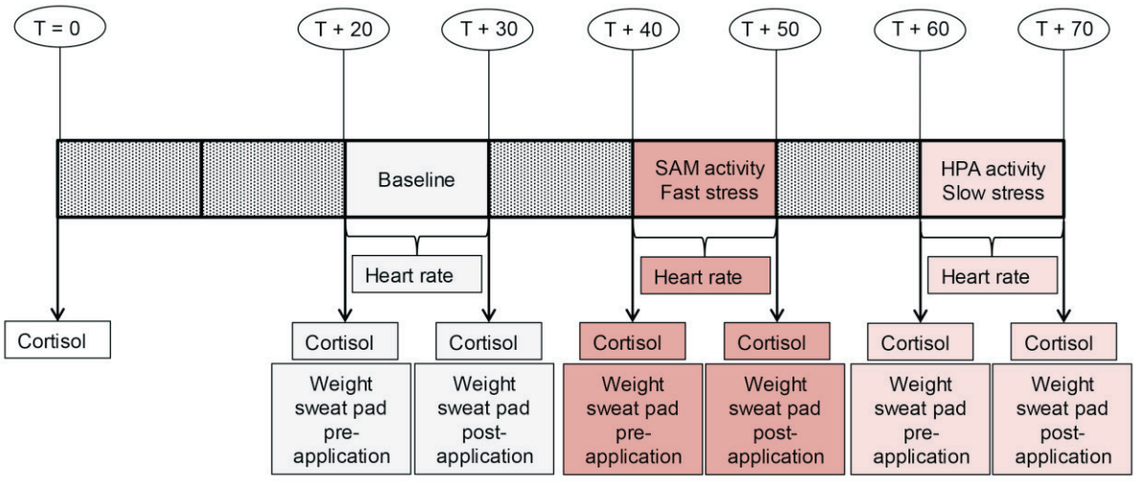

Figure 1. Study design Experiment Part 1. The timeline displays sweat sampling conditions: baseline, fast stress (i.e., SAM activity), slow stress (i.e., HPA axis activity), and measurements: heart rate, cortisol, sweat production. *T* = time (*T* + 20 = 20 min passed since the start of the experiment).

Prior to each sweat sampling session, donors rinsed and dried their armpits with water and paper towels. The experimenter wore vinyl gloves to avoid bacterial contamination and used hypoallergenic tape to attach a pre-weighed pad under each armpit. Donors put on a new t-shirt and sweater before entering the cubicle (23 °C) in which the experiment was run. The heart rate sensor was applied to the ear lobe. Once the experimental condition was finished, the participant called the experimenter, who removed the ear lobe sensor and sweat pads. Salivettes were frozen at -22 °C. All sweat pads were weighed and stored separately in vials at -22 °C. The hedonic properties and intensity of sweat would not be affected by stimulus freezing (Lenochova, Roberts, & Havlíček, 2009). When the third sweat sampling condition was finished, donors were debriefed and they received €30 for their participation.

Statistical analysis

According to a Shapiro-Wilk test, cortisol, heart rate, and sweat pad weight data were normally distributed. Analysis of Salivettes was performed by a specialized relation lab of U-diagnostics (Utrecht, the Netherlands), who provided us with the cortisol levels (nmol/l). There were no missing cortisol and sweat pad weight data. Heart rate data contained substantial artifacts in a number of cases. The start and end points of these artifacts were documented and artifact deletion was applied before calculating mean heart rate (beats per minute, bpm). In two cases, heart rate data was incorrectly recorded, and stochastic regression imputation including a random error term was applied. The material of eight

senders would be sufficient to present to 32 receivers in Experiment Part 2. Nevertheless, 10 participants were tested in total, because two donors did not adhere to the protocol/instructions. Their material was not used and their data were not analyzed.

Part 2

Participants and design

Informed consent was obtained from 32 female participants ("receivers"); 1 participant was excluded from data analysis as this person had participated in a similar study before (N = 31: M_{age} = 21.00, SD_{age} = 2.02). Only females were recruited as chemosignal recipients as they generally have a better sense of smell and greater sensitivity to emotional signals (cf. Zhou & Chen, 2009; de Groot et al., 2012). Moreover, gender differences in chemosignal reception exist with only female receivers showing the behavioral (de Groot et al., 2014b) and neural (Radulescu & Mujica-Parodi, 2013) consequences of fear after fear sweat exposure. Participants had passed the pre-experimental screening that excluded left-handers, smokers, and individuals who had a psychological disorder, respiratory disease, illness, cold or allergy. All participants were assessed by means of a standardized psychophysical test of olfactory function (Sniffin' Sticks, Burghart Instruments, Wedel, Germany); 29 participants had a normal sense of smell [phenethyl alcohol (PEA) threshold: M = 10.35 (binary dilution steps – corresponding to 6.11×10^{-2}% liquid concentration), SD = 3.04, range: 3.25 (i.e., 8.41×10^{-1}%)–15.25 (i.e., 2.05×10^{-4}%)] (Hummel, Sekinger, Wolf, Pauli, & Kobal, 1997) and the scores of 3 participants (≤ 5 binary dilution steps) would label them "hyposmic" (Wolfensberger, Schnieper, & Welge-Lüssen, 2000). Only non-smellers would be excluded and none were encountered. Participants enrolled in a counterbalanced 3 x 4 x 5 within-subjects design with odor (3 levels: baseline, fast stress, slow stress), facial expression (4 levels: fear, disgust, happiness, neutral) and the degradation level of the presented facial expression, "noise level" (5 levels: 20, 40, 60, 80, 100%), as within-subjects factors.

Measures and materials

Odor stimulus composition. Sweat pads that were obtained in the donor phase had to be prepared before presentation to receivers. The first step consisted of cutting each sweat pad (10 x 10 cm) into eight parts (12.5 cm²) with sterilized scissors. To reduce effects of inter-individual variability in sweat production, each vial that would eventually be presented to receivers contained pad parts (four in total) that came from a different donor and stemmed from either the left (two parts) or right (two parts) armpit in a pre-determined randomized

order. Each participant was exposed to the same combination of pad parts across odor conditions. Odor presentation was double-blind, because each vial was marked by a code representing the odor condition by a researcher that was not involved in running the experiment.

Handedness scale. A Handedness scale was included to corroborate the right-handedness of the sample and to control for possible handedness-related differences in facial muscle activity. On a 10-item questionnaire (Van Strien, 1992) (Cronbach's $\alpha = .98$), participants indicated which hand(s) they use to perform a range of activities. All participants were right-handed ($M = 9.39$, $SD = 1.05$).

Facial electromyography. Facial electromyographic (EMG) activity was recorded bipolarly with sintered Ag/AgCl electrodes that were applied to the left side of the face—the side most strongly involved in spontaneous affective reactions in right-handed participants (Dimberg & Petterson, 2000). Following general guidelines (Fridlund & Cacioppo, 1986), electrodes filled with hypoallergenic conductive gel (Lectron II, Newark, NJ) were applied to the muscle that lifts the eyebrow, *medial frontalis*, and to the muscle that furrows the brow, *corrugator supercilii*. The reference electrode was placed on the middle of the forehead. EMG signals were recorded with Biolab Acquisition Software (Version 3.0.10) and filtered online with a .5 Hz low cutoff filter and 200 Hz high cutoff filter. The EMG signal was rectified and smoothed with a 20 Hz low pass filter with a time constant of 100 ms.

Noisy Facial Expression Classification Task. In the Noisy Facial Expression Classification Task (NFECT), participants had to classify four types of facial expressions. The expressions were negatively valenced (fear, disgust), positively valenced (happiness), and neutral. All photos stemmed from the Radboud Faces Database (RFD) (Langner et al., 2010) (codes: m23, v02, m33, v12, m25, v22, m71, v27). The facial expressions that were used in the experiment were first converted to grey-scale in Adobe Photoshop (CS6, Adobe systems Inc., San Jose, CA), after which a Gaussian noise filter (20%, 40%, 60%, 80%, 100%) was applied to only the face (i.e., not to the hair, clothes, and background). A 100% noise filter did not imply that the facial expression was invisible. However, quick stimulus presentation (50 ms) made it relatively difficult to classify the "noisier" expressions. Noise level was manipulated for exploratory purposes, namely to examine whether body odors related to fear would enhance the accuracy/speed of detection of facial cues even when these cues were difficult to detect.

Full facial expression classification. This task was used to check whether static facial expressions would lead to facial mimicry. Participants viewed 24 full-colored pictures from the Radboud Faces Database (RFD) (Langner et al., 2010) (codes: m23, v02, m33, v12, m25, v22, m71, v27). Of the 24 stimuli, 12 pictures displayed a (fe)male actor; 6 faces contained a fearful, disgusted, happy, or neutral expression.

Empathy Questionnaire. Because the emergence of a simulacrum may depend on the level of empathy of a receiver, a translated digital version of the empathy quotient (EQ) questionnaire (Baron-Cohen & Wheelwright, 2004) was administered. On this 60-item questionnaire (including 20 filler items), participants had to indicate on a 4-point Likert scale to what extent they agreed with statements related to empathy (0 = "strongly disagree", 1 = "slightly disagree", 2 = "slightly agree", 3 = "strongly agree"). With a mean score of 47.42 (*SD* = 7.61), the current sample fell within the normal score range (<1 *SD* above the *M*; Baron-Cohen & Wheelwright, 2004).

Reading the Mind in the Eyes Task. Because the EQ may be susceptible to reporting bias, a computerized adaptation of the revised "Reading the Mind in the Eyes Task" (RMET) (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001) was used to objectively assess participants' ability to infer another person's emotional state. The revised RMET consists of 36 photographs depicting the eye region of different (fe)male actors. Participants were asked which one of four descriptions of the photograph best described the state of the person. The current sample had an RMET score that fell in the normal range (*M* = 27.68, *SD* = 2.97) (Baron-Cohen et al., 2001).

Odor ratings. In a pre-determined counterbalanced order, participants evaluated the odors they were exposed to (baseline, fast stress, slow stress) on pleasantness and intensity (7-point Likert scale; 1 = "very unpleasant/weak"; 4 = "neither unpleasant/weak, nor pleasant/strong"; 7 = "very pleasant/strong").

Odor discrimination test. To assess participants' ability to discriminate the presented odors, the 2-Alternative Forced-Choice Reminder (2-AFCR) task was conducted (Van Hout, Hautus, & Lee, 2011). On four trials, participants indicated which of two odor stimuli (presented second or third) corresponded to the reminder (R) odor stimulus (presented first). Comparisons were made between odors obtained from the conditions: fast stress (R) and slow stress (trial 1, 2), baseline (R) and slow stress (trial 3), and baseline (R) and fast

stress (trial 4). Comparison stimuli were presented in a pre-determined counterbalanced order.

Smell threshold test. Smell threshold was assessed with Sniffin' Sticks (Burghart Instruments, Wedel, Germany), using a triple-forced choice staircase method (Hummel et al., 1997). While blindfolded, participants were presented with three markers in a row and asked to identify the single marker that contained the target smell (phenethyl alcohol). Each marker was randomly presented (2 s) about 2 cm below the nostrils of the participant. The odor concentration of the target marker was increased each time ($1.22x10^{-4}$%-4%, with 1:2 binary dilution steps) until participants made two consecutively correct identifications, after which they were presented with a lower concentration (first reversal). If participants erred, they were again presented with a higher concentration (second reversal). The smell threshold was calculated by taking the mean of the final four (out of seven) reversal points.

Awareness check. Funneled post-experimental debriefing (Bargh & Chartrand, 2000) revealed that 4 participants identified the odor stimulus as sweat. When probed for suspicion regarding the purpose of the study, no participant correctly guessed the hypothesis.

Procedure

After receiving information about the experiment, participants made an informed decision whether they wanted to participate. If yes, they filled in a screening and handedness questionnaire. Appointments were made with participants that met the inclusion criteria.

All participants provided written informed consent in the lab. A female experimenter carried out the experiment, because in body odor experiments the presence of a male experimenter was shown to increase mood in female participants (Jacob, Hayreh, & McClintock, 2001). Odor stimuli were defrosted 30 minutes prior to use and each participant received a new vial.

Participants received the instruction that physiological measures would be applied to their face, after which they had to perform computer tasks and a series of other tests. Participants were seated in a cubicle. The skin on the middle and left side of their forehead was cleaned with abrasive lotion (Lemon Prep, Mavidon, Lake Worth, FL) and alcohol to reduce the impedance of the EMG signal. The application of alcohol additionally served to wipe out the potentially confounding influence of Lemon Prep scent. EMG electrodes were applied next. The impedance of EMG electrodes was measured; in rare cases that the impedance exceeded 30 kΩ, an online check of the EMG signal was performed by the experimenter to determine whether the signal was reliably discernible from noise. To this

end, participants had to lift (*medial frontalis*) and knit (*corrugator supercilii*) their brows—no references to emotions were made. Electrode replacement turned out to be unnecessary.

Participants sat on an adjustable chair with their head placed in a chin rest. The chin rest both stabilized the head of the participant and supported the vial that was placed about 2 cm below the nose of the participant. Before the odor-containing vial was opened, participants completed four practice trials of the NFECT. The facial expressions included fear (actor: v02, 80% noise), happiness (m23, 40%), and neutral (v02, 40%; m23, 80%) (Langner et al., 2010). Picture presentation was controlled by Presentation software (Version 16.4) installed on a computer (19-in. FlexScan S1932 screen, 1280 x 1024 screen resolution). Participants were told to classify as soon and accurately as possible the facial expression displayed on the screen as "emotion" or "no emotion" by pressing a designated key. These keys were counterbalanced across participants. The facial expression appeared on the screen for 50 ms and was preceded by a fixation cross (500 ms) and followed by a response window (maximum duration: 2 s). The inter-stimulus interval was 1.5 s.

When the practice trials were finished, participants were exposed to each of three odor stimuli (baseline, fast stress, slow stress) in a pre-determined counterbalanced order. Participants wore a nose clip to prevent preliminary sniffs. The nose clip was removed directly after the opening of the vial. The video capture embedded in EMG analysis software would reveal the moment of odor exposure (100 ms accuracy). As soon as the vial was opened, participants saw a black fixation cross that was presented on a grey background in the middle of the screen for 5 seconds. Then, they performed 40 unique trials of the NFECT. Of these 40 trials, 10 contained either a fearful, disgusted, happy, or neutral expression. Half of the trials displayed a (fe)male actor and the expression of each actor had a different level of degradation (i.e., "noise level": 20, 40, 60, 80, 100%). When the first block of 40 trials was finished, participants took a short break. After this break, the next odor was presented and the cycle was repeated.

After three blocks, participant fulfilled 24 trials of the full facial expression classification task. The trial sequence was similar to that of the NFECT. After this task, participants performed the EQ and RMET. When participants finished the empathy questionnaires, the experimenter removed the electrodes.

In a separate room, participants were asked to rate the pleasantness and intensity of the baseline, fast stress, and slow stress odor and they had to discriminate between these odors, before they performed a smell threshold test. Finally, they completed the funneled debriefing procedure, were debriefed, thanked, and paid €12.

Statistical analysis

Sample size was determined by a priori power analysis (G*Power 3.1) (Faul, Erdfelder, Lang, & Buchner, 2007) for analysis of variance, $f = .25$, power = .80, $\alpha = .05$. Effect size f was converted (Cohen, 1988) from the lowest effect size ($\eta^2 = .06$) obtained in similar research measuring the impact of sweat obtained from fearful individuals on *medial frontalis* and *corrugator supercilii* activity (de Groot et al., 2014a, 2014b). The manner of handling the data was determined as follows. For all EMG and reaction time variables, outliers were identified with the most robust scale measure in the presence of outliers, by means of values that surpassed 2 median absolute deviation (MAD) units (Leys, Ley, Klein, Bernard, & Licata, 2013). When outliers were revealed for a particular variable, these values were altered to be one unit above the next extreme score on that variable according to the method described in Field (2009). Missing values due to measurement error were handled by means of stochastic regression imputation (i.e., deterministic regression imputation with an added random error component). Removing three hyposmic individuals from the sample did not affect the outcome of the main analyses. The analyses were based on 31 participants.

Results

Part 1 ("senders")

Sweat was collected from *senders* to serve as odor stimuli presented to *receivers* in Part 2. The small yet sufficient sender sample ($N = 8$) means that the results reported for this sample should be interpreted with caution. Compared to both the baseline and fast stress condition, higher heart rate and sweat production was expected in the fast stress condition (i.e., SAM activity), whereas the slow stress condition was expected to be characterized by high levels of cortisol (i.e., HPA activity).

A repeated measures ANOVA on heart rate with Greenhouse-Geisser correction of degrees of freedom ($\varepsilon = .54$) revealed a marginally significant main effect of condition (3 levels: baseline, fast stress, slow stress), $F(2,14) = 5.21$, $p = .052$, $\eta_p^2 = .43$. In line with what was expected, planned paired t-tests showed that heart rate was highest in the fast stress condition ($M = 91.91$ bpm, $SD = 25.75$ bpm) (Figure 2A). Compared to the fast stress condition, heart rate was significantly lower in the baseline condition ($M = 70.96$, $SD = 11.34$), $t(7) = 2.37$, $p = .050$, $r^2 = .45$. However, a similar difference between the fast stress and slow stress condition ($M = 72.30$, $SD = 9.68$) was only marginally significant, $t(7) = 2.25$, $p = .059$. Finally, heart rate did not differ significantly between the baseline and slow stress condition, $t(7) = .65$, $p = .54$.

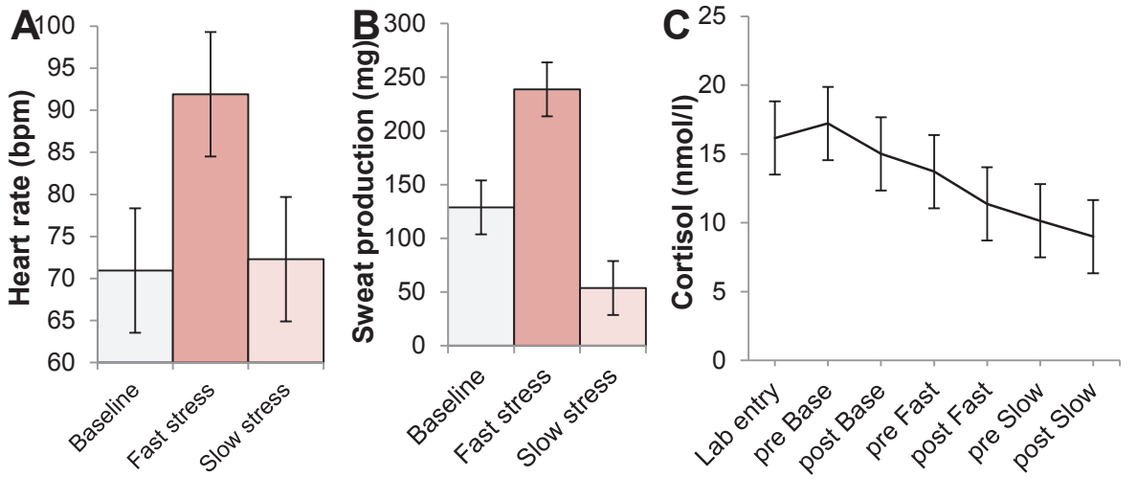

Figure 2. Physiological outcomes senders. Physiological measurements obtained from senders during three conditions: pleasant-neutral baseline, preparation for a speech (i.e., fast stress, SAM axis activity), and recovery from speech preparation (i.e., slow stress, HPA axis activity). (A) Mean heart rate (bpm) per condition. (B) Mean sweat production (mg) per condition. (C) Mean salivary cortisol (nmol/l) over time, including a measure following lab entry and measurements before and after each experimental condition (Base = Baseline; Fast = Fast stress; Slow = Slow stress). Error bars ± 68% within-subjects confidence interval based on the mean square error of the main effect (for formulas, see Loftus & Masson, 1994; for the choice of a 68% confidence interval, see Estes, 1997).

A rather similar pattern of results emerged for sweat production (Figure 2B). A repeated measures ANOVA on sweat production indicated a significant main effect of condition (3 levels: baseline, fast stress, slow stress), $F(2,14) = 14.55$, $p < .001$, $\eta_p^2 = .68$. Participants produced significantly more sweat in fast stress condition ($M = 226.3$ mg, $SD = 142.62$ mg) compared to both the baseline condition, $t(7) = 2.60$, $p = .035$, $r^2 = .49$ ($M = 126.30$, $SD = 81.76$), and slow stress condition, $t(7) = 5.29$, $p = .001$, $r^2 = .80$ ($M = 56.20$, $SD = 43.40$). Furthermore, participants perspired more in the baseline condition than in the slow stress condition, $t(7) = 3.17$, $p = .016$, $r^2 = .59$. Notably, heart rate did *not* differ between the baseline and slow stress condition; these apparently contradicting findings may be explained by excitement experienced by participants during the first time of sweat pad application. This excitement was not measured, as the heart rate electrode was applied after sweat pad application.

Next, salivary cortisol levels were analyzed. A repeated measures ANOVA with time (7 levels: lab entry, before baseline, after baseline, before fast stress, after fast stress, before slow stress, after slow stress) as single factor revealed a significant effect of time, $F(6,42) =$

6.24, $p = .023$, $\eta_p^2 = .47$ ($\varepsilon = .24$). Contrary to the expectation, participants' cortisol levels were highest around the beginning of the experimental procedure and values decreased over time (Figure 2C). Planned paired t-tests supported that compared to time point 5 to 7, higher cortisol levels were observed on time point 2 (before baseline), 3 (after baseline), and 4 (before fast stress), $ps \leq .30$. All other comparisons (i.e., barring the comparison between time point 2 and 4, $p = .025$) were not significant, $ps > .05$.

In sum, higher cortisol levels during the beginning (vs. end) of the experiment suggested that preparing for a speech triggered less HPA activity than being unfamiliar with the experimental procedure. Nevertheless, HPA activity was not related to axillary sweat production. Alternatively, high heart rate and sweat production—signs of sympathetic and adrenal medullary activity, respectively—were observed during speech preparation (fast stress). Arguably, SAM system activity caused the apocrine sweat glands to produce a distinctive olfactory signature of fear. Next, we examined whether the odor sampled in the fast stress condition induced in receivers a simulacrum of the senders' experience.

Part 2 ("receivers")

Facial muscle activity indicative of a fearful expression (i.e., increased *medial frontalis* and *corrugator supercilii* activity) was first analyzed over a time window that would typically encompass two sniffs (Sela & Sobel, 2010). Because previous research has shown that in the context of fear odor, the second sniff (i.e., occurring ~3-5 s after odor onset) would coincide with the emergence of a fearful facial expression (de Groot et al., 2012, 2014a), we expected a significant interaction between odor and time on both the *medial frontalis* and *corrugator supercilii* muscle (see Du, Tao, & Martinez, 2014, for a list of facial muscles related to emotion categories, and see Hess & Fischer, 2013, for a critique on whether facial EMG can be used to discriminate discrete emotions in an emotional facial mimicry setting). A 3 x 5 repeated measures ANOVA on mean *corrugator supercilii* activity with odor (3 levels: baseline, fast stress, slow stress) and time (5 levels: 0-1 s, 1-2 s, 2-3 s, 3-4 s, 4-5 s) as factors revealed a significant main effect of odor, $F(2,60) = 3.30$, $p = .044$, $\eta_p^2 = .10$, and time, $F(4,120) = 20.06$, $p < .001$ ($\varepsilon = .66$). As predicted, the main effects were qualified by an interaction between odor and time, $F(8,240) = 3.27$, $p = .013$, $\eta_p^2 = .10$ ($\varepsilon = .52$) (Figure 3A). Follow-up non-parametric Wilcoxon signed-rank tests indicated significantly higher *corrugator supercilii* activity in the 4th and 5th second after fast stress odor onset, compared to baseline, $Z = 1.86$, $p = .063$; $Z = 2.14$, $p = .033$, and slow stress, $Z = 2.14$, $p = .033$; $Z = 2.04$, $p = .042$. In addition, lower *corrugator supercilii* activity was encountered in the baseline

condition compared to the slow stress, $Z = -2.37$, $p = .018$, and fast stress condition, $Z = -2.12$, $p = .034$. Other comparisons did not yield significant differences, $p > .05$.

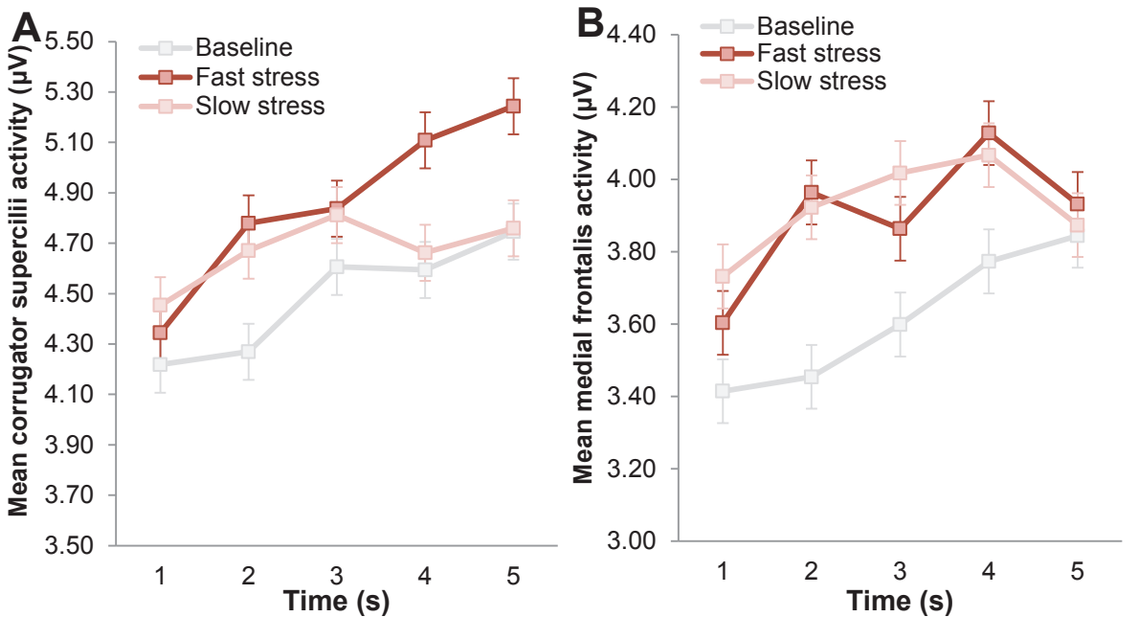

Figure 3. Mean facial muscle activity of receivers over time as a function of odor. (A) Mean *corrugator supercilii* activity (i.e., brow knit) following odor onset (in seconds). (B) Mean *medial frontalis* activity (i.e., brow lift) following odor onset (in seconds). Facial muscle activity displayed here was measured before the start of the facial expression classification task, to isolate the effect of odor. Error bars reflect 68% within-subjects confidence interval of the mean square error of the interaction between odor and time.

Another 3 x 5 repeated measures ANOVA on *medial frontalis* activity indicated a marginally significant effect of odor, $F(2,60) = 2.71$, $p = .075$, $\eta_p^2 = .08$, and a significant effect of time, $F(4,120) = 7.24$, $p = .002$ ($\varepsilon = .50$). More importantly, these effects were qualified by an interaction between odor and time, $F(8,240) = 2.46$, $p = .040$, $\eta_p^2 = .08$ ($\varepsilon = .58$) (Figure 3B). Follow-up Wilcoxon signed-ranks tests indicated significantly higher *medial frontalis* activity on the 2nd second following fast stress odor onset compared to baseline, $Z = 2.55$, $p = .011$ (comparison between slow stress and baseline: $Z = 1.88$, $p = .06$). The other comparisons were not significant, $p > .05$.

Taken together, the present findings indicate that highest co-activation of the *medial frontalis* and *corrugator supercilii* muscle indicative of fear occurred after exposure to fast stress odor (Figure 4). Aside from the five seconds directly following odor onset, facial EMG was measured while participants performed the emotional facial expression classification task (NFECT). Receivers were expected to show increased *corrugator supercilii* and *medial*

frontalis activity when fearful facial expressions were presented in the context of fast stress odor.

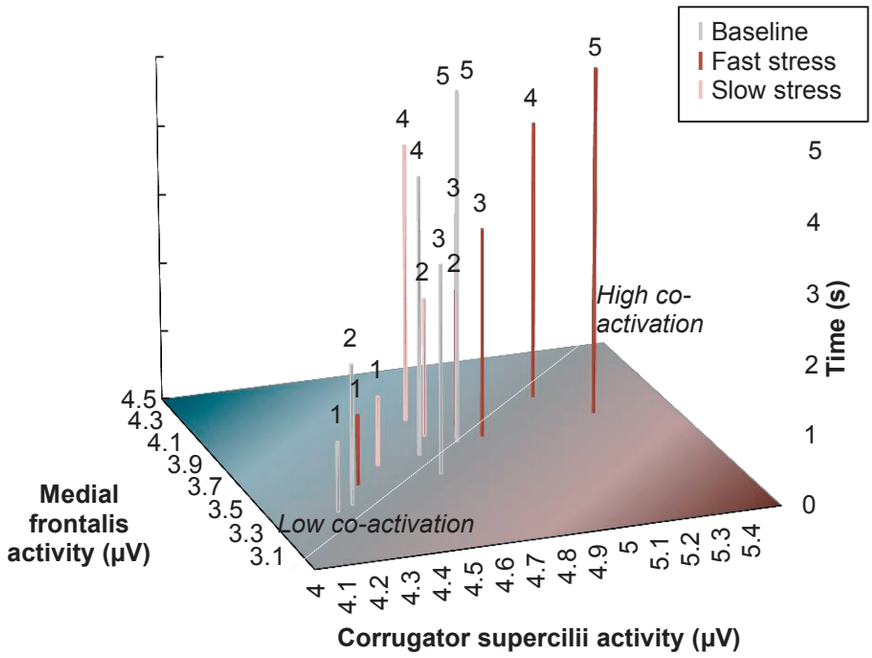

Figure 4. Mean facial muscle co-activation of receivers over time as a function of odor. Facial muscle activity displayed here was measured before the start of the facial expression classification task, to isolate the effect of odor. Above each bar, the time after odor onset (in seconds) is depicted (see Y-axis). The more each bar is located toward the upper-right end point (vs. bottom-left starting point) of the dashed diagonal, the more the *medial frontalis* and *corrugator supercilii* muscles co-activated (µV), resembling a fearful facial expression (cf. de Groot et al., 2014a, 2014b).

First, a 3 x 4 x 5 repeated measures ANOVA on *corrugator supercilii* activity with factors odor (3 levels: baseline, fast stress, slow stress), facial expression (4 levels: fear, disgust, happy, neutral), and noise level (5 levels: 20, 40, 60, 80, 100%) revealed a main effect of odor, $F(2,60) = 5.82$, $p = .005$, $\eta_p^2 = .16$. Planned post hoc tests revealed *corrugator supercilii* activity that mirrored the pattern of the first five seconds after odor onset, with higher activity in the fast stress condition ($M = 5.93$ µV, $SE = .56$ µV) compared to the baseline, $p = .008$ ($M = 5.42$, $SE = .47$), and slow stress condition, $p = .013$ ($M = 5.38$, $SE = .45$) (Figure 5A; cf. Figure 3A). However, there was neither an interaction between odor and facial expression, $F(6,180) = 2.21$, $p = .068$ ($\varepsilon = .70$), which was contrary to our expectation, nor was there a significant three-way interaction between odor, facial expression, and noise level, $F(24,720) = 2.01$, $p = .060$ ($\varepsilon = .27$). In addition, noise level did not significantly

impact mean *corrugator supercilii* activity, $F < 1$. However, the repeated measures analysis did reveal a main effect of facial expression, $F(3,90)$, $p = .002$, $\eta_p^2 = .17$ ($\varepsilon = .73$). Post hoc tests indicated that highest levels of *corrugator supercilii* activity were measured while participants classified neutral faces ($M = 5.66$, $SE = .50$) compared to happy, $p = .004$ ($M = 5.52$, $SE = .48$), fearful, $p = .007$ ($M = 5.53$, $SE = .47$), and disgusted faces, $p = .033$ ($M = 5.59$, $SE = .49$). Participants presented with happy facial expressions additionally showed lower *corrugator supercilii* activity compared to disgust, $p = .042$.

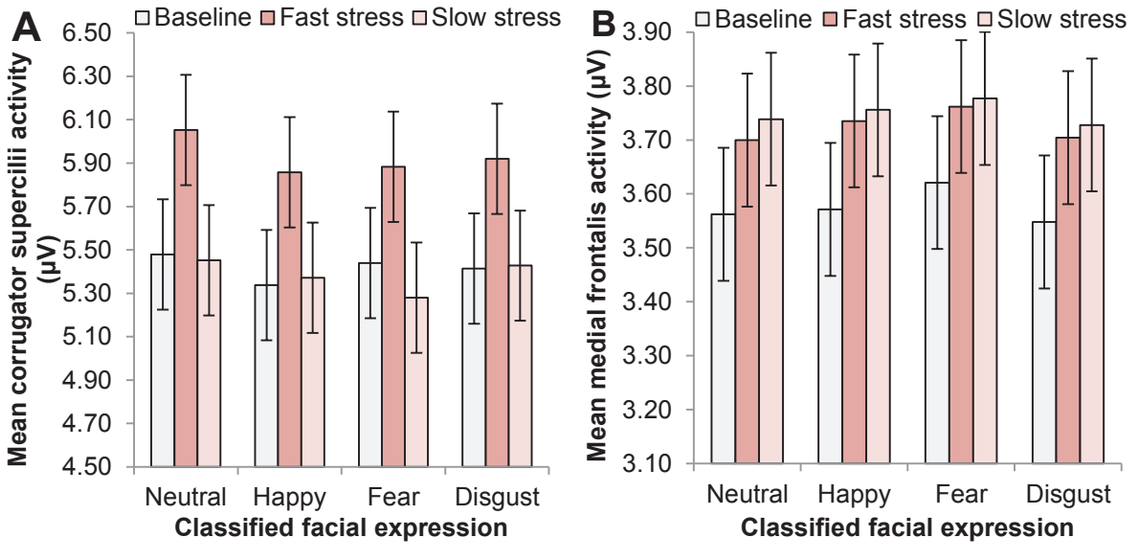

Figure 5. Mean facial muscle activity of receivers per odor condition during classification of presented (emotional) facial expressions. Odor condition: Baseline, fast stress, slow stress. Facial expressions that had to be classified: Neutral, happy, fear, disgust. For clarification purposes, the display of mean facial muscle activity on the emotional facial expression classification task was collapsed over the variable noise level (20%, 40%, 60%, 80%, 100%). (A) Mean *corrugator supercilii* activity, averaged over 1 second following the onset of the presented expression. (B) Mean *medial frontalis* activity, averaged over 1 second following the onset of the presented expression. Error bars reflect 68% within-subjects confidence interval of the mean square error of the main effect of odor.

Although facial muscle activity patterns reported for the *corrugator supercilii* muscle were similar to *medial frontalis* muscle activity patterns, our hypotheses were not supported. Another 3 x 4 x 5 repeated measures ANOVA on *medial frontalis* activity indicated a nonsignificant effect of odor, $F(2,60) = 2.36$, $p = .111$ (Figure 5B). Contrary to what was expected, the interaction between odor and facial expression was not significant, $F < 1$. Furthermore, the three-way interaction between odor, facial expression, and noise, $F(24,720)$

= 2.10, p = .062 (ε = .23) did not exceed the threshold of significance. However, the interaction between facial expression and noise level was significant, $F(12,360) = 3.04$, p = .009, η_p^2 = .09 (ε = .46). An examination of the remaining main effects revealed that there was no significant effect of noise level on *medial frontalis* activity, $F < 1$. Nevertheless, there was a significant main effect of facial expression, $F(3,90) = 4.84$, p = .004, η_p^2 = .14. Participants displayed higher *medial frontalis* activity following the presentation of a fearful facial expression (M = 3.72, SE = .36), compared to a neutral, p = .012 (M = 3.67, SE = .35), disgusted, p = .003 (M = 3.66, SE = .35), and happy expression, p = .067 (nonsignificant trend) (M = 3.69, SE = .35).

In sum, the pattern of facial muscle activity that was established in the first five seconds after odor onset was maintained during the task, a finding that replicates previous research (de Groot et al., 2012, 2014a). The next analysis was performed to examine whether receivers exposed to fast stress odor would show signs of increased speed and/or accuracy with regard to the classification of fearful facial expressions.

A 3 x 4 x 5 repeated measures ANOVA on reaction time (RT) with factors odor (3 levels: baseline, fast stress, slow stress), facial expression (4 levels: fear, disgust, happy, neutral), and noise level (5 levels: 20, 40, 60, 80, 100%) yielded a significant main effect of odor, $F(2,60) = 3.24$, p = .046, η_p^2 = .10, facial expression, $F(3,90) = 35.58$, $p < .001$, η_p^2 = .54, and noise level, $F(4,120) = 80.90$, $p < .001$, η_p^2 = .73 (ε = .53). A planned post hoc test following up on the main effect of odor indicated that participants were significantly faster in classifying *all* facial expressions in the fast stress condition (M = 627.17 ms, SE = 15.62 ms) compared to the baseline, p = .019 (M = 656.69, SE = 17.78) and slow stress condition, p = .068 (nonsignificant trend) (M = 646.76, SE = 13.22) (see Figure 6A). RT did not significantly differ between the baseline and slow stress condition, p = .451. The three-way interaction between odor, facial expression, and noise level was not significant, $F(24,720)$ = 1.70, p = .074 (ε = .45). Concerning the two-way interactions, only the interaction between facial expression and noise level was significant, $F(12,360) = 9.19$, $p < .001$. A post hoc test following up on the main effect of facial expression indicated a typical response pattern (cf. Leppänen & Hietanen, 2003). That is, participants were significantly faster in detecting happy facial expressions (M = 584.93, SE = 12.10) compared to neutral (M = 697.93, SE = 15.59), fearful (M = 645.49, SE = 17.77) and disgusted (M = 645.80, SE = 16.40) expressions, ps < .001. At the same time, participants were significantly slower in detecting neutral expressions relative to expressions that contained emotional expressions, ps < .001. Finally, a post hoc test on noise level indicated that receivers showed the fastest classification

responses when expressions were least degraded: 20% (M = 558.12, SE = 10.16), followed by 40% (M = 594.39, SE = 12.78), 60% (M = 636.17, SE = 12.94), 80% (M = 706.41, SE = 18.41), and 100% noise (M = 722.61, SE = 21.60); all comparisons (i.e., barring the comparison between 80-100%), $p < .001$.

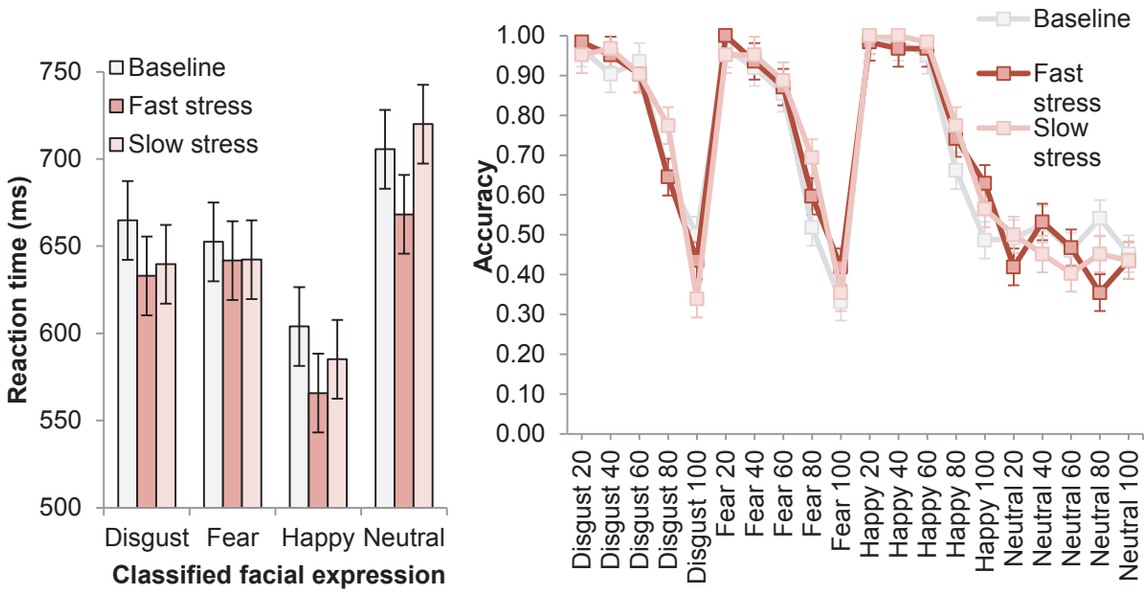

Figure 6. Mean speed and accuracy of receivers to classify (degraded) facial expressions per odor condition. (A) Mean reaction time (ms) of facial expression classification (disgust, fear, happy, neutral) per odor condition (baseline, fast stress, slow stress), collapsed over noise levels (for clarification purposes). (B) Mean accuracy (proportion) of facial expression classification (disgust, fear, happy, neutral) per odor condition (baseline, fast stress, slow stress), and noise level (20-100%). Error bars reflect 68% within-subjects confidence interval of the mean square error of the interaction between odor and facial expression.

Another 3 x 4 x 5 repeated measures ANOVA on accuracy with odor (3 levels: baseline, fast stress, slow stress), facial expression (4 levels: fear, disgust, happy, neutral), and noise level (5 levels: 20, 40, 60, 80, 100%) as factors did not reveal a significant main effect of odor, $F < 1$; yet, there was a main effect of facial expression, $F(3,90) = 19.44$, $p < .001$ ($\varepsilon = .42$), and noise level, $F(4,120) = 113.93$, $p < .001$ ($\varepsilon = .50$) (Figure 6B). Follow-up post hoc tests on facial expression revealed that classification of happy facial expressions occurred with the highest accuracy compared to all other expressions, ps < .016 (happy: M = .85, SE = .02; disgust: M = .79, SE = .02; fear: M = .75, SE = .02). In contrast, classification of neutral expressions occurred with the lowest accuracy, ps < .001 (neutral: M = .47, SE = .07). Furthermore, post hoc tests on noise level indicated that participants displayed significantly lower accuracies (i.e., barring the 20-40% comparison) with each decrement in

noise level, *p*s < .009 (100%: *M* = .45, *SE* = .03; 80%: *M* = .63, *SE* = .03; 60%: *M* = .81, *SE* = .02; 40%: *M* = .84, *SE* = .02; 20%: *M* = .85, *SE* = .02). Concerning the two-way interactions, the only significant interaction was between facial expression and noise level, $F(12,360) = 15.96$, $p < .001$ ($\varepsilon = .51$). Finally, the three-way interaction between odor, facial expression, and noise level was not significant, $F(24,720) = 1.04$, $p = .41$ ($\varepsilon = .47$).

In sum, receivers exposed to fast stress odor demonstrated a *general* increase in speed (vs. accuracy) with regard to the classification of *all* facial expressions. Hence, fast stress odor appeared to have induced sensory vigilance—replicating previous research findings (de Groot et al., 2012).

To assess whether receivers mimicked the fully visible facial expressions (fear, disgust, happy, neutral) of the actors in the NFECT, another repeated measures ANOVA was conducted. Negatively valenced expressions (i.e., fear, disgust) were expected to lead to significantly higher *corrugator supercilii* activity compared to happy and neutral, whereas fearful facial expressions were expected to induce increased *medial frontalis* activity. Although a main effect of *medial frontalis* activity was encountered, $F(3,90) = 3.16$, $p = .049$ ($\varepsilon = .67$), the results were not in line with our hypothesis, as *medial frontalis* activity was significantly lower in the neutral condition compared to all other conditions, *p*s < .039 (neutral: *M* = 3.46 μV, *SE* = .31 μV; fear: *M* = 3.51, *SE* = .31; happy: *M* = 3.55, *SE* = .31; disgust: *M* = 3.53, *SE* = .31); all other comparisons were not significant. Furthermore, no main effect of *corrugator supercilii* activity emerged, $F(3,90) = 1.17$, $p = .32$ ($\varepsilon = .64$) (neutral: *M* = 5.48 μV, *SE* = .52 μV; fear: *M* = 5.45, *SE* = .52; happy: *M* = 5.35, *SE* = .53; disgust: *M* = 5.45, *SE* = .52). The absence of evidence for facial mimicry during the classification of facial expressions might be due to the absence of a social context in which mimicry would normally occur (Hess & Fischer, 2013).

Additional analyses were performed on participants' ratings of the pleasantness and intensity of body odor to demonstrate that these variables did not drive facial EMG responses (Table 1). A repeated measures ANOVA on self-reported pleasantness revealed a nonsignificant effect of odor, $F(2,60) = .79$, $p = .458$. Another repeated measures ANOVA on intensity revealed a nonsignificant trend, $F(2,60) = 2.74$, $p = .077$ (Table 1). Furthermore, participants could not discriminate the baseline, fast stress, and slow stress odor, as was demonstrated by binomial analysis of odor discrimination task scores (H_0 = 50% correct), *p*s > .071 (% correct, Trial 1-4: 52%, 32%, 58%, 58%, respectively). Hence, concurring with what was reported in previous research (e.g., Zhou & Chen, 2009; de Groot et al., 2014a)

there is no evidence for glaring differences in the perceptual properties of the odors that may have accounted for differences in facial EMG responses; odor-evoked facial muscle responses were not relatable to verbal reports.

Table 1

Receivers' ratings of sweat sampled from senders under different conditions

	Baseline	Fast stress	Slow stress
Intensity	4.03 (1.60)	4.61 (1.20)	4.42 (1.63)
Pleasantness	3.35 (1.14)	3.13 (1.15)	3.19 (1.22)

Note. Mean (SD) intensity and pleasantness ratings (7-point Likert scales) of sweat presented to receivers sampled from senders during different phases (baseline, fast stress, slow stress).

Discussion

By demonstrating that receivers showed a simulacrum of the fear experience of senders, the current results supported the main hypothesis that the release of what has been labeled fear sweat is driven by a rapidly activated stress response in the sender that is part of the fight/flight response, namely the sympathetic-adrenal medullary (SAM) system. Experiment Part 1 showed that when participants had to prepare for a speech, heart rate was higher and sweat production was increased relative to a baseline and slow stress (i.e., later time interval) condition. Specifically, activation of the sympathetic part of the SAM system resulted in increased heart rate, and since the adrenal medulla is part of the SAM system, the subsequent release of adrenalin arguably activated the apocrine sweat glands. Sweat sampled in the fast stress condition contained a distinctive signature, as receivers exposed to this odor showed a fearful facial expression (i.e., co-activation of *corrugator supercilii* and *medial frontalis* muscle) and vigilant behavior (i.e., faster reaction times in general when classifying facial expressions). Notably, the facial expression that emerged in the five seconds after odor onset was maintained for several minutes during the task, replicating previous research (de Groot et al., 2012, 2014a). The combined results suggest that SAM activity results in the release of a *qualitatively* different odor stimulus by the sender, one that has a distinctive and communicable chemical signature capable of inducing in receivers a simulacrum of fear.

The current results were interpreted by combining evidence from multiple variables (i.e., facial EMG, RT) (Cacioppo & Tassinary, 1990) as opposed to examining each variable in isolation. For instance, when *medial frontalis* activity is examined in isolation, the absence of a significant difference between the fast stress and slow stress condition could be problematic with regard to our conclusion that receivers displayed a simulacrum of fear after

fast stress odor exposure. Many reasons can be provided for the absence of a difference, such as the occurrence of an orientation response (Delplanque et al., 2009) that would briefly emerge in case the odor exceeded a certain level of intensity (cf. Table 1). However, this explanation is less likely when facial EMG data and vigilant behavior are examined together. The advantage of this approach is that it increases the likelihood that one particular type of behavior is observed (e.g., fear) and not another (e.g., disgust, anger, or an orientation response) (Cacioppo & Tassinary, 1990).

Although the current research provided information about the time course and physiology of "fear odor" release by senders, many epistemic gaps still need to be filled on the part of the receiver. First, a particular odor, such as fear odor, is assumed to have a distinctive signature, in the sense that it is comprised of distinctive chemical compounds, similar to what other researchers have demonstrated for gender (Penn et al., 2007), individuals (Penn et al., 2007) and disease (Olsson et al., 2014). Arguably, specific odor compounds related to fear may have become associated with particular situations in which they naturally occur (e.g., fear-inducing contexts such as academic examinations). Subsequently, a population of multimodal neurons, processing not only olfactory (i.e., *odor object* information; Wilson & Stevenson, 2006) but also auditory and visual information, may be involved in creating a representation of this event (Barsalou, 2009). Encountering fear odor may then reactivate these previously stored representations.

Since the original state is never completely reinstated in a receiver (Barsalou, 2009), exposure to compounds related to fear induce a simulation of fear that is *partial*. A partial simulation of fear may include activation of (parts of) a neuro-motor program of fear, resulting for instance in the emergence of a fearful facial expression (e.g., Ekman, 2003). Taking on a fearful facial expression could be vital in dangerous situations, as lifting the eyebrows (i.e., *medial frontalis*) would lead to increased visual field size and enhanced sensory intake (Susskind et al., 2008). The results obtained in previous research (de Groot et al., 2012) and that of the current research seem to fit with this perspective, as exposure to fear odor elicited not only a facial expression of fear, but also behavior indicative of sensory vigilance. Vigilant behavior ranged from more effective eye movements and enhanced performance on an easy visual search task in previous research (de Groot et al., 2012) to increased speed of classifying facial expressions in the present research.

Previous research reported facilitated recognition of fearful facial expressions when these expressions were presented together with fearful voices (Dolan et al., 2001). In a similar vein, we expected that exposure to fast stress odor (i.e., olfactory modality), would

led to faster and/or more accurate detection of fearful facial expressions (i.e., visual modality). However, the results of the current research did not support this hypothesis. Previous research showed that exposure to sweat obtained from senders induced to be in a fearful state increased amygdala activity in (female) receivers (Mujica-Parodi et al., 2009; Radulescu & Mujica-Parodi, 2013). A locationist perspective invites relating the amygdala to fear behavior (e.g., LeDoux, 2003). Alternatively, the amygdala was suggested to play a role in fixating on and paying attention to visual information of all facial emotions (Adolphs et al., 2005). The amygdala was argued to be neither a fear module, nor a negative-emotions-dedicated subsystem, but rather a relevance detector (Sander, Grafman, & Zalla, 2003). The psychological constructionist view similarly states that the amygdala is part of a network that signals the motivational salience of the stimulus (Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012). Hence, similar to what has been observed in previous research (Mujica-Parodi et al., 2009; Radulescu & Mujica-Parodi, 2013), the motivational salience of the fast stress odor may be processed, amongst other brain regions, at the level of the amygdala. What followed was increased vigilance toward (other) relevant social stimuli in the environment (e.g., facial expressions), ultimately resulting in increased classification speed of *all* facial expressions.

One can ask whether the experience of receivers, and that of senders, can be classified as the emotion category *fear*. Labeling particular behaviors and facial expressions as discretely fearful may not match with the person's actual experience (Barrett, 2009a). Instead, emotions were argued to be rooted in *core affect*, characterized by the components valence and arousal (e.g., Barrett, 2009a; Wilson-Mendenhall, Barrett, & Barsalou, 2013). Emotion categories such as fear would emerge from the interplay of these basic operations in part determined by the content of the experience and the context in which the experience occurs (Lindquist et al., 2012). With regard to the current research, *senders* that produced sweat in the context of preparing for a speech may have labeled their arousing negative affective experience as "fear" or "anxiety". However, apart from the odor itself, receivers exposed to fast stress sweat had no clear-cut contextual information to make sense of their experience, which leaves open the question whether there is *emotion-specificity* in the response of receivers. Future research could examine whether exposure to odors from senders experiencing anger—another emotion category related to sympathetic-adrenal medullary (SAM) activity—leads to the release of markedly different odor compounds to which receivers respond in an emotion-specific manner. If receivers do not display emotion-specificity, then this may require rethinking the *signaling* value of chemosignals. What is

then chemically transferred between a sender and receiver may not be a discrete emotion package, but rather a *cue* that elicits particular behavior based on, for instance, the receiver's previously stored association with the odor. Notably, a *cue* could acquire *signal* properties, in case *many* individuals have stored fear odor objects. In that case, the odor emitted by one person as a function of fear may trigger in another person a partial simulation of their previously stored fear experience.

Although previous research provided neural and behavioral evidence showing that receivers displayed a *simulacrum* of the fear experience following exposure to sweat sampled from fearful senders (e.g., Mujica-Parodi et al., 2009; Zhou & Chen, 2009; de Groot et al., 2012; Prehn et al., 2006), remarkably little was known about the time course and physiological mechanism responsible for the release of this apparently distinctive chemical signature. The current research provided evidence suggesting that the release of that what has been labeled *fear sweat* is driven by rapid physiological changes that accompany a well-known concomitant of fear, the fight/flight response (Cannon, 1932). Indeed, patterns of facial muscle activity that were observed in receivers following fast stress (i.e., sampled from senders during 10 minutes) odor onset resembled patterns obtained in previous research using sampling intervals that were on average three times longer (de Groot et al., 2012, 2014a, 2014b). Hence, the apparently distinctive fear signature was created relatively rapidly as a function of the SAM system. Based on the current findings and previous research showing that sweat sampled during an interval marked by the absence of a cortisol response still induced fear-related responses in receivers (Ackerl et al., 2002), we presume that not HPA axis, but SAM axis activity was responsible for the chemical transfer of fear from sender to receiver.

Chemical analysis needs to determine the relation between SAM activity and the apparent emergence of distinctive sweat compounds. By narrowing down on the common physiological process (i.e., SAM activity) underlying fear/anxiety sweat production, the current research provided guidelines for future research to become more effective in inducing and measuring the *particular* state that drives the release of so-called fear/anxiety sweat. Furthermore, given the relatively rapid operation of the SAM axis, the current research has implications with regard to sampling time. Previous research demonstrated that sampling time (12 versus 24 hours) was an important determinant of the pleasantness and intensity of body odor samples (Havlíček et al., 2011); yet, the present research adds to these findings that regardless of differences in pleasantness and intensity, changes in body odor composition

may occur during relatively short time intervals. In sum, the changes implied by the present research are not only theoretical but also methodological.

Based on the steadily increasing number of contributions to the topic, research on emotional chemosignaling can be considered an emerging field. Even though pheromone communication is unlikely in humans, since we lack a functional vomeronasal organ (e.g., Witt & Wozniak, 2006), odors may still affect humans in a consistent manner by means of associations that emerge between an odor and the context in which the odor is typically emitted and experienced. The present research is one of a number of studies demonstrating that the sense of smell is more important than usually assumed. Although humans have difficulty naming even the most common odors (Lorig, 1999), an estimated one trillion plus odors can be discriminated (Bushdid, Magnasco, Vosshall, & Keller, 2014). By delving into the underlying physiological mechanism of fear chemosignaling, the current research opened new lines of research that could further our understanding about how humans transfer information to each other by using the sense of smell.

Chapter 8

General discussion: A situated perspective on chemosignaling

This chapter is based on:

de Groot, J. H. B., Semin, G. R., & Smeets, M. A. M. (in prep). The situated nature of communication via smell in humans.

Abstract

Humans use multiple senses to navigate the social world. Among these senses, the sense of smell is arguably the most underestimated one. However, recent studies estimated that humans can discriminate more odors than colors and tones combined. We even share abilities with rats and dogs such as being able to track a scent-trail through a field. The sense of smell has many important functions in humans. We can judge the edibility of food through smell, avoid environmental hazards, and gather social information from other individuals about emotions, gender, age, and personality, inter alia. Essentially, by providing information about a sender to a receiver, body odors serve as a communicative medium. Unlike pheromones, however, this information is likely to be acquired by individuals through the extraction of natural relations between certain odors and situations in which they typically occur. Although such a situated perspective can account for the complexity of responses to body odors including individual variance, the situation component has remained a neglected facet in emerging research on what has been called “chemosignaling”. By adopting a situated perspective, the current review aims to provide a plausible, dynamic, and flexible basis for human chemosignaling.

The situated nature of communication via smell in humans

> "Nothing is more memorable than a smell. One scent can … conjure up a childhood summer beside a lake in the mountains. ... Smells detonate softly in our memory like poignant land mines hidden under the weedy mass of years. Hit a tripwire of smell and memories explode all at once. A complex vision leaps out of the undergrowth." (Ackerman, 1990, p. 5)

This poetic illustration stands in stark contrast to the relative neglect of the significant role and functions fulfilled by the human sense of smell. Among these functions, the relatively well-known ones are: avoiding environmental hazards and determining whether something is edible or not (Stevenson, 2010). However, one of the features of the sense of smell that makes it of considerable interest is its telereceptive function, namely its propensity to pick up social information contained in certain human odors, in particular *chemosignals*[1]. Recent research has indicated that body odors contain social information ranging from (relatively) static features such as gender (Penn et al., 2007) and age (Mitro, Gordon, Olsson, & Lundström, 2012) to more dynamic characteristics such as the emotional state of fear (e.g., Zhou & Chen, 2009; Prehn, Ohrt, Sojka, Ferstl, & Pause, 2006; de Groot, Smeets, Kaldewaij, Duijndam, & Semin, 2012; Mujica-Parodi et al., 2009). Although the range of social information conveyed by body odors is multifarious, receivers generally respond only to the most salient information. What is salient is determined in part by the context at hand, the receiver's goals, the properties of the odor, and existing associations with the odor.

Indeed, as Edgar Allan Poe noticed centuries ago (1902/2009, p. 232), "odors have an altogether peculiar force, in affecting us through association". Sometimes these associations have an idiosyncratic nature, such as when a perfume of a grandparent takes you back years in time. Of course, ritualized relations between certain odors (e.g., incense) and the situations in which they typically occur (e.g., holy services) render it more likely that many different individuals report similar feelings (e.g., a "sensed presence"). These examples are about non-human odors; yet, there is a reason to assume that human chemosignaling follows the same situated principles. In fact, these examples set the tenor for this review by placing the human sense of smell in a broader context, which will also lead to a reframing of the social

[1]With *chemosignals* we mean odoriferous volatiles emanating from the human skin, produced by a sender and potentially registered by a receiver via the olfactory epithelium in the nose (i.e., chemical sense).

implications of human odors. By taking a dynamic situated perspective on human chemosignaling the current review is aimed at providing a plausible basis for human chemosignaling.

Although others have aptly documented evidence for the social communicative function of chemosignals in humans (Stevenson, 2010; Wysocki & Preti, 2004), these reviews have not taken into account the role of the situation. This absence is understandable given the static relation between stimulus and response in animals assumed under the pheromone concept[2]. As a consequence, the role of the situation in for instance acquisition processes related to chemosignaling has remained unaddressed. Moreover, a pheromone-like definition of chemosignals can paradoxically lead researchers to flexibly interpret what they assume to be inflexible behavior. For instance, the observed risky behavior of receivers in one experiment (Haegler et al., 2010) and cautious behavior in another (Chen, Katdare, & Lucas, 2006) can both be interpreted as fear responses that changed in line with the fearful state of a sender, regardless of context. A situated perspective would counteract this inclusivity problem and would provide a better fit with reality, as it suggests that human olfactory communication takes a more complex form, with responses depending on the context, the goals of the receiver, and the receiver's association with and interpretation of the odor.

General overview

We start this review by highlighting that the human sense of smell is not per definition inferior to that of other species and to vision and hearing. With the modalities vision and hearing, inter alia, the sense of smell can be used to make sense of the larger multimodal context; these modalities are employed in concert by senders and receivers to achieve a common basis. As is shown in the Brief overview section, research on olfactory

[2]A definition of chemosignals that is based on the workings of pheromones in animals implies that chemosignals meet the following criteria (Beauchamp, Doty, Moulton, & Mugford, 1976): (1) species-specificity; (2) having a well-defined behavioral or endocrinological function; (3) showing a large degree of genetic programming; (4) involving only one, or at most, a few compounds; (5) uniqueness of the compound(s) in producing the behavioral or endocrinological response (also see Doty, 2010). First of all, species-specificity has never been tested (Doty, 2010). More importantly, body odor that contains chemosignals consists of multiple volatile organic compounds (e.g., Gallagher et al., 2008) and responses to these chemosignals or putative pheromones are highly variable, experience-oriented, and on numerous occasions may fail to match the predicted effects (e.g., Bronson, 1976; Doty, 2010). Rather than constituting "keys" that "unlock" preprogrammed behavior, chemosignals are not pheromones but complex odors that exert their effects in receivers by simultaneously relying on the top-down influence of the context or situation.

communication started by examining putative pheromones[3]. In Part I (Theoretical Framework), a case will be build against the pheromone perspective and a plausible basis for chemosignaling is constructed by integrating different theories on (odor) learning and accounts that stress the importance of top-down factors such as the situation in shaping body odor perception. A situated framework is advanced to ground the rapidly accumulating findings in the field of chemosignaling. What then follows is a systematic review of the chemosignaling literature, which is split into two parts (Part II and III). Part II contains a review of the evidence for chemosignaling of (relatively) stable characteristics such as gender, age, and personality. Part III is reserved for emerging research on the dynamic chemosignaling of emotions. Finally, Part IV contains a short summary and conclusions.

The sense of smell

Animals are known to use odors to communicate within and between species (e.g., Karlson & Lüscher, 1959), yet the same statement becomes controversial when it is applied to humans. In humans, the sense of smell was historically considered to be "extremely rudimentary" and olfaction was reported to play no more than an "insignificant role" (Grinker, 1943, p. 337). Since humans lifted their noses from the ground by adopting a bipedal stance, human evolution was characterized by the increased dominance of vision and the reduced significance of the olfactory receptor repertoire (see Shepherd, 2004, for a further discussion of this theory). The declining number of functional olfactory receptor genes was believed to translate directly into olfactory ability; yet, this assumption was recently challenged. Recently, researchers estimated that humans could discriminate one trillion odors (Bushdid, Magnasco, Vosshall, & Keller, 2014)—figures that by far exceed the ability to discriminate colors (2.3-7.5 million) and tones (~340.000) (see Bushdid et al., 2014). Humans are remarkably good at detecting odorants even at very low concentrations (i.e., parts per billion; cf. Yeshurun & Sobel, 2010). Moreover, like "great smellers" such as rats and dogs, humans were shown capable of tracking a scent (i.e., chocolate essential oil) through a field (Porter et al., 2007). Although difficulties may arise when having to name even the most common household smells (for a potential explanation, see Lorig, 1999), human olfaction is

[3]A (detailed) discussion of putative pheromones falls outside the scope of this review. Their existence, such as in the case of menstrual synchrony (McClintock, 1971), has been challenged on numerous occasions (e.g., Wilson, 1992; Ziomkiewicz, 2006; Yang & Schank, 2006; Schank, 2006). More evidence is required to classify certain odors as putative pheromones.

thus not as manifestly inferior to that of other species and other senses as had been thought previously.

However, the sense of smell is not as fast acting as the visual and auditory system, as odor molecules need to be released and travel through space before they potentially reach a recipient's nose (Wyatt, 2003). Nevertheless, the unique advantages of the olfactory system become apparent from the fact that chemical signals can be carried over long distances, cross barriers, and signal information when the signaler has long gone (for a more extensive overview, see Wyatt, 2003). These properties are shared by odors produced by the human body, *chemosignals*, which serve as a medium to transfer social information from a sender to a receiver. Next to vision, hearing, and touch, humans can use their sense of smell to navigate the social world (Semin & de Groot, 2013). That is, multiple modalities make sense of the larger multimodal context and these modalities are employed in concert by senders and receivers of body odors to achieve a common basis between individuals (Semin & de Groot, 2013). Establishing similarity of perspectives constitutes an indispensable requirement for any successful communication that ultimately enables group living and chemosignals contribute to such a process (Semin, 2007).

Brief overview: Putative pheromones

Research on human chemosignaling started more than a decade (McClintock, 1971) after the development of the pheromone concept by Karlson and Lüscher (1959). They defined pheromones as "substances which are secreted to the outside by an individual and received by a second individual of the same species, in which they release a specific reaction, for example, a definite behavior or a developmental process". Among the many behaviors elicited by pheromones are mate selection, predator avoidance, territorial marking, and kinship recognition (Wyatt, 2003). Although pheromones are the primary means of motivating behavior in many species (Gottfried, 2006), this is not the case for humans. The difference is that most species, including reptiles, amphibians, and certain mammals, have a fully functional pheromone-detecting vomeronasal organ (VNO) (Witt & Wozniak, 2006). The human VNO, however, is a vestigial structure (Boehm, Roos, & Gasser, 1994) that does not function as a sensory organ in adult humans (Trotier et al., 2000), as it has no receptor cells (Boehm & Gasser, 1993). Human pheromone communication was instead alleged to be mediated by the main olfactory epithelium (Wysocki & Preti, 2004), and evidence for human pheromones—in contrast to *chemosignals*—has remained unconvincing. Although pheromones may elicit context-free behavioral changes in most animals, humans lack the

sensory structures animals have. Human chemosignaling is ostensibly more complex and situated and this becomes clear when observing the reactions of body odor recipients.

The idea that chemosignals elicit rather inflexible responses in receivers that are unaffected by the context may have resulted from a direct extension of the animal-based pheromone concept to humans. In humans, olfactory information is processed predominantly by limbic brain regions. One of the unique anatomical features of the human sense of smell is that brain regions related to olfactory processing, such as the amygdala, entorhinal cortex, striatum, orbitofrontal cortex, hypothalamus, and hippocampus, overlap with areas related to the processing of emotions (e.g., Gottfried, 2006). The amygdala-hippocampal complex is critically involved in forming and remembering emotional associations and odors can easily be linked to emotions through associative learning (Herz & Engen, 1996). Olfaction, not surprisingly, is therefore often regarded as the "most emotional sense" (Chrea et al., 2009). The formation of an emotional association with an odor requires neither the intention to learn nor awareness of the odor (Köster, 2002). As receivers often display highly variable affective reactions to odors and since many odors contain hundreds of different compounds, human olfaction can be a challenging and complex research area (Hudson & Distel, 2002). Nevertheless, multiple individuals may extract the same statistical regularities from the environment, resulting in a coupling of olfactory and contextual or situational information. A coupling of this kind may lead to rapid and consensual responses to odors that may erroneously be interpreted as predetermined and invariant as opposed to having resulted from the systematic acquisition of situated information from multiple modalities.

I. Theoretical framework

The theoretical framework advanced here argues against a pheromone perspective and explains emerging research findings in the field of human chemosignaling by incorporating different ideas on odor learning present in the literature to date. These ideas include accounts that stress the importance of top-down processing in odor perception (e.g., Dalton, 1996), odor object theory (e.g., Wilson & Stevenson, 2006), a modified version of odor object theory (Yeshurun & Sobel, 2010), and a situated perspective (e.g., Barsalou, 2003). The focus on the role of learning and situational factors is what binds these conceptual frameworks together.

"Bottom-up"

In contrast to the perspective that all human reactions to odors are learned reactions (e.g., Herz, 2002), a pheromone perspective would suggest that certain odors can warn

individuals *prior to* learning. First, labeled-line theory suggests that at least some odorants[4] are coded by specific olfactory receptors that have a direct "line" to the cortex (Boeckh, Kaissling, & Schneider, 1965), the consequence of which is that certain odorants—at least in animals—can evoke innate (avoidance) responses (e.g., Suh et al., 2004). However, Wilson and Stevenson (2006) report abundant evidence that discourages a possible application of labeled-line theory to humans. Second, many odorants can stimulate the endings of the trigeminal nerve (i.e., the 5th cranial nerve) in the nose, leaving a tingling, prickling, stinging sensation that may even border on pain (e.g., Doty et al., 1978). Ammonia, for instance, strongly stimulates the trigeminal nerve and the resulting irritation is accompanied by an automatic avoidance response (Herz, 2002). However, odorants usually only stimulate the trigeminal nerve at concentrations that well exceed the threshold of odor awareness. Body odors are the type of olfactory stimuli that do not always reach conscious awareness and they mainly consist of substances that do not stimulate the trigeminal nerve (Pause, Krauel, Sojka, & Ferstl, 1998; Zernecke et al., 2010, but also see, Lundström, Boyle, Zatorre, & Jones-Gotman, 2008, for a different perspective). In sum, chemosignaling is unlikely to be driven (only) by bottom-up factors such as the odor stimulus' trigeminal properties, suggesting that body odor perception is (largely) influenced by top-down processes.

"**Top-down"**

Top-down processes can play a role both during odor perception but also while associations with odors are formed. Previous research has indicated that humans have the capacity to learn that certain odors that were not encountered previously signal danger (e.g., Cain & Turk, 1985). Previously neutral odors (i.e., conditioned stimuli) can become warning signals through the coupling with the (e.g., threatening) meaning of chemical exposure (i.e., unconditioned stimulus) (e.g., Bulsing, Smeets, Hummel, & van den Hout, 2007; Bulsing et al., 2010). A historical example may illustrate this capacity. During the later stages of the Second World War, gas attacks were a common threat to Japanese citizens and posters were designed to warn citizens against chemical weapons. On these posters, typically neutral or even pleasant odors such as hay and geraniums were associated with the respective danger of phosgene and mustard gas (Stevenson, 2010). In addition to anecdotal evidence, experimental

[4]Before reaching the receptors in the olfactory epithelium, odoriferous volatile molecules (i.e., the physical stimuli) are commonly referred to as *odorants*; *odor* perception is the sensation resulting from stimulation of the olfactory organs. When odoriferous volatile molecules are stemming from the body, however, researchers often refer to the physical stimulus as "body odor" even before the odor is perceived.

research showed that odors can be rapidly disliked in the presence of a negative verbal label (Herz & von Clef, 2001) or when the odor is associated with adverse physiological effects (Van den Bergh et al., 1999), such as when humans (incorrectly) believe that the odor is noxious (Dalton, 1996). These are but a few examples that illustrate top-down modulation of odor perception.

Odor object theory

Human odor perception is more complex than what a pheromone-like perspective on olfaction would assume: odorants are not specific keys that unlock specific receptors leading to the execution of preprogrammed behavior (i.e., bottom-up effects). Indeed, most environmental odorants are complex mixtures consisting of hundreds of compounds (e.g., Livermore & Laing, 1998). Each compound in the mixture will stimulate one or multiple olfactory receptors, and many receptors will be stimulated by more than one chemical compound (Buck & Axel, 1991). Information from all receptors travels via the olfactory bulb further into the brain, where it is combined into a combinatorial code that is unique to that mixture (Buck & Axel, 1991). According to odor object theory (Wilson & Stevenson, 2006), what is stored in memory as a template or "object" is the complete odor mixture, rather than the individual parts of the mixture. For instance, once we encounter a lemon, a template-matching process occurs on the basis of the complete set of volatiles (e.g., limonene, citral, pinene, terpinene). Once the best matching template is selected, a stable, background-detached odor representation can be formed (Wilson & Stevenson, 2006). Once learned, the activation of a lemon odor object can also prime information that had become associated with the odor, such as the visual image of a lemon. Odor object theory likens odor objects to visual objects, as both are the result of a pattern-matching system that recognizes discrete sets of spatial and temporal features (Stevenson & Wilson, 2007).

Alternative odor object theory

Alternatively, Yeshurun and Sobel (2010) argued that odor objects are different from visual objects in the sense that the physical odor and background odor are perceived as a unitary perceptual object and only other-modality sensory information and context would allow for their separation (cf. Stevenson & Wilson, 2007). The interaction between bottom-up and top-down influences becomes apparent from the perspective that odor objects were suggested to be the integrative product of the odor's inherent pleasantness with the subjective state at the moment of perception (Yeshurun & Sobel, 2010). For example, the smell of steak would activate a different odor object when one is satiated compared to when one is hungry.

The influence of the steak's odor thus only tells a part of the story and this alternative odor object theory argues that we have learned to link the pleasantness of odors to a visual image, context, and label (Yeshurun & Sobel, 2010).

Whereas odor object theory (Wilson & Stevenson, 2006; Stevenson & Wilson, 2007) and its modified version (Yeshurun & Sobel, 2010) have only been applied to non-body odors, all signs suggest that these theories can (partly) be incorporated into a broader theory of chemosignal reception. Before a synthesis of the different theories is provided, the next section discusses a situated perspective that will stress and describe in rich detail the importance of the situation. Notably, the situation plays an important role both during the *formation* of an association with the odor and when previously stored odor experiences are *reenacted*. Indeed, both processes are central to the argument that chemosignal reception is socially situated.

Situated perspective

During the acquisition process that leads up to the formation of (body) odor objects, the situation plays a quintessential role. The situation influences which goals, actions, and emotions are relevant and will be executed (Barsalou, 2005a). When one prepares breakfast with a toaster, for instance, the smell of smoke will mean something entirely different and necessitates a different response than when smoke comes from the barbecuing neighbors' garden on a summery evening. In other words, each situation asks for a different situated action. Different situations lead to different predictions of what constitute likely events and entities (Barsalou, 2005a). Because certain events and entities occur more often in some situations than others, knowledge of the current situation limits the number of correlated events and entities that are likely to be encountered and vice versa (Yeh & Barsalou, 2006). Hence, rather than having to search through a knowledge reservoir of all situations that are stored in memory, processing is simplified by making inferences about likely events and entities based on the current situation (Yeh & Barsalou, 2006).

Some odors may be frequently present in particular contexts and these statistical regularities can be extracted by individuals to form general—as opposed to idiosyncratic—associations between the odor and the specific situational information. For most people, the smell of roses evokes positive feelings because of the symbolic meaning (e.g., friendship, love) that is attached to giving or receiving them. Indeed, odor compounds can become rapidly associated with the context or situation in which they are typically emitted and so-called statistical regularities can also be extracted for body odors. For instance, when

individuals are exposed to body odor that had frequently been associated with danger, what is likely to be represented by those individuals is not only the body odor, but also the typical situation in which the body odor is emitted, the visual appearance of danger, the sound of danger, along with the likely emotional response. In sum, situations can play an important role in the formation of individual or general associations with odors by giving odors their informative properties (i.e., aside from their pleasantness, intensity).

The importance of the situation should become clear from the view that conceptual knowledge is grounded in modality-specific systems in the brain (e.g., Barsalou, 1999, 2003). Concepts, take for instance "danger", are abstracted from different situations that activate modality-specific brain areas (e.g., vision, hearing, olfaction). Association areas in so-called convergence zones (Damasio, 1989; Barsalou, 2005b) capture patterns of brain activation for later use within a modality, while higher association areas in the temporal, parietal, and frontal lobes integrate activation across modalities (Barsalou, 2005b). When knowledge is required to represent "danger" on a later occasion, multimodal representations are reactivated to simulate how the brain represented perception, action, and introspection on an earlier occasion (Barsalou, 2008). Situations are intrinsic parts of perceptual experiences and what follows from the situated perspective is that *simulators* are constructed that represent a category (e.g., danger) in a relevant perceptual situation, not in isolation (Yeh & Barsalou, 2006).

During their lives, people experience many situations repeatedly and knowledge about these repeated situations becomes entrenched in memory (Barsalou, 2005b). Entrenched knowledge allows individuals to make inferences about the situation and can guide interactions in these familiar situations but also in similar novel situations (e.g., Andersen & Chen, 2002). The capacity to simulate how a predicted situation is going to unfold is essential for human survival, as individuals can prepare themselves for action that will achieve their goals. Barsalou (2003) referred to one particular package of situation-specific inferences as a situated conceptualization. Essentially, a situated conceptualization is a multimodal simulation of a multicomponent situation, with each modality-specific component simulated in the respective brain area (Barsalou, 2005b).

Once multimodal (e.g., visual, auditory, olfactory) information has been stored with respect to a particular category (e.g., danger), the situation may simulate a particular component of a pattern in memory (Barsalou, 2005b). For instance, the "smell of danger" can be *simulated* as a subset of the simulator (i.e., danger); the simulator includes multimodal information and concept-related goals, actions, and feelings. Modality-specific reenactments

can result in a partial—potentially unconscious and biased—reinstatement of the original state (Barsalou, 2005b). The situational components that may not have been observed yet can be filled in by pattern completion inferences (Barsalou, 2005b). This enables individuals to make educated guesses about how the situation will unfold.

Synthesis: The case of chemosignal reception

Human chemosignaling research can profit from integrating different ideas on odor learning present in the literature to date, including the discussed top-down accounts (e.g., Dalton, 1996), odor object theory (e.g., Wilson & Stevenson, 2006), a modified version of this theory (Yeshurun & Sobel, 2010), and a situated perspective (e.g., Barsalou, 2003). Whereas odor object theory (e.g., Wilson & Stevenson, 2006; Stevenson & Wilson, 2007) and its modified version (Yeshurun & Sobel, 2010) have only been applied to non-body odors, all signs suggest that these theories can (partly) be incorporated into a broader situated theory of chemosignal reception. By weaving existing (modified versions of) odor object theory into a situated perspective on chemosignaling, a detailed and inclusive framework is created that helps understand chemosignal reception. The situation plays an important both during the *formation* of an association with the odor and when previously stored odor experiences are *reenacted*.

1) Formation

What distinguishes body odors from certain non-human odors is that body odors carry *multifarious* information about factors such as gender, age, personality, and emotions. That is, body odors have the potential to form and activate multiple odor objects, depending on receivers' associations between a particular set of odoriferous compounds that can reliably be related to specific situations and experiences. Although body odors contain hundreds of odoriferous compounds, receivers may learn to predict how situations unfold based on the odor's *non-accidental properties* (Kosslyn, 1994). Non-accidental properties are relatively *constant* to a category (Kosslyn, 1994). Take for instance a chair, which is characterized by the "non-accidental" horizontal support held by one or more vertical support(s), enabling a person to sit. Similarly, body odors are likely to have certain non-accidental properties (e.g., related to age, gender, individuality, and emotions) and these properties could have gained predictive value by occurring more frequently in certain situations, resulting in the synthesis of multiple odor objects.

2) Re-enactment

Given the complex molecular constellation of body odor, certain non-accidental properties of the body odor are expected to trigger in a bottom-up fashion likely body odor object templates to initially match the input. In a top-down fashion, additional information sources help hone in on the best matching template by activating other-modality representations in associative memory, which are related to the context or situation in which that template was originally formed. It is this two-way and iterative process that makes body odor perception situated. A threatening situation may for instance prime attention to certain non-accidental properties in body odor that result in the activation of the fear odor object. In case of impoverished input, the best matching template is selected on the basis of pattern completion inferences (e.g., Kosslyn, 1994; Wilson & Stevenson, 2006).

In sum, the situation plays a role both during the formation of associations with body odor and while receivers re-enact or simulate previously stored experiences. First, body odors have certain constant properties such that information about them can be stored as "odor objects", given that these body odor compounds are encountered more frequently in particular situations (i.e., non-accidental properties). After storage, the situation—including the multimodal information that makes up the situation—plays an important part in influencing which odor object is selected. The selection of a "body odor object" often occurs without the individual's conscious awareness and additionally involves simulating associated multimodal states, actions, goals, and feelings.

Theoretical framework to interpret research on chemosignaling

The abovementioned synthesis of learning theories provided us with a framework to interpret chemosignaling research and the remaining part consists of a review of the chemosignaling literature. Although chemosignaling is a process that involves the transfer of information from a sender to a receiver, the response of the receiver is arguably driven by the selection of a particular body odor object depending on the situation and odor-related associations the individual has. Non-accidental properties of body odor can be responsible for the fact that many individuals have similar odor-related associations. For the characteristics individuality, gender, and age, biochemical evidence has been documented that supports the extractable non-accidental properties assumption. As a consequence, evidence for the chemosignaling of these (relatively) stable constructs, including personality, will be reviewed first. Research on emotional chemosignaling, which received increased attention during the last decade, will be reviewed in Part III.

II. Chemosignaling "stable" states

Individuality, gender, age, and personality

In short, accumulating evidence has indicated that body odor can contain multifarious information about relatively stable characteristics such as individuality, gender, age, and personality. In the following sections, the documented evidence is reviewed from a situated perspective and each characteristic is addressed in turn.

Individuality

First, different individuals produce different body odors. As a consequence, we can learn to distinguish individuals on the basis of their body odor or "chemical profile". Biochemical analysis of axillary sweat by means of gas-chromatography mass-spectrometry (GC-MS) revealed consistent differences in the chemical profiles of individuals (Penn et al., 2007). Axillary sweat was obtained from multiple individuals over a 10-week sampling period and GC-MS showed that 373 out of 4941 peaks were consistent over time. Specifically, GC-MS identified the chemical structure of 44 "individual compounds". Individual differences were marked by the presence (and absence) of compounds; yet, relative ratios of compounds also varied between individuals. What has remained unknown is whether these individual differences are caused by differences in food habits, axillary microflora, genetics, and so on. For instance, evidence suggests that individual differences in marker compounds may be related to genetically determined odors such as those associated with the immune system (i.e., major histocompatibility complex, MHC; see Havlíček & Roberts, 2008, for a review on body odors and MHC).

In sum, this finding shows that particular body odors have non-accidental properties that can be associated with particular individuals. Once an association has been formed between the odor and the individual, the odor has become an information source for the recipient. Detecting individuals by smell can be important in early life, for instance when hungry neonates search for their (breastfeeding) mother (Cernoch & Porter, 1985). Not only the mother's odor, but also odors associated with breastfeeding can lead to the formation of an associative link that can persist into at least toddlerhood (Delaunay-El Allam, Soussignan, Patris, Marlier, & Schaal, 2010). In a given social situation, encountering the body odor of a familiar individual may evoke actions, feelings, and goals related to that individual.

Gender

Individuality was not the only source for differences in chemical profiles, as gender was shown to be distinguishable on the basis of body odor as well. For instance, male and female raters were significantly better than chance in detecting gender based on smells of t-shirts worn over the course of three consecutive nights (Sorokowska, Sorokowski, & Szmajke, 2012). Essentially, GC-MS indicated that no single marker compound was universally present in the axillary sweat of one gender versus the other (Penn et al., 2007). Instead, the distribution of marker compounds was multivariate and the genders could be classified with high accuracy into the right gender category (75%) based on 14 key markers (e.g., males: hexadecanoic acid, females: nonadecane; for a complete list, see Penn et al., 2007). What has remained unknown is whether the different compounds that are present in male and female sweat change the hedonic properties and intensity of the body odor. Although performance on odor detection tasks indicated that body odors and breath odors could be assigned significantly more often than chance to the right gender category (e.g., Doty, Orndorff, Leyden, & Kligman, 1978; Doty, Green, Ram, & Yankell, 1982), these findings could be explained by the fact that stronger and less pleasant odors were attributed more often to males (Doty et al., 1978; Doty et al., 1982).

There are at least four explanations why humans perform above chance in detecting gender based on body odor. First, individuals may have learned to associate particular compounds that are produced more often or uniquely by either sex with the category "male" or "female" (i.e., qualitative differences) (Zeng et al., 1991; Zeng, Leyden, Spielman, & Preti, 1996). Second, the bacteria present in the axilla are different for males and females; males have higher populations of coryneform bacteria responsible for the production of a more pungent odor (Pause, 2004) (i.e., qualitative differences). Third, males may produce stronger (and less pleasant) body odors because, compared to females, they have larger and more active apocrine glands causing them to produce *more* of the same components (i.e., quantitative differences). Of course, combinations of these explanations are also possible. Furthermore, body odor intensity may be used as a gender-classification cue in more than one way. For instance, "strong" is a physical property of an odor that may also be attributed to one sex based on mere linguistic relatedness, namely to the sex that is generally viewed as physically "stronger".

Hence, unlike what seems to be the case for the detection of individuals, prior exposure to body odors of males and females is not a necessary requirement for above chance classification of odors stemming from males and females. Nevertheless, given that the body odors produced by males and females differ, these odors could have become associated with

situated (multimodal) information related to gender, resulting in the synthesis of a "gender body odor object". Specific situations may increase the accessibility of the gender body odor object by activating situation-specific states, goals, and motives.

Age

Besides individuality and gender, another factor that can be "expressed" in body odor is age. What has been found is that strangers' estimations of the age of body odor donors is positively correlated with the actual age of donors (Sorokowska et al., 2012). Biochemical evidence for "old age smell" has been provided by studies showing the unique presence of a greasy and grassy odor in people aged over 40 caused by 2-nonenal (Haze et al., 2001; Yamazaki, Hoshino, & Kusuhara, 2010). What has remained unknown is the reason why 2-nonenal was more abundant in older individuals (but for plausible reasons, see Haze et al., 2001). Other researchers have contested 2-nonenal as the unique marker of "old age" in humans (Curran, Rabin, Prada & Furton, 2005; Gallagher et al., 2008). In a Western sample, 2-nonenal was detected in the body odor of individuals younger than 40 (Curran et al., 2005), whereas for individuals over 40, the unique body odor compound appeared to be nonanal, not 2-nonenal (Gallagher et al., 2008).

Regardless of whether specific compounds are present in the body odor of older individuals, there is one study that documented evidence for the capability to detect old age smell (Mitro et al., 2012). Participants were significantly better than chance in discriminating, labeling, and grouping together the body odor of old individuals (75-95 years), compared to that of middle-aged (45-55 years) and young (20-30 years) individuals (Mitro et al., 2012). This detection capacity was alleged not to have been caused by differences in the odors' intensity and pleasantness, even though "old age smell" was judged as slightly more pleasant (Mitro et al., 2012). The authors acknowledged that in real world settings, "old age smell" is usually interpreted negatively. This negativity may arise from the relatively greater weight that is assigned to copresent situational (e.g., nursing homes) and audiovisual information (e.g., indicators of declining health) that is interpreted as negative, thereby overriding the initial stimulus-driven pleasant reaction to old age smell.

Personality

Hence, biochemical and in some cases experimental evidence has indicated that body odors differ as a function of individuality, gender, and age. Although biochemical evidence has not yet been documented for another stable trait, personality, there are several experiments showing that certain personality traits can be conveyed by body odor (e.g.,

Sorokowska et al., 2012). These experiments were conducted as follows. First, donors self-assessed their personality traits on a personality questionnaire (NEO Five-Factor Inventory) and "aggressive dominance" scale (D-26). These scores were compared to the personality trait scores that were given by 200 raters to donors; raters based their score solely on body odor that was sampled during three consecutive nights. Significant correlations emerged between self-other judgments of "high arousal" personality traits such as neuroticism, extraversion, and dominance, but not between the low arousal personality traits openness to experience, agreeableness, and conscientiousness. Based on body odor alone, both male and female raters were more accurate than chance in detecting "extraversion", whereas female raters in particular were accurate detectors of "neuroticism". Because extraversion and neuroticism are accompanied by frequent occurrences of (high arousal) positive and negative affect, respectively, the current findings dovetail with results obtained in studies on emotional chemosignaling (reported in Part III). Highly arousing states apparently led to the production of different body odors that could become associated with emotional information that was congruent with the affective situation in which the body odor was produced.

To replicate and extend the findings of the first study, a second study additionally provided receivers with visual cues to judge donors' personality traits. Body odors were sampled by means of cotton pads during a 12-hour daytime period. Strangers were asked to rate donors' personality traits based on either their body odor, a picture of their face, or a combination of olfactory and visual cues (Sorokowska, 2013a). When raters had to rely solely on donors' facial pictures, significant overlap was observed between donors' self-assessed extraversion and neuroticism, respectively, and the manner in which strangers rated donors' extraversion and the way knowledgeable informants judged donors' neuroticism. Notably, personality judgments did not change by adding body odor to the facial pictures of donors. However, having only body odor as an information source, significant overlap was encountered between donors' self-assessed neuroticism and dominance and strangers' ratings of these two traits. Hedonic ratings of odors may have affected personality judgments based on body odor, as strangers associated body odors judged as more attractive more often with (self-assessed) extraverted individuals and body odor judged as less attractive with (self-assessed) neurotic individuals.

In a third study, the influence of age on the correctness of body odor-based personality judgments was assessed (Sorokowkska, 2013b). Whereas adults' judgments of dominance and neuroticism corresponded significantly to donors' self-assessed dominance and neuroticism, children could only correctly detect the body odor of "neurotic" adults more

often than chance. Neuroticism is related to episodes of emotional instability and negative affect and children may have learned to associate body odor produced during frequent negative affective states with negative consequences registered by other senses (e.g., yelling, angry facial expressions). Obviously, the development of a consistent pairing between body odor and other-modality information necessitates the release of a distinctive odor that is produced as a function of a particular state, such as during high arousal positive affect (i.e., related to extraversion) and high arousal negative affect (i.e., related to neuroticism). Over the course of life, the type of situations one encounters can be different and different types of information can be salient, resulting in the development of different "body odor objects" in the face of what can be similar physical odor stimuli.

Other factors impacting chemosignal reception

In a similar vein, information related to "dominance" could become more important when individuals become aware of social status, have higher testosterone levels, and have repeated exposure to body odor from dominant peers with high androgen levels. Indeed, one study showed that higher levels of testosterone in receivers were related to higher sensitivity to androstenone (Lübke & Pause, 2014). Androstenone was shown to elicit "competition" in (socially anxious) males, evidenced by increased skin conductance responses (vs. body odor sampled during exercise: sport sweat) (Adolph, Schlösser, Hawighorst, & Pause, 2010). Rather than communicating "competition", however, body odors sampled during a competitive match probably contained androgen-derivates and how these compounds are evaluated depends on the individual's situation, state, and goals. For instance, women in the fertile phase of their menstrual cycle *preferred* the body odor of self-assessed dominant males (Havliček, Roberts, & Flegr, 2005). Hence, "the smell of dominance" may be related to androstenone and this body odor elicited threat in socially anxious males and liking in fertile women.

Sexual orientation can also play a role in the processing of body odor (e.g., Martins et al., 2005). For instance, homosexual men had higher olfactory sensitivity compared to heterosexual men to the earlier mentioned compound that is predominantly present in male body odor: androstenone (Lübke, Schablitzky, & Pause, 2009). On a more general level, homosexual men, heterosexual men, and lesbian women apparently allocated more attention to odors of their preferred sexual partner, as was evidenced by shorter P2 latencies (Lübke, Hoenen, & Pause, 2012). The early processing advantage for body odors of desirable sexual

partners may be related to learning effects, as repeated exposure to body odors results in enhanced sensitivity and shifts in the evaluation of body odors (also see, Lübke et al., 2012).

Hence, body odors are *social stimuli* that ostensibly acquired this quality through learning. One study showed that when individuals high (vs. low) in social openness were exposed to body odor, more activity was recorded in regions related to activation of the mirror neuron system (i.e., inferior frontal gyrus) and the processing of reward (i.e., caudate nucleus) (Lübke et al., 2014). Indeed, a positron emission tomography (PET) study showed that body odors were processed differently as they additionally activated non odor-related brain areas compared to perceptually similar common odors (see Lundström et al., 2008). The social implications of body odor can also be derived from the influence of familiarity. Body odors stemming from friends evoked less negative emotions compared to the body odor of strangers, and emotions were better recognized on the basis of body odor when these individuals were familiar to the person (Zhou & Chen, 2011).

In sum, there are a plethora of factors that can influence body odor perception. These factors clearly indicate that the perception of body odor occurs in a rich context, not in isolation. Simple one-to-one relations between body odors produced by a sender and perception by a receiver do not exist. Instead, receivers pick out the type of olfactory information that is most salient to them, strongly depending on learned associations. More evidence for this claim is provided in the next section, which will focus on the chemosignaling of dynamic states[5], namely emotions.

III. Chemosignaling "dynamic" states

When dealing with emotional chemosignaling, one has to have a clear grounding of what is meant with emotions and how they can be communicated from a sender to a receiver. This is the subject of the next section. Before reviewing emerging research on emotional chemosignaling from a situated perspective, we introduce and briefly discuss different emotion perspectives. Of these perspectives, the discrete emotion perspective has generally been used as a theoretical anchor in emotional chemosignaling research. Notably, a discrete emotion perspective may be adopted to support a pheromone-like view of chemosignals, when it is expected that exposure to the body odor of a fearful sender will *always* lead to a

[5]For a recent study on the scent of disease, the reader is referred to the work of Olsson et al. (2014). With regard to the chemosignaling of dynamic states, we include in this review only those dynamic states that have been reported in more than one study, such as is the case for emotional chemosignaling.

fearful receiver. However, the discrete emotion perspective does not seem to adequately account for the situated responses displayed by receivers exposed to emotional chemosignals.

Chemosignals and (discrete) emotions

Before addressing the actual research on emotional chemosignaling, we first introduce and briefly discuss three main perspectives on emotions. Notably, all studies on emotional chemosignaling published to date followed one of these perspectives to interpret the experience of body odor producers and recipients, namely the discrete emotion perspective. The discrete emotion perspective appears to fit well with a pheromone-like definition of chemosignals, in the sense that stable and fixed reactions are expected to occur to body odors that are produced as a function of a discrete state. The standard idea of emotions is that they are innate and universal and they emerge from the organism's biological heritage as opposed to being learned (e.g., Ekman, 1992; Izard, 2007; Panksepp, 2007). Even though body odors may activate the primitive, limbic regions of our brain, the evidence reported below suggests that the experience of the chemosignal recipient and therefore chemosignaling as a whole is more complex and situated.

Compared to discrete emotion theories, appraisal theories suggest that one individual may interpret a situation as threatening, whereas another could interpret the same situation as challenging and these situations can be reappraised (e.g., Lazarus, 1991). Indeed, even within categories of emotion experience, there is tremendous variation that cannot be captured by the basic emotion concepts of happiness, disgust, fear, anger, surprise, and sadness (Barrett, 2009b, 2013). Less typical fear experiences, such as riding a rollercoaster, do not always evoke negative affect and can even be interpreted positively by some individuals (Wilson-Mendenhall, Barrett, & Barsalou, 2014). In addition, the type of fear in a social situation can evoke different actions, feelings, goals, and expressions, than being in a situation in which physical harm could occur. That is, there is non-homogeneity *within* emotion categories (Lebois, Wilson-Mendenhall, Simmons, Barrett, & Barsalou, under review). In addition, both fear and anger may be associated with activation of the fight/flight response and similar brain areas may be dedicated to the processing of these emotions (for a review, see Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012). Since all emotions tend to utilize the same neural systems (e.g., amygdala, insula, orbitofrontal cortex) on some occasions, there is non-selectivity *across* emotion categories (Lebois et al., under review; Duncan & Barrett, 2007; Pessoa, 2008, 2012). In sum, recent evidence suggests that "emotion" as a category represented by the brain does not emerge from activation of innate circuits, but instead results

from computational strategies in the brain, involving core affect, conceptual knowledge, and sensory input from the situation.

Empirical evidence has shown that participants use background settings to situate categories (Vallée-Tourangeau, Anthony, & Austin, 1998). For instance, the category social fear may be situated in a setting in which someone has to give an impromptu oral presentation in front of an expert audience. Categories are thus associated with situations and both are activated in situated conceptualizations (Barsalou, 2005b). The situated representation produces inferences by priming relevant actions in the motor system. Situated action could be inferred from emotional facial expressions. These facial expressions can either be taken over by a receiver once displayed by a sender and in the least case these facial expressions can be used as information source. In both cases, the adopted somatosensory and motor states allow individuals to make conceptual inferences about categories such as emotions, facilitating communication. In the end, conceptual knowledge, sensory input from the world, and core affect (i.e., the dimensions of valence and arousal) influence one another to produce an emergent state that can be measured as a discrete emotion (Lindquist et al., 2012).

Emotional chemosignaling research: A systematic review

Whereas odors are produced and perceived in congruent situations in a real world setting, the actual study of the perception of chemosignals has been performed in a laboratory context. The laboratory context cuts out important situational information, as it isolates the effects of body odors such as those produced during certain emotional states. Although research on emotional chemosignaling has been performed mostly in a decontextualized setting, the pattern of results indicated at least four signs suggestive of *situatedness*: (1) multiple individuals showed signs of having extracted statistical regularities with regard to odors and the typical situation in which they would be experienced; (2) some individuals showed stronger responses or reacted to different properties of certain odor stimuli than others (i.e., individual variation); (3) in the absence of contextual information, individuals experienced more difficulty labeling or making sense of their emotional experience; (4) strongest responses were encountered when congruence existed between particular body odor and situation in which the body odor would be typically produced and perceived.

Our literature search showed that 23 empirical studies were published that reported on *emotional chemosignaling* (see Table 1). Authors used similar yet different terms to describe the communicative medium. Most authors used the short definition adopted here,

chemosignals (e.g., Zhou & Chen, 2009; Zernecke et al., 2011; de Groot et al., 2012; Dalton, Mauté, Jaén, & Wilson, 2014), whereas others speak of "chemosensory signals" (e.g., Adolph, Meister, & Pause, 2013; Haegler et al., 2010), "chemosensory cues" (Mujica-Parodi et al., 2009), or simply (stress-related) "body odors" (Wintermann, Donix, Joraschky, Gerber, & Petrowski, 2013). All 23 studies primarily focused on olfactory communication of discrete fear or stress. The typical fear chemosignaling study would involve sampling "fear odor" from *senders* having absorbent compresses attached under their armpit during the induction of physical or social[6] fear (see Table 1), after which *receivers* exposed to fear odor were expected to show a corresponding fear reaction compared to one or more control conditions (i.e., sport sweat, unused sweat pads, sweat sampled during a neutral state). Four chemosignaling studies additionally explored a positive affective state, happiness (Chen & Haviland-Jones, 2000; Zhou & Chen, 2009, 2011; de Groot et al., 2015a), and another explored a different negative affective emotion (i.e., disgust, de Groot et al., 2012). Evidence for emotional chemosignaling was derived from affect-modulated performance on a multitude of tasks and measures, including odor discrimination tasks, self-report measures, behavioral measures, and neural measures.

Below we sum up and critically review evidence for emotional chemosignaling. To sketch a comprehensive picture of the pattern of results, the 23 studies on chemosignaling were grouped per main outcome variable. The overarching questions were: (1) Are the effects induced by chemosignals likely to be socially situated instead of context-independent? (2) Is there sufficient evidence to state that the experience of the receiver can be considered discrete fear (vs. core affect), and can we thus speak of *fear* chemosignaling?

[6]What is labeled "social fear" in the current review is called anxiety by authors who sampled sweat while participants were *anticipating* an oral exam (e.g., Pause, Ohrt, Prehn, & Ferstl, 2004). We prefer to use the term "social fear" in this review for two reasons. First, social (vs. physical) gives information about the situation in which fear was induced. Fear is a non-homogenous state with different outings in social and physical settings (Lebois et al., under review). Second, there is no evidence evidence to assume that sweat production during "anxiety" draws on a different physiological mechanism than that of "fear", since the apocrine sweat glands responsible for chemosignal production are activated by adrenalin (Harker, 2013; de Groot et al., 2015b) and no relation with another stress-related product such as cortisol was documented in the literature (Harker, 2013). Third, the results are reviewed from a social communication perspective which assumes correspondence between the process observed in a sender and a receiver. That is, receivers display a simulacrum of the state of the sender. Do enhanced startle reflexes mean that receivers exposed to sweat from anxious individuals became anxious as well (i.e., correspondence), or was this a sign of fear or negative affect? These three reasons form the basis of our goal to achieve conceptual clarity by using the terms (social and physical) fear throughout the review.

Even though the results on the diverse measures may converge on the perspective that receivers emulated the discretely fearful state of senders, the alternative explanation cannot be ruled out, namely that receivers experienced a high arousal, negative valence state. At least three reasons should be mentioned with regard to the argument that receivers may not have experienced discrete fear. First, the apocrine sweat glands in the armpit area produce a distinctive odor after adrenalin release (Harker, 2013) following the activation of the fight/flight response (de Groot, Smeets, Semin, 2015b). This could imply that both anger and fear lead to the production of a similar odor that can be associated with anger, fear, both, or with the general category (e.g., "danger", "threat", or "negativity"), depending on situated aspects such as the frequency of co-occurrence between the state and the release of the odor. Second, in most studies *receivers* were not provided with emotion-relevant contextual information from the audiovisual modalities to make sense of their experience, unlike what was the case for *senders*. Since emotion-relevant audiovisual and situated information was available to them for (conscious) introspection (e.g., tandem skydiving), senders were able to label their experience in discrete emotion terms. Third, the measures that were used to target a state of fear (e.g., startle reflex, facial electromyography) in both senders and receivers may not necessarily reflect discrete states, as evidence suggests that these measures are reflective of general states of arousal and positive or negative valence (e.g., Russell & Barrett, 1999; Lang, 1995; Larsen, Norris, & Cacioppo, 2003).

Table 1

Overview of the 23 published studies on emotional chemosignaling

Authors	**Year**	**Induction method**	**Sampling T (min)**	**Odor exposure**	**N sender**	**N receiver**	**Main finding senders**	**Main dependent variable receivers**
Chen & Haviland-Jones	2000	Videos (physical)	13	Glass bottles	14F&11 M	40F&37M	SR: mod. > fear	Odor identification
Ackerl, Atzmueller, & Grammer	2002	Videos (physical)	70	Plastic bottles	42F	62F	SR: > state anxiety Φ: no > cortisol	Odor judgment
Pause, Ohrt, Prehn, & Ferstl	2004	Prior to academic examination (social)	90	Olfactometer	12M	8F&8M	SR: > aroused, anxiety; < happy, dominant, pleasant	Judgment neutral facial expressions preceded by face prime
Chen, Katdare, & Lucas	2006	Videos (physical)	20	Above lip	3F&4M	68F	SR: > fear, anxiety, disgust, Φ: no > HR, SCL, RSA	Word association task
Prehn, Ohrt, Sojka, Ferstl, & Pause	2006	Prior to academic examination (social)	90	Olfactometer	12M	3F&4M	SR: > anxiety, arousal; < pleasure, happy, dominant	Startle reflex
Zhou & Chen	2009	Videos (physical)	20	Above lip	6M; 2M	48F; 16F	SR: > fear Φ: > HR	Judgment morphed facial expressions
Pause, Adolph, Prehn-Kristensen, & Ferstl	2009	Prior to academic examination (social)	90	Olfactometer	21F& 28M	16F&16M	-	Startle reflex
Prehn-Kristensen et al.	2009	Prior to academic examination (social)	60	Olfactometer	21F& 28M	14F&14M	SR: > anxiety, surprise, angry, disgust, sad, < happy, dominant, Φ: > cortisol, testosterone	fMRI
Mujica-Parodi et al.	2009	Tandem skydive (physical)	20 (dive: 5)	Olfactometer	52F& 92M	21F&25M	SR: > state anxiety Φ: > cortisol	fMRI; threat detection from facial expression
Pause, Lübke, Laudien, & Ferstl	2010	Prior to academic examination (social)	60	Olfactometer	21F& 28M	12F& 16M; 8F&8M	-	EEG
Haegler et al.	2010	High rope course (physical)	2 x 30	Above lip	21M	16F&14M	SR: > state anxiety	Risk game
Zhou & Chen	2011	Video (physical)	20	Polypropene jars	20M& 20F	20M& 20F	SR: > fear, Φ: > SCL, HR	Odor identification
Albrecht et al.	2011	High rope course	20	Above lip	13M	20F	SR: > state anxiety,	Self-reported state

		(physical)					Φ: no > HR, blood pressure	anxiety
Zernecke et al.	2011	High rope course (physical)	30	Above lip	21M	15M	SR: > anxiety	Judgment morphed facial expressions
Rubin, Botanov, Hajcak, & Mujica-Parodi	2012	Tandem skydive (physical)	20 (dive: 5)	Olfactometer	64M	8F&6M	-	EEG
de Groot, Smeets, Kaldewaij, Duijndam, & Semin	2012	Videos (physical)	30	Polypropene jars	10M	35F	SR: > state anxiety, Φ: mod. > HR, SCL	Facial EMG; sensory vigilance
Adolph, Meister, & Pause	2013	Prior to academic examination (social)	90	Olfactometer	20M	40F; 36F	SR: > unpleasant, aroused, anxious, < happy	EEG; startle reflex; Judgment of facial expressions
Radulescu & Mujica-Parodi	2013	Tandem skydive (physical)	20 (dive: 5)	Olfactometer	20F& 20M	8F&8M	-	fMRI
Dalton, Mauté, Wilson, & Jaén	2013	Trier Social Stress Task (social)	15	Glass bottles	44F	72F&48M	SR: > anxiety, stress, Φ: > HR	Judgment of third person (women) in neutral video clips
de Groot, Semin, & Smeets	2014	Videos (physical)	30	Polypropene jars	8M	30F	SR: > state anxiety, fear, < calm	Facial EMG
de Groot, Semin, & Smeets	2014	Videos (physical)	30	Polypropene jars	13F& 13M	26F& 26M	SR: > fear, disgust Φ: > sweat production	Facial EMG
de Groot, Smeets, Rowson, Bulsing, Blonk, Wilkinson, & Semin	2015	Videos (physical)	30	Polypropene jars	9M	35F	SR: > fear (fear), > happiness (happy) Φ: > sweat production	Facial EMG; global-local task
de Groot, Smeets, & Semin	2015	Trier Social Stress Task: Anticipation phase (social)	10	Polypropene jars	8M	31F	Φ: > HR, sweat production, < cortisol	Facial EMG; classification of facial expressions

Note. Situation in which fear was induced displayed between parentheses (physical or social) under "Induction method". N = sample size, M = male, F = female. Measures: SR = self-report measure, Φ = physiological measure; HR = heart rate, EEG = electroencephalography, EMG = electromyography, fMRI = functional magnetic resonance imaging, SCL = skin conductance level, RSA = respiratory sinus arrhythmia.

Emotion identification

The first experiment on emotional chemosignaling asked receivers to identify the emotion of the senders based on body odor alone. Senders were induced to be in a fearful and happy state by means of video clips (Chen & Haviland-Jones, 2000). Receivers had to discriminate between fear odor, happy odor, and unused cotton pads on six (3-choice and 6-choice) different identification tasks. When receivers had the task to pick "the odor of people when they were afraid", both men and women performed above chance in selecting male (but not female) fear odor. Furthermore, male receivers identified "the odor of people when they were happy" above chance when it concerned female senders, whereas female receivers identified above chance the happy odor of women *and* men.

There are at least three limitations that can be noted with regard to this study. First, since fear and happiness map on opposing sides of the valence dimension, evidence as to whether receivers distinguished between sweat on a *discrete* emotion basis rather than a valence (positive-negative) basis cannot be unambiguously inferred. Neither were other negative and positive emotion control conditions included, nor were receivers provided with different discrete emotion labels when selecting body odor. For instance, when receivers would be asked to identify "the odor of people when they were angry" from unused pads, fear odor, and happy odor, receivers may in this case select fear odor (i.e., another negative emotion) above chance. Third, the finding that receivers discriminated body odors based on the emotional state of the sender does not imply that receivers emulated the state of the sender—one of the key principles of social communication theory.

The minimal conclusion that can be drawn from findings reported in this pioneering body odor emotion identification study is that humans produce and perceive *at least* two distinctive body odors, one (high arousal) positive affect-related odor and one (high arousal) negative affect-related odor. Although body odors partly consist of trigeminal components that may evoke negative affective responses such as irritation, these components were apparently not (solely) responsible for the observed effects, as receivers could pick out body odors related to positive affect. Hence, the current study provided the first hint that certain odors may have become associated with negative affect, whereas others were associated with positive effect and these are findings that can be explained from a situated perspective.

Self-report

Three studies went further and examined whether sweat produced during an instance of negative affect, namely fear, would modulate the subjective experience of a receiver to become similar to the experience of the sender (Ackerl, Prehn, & Atzmueller, 2002; Albrecht et al., 2011; Dalton et al., 2014). Although all three studies reported changes in the subjective experience of receivers that were more or less "in line with the state of the sender" in the broad sense, not all studies could show that receivers experienced *discrete* fear. In fact, only one study delivered preliminary evidence in favor of correspondence between a sender and a receiver. Specifically, receivers that were exposed for a long time (i.e., 20 min vs. 5 min) to the odor of fearful high rope course participants reported increased state anxiety (Albrecht et al., 2011). However, another study showed that when receivers judged the affective state of horror (vs. neutral) movie-watching senders using multiple verbal labels, odors were rated as significantly more intense, unpleasant, and aggressive, but not fearful (Ackerl et al., 2002). Similar findings were reported in a third study, which examined the influence of fear odor on ratings of a third person (Dalton et al., 2014). Compared to sweat sampled during a social fear manipulation when sweat glands were blocked with antiperspirant, receivers exposed to untreated fear sweat and sport sweat rated women in muted neutral video clips as less trustworthy, less competent, and less confident, but these women were *not* judged as being more stressful.

In sum, these mixed results indicate that exposure to fear odor did not generally lead to the preference of the labels "anxious", "fearful", or "stressed" to describe the odor (Ackerl et al. 2002), the receiver's own situation (Albrecht et al., 2011), or characteristics of a third person (Dalton et al., 2014). The lack of emotion-related (audiovisual) information seemed to have precluded receivers from interpreting the olfactory experience in discrete emotion terms. Instead, subjective measures indicated that receivers selected general (high arousal) negative valence terms to describe the odor, their situation, and characteristics of a third person. Although self-report measures are widely used in the field of psychology to the extent that studies not including explicit ratings seemingly have a harder time finding the light of publication (Baumeister, Vohs, & Funder, 2007), the relation between olfaction and language is weak (Lorig, 1999). Insufficient development of vocabulary for odors and the effects they induce may therefore alternatively account for the lack of consensus in describing what the smell induced. Essentially, the question that has

remained is whether explicit labels form an accurate description of the *actual* state of the receiver induced by body odor. The next set of studies was aimed to answer the question whether exposure to the body odor of fearful individuals changed the *perception* and actual *behavior* of receivers.

Perception

A number of studies on fear chemosignaling examined whether sweat sampled during the induction of physical or social fear modulated the visual perception of receivers in a manner that reflected the state of the sender. The overall pattern of results indicated that receivers showed the most typical responses interpreted as indicators of a "fear experience" when the (negative) valence of the odor stimulus was incongruent with a simultaneously presented positively valenced or ambiguous visual stimulus (i.e., facial expression).

First support for this olfactory-visual valence mismatch effect came from a study that presented participants with different facial expressions in the presence of fear sweat (vs. sport sweat). When neutral faces were preceded by subliminally presented *happy* (vs. fearful, sad) facial expressions, these neutral faces were judged as less pleasant by receivers in the presence of fear sweat (Pause et al., 2004). Fewer positive judgments do not necessarily have to be related to fear, as they could indicate the likely presence of negative affect, the absence of positive affect, or both (i.e., when following the idea that positive and negative affect are independent; e.g., Larsen, McGraw, Cacioppo, 2001). Additional evidence was reported by studies that presented receivers with ambiguous facial expressions to examine whether they would disambiguate the ambiguous facial expressions as fearful. Indeed, facial expressions morphed halfway between happy and fearful were identified significantly more often as fearful when presented together with fear odor (vs. unused pads) (Zhou & Chen, 2009). When participants were asked to detect the level of threat on the basis of facial expressions morphed between neutral and angry, exposure to fear odor (vs. sport sweat) led to more accurate "threat" and "no threat" decisions in the relatively more ambiguous cases (Mujica-Parodi et al., 2009). Another study showed that facial expressions morphed between neutral and happy were judged as more scary (or less happy) by male receivers when presented together with fear odor (vs. sport sweat, unused pads) (Zernecke et al., 2011).

In sum, the reviewed results went beyond observations from the domain of visual perception that revealed the dominant impact of bottom-up information in cases of conflict with top-down information (Pylyshyn, 1999; Barsalou, 1999). Research showed that modulation of visual perception by fear odor was strongest when visual information was ambiguous or positive, thereby creating a valence mismatch between the olfactory and visual stimulus. When negative information from the olfactory modality contrasted ambiguous or positive visual information, visual information was seemingly outweighed by information the olfactory modality. Hence, humans seem to be capable of flexibly deploying attention to relevant information in the environment, in accord with a situated account of chemosignaling. Chemosignal reception was more complex than the simple context-free communication of fear that would be expected based on an animal-based pheromone-like definition of chemosignaling. The studies on perceptual modulation by fear odor furthermore could not provide definitive evidence about whether receivers experienced discrete fear, because all studies used dichotomous ratings of facial expressions. That is, receivers had to contrast a positive affective state (i.e., pleasant, not threatening, and happy) with a negative affective state (i.e., unpleasant, threatening, fearful, scary) on each occasion. Multiple qualifiers of negative affect are required to verify whether receivers experienced discrete fear in the presence of fear odor. Examining the impact of chemosignals on behavior may provide more conclusive evidence to this respect.

Behavior

Most chemosignaling studies measured behavior to observe a correspondence between the state of the sender and receiver. Researchers gathered their evidence mainly from modulation of the startle reflex, behavior related to a risky or cautious strategy, and emotional facial expressions via facial electromyography (EMG). Below, studies are grouped per outcome variable and addressed in their respective order.

Three chemosignaling studies examined whether fear odor modulates a motor response that is often related to fear: the startle response. The startle response is a defensive reflex consisting of a rapid series of motor actions following exposure to an abrupt, intense stimulus (e.g., Lang, 1995). The startle response is often evoked in an experimental paradigm with a brief (50 ms) 95-110 decibel acoustic startle probe (Mauss & Robinson, 2009). The most robust behavioral component of the startle

reflex is the eye blink, which can be measured with facial EMG (Mauss & Robinson, 2009). However, the startle reflex appears to be an indicator of negative affect rather than fear and this assumption is supported by evidence. Specifically, the magnitude of the eye blink startle response was enhanced in the context of unpleasant stimuli compared to neutral control stimuli, whereas positive stimuli resulted in the opposite effect and diminished the magnitude of the startle response (Lang, 1995; Cuthbert, Bradley, & Lang, 1996).

Using a small sample ($N = 7$), Prehn and colleagues (2006) were the first to demonstrate increased startle eye blink magnitude in the presence of sweat sampled from senders anticipating an oral exam (vs. sport sweat and unused cotton pads). Their findings were replicated and extended in two larger studies showing particularly pronounced startle responses when fear odor was presented to (highly) socially anxious individuals (Pause, Adolph, Prehn-Kristensen, & Ferstl, 2009; Adolph et al., 2013). Socially anxious individuals may indeed be specifically attuned to body odor produced during social evaluative threat. In line with the situated perspective, these individuals were more likely to have established strong associations between fear odor and (multimodal) situational information related to fear. Socially anxious individuals may not only be sensitive to fear-related social information, however, as they may turn attention to any type of stimulus that contains (negative) social information. Hence, evidence as to whether fear odor induced a *discrete* state of fear as opposed to general negative affect has remained inconclusive, as will be outlined below.

Evidence for *non*-emotion specificity in receivers' responses comes from a study presenting fearful facial expressions in the presence of fear odor, as these fearful facial expressions were not evaluated as more fearful but as "more unpleasant" in general (Adolph et al., 2013). Nevertheless, when receivers had to describe which discrete state would best fit the state of the (social) fear odor-producing senders, "anxious" was selected more often, whereas "joyful" was considered to be the best fitting state of senders producing sport sweat (Pause et al., 2009). Notably, the valence of the emotion label that was ascribed to the sender was congruent with the direction of the startle response, as compared to the neutral condition, startle responses were *diminished* in the presence of sport sweat (Pause et al., 2009).

A general conclusion with regard to the startle response would be that exposure to fear odor enhanced the magnitude of the startle response, in particular in socially anxious individuals. Because fear odor was not rated as significantly more

unpleasant than sport sweat and unused pads, startle responses were apparently not driven by the odors' hedonic properties. However, the degree of emotion-specificity of the startle response can be questioned, as its modulation is usually related to negative affect (Lang, 1995). The question is whether odors produced during other negative affective states (e.g., anger) could affect the startle response in a similar manner. The startle reflex serves to protect the organism from injury, which is adaptive for many negative emotions, but it also facilitates vigilance toward potential threat (see Lang, 1995; Mauss & Robinson, 2009). The common neural "ground" between the startle reflex, vigilant behavior, and threat detection is the amygdala (e.g., Davis, 1992; Angrilli et al., 1996). However, before we turn to discussing the neural correlates of fear odor perception, five behavioral studies are highlighted that may give a more conclusive picture as to whether receivers displayed behavior associated with discrete fear in the presence of body odor produced by fearful senders.

Compared to a view on fear chemosignaling that extends the animal-based definition of pheromones to humans, a situated perspective would incorporate the context and would better account for large inter-individual variation in the manner in which receivers respond to fear odor. The task at hand constitutes an important contextual factor that determines how receivers respond to fear odor. To exemplify, receivers in the presence of fear odor (vs. sport sweat, neutral sweat, unused pads) spent more time on a cognitively demanding task in order to decide with greater accuracy that two words from similar categories (i.e., threat-related and not threat-related) were indeed similar (Chen et al., 2006). However, when receivers played a card game that included risky and less risky decisions in the presence of fear odor, they chose the most risky option more frequently (Haegler et al., 2010).

The question is how fear odor can elicit cautious behavior in one study and risky behavior in another. One possible yet speculative explanation is that receivers associated both avoidance motivation-related negative affect (e.g., fear) and approach motivation-related negative affect (i.e., anger) (Carver & Harmon-Jones, 2009) with what is typically considered to be fear odor, in case fear and anger may lead to the production of a relatively similar body odor based on activation of the fight/flight response (see de Groot et al., 2015b). Aspects of the situation, such as the experimental task at hand, may then determine whether exposure to "fear odor" predominantly activates approach-related or avoidance-related aspects of the previously stored situated conceptualization. In sum, these behavioral studies

provided further evidence that fear odor elicits behavior that is socially situated and that cannot be neatly categorized in terms of discrete fear, compared to the broader umbrella term negative affect.

Five more studies relied on a particularly sensitive and implicit behavioral outcome, facial EMG, and assessed whether receivers displayed a simulacrum of the discretely fearful state of the sender. All studies indicated that fear odor induced, inter alia, a fearful facial expression, evidenced by increased *medial frontalis* (de Groot et al., 2012) and *corrugator supercilii* activity (de Groot, Semin, & Smeets, 2014a) in female receivers (de Groot, Semin, & Smeets, 2014b). Increased *medial frontalis* activity (i.e., lifting the eye brow) would be particularly adaptive in the case of fear, as it increases visual field size allowing individuals to take in more visual information (Susskind et al., 2008). The seemingly automatic "matched" motor response of the receiver therefore resembled the state of the sender and could be classified as a case of emotional contagion (e.g., Hatfield, Cacioppo, & Rapson, 1993). However, some researchers are skeptical whether emotional mimicry extends beyond positive and negative affect and a recent review noted the absence of solid evidence for the emotional facial mimicry of discrete states (Hess & Fischer, 2013). The discrete emotion discussion will be used as a thread connecting each study that will now be discussed in more detail.

The first study that explored facial muscle reactions to fear odor was aimed to provide multi-faceted evidence for the social communication of discrete states by means of chemosignals (de Groot et al., 2012). Not only facial EMG, but also eye scanning behavior, sniffing behavior, and perceptual sensitivity were measured in response to fear odor compared to another negative emotion (i.e., disgust) and unused sweat pads. Exposure to fear odor induced sensory vigilance, evidenced by increased *medial frontalis* activity, more effective eye scanning in a visual search paradigm, and enhanced accuracy when the search task was easy (de Groot et al., 2012). In contrast, exposure to body odor that was obtained during an episode of disgust led to sensory rejection, evidenced by decreased visual search task performance, less effective eye scanning strategies, and the emergence of a disgusted facial expression (i.e., *levator labii* activity). While these facial muscle patterns appear to fit with the discrete emotion perspective, the odor of individuals that were induced to be disgusted was judged as more intense and more unpleasant compared to fear odor. Hence, the perceptual properties of the odor may have driven the disgust response in this case.

Alternatively, biochemical analyses could point out that disgust leads to the production of a qualitatively different odor than the odor produced during an episode of fear. Given that the typical effects evoked by fear odor are usually not driven by differences in pleasantness and intensity, evidence is required from multiple sources (e.g., biochemical studies, replication studies of behavior) to determine whether discrete states other than "fear" can be carried over from a sender to a receiver by means of chemosignals.

Rather than focusing on disgust, a second (de Groot et al., 2014a) and third study (de Groot et al., 2014b) explored the boundary conditions of effective fear chemosignaling. Whereas one study examined the potential overriding effects of audiovisual information, another was aimed at testing for sex differences in chemosignal reception. With regard to the former, facial EMG responses to fear odor (vs. neutral odor) were examined while receivers were exposed to different situations. They viewed audiovisual scenes containing emotional information that was either congruent with the odor or not (i.e., fear and neutral). Like what was observed in a similar previous study (de Groot et al., 2012), the fearful facial expression (i.e., *medial frontalis* and *corrugator supercilii* activity) emerged a couple of seconds after odor onset and the expression was maintained over the course of minutes. Importantly, the fearful facial expression was strongest when fear-inducing audiovisual scenes were presented together with fear odor. In contrast, the weakest facial expression taken as an indicator of fear was recorded when neutral scenes were presented together with neutral odor—the two incongruent conditions ranked in-between the congruent ones (de Groot et al., 2014a).

The abovementioned results were obtained in a female receiver sample. It has to be noted that women are generally more sensitive to emotional signals and have a better sense of smell (e.g., Brody & Hall, 2000). As a consequence, fear chemosignal reception was expected to be characterized by sexual asymmetry. Indeed, when receivers were exposed to (male and female) fear odor, only female receivers displayed a *simulacrum* of the fearful state of the sender (i.e., increased *medial frontalis* and *corrugator supercilii* activity). Strikingly, men showed a similar albeit somewhat weaker response as females, but this occurred only when they were presented with the odor stemming from female senders (de Groot et al., 2014b). Hence, facial muscle responses that were recorded in receivers may not have reflected the presence of discrete fear, but may rather have been an indication of vigilant

attention toward information that was most salient to the receiver. To restate, the type of information that is salient to a receiver depends on aspects of the situation and the individual's goals.

The studies that were aimed to examine the boundary conditions of fear chemosignaling were complemented by a fourth and fifth study. One study focused on the sender and showed that activation of the fight/flight response (i.e., participants had to prepare for a speech) led to the production of typical "fear odor" (vs. control conditions) (de Groot et al., 2015b). This was evidenced in the case of the emergence of a negative affective facial expression (i.e., significantly higher *corrugator supercilii*, but not *medial frontalis* activity) in receivers, who additionally showed increased speed with regard to the classification of emotional facial expressions (de Groot et al., 2015b). The increase in classification speed occurred across the board and was not specific to fearful facial expressions, which indicates a general vigilance effect that was induced by the odor. Because the apocrine sweat glands can be activated by adrenalin, they may be activated by the fight/flight response, but also by highly arousing positive affect. Another study focused on obtaining behavioral evidence for the chemical transmission of positive affect from a sender to a receiver (de Groot et al., 2015a). This study indicated that receivers exposed to the odor of individuals induced to be in a happy state (vs. fear and neutral) led to a simulacrum of happiness in receivers, evidenced by facial muscle activity over the *zygomaticus major* and *orbicularis oculi* and a relatively more global perceptual focus (vs. fear) (de Groot et al., 2015a). Hence, certain body odors appeared to have been associated with positive information, disproving the possible assumption that receivers simply responded to the trigeminal properties of body odors with a negative valence or vigilance response.

In sum, studies that relied mainly on facial EMG provided relatively robust evidence for the emergence of a fearful (or negative affective) and happy (or positive affective) facial expression following exposure to body odor produced during instances of fear and happiness, respectively. Although activity over the *medial frontalis* and *corrugator supercilii* muscles may be related to an expression of fear (e.g., Du, Tao, & Martinez, 2014; Susskind et al., 2008), some researchers argue that only positive and negative affect can reliably be distinguished on the basis of facial EMG (e.g., Larsen, Norris, & Cacioppo, 2003; Hess & Fischer, 2013). Notably, receivers showed a typical fearful facial expression shortly after fear odor onset. This

expression was maintained over the course of minutes and previous research indeed indicated that compared to common odors, body odors may induce effects that are less prone to habituation (McClintock, 2002; Pause, Lübke, Laudien, & Ferstl, 2010). The combined set of studies additionally indicated that (1) the effects elicited by fear odor were most pronounced in the context of congruent audiovisual information, allowing individuals to make better inferences or educated guesses about how the situation will unfold (2); male receivers responded differently to fear odor than female receivers, reflecting different strategies of attending to olfactory information based on the salience of olfactory information. What is most salient to individuals depends on the context, the goals of the receiver, and the receiver's association with and interpretation of the odor. In sum, these behavioral studies highlighted the situated form of human olfactory communication on the receiver side. Next, we turn to studies that measured brain activity to study the effects of fear chemosignals.

EEG

Three studies recorded electroencephalograms (EEGs); event-related potentials (ERPs) were measured to capture the specific impact of fear odor on the brain in a time-sensitive manner. For this type of research, the timing of odor stimulus presentation is crucial and this necessitates the use of an olfactometer. The olfactometer makes use of a continuous airflow and odors are presented to a participant once a valve is opened with a pre-programmed trigger. The three studies that used the olfactometer to present fear odor showed increased amplitudes of various components of the ERP in (socially anxious) receivers, which was interpreted as a processing bias for fear odor. Consistent with other research on emotional chemosignaling, fear odor was shown to increase vigilance and this increase was particularly noteworthy in females and socially anxious individuals (Pause et al., 2010; Adolph et al., 2013).

In one ERP study, receivers were exposed to "fear odor" obtained from senders that had their first tandem skydive. Simultaneously, receivers viewed morphed faces containing angry, neutral, and ambiguous (i.e., morphed between neutral and angry) expressions (Rubin, Botanov, Hajcak, & Mujica-Parodi, 2012). Exposure to fear odor increased amplitudes of the early (250-400 ms) and late (400-600 ms) positive potential, irrespective of simultaneously presented angry, neutral, and ambiguous facial expressions. Regardless of simultaneously presented fearful

facial expressions, a second study showed that only socially anxious individuals exposed to fear odor had increased amplitudes on the late positive potential (400-600 ms), reflecting higher motivated attention toward fear odor in these participants (Adolph et al., 2013). In fact, prior research had already shown that socially anxious (female) receivers had greater ERP amplitudes in frontal scalp areas (Pause et al., 2010). The difference was that for socially anxious receivers, faster amplitude differences were encountered (i.e., at the N1 component of the ERP), ostensibly indicating alertness (Pause & Krauel, 2000). Female receivers showed higher peak amplitudes in medial and frontal brain areas at P3 (700-900 ms post onset), indicating greater emotional involvement on their part (Pause & Krauel, 2000).

Hence, exposure to fear odor arguably signaled to the receiver that "something important is going on", resulting in the recruitment of additional neural resources. Based on increased ERP amplitudes, females and socially anxious individuals appeared to have been particularly sensitive to the information that was transferred by fear odor. These findings dovetail with the situated perspective and other research on chemosignaling that used for instance behavioral measures and functional fMRI, discussed in the next section.

fMRI

Neural evidence for fear chemosignaling was delivered by three carefully designed studies that made use of functional magnetic resonance imaging (fMRI). Compared to sport sweat, exposure to (social) fear odor induced activity in a brain network that—according to the authors—was related to the processing of empathy (Prehn-Kristensen et al., 2009). Furthermore, exposure to (physical) fear odor evoked amygdala activity that was related to the experience of fear (Mujica-Parodi et al., 2009; Radulescu & Mujica-Parodi, 2013). However, the utilization of a particular neural resource such as the amygdala may be relevant across many emotions and therefore does not provide conclusive evidence with regard to the presence of discrete fear (Lindquist et al., 2012). Each study will now be examined in more detail.

Aside from eliciting brain activity in the left cerebellum, anterior lobe, right inferior temporal gyrus (BA 20), and right precuneus (BA 7), body odor obtained from tandem skydivers resulted predominantly in activation of the *left* superficial amygdala (Mujica-Parodi et al., 2009). However, a second study using similar stimuli revealed activation in the superficial nucleus of the *right* amygdala and this effect was more pronounced in females (Radulescu & Mujica-Parodi, 2013). Apparently,

receivers did not respond merely to the trigeminal properties of the odor, as activation of the superficial amygdala is involved in the processing of social stimuli (Goossens et al., 2009). Essentially, the amygdala signals whether external sensory information is motivationally salient, irrespective of valence (e.g., Sander, Grafman, & Zalla, 2003). Rather than being involved in the processing of discrete fear, the amygdala is alleged to be part of a distributed network that realizes core affect (Lindquist et al., 2012).

In line with this argument, another study showed that exposure to (social) fear odor did not exclusively activate brain regions related to the processing of fear. Compared to the sport sweat condition, body odor sampled during a socially threatening situation activated a number of brain areas, namely the right insula (BA 44, 47, 48), the right precuneus (BA 4, 5), the left supramarginal gyrus (BA 40), the right thalamus, the dorsomedial frontal gyrus (BA 6, 8, 9), the right inferior frontal gyrus (BA 44), the right cingulated gyrus (BA 23, 24, 29), the right substantia nigra, the left fusiform gyrus (BA 37), the left cerebellum (BA 19,30), and the medial vermis (Prehn-Kristensen et al., 2009). A couple of noteworthy patterns could be extracted from these data. For instance, the cingulate cortex was found to be activated in empathy-related mind-reading tasks (Völlm et al., 2006). Furthermore, a meta-analysis showed that activation of the right insula (BA 47)—amongst other brain regions—was related to affective empathy (Fan, Duncan, de Greck, & Northoff, 2011) and the explicit evaluation and awareness of affective feelings (Lindquist et al., 2012).

Notably, what binds the research findings of the three fMRI studies on chemosignaling is that exposure to social fear odor activated brain regions that were also involved in the acquisition process of *simulating* instances of physical fear, social anger, and physical anger (Lebois et al., under review). The situated perspective suggests that certain individuals have certain associations with body odors based on encountered statistical regularities. Empirical data showed that social and physical fear ostensibly led to the production of a similar body odor that activated in receivers the relevant situated conceptualization—one that was relatively broad and rooted in core affect (e.g., "threat", "danger"). The experience of core affect is associated with certain action representations that can play an essential role in the display of empathic behavior (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003).

In sum, although brain activity may not directly translate into overt behavior and symbolic expressions, the neural activation observed after fear odor exposure

(e.g., amygdala, insular cortex) can be counted within a network that rather than with discrete emotion experiences has been associated with core affect (Lindquist et al., 2012).

Conclusions and recommendations for emotional chemosignaling research

Even though the results on the diverse measures seem to indicate that receivers emulated the discretely fearful state of the senders, this conclusion should at least be drawn with caution based on the current evidence, as receivers may have experienced affect on two dimensions, namely (high) arousal and (negative) valence. Importantly, the measures that were used to target a state of fear (e.g., startle reflex, facial electromyography) do not necessarily reflect a discrete state of fear, as evidence suggests that these measures are affected by a general state of high arousal and negative valence (e.g., Russell & Barrett, 1999; Lang, 1995; Larsen, Norris, & Cacioppo, 2003; Hess & Fischer, 2013). However, receivers were shown to display vigilant behavior following exposure to fear odor in most studies and vigilant behavior is often associated with a state of fear (e.g., Susskind et al., 2008). Nevertheless, high intensity information may generally induce vigilance regardless of valence: individuals can make situational inferences, such as "sthing important is going on". Some individuals were more vigilant than others and this indicates that fear-related olfactory information was more salient to them. These individual differences can be explained from a situated perspective.

Obviously, experiences can be interpreted and labeled as fear in the proper context. For instance, when someone walks close to the edge of a cliff, the arousal that is induced by the sight of this situation may evoke feelings of being scared. These feelings may prevent the person from engaging in risky behavior and thus may save lives. Most studies did not provide (emotion-relevant) situational information from the audiovisual modalities, which could have aided receivers in making sense of their experience in discrete emotion terms. The mere smell of fear is arguably insufficient to evoke a conscious reenactment of "fear", as even the formation of associations between body odor and other-modality situational information does not require conscious awareness (Köster, 2002). Strong manipulations of the situation such as what has been reported in Lebois et al. (under review) or field experiments could shed further light on the role of the situation in emotional chemosignaling.

Different researchers used different ways to induce fear, namely they induced fear in physical and social situations. Future research could focus on the homogeneity of fear odor. Apocrine sweat glands in the armpit area produce a distinctive odor after adrenalin release (Harker, 2013) by for instance the fight/flight response (de Groot et al., 2015b). This implies that both anger and fear may lead to the production of a similar odor that can be associated with anger, fear, both, or with the general category (e.g., "danger", "threat", or "negativity"). Situated aspects such as the frequency of co-occurrence between the state and the release of the odor play an important role in the formation of category-related information that may be retrieved on a later occasion.

A general recommendation with regard to the emotional chemosignaling literature is to provide multi-faceted evidence for correspondence between a sender and receivers in terms of their emotional state. Each variable in itself may have its own problems, but the combination of self-report, perception, behavior, and neural measures paints a relatively coherent picture of the state of the receiver and whether it is indeed similar to the state of the sender. Obviously, definitions of "correspondence" should not be too inclusive and need to be well-defined a priori. The fact that chemosignals induce "correspondence" does not mean that they elicit pheromone-like responses in all individuals. Because natural relations occur between the odor and the situation in which it is typically emitted, multiple individuals can have a similar association and this previously stored association can be triggered by the mere presentation of an odor. Hence, what *seems* like rigid communication may in fact be viewed as a situated form of social regulation, given that chemosignals impact different individuals (e.g., socially anxious individuals and females) to a different extent.

Worst case scenario: Odor hedonics and trigeminal properties

One argument that could be given for the responses that were observed in receivers was that it was not "a negative affective" or "fearful" state that was carried over, but these effects emerged because the odor itself was an aversive stimulus. However, only three out of 23 studies on emotional chemosignaling reported differences in pleasantness between fear odor and the control odors (e.g., sport sweat, "neutral" sweat, and unused pads). Hence, what may be unpleasant is not the odor itself, but what it evokes in a particular context. Alternatively, self-report Likert scales

may not be sensitive enough to capture the dislike of a participant compared to for instance facial EMG. It could also be argued that body odors have properties that stimulate the trigeminal nerve and these properties may partly explain the negative affective and vigilant feelings in receivers. However, trigeminal properties cannot account for the effects that have been found for body odors produced during positive affect (Chen & Haviland-Jones, 2000; Zhou & Chen, 2009, 2011; de Groot et al., 2015a). Furthermore, male receivers responded more vigilantly to the body odor of female senders and this cannot be attributed to trigeminal properties either. Most importantly, the concentration of compounds present in body odor is likely not high enough to stimulate the trigeminal nerve. Instead, human olfactory communication takes a more complex form and responses depend on multiple factors, including the context, the goals of the receiver, and the receiver's association with and interpretation of the odor.

IV. Summary and Conclusions

Research on chemosignaling started to accumulate slowly but steadily right after the beginning of the 21st century. Currently, evidence for chemosignaling is expanding at an almost exponential rate. Dozens of studies have investigated whether body odors produced by certain individuals, called "senders", contained particular information that could influence or that could be picked up by "receivers". Dynamic states such as emotions, but also more static features such as age, gender, individuality, and personality, could be transferred by means of so-called chemosignals. Large individual variation in responses to body odors and the absence of firm evidence for the experience of discrete emotions in receivers indicated the situated nature of chemosignal reception in particular and thus chemosignaling as a whole.

The range of information that can be transferred via smell is arguably only limited by the amount of different body odors an individual can produce in different situations that reliably co-occur. Body odors are social stimuli and the association between body odors and multimodal information present in particular situations may explain why body odors can have a relatively richer meaning than simply being pleasant, unpleasant, intense, and familiar.

People experience many situations repeatedly and knowledge about these situations becomes entrenched in memory (Barsalou, 2005b). Early learning combines

olfactory and other-modality events that have common causes and consequences into complex networks, according to an ecological model of memory development (Spear, 1984). The rate, duration, and timing of reappearance of the elements in the environment then determine whether associations are preserved or become discarded (Spear, 1984). As certain body odors occur more often in certain contexts or can predict aspects of the situation, multiple individuals can extract these statistical regularities and the body odor becomes "informative". For instance, once a smell is encountered in a situation that is related to danger, this may result in an incomplete reinstatement of the original state. The remaining pattern components that may not have been observed in the situation yet can be filled in (Barsalou, 2005b). That is, the presence of a mere smell in a situation could be sufficient to establish so-called situational pattern completion, which enables individual to make educated guesses about how the situation will unfold based on other-modality components that frequently co-occurred with the odor on previous occasions. Statistical models could be developed that help understand which odors are more likely to be emitted in which contexts and to target whether exposure is different for different individuals, as these factors help explain large individual variation in body odor perception.

Obviously, there are certain odors that cause immediate avoidance reactions and these reactions have not been learned. Most odors including body odors contain properties that stimulate trigeminal nerve endings in the nose, causing a pungent, burning, and stinging sensation. Automatic responses to trigeminal components in body odor may obviously constrain the impact of the situation on how the odor is perceived. However, the range of reactions to body odors reviewed here (e.g., positive affect) is too rich to be explained by trigeminal stimulation alone. Notably, our ability to quickly couple olfactory with emotional information may well be an evolutionary remnant. Humans have no functional vomeronasal organ (e.g., Trotier et al., 2000), unlike certain animals (Witt & Wozniak, 2006). Hence, humans cannot detect pheromones, but this does not mean that individuals cannot be influenced by body odors in a relatively consistent manner. The sense of smell has been argued to have lost its importance when humans took a bipedal stance (Shepherd, 2004) and obviously a good nose would be useful for ground-dwelling species. Nevertheless, the sense of smell could have been useful for humans even during later evolutionary stages (e.g., hunter-gatherer societies), as chemical signals can be carried over long distances and transfer information when the signaler has long gone (Wyatt, 2003).

Next to vision, hearing, and touch, humans used and still use their sense of smell to navigate the social world (Semin & de Groot, 2013). Multiple modalities are employed to make sense of the larger multimodal context and these modalities have media that signal information between a sender and receiver and function to achieve a common basis (Semin & de Groot, 2013). Establishing similarity of perspective by means of a medium such as chemosignals constitutes an indispensable requirement for any successful communication that ultimately enables group living (Semin, 2007).

Human communication takes place in a social context (Smith & Semin, 2004, 2007) and there is no reason to assume that chemosignals escape this premise. Although a communication perspective invites thinking about chemosignaling as a process entailing the *intentional* transfer of one particular "package" of information (e.g., a discrete emotion), communication is merely a term that is used here to highlight that the transfer of information takes place between a communicative dyad, consisting of a sender and a receiver. In fact, since chemosignals are not produced intentionally, they are "informative" signals rather than "communicative" signals (Poggi & D'Errico, 2010). Although body odors contain multifarious information and this information can be stored in multifarious odor objects, empirical evidence has revealed that receivers responded only to the most salient information. What is salient is determined in part by the context at hand, the goals of the receiver, the properties of the odor, and existing associations with the odor.

The start of this review was marked by the uncontroversial assertion that associations with odor can be highly idiosyncratic. However, what makes odor perception in general and chemosignaling in particular a topic of empirical interest is that certain non-accidental properties enable multiple individuals to extract similar information, resulting in general associations with odors. In the end, odor sensations are not the result of a simple equation. The complex computations performed by the brain involve many variables and one of these variables is an often-overlooked one, namely the situation. The situation plays a pivotal role in both the formation of associations with odors and during the (partial) reenactment of stored multimodal representations of particular odors. The interaction between bottom-up and top-down factors becomes clear from the assumption that incoming body odors (i.e., physical stimuli) are matched to existing templates or "body odor objects", the accessibility of which is influenced by top-down factors. Although a situated perspective can account for the complexity of responses to body odors including individual variance, the

situation has remained a neglected facet in emerging research on what has been called chemosignaling. Eventually, the situated perspective can be applied to the processing of any odor *in situ*, not just body odors. By adopting a situated perspective, the current review attempted to provide a plausible, dynamic, and flexible basis for human chemosignaling.

Summary in Dutch

(Samenvatting)

Achtergrond

Het dierenrijk barst van de diersoorten die lichaamsgeuren gebruiken om te communiceren met soortgenoten. Dit geldt niet alleen voor ongewervelde dieren zoals zeeanemonen, mieren en bijen, maar ook voor gewervelde soorten zoals bepaalde soorten vissen en zoogdieren (ratten en muizen). De door het lichaam geproduceerde communicatieve geuren staan waarschijnlijk beter bekend als feromonen. Het woord feromoon is een samentrekking van het Griekse *pherein* (dragen of doorgeven) en *hormōn* (opwinden, stimuleren). Feromonen werden in 1959 ontdekt bij insecten door Karlson en Lüscher. Volgens hen zijn feromonen: "substanties die uitgescheiden worden door één individu en ontvangen worden door een ander individu van dezelfde soort, waar deze substanties een specifieke reactie ontlokken".

Feromonen worden meestal geassocieerd met seksueel gedrag, maar sommige diersoorten, knaagdieren bijvoorbeeld, produceren feromonen na bedreigd te zijn geweest. Deze feromonen kunnen opgepikt worden door soortgenoten. Na blootstelling aan alarmferomonen van soortgenoten werden knaagdieren (als onderdeel van de stress) alerter. Verdere tekenen van stress waren verhoging van de lichaamstemperatuur en onderdrukking van de afweerreactie op ziekteverwekkers.

Na de ontdekking van feromonen in 1959 werd veel onderzoek gedaan bij verscheidene niet-menselijke diersoorten zoals knaagdieren. Het duurde zeker 12 jaar voordat onderzoek verscheen naar het bestaan van feromonen bij mensen. Het zogenoemde "McClintock-effect" houdt in dat de menstruele cyclus van vrouwen die samenwoonden op een universiteitscampus op den duur (meer) gelijk ging lopen. Dit effect werd toegeschreven aan feromonen. In de loop der jaren kreeg dit onderzoek echter kritiek te verduren op de methodologie, statistiek en theorie. Ergo, het bestaan van feromonen bij mensen bleef controversieel.

Volgens vooraanstaand geuronderzoeker Richard Doty is het bestaan van menselijke feromonen zelfs een mythe. Om als feromoon te worden beschouwd moeten geuren slechts één (of een paar) component(en) bevatten die op een genetisch voorgeprogrammeerde manier bij soortgenoten bepaald gedrag (of een fysiologische reactie) veroorzaakt. De meeste geuren, inclusief menselijke lichaamsgeuren, bevatten echter vele honderden componenten; de reacties hierop zijn vaak te variabel om

gezien te worden als reacties op feromonen. Menselijke lichaamsgeuren zijn geen sleutels die het slot tot voorgeprogrammeerd gedrag ontsluiten. Mensen lijken ook de sensorische apparatuur te missen om feromonen te detecteren. Sommige mensen hebben in hun neus echter wel wat wordt genoemd een vomeronasaal orgaan (VNO). Zo gebruiken de meeste dieren het VNO voor feromooncommunicatie. Bij mensen is het VNO echter, als het al aanwezig is, een doodlopend kanaal.

Het bestaan van feromonen bij mensen wordt dus door sommige onderzoeken betwist, maar dit neemt niet weg dat er een sterk verband kan zijn tussen geuren en emoties. Zowel geuren als emoties worden namelijk voornamelijk verwerkt in dezelfde, relatief meer primitieve en dieper gelegen hersengebieden. Door sterke zenuwverbindingen tussen deze regio's is het geen wonder dat het reukvermogen meestal wordt aangemerkt als het meest "emotionele" zintuig. De sterke link tussen geuren en emoties maakt de weg vrij voor het menselijk vermogen om emoties over te dragen door middel van lichaamsgeur.

Overdracht van emoties via geur

Op de toepassing van het feromoonconcept op mensen kan veel kritiek gegeven worden, maar juist deze feromonen inspireerden het eerste onderzoek naar de overdracht van emoties via (oksel)geur. Het idee was als volgt: omdat ratten hun gestreste en niet-gestreste soortgenoten konden onderscheiden op basis van hun geur, zouden mensen dat eventueel ook kunnen. De eerste onderzoekers op dit gebied (Chen & Haviland-Jones, 2000) verzamelden okselgeur op absorberende kompressen van personen in een ofwel neutrale, ofwel angstige, ofwel blije staat. In de tweede fase van het experiment werd een groep onwetende participanten gevraagd om de okselgeur eruit te pikken van personen die angstig waren en tevens van personen die blij waren. De participanten wisten dit beter te doen dan wat men zou verwachten op basis van kans. Daarmee kan dit onderzoek worden gezien als eerste demonstratie van de communicatie (in de ruime zin) van emoties via geur.

Na dit onderzoek volgden nog 13 onderzoeken naar de overdracht van emoties via okselgeur (*chemosignalen*). Verschillende onderzoeksgroepen onderzochten of blootstelling aan de okselgeur van angstige personen leidde tot een angstreactie bij een andere persoon. Deze onderzoeken lieten zien dat proefpersonen die werden blootgesteld aan angstzweet meer angst rapporteerden, grotere schrikreacties vertoonden en meer activiteit lieten zien in regio's van het brein die gelinkt worden aan de ervaring van angst. Dit in tegenstelling tot (1) blootstelling aan sportzweet, (2)

zweet dat middels kompressen werd afgenomen tijdens een neutrale staat en (3) ongebruikte kompressen. Deze onderzoeken lijken andermaal te hebben bewezen dat mensen, net als sommige dieren, de emotie angst kunnen overdragen door middel van lichaamsgeur.

Van problemen eerder onderzoek naar oplossingen huidig onderzoek

Bij eerder onderzoek naar de overdracht van emoties via geur zijn ten minste drie problemen te benoemen. Ten eerste is het bewijs dat is aangeleverd voor dit fenomeen nogal indirect en onsystematisch. Ten tweede ontbrak een adequaat theoretisch kader, waardoor veel verschillende gedragingen nogal wenselijk werden geïnterpreteerd onder dezelfde noemer (er dienen echter scherpe criteria te zijn op basis waarvan een wetenschappelijke aanname verworpen kan worden). Ten derde is niet onderzocht wat de grenzen zijn van het menselijk vermogen om emoties over te dragen via lichaamsgeur. Hieronder worden deze punten in meer detail besproken.

1. Bewijs

Eerdere onderzoeken leverden gefragmenteerd bewijs voor de overdracht van emoties via geuren. Het ene onderzoek mat bijvoorbeeld de toename van riskant gedrag na blootstelling aan angstzweet, terwijl het andere onderzoek voorzichtiger gedrag interpreteerde als teken dat angst middels geur overgedragen was. Weer andere onderzoeken maten schrikreacties en verhoogde activiteit in bepaalde hersengebieden, maar het is de vraag in hoeverre deze reacties en activiteit een symbool zijn van *pure* angst in tegenstelling tot een algemeen negatief gevoel. In de huidige dissertatie tracht ik—in tegenstelling tot eerder onderzoek— direct en systematisch bewijs te vinden voor de overdracht van specifieke emoties door middel van geur.

2. Theoretisch kader

Hierbij helpt een adequaat theoretisch kader empirisch onderzoek vooruit: het voorziet de onderzoeker van een set duidelijke voorspellingen welke uiteindelijk wel of niet uitkomen. Voorgaand onderzoek heeft vooral de dierlijke feromoon-logica toegepast op mensen; dit doet echter geen recht aan de complexiteit en dynamiek van menselijke reacties op geuren. In dit proefschrift ga ik in op de vraag of de overdracht van emoties via geuren gezien kan worden als vorm van sociale communicatie. De theorie van sociale communicatie gaat uit van het feit dat de psychologische en fysiologische processen bij een "ontvanger" een soort kopie kunnen zijn van de staat van een "zender". Dit stelt de ontvanger in staat om de zender te begrijpen. Het

overnemen van de staat van een zender kan bij de ontvanger worden veroorzaakt door (sociale) stimuli, welke mensen registeren met hun ogen en oren en waarschijnlijk ook neus. Geuren kunnen bijvoorbeeld gezien worden als communicatieve "signalen" indien zij gekoppeld zijn aan gelijksoortige (emotionele) audiovisuele informatie. Na verloop van tijd kan een associatie zodanig sterk zijn, dat geuren *an sich* emoties zoals angst kunnen overdragen van één individu naar een ander.

3. Grenzen van het fenomeen

Ook al is het zo dat we emoties zoals angst kunnen ruiken, dan nog vertrouwen wij onze ogen en oren meestal meer. Zo zouden we denken dat de informatie die we binnenkrijgen via geuren makkelijk overschreven kan worden door hetgeen we zien en/of horen. Eerder onderzoek heeft hier nog niet naar gekeken. De sociale communicatie theorie gaat ervan uit dat sociale informatie via meerdere kanalen overgedragen kan worden van een zender naar een ontvanger. Een dergelijk model is tevens dynamisch en veronderstelt dat verschillende individuen op verschillende wijze beïnvloed kunnen worden door geuren.

Conclusie

De wetenschappelijke kennis over de overdracht van emoties via geur is momenteel nog incompleet en derhalve is het begrip van dit fenomeen zeer beperkt. Het huidige proefschrift probeert een beter beeld te scheppen van dit opmerkelijke fenomeen, onder andere door te trachten om direct en systematisch bewijs te leveren voor de overdracht van emoties via geuren. Er wordt in dit proefschrift getoetst vanuit een breed en dynamisch theoretisch kader, zodat zowel het fenomeen alsmede de grenzen ervan helder in kaart gebracht kunnen worden.

Het huidige proefschrift

Algemene opzet experimenten

Geuronderzoek: hoe doe je dat? De huidige en hier gerapporteerde experimenten bestaan elk uit een fase waarin lichaamsgeuren werden verzameld van een groep "donoren" (ook wel "zenders" genoemd) en een fase waarin een nieuwe groep onwetende participanten ("ontvangers") aan deze verzamelde lichaamsgeuren blootgesteld werd. Daarbij vroegen wij niet simpelweg hoe mensen zich voelden na blootstelling aan angstzweet (het is meestal moeilijk om de invloed van een geur onder woorden te brengen), maar we maten subtiele indicatoren van emoties, zoals emotionele gezichtsuitdrukkingen (via elektroden) en alert gedrag (via computertaken, oogbewegingen, de hoeveelheid ingeademde lucht). Angstzweet werd via kompressen

onder de oksel verzameld van donoren, terwijl zij beangstigende films keken of terwijl zij zich voorbereidden op een presentatie. Van dezelfde donoren werd lichaamsgeur verzameld terwijl zij in een even warme ruimte (23 graden) door film clips in een zoveel mogelijk neutrale staat werden gebracht. Om de communicatie van emoties via lichaamsgeur zo goed mogelijk te kunnen observeren, hielden de donoren zich vanaf 48 uur vóór het experiment aan een uitgebreid protocol om "geurbesmetting" te voorkomen. Zo mochten zij onder andere niet roken, geen alcohol drinken en geen sterk geurende producten nuttigen zoals knoflook en asperges. Omdat de invloed van geuren erg kan verschillen van mens tot mens, stelden we dezelfde "ontvangers" bloot aan zowel angstzweet als neutraal zweet. Veruit het grootste deel van de participanten kon niet benoemen waaraan ze werden blootgesteld. De onderzoeksvraag was in het algemeen: nemen "ontvangers" die worden blootgesteld aan angstzweet (zonder het te weten) de emotie angst over van de "zenders"?

Overzicht hoofdstukken

Het huidige proefschrift bevat 8 hoofdstukken.

In *Hoofdstuk 1* wordt een algemene samenvatting gegeven van het huidige proefschrift. Het schetst de achtergrond van het huidige onderzoek, de problemen met betrekking tot eerder onderzoek en legt uit hoe het huidige proefschrift deze problemen verwacht op te lossen.

Hoofdstuk 2 zet kort de theorie uiteen. Hier wordt beargumenteerd waarom het reukzintuig in sommige gevallen een plek verdient naast de "traditionele" communicatiekanalen zicht en gehoor. De sociale communicatie theorie wordt getoetst in Hoofdstuk 3-7.

In *Hoofdstuk 3* wordt op systematische wijze getest of verschillende negatieve staten, angst en walging, overgebracht kunnen worden van zender op ontvangers door middel van lichaamsgeur. Dit hoofdstuk laat zien dat blootstelling aan okselgeur dat werd verzameld ten tijde van angst leidde tot een angstige gezichtsexpressie bij ontvangers alsmede alerter gedrag, terwijl blootstelling aan de geur van gewalgde proefpersonen leidde tot een gewalgde gezichtsexpressie en het zoveel mogelijk afwijzen van prikkels in de omgeving.

Hoofdstuk 4 had als doel om te testen of de invloed van angstzweet overschreven zou worden door tegenstrijdige (namelijk neutrale) informatie welke via de ogen en oren geregistreerd zou worden. Wat gevonden werd is dat de overdracht

van angst (gemeten aan de hand van gezichtsspieractiviteit) plaatsvond, ongeacht of de angst werd verspreid door beangstigende filmpjes of angstzweet. Bovendien werd de invloed van angstzweet niet verzwakt door de aanwezigheid van neutrale filmpjes. De mate waarin de emotie angst wordt overgedragen lijkt op basis van deze bevindingen sterker dan eerder werd aangenomen.

Hoofdstuk 5 ging verder met het onderzoeken van de grenzen van het vermogen om angst te communiceren door middel van lichaamsgeur. Aangezien vrouwen over het algemeen beter kunnen ruiken en gevoeliger zijn voor emotionele signalen, werd aangenomen dat zij in sterkere mate dan mannen de emotie angst zouden overnemen (wederom gemeten aan de hand van gezichtsspieractiviteit). De data ondersteunde deze hypothese. Dit hoofdstuk toont aan dat de overdracht van emoties via lichaamsgeur niet symmetrisch is (niet voor elk geslacht hetzelfde).

Hoofdstuk 6 bekijkt of het vermogen om emoties over te dragen door middel van lichaamsgeur zich niet alleen beperkte tot negatieve emoties. Sterke positieve emoties kunnen namelijk ook transpiratie veroorzaken. Eerdere onderzoeken lieten al indirect zien dat positieve emoties gecommuniceerd kunnen worden middels lichaamsgeur. Het huidige onderzoek liet inderdaad zien dat de geur van personen in een positieve staat resulteerde in een blije gezichtsexpressie bij ontvangers, alsook een met positieve emoties geassocieerde "bredere kijk" (het bos zien in plaats van de bomen).

Het sluitstuk qua empirische hoofdstukken, *Hoofdstuk 7*, was meer mechanistisch van aard. In dit hoofdstuk wordt het onderliggende mechanisme dat verantwoordelijk is voor de productie van "angstzweet" belicht. Het bleek dat de snellere van de twee stress-systemen (niet het systeem dat zorgt voor de productie van cortisol, maar het systeem dat adrenaline laat vrijkomen) verantwoordelijk was voor de productie van angstzweet. Ontvangers vertoonden namelijk specifiek na blootstelling aan deze geur een angstige (negatieve) gezichtsexpressie en men werd bovendien alerter. Dat wil zeggen, de ontvangers beslisten sneller (zonder in te leveren op accuratesse) of de kort op het beeldscherm gepresenteerde gezichten emoties bevatten of niet.

Hoofdstuk 8 bevat als afsluitend werk een kritische beschouwing van het gehele onderzoeksveld inclusief het in dit proefschrift vermelde onderzoek. Het hoofddoel van dit hoofdstuk was om uit te leggen hoe de overdracht van emoties via geuren naar alle waarschijnlijkheid werkt.

Belang van huidig onderzoek

Het huidige onderzoek is fundamenteel van aard. Het primaire doel is om meer begrip te krijgen van hoe emoties via geuren overgedragen kunnen worden. Dit type onderzoek is niettemin ook maatschappelijk gezien belangrijk, omdat het laat zien dat geuren een sterkere impact kunnen hebben op het gedrag van mensen in tegenstelling tot hetgeen men jaren geleden dacht. Ander onderzoek wees namelijk al uit dat mensen, net als andere dieren, geursporen kunnen volgen. Tevens kunnen mensen naar schatting meer geuren onderscheiden dan kleuren en tonen samen. Het feit dat het reukzintuig belangrijker is dan eerder werd gedacht heeft implicaties voor de erkenning van bepaalde patiëntgroepen, in het bijzonder groepen waarbij het reukvermogen is aangetast of in zijn geheel niet meer functioneert (anosmie). Deze patiënten rapporteren vaak depressieve klachten, niet in de minste plaats omdat geuren meestal sterke emoties teweeg kunnen brengen en sociale informatie bevatten. Huidig onderzoek draagt bij aan meer erkenning voor deze patiëntgroepen.

Angstzweet zou ook een rol kunnen spelen bij het in stand houden van veel voorkomende angststoornissen zoals sociale fobie. Als iemand angstig is, produceert deze persoon transpiratie met een bepaalde geur. Deze geur kan leiden tot een (verdere) versterking van de reeds aanwezige angst. Om deze vicieuze cirkel te doorbreken kan gekeken worden naar het verminderen van de hoeveelheid transpiratie en wat dit voor effect heeft op de symptomen van de stoornis.

Huidig onderzoek vormt tevens een startpunt voor toekomstig biochemisch onderzoek. De onderzoeken in dit proefschrift werpen vragen op zoals: zijn er verschillen in de biochemische “geurafdruk” als gevolg van de emotionele staat van een persoon. Zijn er bepaalde geurcomponenten die op relatief constante wijze voorkomen in lichaamsgeur? Welke componenten zijn variabel en waarom? Deze type vragen tonen aan dat multidisciplinair onderzoek de volgende stap is in onderzoek naar de overdracht van emoties via geur. Het huidige proefschrift vormt daarbij een eerste “psychologische” stap in die richting.

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Appendix A

Supplemental Section: Chapter 3

Part 1: Senders (body odor donors)

Emotion induction

First, we checked whether emotion induction in donors was successful. Because normality assumptions were violated for self-report data, non-parametric Wilcoxon signed-rank tests ($df = 10$) were used. This analysis revealed that donors in the fear condition did not report significantly more fear than in the disgust condition, $Z = .85$, $p = .395$ (Table 1). In the fear condition, self-reported state anxiety levels did not increase from baseline, $Z = 1.03$, $p = .305$. These findings are consistent with the observation that self-report and physiological measures often diverge in the assessment of fear in men (Pierce & Kirkpatrick, 1992). Compared to the fear condition, donors reported stronger feelings of disgust in the disgust condition, $Z = 2.83$, $p = .005$, effect size (r) = .90, and they evaluated their feelings of surprise significantly higher in this condition, $Z = 2.25$, $p = .024$, $r = .71$. As predicted, donors did not report increased levels of state anxiety after the disgust-inducing video compared to baseline, $Z = 1.58$, $p = .114$.

Part 2: Receivers

Stimulus evaluation and discrimination

We further examined how receivers evaluated body odor and control pads (Table 2). Wilcoxon signed-rank tests ($df = 36$) that compared disgust odor, fear odor, and control pad ratings revealed that disgust odor was perceived as significantly more intense and less pleasant than fear odor (intensity: $Z = 2.71$, $p = .007$, $r = .45$; pleasantness: $Z = -2.00$, $p = .045$, $r = .33$), and control pads (intensity: $Z = 3.14$, $p = .002$, $r = .52$; pleasantness: $Z = -2.76$, $p = .006$, $r = .46$). Differences between fear odor and control pads in reported intensity ($Z = 1.14$, $p = .251$) and pleasantness ($Z = -1.14$, $p = .213$) were not significant. Despite these findings, participants were unable to discriminate between stimuli. With the minimum number of correct detections in the triangle tests being 18 for rejection of the no-discrimination hypothesis (given: $N = 36$, $\pi = ⅓$; Meilgaard, Civille, & Carr, 1991), participants could not discriminate

between the body odor of fearful vs. disgusted individuals (13), control vs. disgust odor (12), and control vs. fear odor (9).

Facial EMG

Although exposure to unused control pads did not evoke emotional facial expressions, fear (disgust) chemosignals elicited a facial expression of fear (disgust). Fear chemosignals induced *medial frontalis* activity (cf. Chapter 3) that significantly increased from baseline in the third and fourth second after exposure (3rd second: p = .032; 4th second: p = .028) rather than the first two seconds (1st second: p = .166; 2nd second: p = .083), indicated by Bonferroni corrected post-hoc tests. Shortly after disgust chemosignal exposure, an early reduction in *medial frontalis* activity was followed by a marked increase, which contrasted the muscle activity pattern that was displayed in the fear condition, $F(4,116) = 3.12$, p = .018, η^2 = .01 (p values > .817, for all 1s intervals). When adopting a time window that covered the complete visual search task (~7 min), *medial frontalis* activity was neither observed after disgust chemosignal exposure, $F(1,29) = 3.53$, p = .071, nor after control pad exposure, $F(1,25) = .27$, p = .608. Hence, fearful expressions were only reliably generated after fear chemosignal exposure.

Likewise, disgust chemosignals evoked a disgusted facial expression shortly after exposure that was maintained throughout the task (see Chapter 3). Post-hoc tests demonstrated a significant increase in *levator labii* activity from baseline up to the fourth second after exposure (p values < .001, for all 1s intervals). Although significant *levator labii* activity changes were shown after fear chemosignal exposure, $F(4,108) = 5.60$, p < .001, η^2 = .01, post-hoc tests revealed nonsignificant differences (p values > .077, for all 1s intervals). As predicted, a disgusted facial expression remained absent during the remainder of exposure to fear odor, $F(1,27) = 1.29$, p = .266, and control pads, $F(1,26) = .73$, p = .401. Hence, disgusted expressions were only reliably generated after disgust chemosignal exposure.

Sniffing behavior

Next to facial muscle activity, sniffing behavior was explored further. With regard to the first couple of sniffs, follow-up paired t-tests indicated that the magnitude of the first sniff neither differed between the control and fear condition, $t(31) = 2.05$, p = .15, nor between the control and disgust condition, t < 1. The difference between the fear and control condition with respect to the magnitude of the

second sniff was not significant, $t < 1$, whereas a significantly lower sniff magnitude was indeed observed in the disgust condition relative to the control condition, $t(32) = 4.53$, $p < .001$. These combined findings (cf. Chapter 3) reflect the cyclic nature of air intake after chemosignal exposure. While fear chemosignals ostensibly induced rapid sensory acquisition, disgust chemosignals evoked sensory rejection.

Eye scanning

Further support for chemosignal-induced sensory acquisition was obtained from eye tracking data. Exposure to fear odor resulted in fewer fixations on the target (Table 3) compared to the control condition (post-hoc ANOVA: $p = .011$), but not the disgust condition ($p = .145$). Exposure to body odor of fearful individuals furthermore led to shorter average fixation durations compared to the control ($p = .014$), but not the disgust condition ($p = .705$). The eye fixation modulating effects that were induced by fear chemosignals potentially reflected the employment of a quick scan search strategy of the entire visual field, rather than mere fixations on individual objects within a space.

Table 1

Physiological and subjective assessments of body odor donors

	Fear condition	Disgust condition	*p* value
Skin conductance level	2.60 (0.79-4.20)	2.22 (0.97-4.00)	0.074
Heart rate	68.54 (48.74-85.50)	56.42 (48.67-65.95)	0.011
Self-reported disgust	2 (1-5)	6 (4-7)	0.005
Self-reported fear	2 (1-4)	1.5 (1-5)	0.395
Self-reported anger	1.5 (1-3)	1 (1-4)	0.785
Self-reported happiness	4 (3-6)	4 (2-7)	0.719
Self-reported sadness	1 (1-4)	1 (1-7)	0.414
Self-reported surprise	2.5 (1-6)	5 (3-7)	0.024

Note. Skin conductance level was measured in microSiemens, heart rate in beats per minute, and self-report on 7-point Likert scales (1 = not at all; 7 = very). Data is presented as means (physiological data) and medians (subjective data), with ranges displayed between parentheses.

Table 2

Receivers' intensity and pleasantness ratings of body odor and odorless pads

	Fear odor	Disgust odor	Control
Intensity	3.00 (1.31)	4.00 (1.45)	3.00 (1.37)
Pleasantness	4.00 (1.10)	3.00 (1.02)	4.00 (1.06)

Note. Evaluations were measured on 7-point Likert scales (1 = not at all; 7 = very) and are presented as medians. Standard deviations are displayed between parentheses.

Table 3

Eye tracking parameters per body odor exposure condition as a function of task difficulty

	Fear odor		Disgust odor		Control	
	Easy	Difficult	Easy	Difficult	Easy	Difficult
Target fixations	0.69 (0.17)	0.76 (0.21)	0.73 (0.24)	0.74 (0.22)	0.78 (0.17)	0.82 (0.19)
Fixation duration	211.80 (37.37)	205.61 (29.35)	215.77 (38.79)	212.66 (27.02)	227.01 (47.82)	221.52 (45.13)
Overall fixations	5.58 (1.46)	11.17 (3.53)	5.55 (1.86)	9.94 (2.73)	5.67 (1.39)	11.22 (2.80)

Note. Depicted are the mean number of fixations on the target, mean fixation duration (ms), and mean number of overall fixations. Standard deviations are displayed between parentheses.

Appendix B

Supplemental Section: Chapter 4

Part 1: Senders

The effectiveness of the emotion induction procedure was determined by sweat donors' self-reported feelings. Because Shapiro-Wilk tests indicated that normality assumptions were violated, self-reported feelings data was subjected to non-parametric tests.

A Wilcoxon-signed ranks test revealed that donors reported significantly stronger feelings of anger ($Z = 2.03$, $p = .042$, $r = .72$) and disgust ($Z = 2.39$, $p = .017$, $r = .84$) in the fear condition compared to the neutral condition. Since self-reported anger ($Mdn = 2$) and disgust ($Mdn = 3.5$) scores fell in the lower half of the self-report scale (ranged 1-7), the experienced magnitude of these emotions was relatively weak. Furthermore, the fear and neutral condition did not differ significantly with regard to self-reported happiness ($Z = 1.54$, $p = .125$), sadness ($Z = .41$, $p = .680$), neutral feelings ($Z = .00$, $p = .999$), and surprise ($Z = .71$, $p = .481$). The abovementioned results should be interpreted with caution given the small sample size ($N = 8$). Nonetheless, the combined results (cf. main text) indicate that above all fear ($Mdn = 4$) was triggered in the fear condition, whereas above all calmness ($Mdn = 6.5$) was induced in the neutral condition.

Part 2: Receivers

Next, we conducted a further examination of EMG activity averaged over the complete duration of the task (~12 min) as a combined function of olfactory (fear, neutral) and audiovisual (fear, neutral) input. Planned paired t-tests were performed on facial muscle activity (*medial frontalis*, *corrugator supercilii*) indicative of emotional contagion. Relative to the olfactory and audiovisual neutral condition, *medial frontalis* and *corrugator supercilii* activity was increased in the olfactory fear, audiovisual neutral: *medial frontalis*, $t(29) = 2.29$, $p = .03$, $d = .26$; *corrugator supercilii,* $t(29) = 1.82$, $p = .079$, $d = .29$, olfactory neutral, audiovisual fear: *medial frontalis*, $t(29) = 2.28$, $p = .024$, $d = .19$; *corrugator supercilii*, $t(29) = 3.34$, $p = .002$, $d = .45$, and olfactory and audiovisual fear condition: *medial frontalis*, $t(29) = 4.23$, $p < .001$, $d = .48$; *corrugator supercilii*, $t(29) = 3.54$, $p = .001$, $d = .54$. Interestingly, there were no significant differences between the conditions that contained a single

fear signal (olfactory fear, audiovisual neutral vs. olfactory neutral, audiovisual fear condition: *medial frontalis*, $t(29) = .75$, $p = .46$; *corrugator supercilii*, $t(29) = -.72$, $p = .475$. Finally, when fear-inducing audiovisual information was presented together with olfactory fear signals, *medial frontalis* and *corrugator supercilii* activity was increased relative to the olfactory fear, audiovisual neutral condition, $t(29) = 1.66$, $p = .108$; $t(29) = 1.79$, $p = .083$, $d = .21$, and the olfactory neutral, audiovisual fear condition, $t(29) = 3.50$, $p = .002$, $d = .32$; $t(29) = 1.30$, $p = .204$. Although not every comparison yielded a statistically significant difference, the combined results suggest that fear-related information communicated by different media adds up to create an enhanced fear response.

Besides measuring emotional contagion via facial EMG, the Chinese symbol task was used to measure implicit affect. While being exposed to olfactory signals (fear, neutral), each clip (audiovisual fear, neutral) was followed by Chinese symbols that were rated as either less or more threatening than the average symbol. Participants rated significantly more Chinese symbols as threatening ($M = .57$, $SD = .13$) after seeing the fear-inducing audiovisual scenes compared to the neutral scenes ($M = .47$ $SD = .13$), $F(1,29) = 7.47$, $p = .011$, $\eta_p^2 = .21$. While participants consciously processed audiovisual information, the manipulation that ostensibly escaped their conscious awareness—that is, the presence of sweat—did not significantly impact Chinese symbol ratings, $F(1,29) = .65$, $p = .426$.

To explore whether fear sweat played a role in receivers' reactions toward in- and outgroup members, we created a subcategory for the audiovisual fear and neutral condition by varying the man's group-membership as being either ingroup (Caucasian) or outgroup (African American). Because there were no significant differences in facial muscle activity between different levels of group-membership: *corrugator supercilii*, $F(1,29) = .06$, $p = .803$; *medial frontalis*, $F(1,29) = .32$, $p = .579$, and the interaction between group-membership and sweat exposure did not reach significance: *corrugator supercilii*, $F(1,29) = .37$, $p = .548$; *medial frontalis*: $F(1,29) = 2.69$, $p = .112$, the levels of the subcategory group-membership were collapsed in the final 2 (olfactory signal: fear, neutral) x 2 (audiovisual signal: fear, neutral) repeated measures analyses.

In sum, fear chemosignals produced by senders induced fear in receivers. This was evidenced by a fearful facial expression that emerged in a receiver, irrespective of copresent audiovisual information.

Appendix C

Supplemental Section: Chapter 5

Binomial analysis of receivers' ability to discriminate male fear sweat from male neutral sweat on the sweat discrimination task (aggregated over the first two trials) revealed that women performed better than chance (25%), $Z = 5.88$, $p = .002$. All remaining comparisons: $p > .05$ (Table 1). When comparing the overall performance of the sexes on the sweat discrimination task, women performed significantly above chance, $Z = 2.75$, $p = .008$, whereas men did not, $Z = .39$, $p = .769$. Hence, consistent with previous research (Brand & Millot, 2001; Chen & Haviland-Jones, 2000), women performed better than men in discriminating between sweat types on the basis of the emotion of the sender.

A further examination of sex differences in self-reported sweat ratings revealed that women judged male fear sweat to be more intense, $t(50) = 2.45$, $p = .018$, and less pleasant, $t(50) = 2.32$, $p = .025$, than did men. In contrast, men rated female fear sweat as more intense than male neutral sweat, $Z = 2.00$, $p = .045$. All other comparisons were not significant (see Table 2). Importantly, facial EMG parameters were not impacted by women's ratings of sweat hedonics and intensity, as comparisons of these values within the female participant group revealed only nonsignificant differences, $p > .05$. Concerning facial EMG activity, the set of outcomes that were not central to the conclusions reported in the main text are presented in Table 3 and Table 4.

Our secondary target was to conceptually replicate previous results regarding facial EMG activity emerging as a consequence of neutral and fear-inducing audiovisual and olfactory information (de Groot, Semin, & Smeets, 2014a). Note that the current contribution did not constitute a direct replication, given the presence of four sweat exposure conditions instead of two, the presentation of six video clips per condition rather than twelve, and the presence of male receivers in addition to female receivers (cf. de Groot et al., 2014a). Analysis of variance nevertheless revealed a main effect of audiovisual information on *medial frontalis* activity, $F(1,50) = 8.07$, $p = .006$, and *corrugator supercilii* activity, $F(1,50) = 15.86$, $p < .001$, with fear-inducing scenes leading to elevated facial muscle activity indicative of fear (Table 5). However, similar effects were not observed for olfactory information, *medial frontalis*, $F(1,50) = 3.78$, $p = .058$; *corrugator supercilii*, $F(1,50) = 1.02$, $p = .32$

(Table 5). To verify its robustness, future research should identify the specific boundary conditions under which fear sweat exerts its fear-inducing effects over time regardless of copresented audiovisual information.

Whereas no sex differences were encountered with regard to mean *medial frontalis* activity, $F < 1$, women showed larger *corrugator supercilii* responses compared to men, $F(1,50) = 20.34$, $p < .001$. Women particularly showed strong *corrugator supercilii* responses following the presentation of fear-inducing audiovisual information, $F(1,50) = 19.12$, $p < .001$, implying that women experienced greater negative affect than men in this condition. All other between-sex comparisons were not significant, $\alpha = .05$.

Table 1

Number of correct and incorrect discriminations between male fear sweat (MF), male neutral sweat (MN), female fear sweat (FF), and female neutral sweat (FN) on each trial (T1-T4).

	Male discriminator		Female discriminator	
	Correct	Incorrect	Correct	Incorrect
T1: MF – MN	14	12	20	6
T2: MF – MN	9	17	16	10
T3: FF – FN	14	12	17	9
T4: FF – MF	17	9	13	13

Table 2

Median (range) pleasantness and intensity ratings of male and female judges per sweat type.

	Male rater		Female rater	
	Pleasantness	Intensity	Pleasantness	Intensity
Male fear sweat	4 (2-6)	3 (1-7)	3 (1-6)	5 (1-6)
Male neutral sweat	4 (2-6)	3 (1-6)	3.5 (1-6)	3 (1-7)
Female fear sweat	4 (1-6)	4 (1-6)	3 (1-6)	4.5 (1-7)
Female neutral sweat	4 (2-6)	3 (1-7)	4 (2-5)	4 (1-6)

Table 3

Additional results from four-way ANOVA on mean facial muscle activity (medial frontalis, corrugator supercilii) with receiver sex (male, female) as between subjects factor and sender sex (male, female), emotion (fear, neutral), and time (0-4 s) as within-subjects factors.

	Medial frontalis		*Corrugator supercilii*	
Effects	*F* (df)	*p*	*F* (df)	*p*
Time	10.37 (4,200)	<.001	12.48 (4,200)	<.001
Emotion	5.58 (1,50)	.022	2.62 (1,50)	.112
Sender sex	3.01 (1,50)	.089	<1 (1,50)	.420
Sender sex x Emotion	6.72 (1,50)	.012	2.05 (1,50)	.158
Sender sex x Time	1.45 (4,200)	.219	<1 (4,200)	.744
Emotion x Time	2.53 (4,200)	.057*	1.07 (4,200)	.371
Sender sex x Emotion x Time	2.90 (4,200)	.023	1.34 (4,200)	.255
Sender sex x Emotion x Receiver sex	4.99 (1,50)	.030	1.97 (1,50)	.167
Sender sex x Emotion x Time x Receiver sex	2.89 (4,200)	.023	<1 (4,200)	.861

Note. *The Greenhouse-Geisser corrected result (Emotion x Time: $\varepsilon = .75$; uncorrected, $p = .042$) was reported only when Mauchly's test indicated that the sphericity assumption had been violated and Greenhouse-Geisser correction of degrees of freedom would lead to a different interpretation of the result, given $\alpha = .05$.

Table 4

Additional results from three-way ANOVA on mean facial muscle activity (medial frontalis, corrugator supercilii) with sender sex (male, female), emotion (fear, neutral), and time (0-4 s) as within-subjects factors.

	Medial frontalis		*Corrugator supercilii*	
Effects	*F* (df)	*p*	*F* (df)	*p*
Female				
Sender sex x Emotion	7.54 (1,25)	.011	2.44 (1,25)	.131
Sender sex x Time	<1 (4,100)	.948	1.55 (4,100)	.192
Emotion x Time	5.15 (4,100)	<.001	2.61 (4,100)	.062*
Sender sex x Emotion x Time	3.06 (4,100)	.020	<1 (4,100)	.560
Male				
Sender sex x Emotion	<1 (1,25)	.710	<1 (1,25)	.973
Sender sex x Time	6.46 (4,100)	<.001	2.73 (4,100)	.052*
Emotion x Time	1.68 (4,100)	.160	7.58 (4,100)	<.001
Sender sex x Emotion x Time	2.45 (4,100)	.051	1.35 (4,100)	.257

Note. *The Greenhouse-Geisser corrected result (Emotion x Time: $\varepsilon = .70$; uncorrected, $p = .040$; Sender sex x Time: $\varepsilon = .72$; uncorrected, $p = .033$) was reported only when Mauchly's test indicated that the sphericity assumption had been violated and Greenhouse-Geisser correction of degrees of freedom would lead to a different interpretation of the result, given $\alpha = .05$.

Table 5

Mean (standard deviation) facial muscle activity (microvolt) per participant group (female, male) as a function of four conditions, involving combinations of olfactory fear (OF), audiovisual fear (AVF), olfactory neutral (ON), and audiovisual neutral (AVN) information.

	Medial frontalis		*Corrugator supercilii*	
	Female	Male	Female	Male
OF, AVF	2.21 (0.77)	2.15 (0.99)	7.07 (3.94)	2.91 (1.73)
ON, AVF	2.19 (0.78)	2.31 (1.41)	6.81 (3.78)	2.90 (1.60)
OF, AVN	1.92 (0.65)	2.11 (0.91)	5.42 (3.49)	2.94 (2.01)
ON, AVN	2.13 (0.90)	2.22 (1.29)	6.10 (3.94)	2.98 (1.87)

Appendix D

Supplemental Section: Chapter 6

Discriminant analysis facial EMG data receivers

Tables 1 to 6 depict a complete list of means and standard errors of each facial EMG parameter classified into the discriminant model. The variables marked blue are those that were selected by discriminant analysis as providing the best fit.

The parameters provided along with discriminant analysis should be interpreted as follows. For the non-baseline corrected method (ITT meth 1), all numbers are expressed relative to mean per subject (i.e., standardized). For example, a figure of .06 on "fro_mean" "_INTO_" "Fear" implies that the parameter in question was, on average, .06 (units—in this case log transformed millivolt) higher in Fear than was typical for subjects across all conditions.

For the baseline corrected method (ITT meth 2), mean figures are standardized mean differences from baseline. A figure of .07 of "fro_mean" "_INTO_" "Fear" means that those classified into the Fear group exhibit an average difference in *medial frontalis* activity (from baseline) that is .07 units (i.e., millivolt) on the log scale greater than the average of this value across all conditions. It follows that on the original (unlogged) scale, average *medial frontalis* activity of the reactions classified as Fear is: $e^{.07} = 1.07$ times (i.e., 7%) higher than the average similar figure across all conditions. Units of measurement: Mean (average value, mV), Max (peak value, mV), TTM (time to maximum: ms), SD (variation: mV).

Table 1

Discriminant analysis: Fear vs Neutral comparison; baseline uncorrected

Fear vs Neutral ITT meth 1

The MEANS Procedure

INTO	N Obs	Variable	Mean	Std Error
Fear	35	fro_mean	0.0573003	0.0280029
		Fro_MAX	0.1719553	0.0641289
		Fro_TTM	-26.6666667	214.4229875
		Fro_SD	0.0449328	0.0131002
		zyg_mean	0.1078145	0.0610542
		Zyg_MAX	0.0074105	0.1081800
		Zyg_TTM	28.5714286	146.6790347
		Zyg_SD	-0.0342139	0.0298434
		orb_mean	0.0900558	0.0404799
		Orb_MAX	-0.0056006	0.0489048
		Orb_TTM	-243.8095238	179.1137610
		Orb_SD	-0.0338610	0.0137920
Neutral	35	fro_mean	-0.0788427	0.0263896
		Fro_MAX	-0.1667879	0.0462353
		Fro_TTM	85.7142857	215.8010535
		Fro_SD	-0.0351871	0.0100235
		zyg_mean	-0.0511916	0.0415507
		Zyg_MAX	-0.0181184	0.1007821
		Zyg_TTM	49.5238095	151.5150467
		Zyg_SD	0.0112275	0.0358101
		orb_mean	-0.0757314	0.0318912
		Orb_MAX	-0.0161852	0.0631037
		Orb_TTM	-154.2857143	179.7554398
		Orb_SD	0.0220801	0.0182015

Table 2

Discriminant analysis: Fear vs Neutral comparison; baseline corrected

Fear vs Neutral ITT meth 2

The MEANS Procedure

INTO	N Obs	Variable	Mean	Std Error
Fear	40	fro_mean	0.0676813	0.0272773
		Fro_MAX2	0.0925846	0.0482642
		Fro_TTM	325.0000000	187.6862797
		Fro_SD	0.0147654	0.0111128
		zyg_mean	0.0485938	0.0378983
		Zyg_MAX2	-0.0568197	0.0918471
		Zyg_TTM	170.0000000	141.0976506
		Zyg_SD	-0.0431095	0.0310958
		orb_mean	0.0044668	0.0350746
		Orb_MAX2	-0.0621723	0.0409298
		Orb_TTM	-93.3333333	171.7647633
		Orb_SD	-0.0332165	0.0135025
Neutral	30	fro_mean	-0.1059551	0.0299222
		Fro_MAX2	-0.1079980	0.0614598
		Fro_TTM	-364.4444444	233.0481746
		Fro_SD	-0.0083172	0.0164119
		zyg_mean	-0.2118246	0.0372307
		Zyg_MAX2	-0.1498259	0.0687352
		Zyg_TTM	-135.5555556	152.6432358
		Zyg_SD	0.0306619	0.0342449
		orb_mean	-0.1358856	0.0446182
		Orb_MAX2	-0.0891620	0.0591491
		Orb_TTM	-340.0000000	184.7672935
		Orb_SD	0.0305443	0.0192161

Table 3

Discriminant analysis: Happy vs Neutral comparison; baseline uncorrected

Happy vs Neutral ITT meth 1

The MEANS Procedure

INTO	N Obs	Variable	Mean	Std Error
Happy	31	fro_mean	-0.0117080	0.0480174
		Fro_MAX	-0.0253187	0.0843039
		Fro_TTM	-8.6021505	192.0708236
		Fro_SD	-0.0194662	0.0152878
		zyg_mean	0.0021469	0.0572112
		Zyg_MAX	0.0371121	0.0917819
		Zyg_TTM	12.9032258	166.2696161
		Zyg_SD	0.0154007	0.0305169
		orb_mean	-0.0082862	0.0353682
		Orb_MAX	-0.000220398	0.0538295
		Orb_TTM	961.2903226	152.4871209
		Orb_SD	0.0112099	0.0200138
Neutral	39	fro_mean	0.0075837	0.0254215
		Fro_MAX	-0.0305652	0.0530449
		Fro_TTM	-37.6068376	218.6642045
		Fro_SD	-0.0052368	0.0115880
		zyg_mean	-0.0767170	0.0416440
		Zyg_MAX	-0.0405001	0.1062873
		Zyg_TTM	-145.2991453	133.3079552
		Zyg_SD	0.0046189	0.0331890
		orb_mean	-0.0207263	0.0300474
		Orb_MAX	0.0141870	0.0547212
		Orb_TTM	-629.0598291	97.0951575
		Orb_SD	0.0102443	0.0164500

Table 4

Discriminant analysis: Happy vs. Neutral comparison; baseline corrected

Happy vs Neutral ITT meth 2

The MEANS Procedure

INTO	N Obs	Variable	Mean	Std Error
Happy	39	fro_mean	-0.0022988	0.0266454
		Fro_MAX2	-0.0040478	0.0530298
		Fro_TTM	-179.4871795	170.0141359
		Fro_SD	-0.0108206	0.0124204
		zyg_mean	0.1367922	0.0402996
		Zyg_MAX2	0.1919889	0.0763405
		Zyg_TTM	-102.5641026	145.6490719
		Zyg_SD	0.0222497	0.0257870
		orb_mean	0.1048344	0.0309683
		Orb_MAX2	0.1464547	0.0457517
		Orb_TTM	471.7948718	171.7730497
		Orb_SD	0.0137193	0.0156271
Neutral	31	fro_mean	-0.0413889	0.0356068
		Fro_MAX2	-0.1007930	0.0547391
		Fro_TTM	169.8924731	254.5047189
		Fro_SD	-0.0124415	0.0143381
		zyg_mean	-0.1858082	0.0406021
		Zyg_MAX2	-0.1747208	0.1064909
		Zyg_TTM	-40.8602151	150.1787838
		Zyg_SD	-0.0067799	0.0401675
		orb_mean	-0.1257375	0.0498972
		Orb_MAX2	-0.1261095	0.0612350
		Orb_TTM	-423.6559140	152.7618581
		Orb_SD	0.0068381	0.0210180

Table 5

Discriminant analysis: Fear vs Happy comparison; baseline uncorrected

Fear vs Happy ITT meth 1

The MEANS Procedure

INTO	N Obs	Variable	Mean	Std Error
Fear	32	fro_mean	-0.0031155	0.0335515
		Fro_MAX	0.0749849	0.0660060
		Fro_TTM	91.6666667	220.0266765
		Fro_SD	0.0355758	0.0139639
		zyg_mean	0.1280456	0.0504423
		Zyg_MAX	0.0925753	0.1020345
		Zyg_TTM	156.2500000	155.4450592
		Zyg_SD	-0.0125854	0.0328996
		orb_mean	0.0644458	0.0396563
		Orb_MAX	0.0189119	0.0492921
		Orb_TTM	-464.5833333	173.7341410
		Orb_SD	-0.0181577	0.0132118
Happy	38	fro_mean	0.0242334	0.0310764
		Fro_MAX	-0.0158804	0.0563751
		Fro_TTM	-85.9649123	164.8005130
		Fro_SD	-0.0176799	0.0114511
		zyg_mean	-0.0829961	0.0346624
		Zyg_MAX	-0.0568053	0.0841021
		Zyg_TTM	-64.9122807	146.5365784
		Zyg_SD	0.0144657	0.0245382
		orb_mean	-0.0394321	0.0276245
		Orb_MAX	-0.0102405	0.0493490
		Orb_TTM	619.2982456	172.6138164
		Orb_SD	0.0064828	0.0171591

Table 6

Discriminant analysis: Fear vs Happy comparison; baseline corrected

Fear vs Happy ITT meth 2

The MEANS Procedure

INTO	N Obs	Variable	Mean	Std Error
Fear	36	fro_mean	0.0721245	0.0291653
		Fro_MAX2	0.1285365	0.0503337
		Fro_TTM	109.2592593	190.9625258
		Fro_SD	0.0308675	0.0135872
		zyg_mean	0.0052287	0.0414487
		Zyg_MAX2	-0.0511644	0.0671220
		Zyg_TTM	214.8148148	158.2780156
		Zyg_SD	-0.0245643	0.0236289
		orb_mean	-0.0269475	0.0321116
		Orb_MAX2	-0.0933371	0.0340539
		Orb_TTM	-231.4814815	190.9871527
		Orb_SD	-0.0285521	0.0135001
Happy	34	fro_mean	-0.0221286	0.0260387
		Fro_MAX2	-0.0531857	0.0455933
		Fro_TTM	-125.4901961	188.4517967
		Fro_SD	-0.0189601	0.0116024
		zyg_mean	0.1367033	0.0339809
		Zyg_MAX2	0.1923018	0.1029831
		Zyg_TTM	-152.9411765	137.0697333
		Zyg_SD	0.0303317	0.0323863
		orb_mean	0.1375683	0.0347682
		Orb_MAX2	0.1976337	0.0525621
		Orb_TTM	500.0000000	181.4151802
		Orb_SD	0.0203875	0.0170498

Receivers: Canonical plots facial EMG data

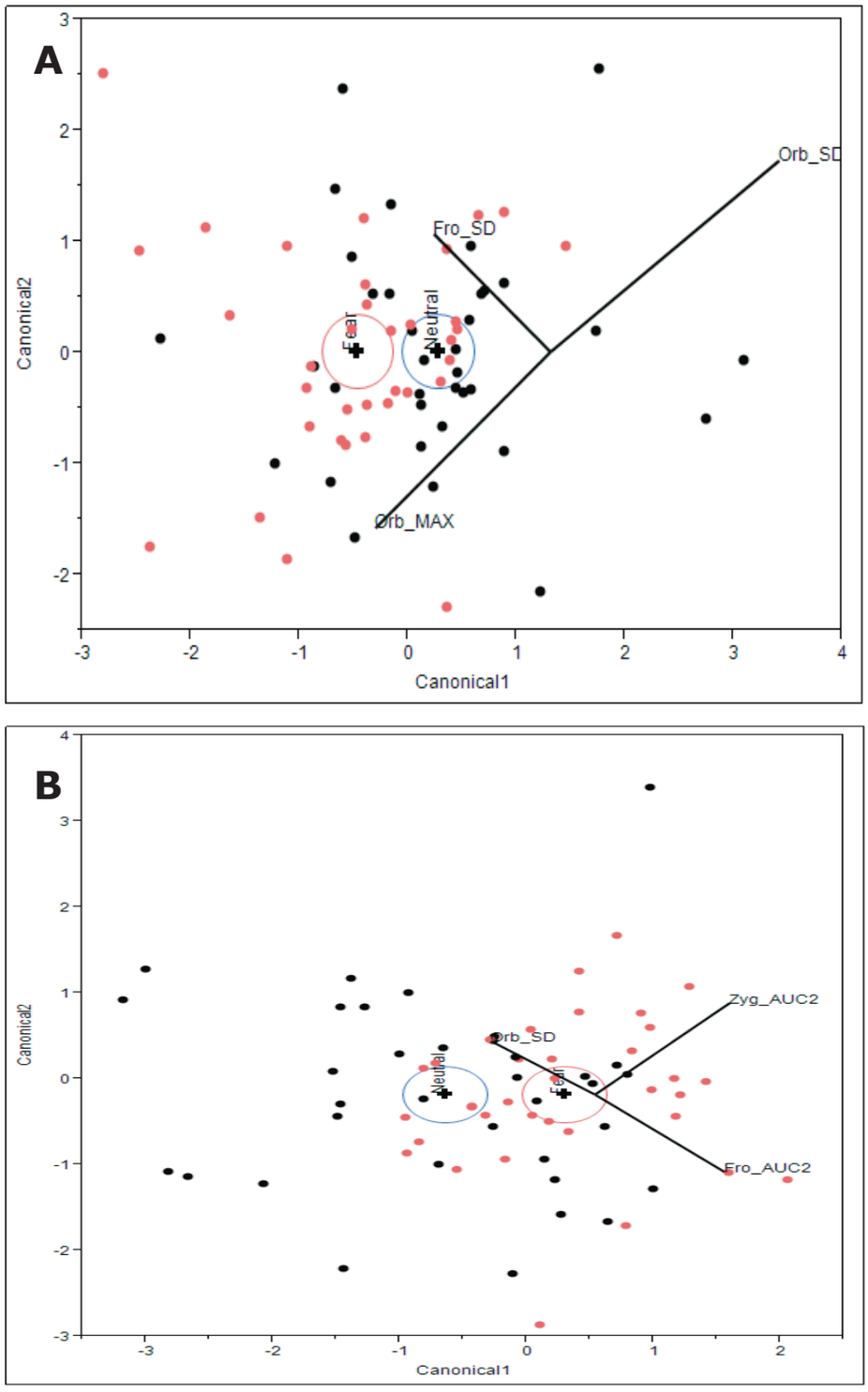

Figure 1. Displays data in two dimensions that best separate the groups (red: Fear, black: Neutral). Circles are confidence intervals for mean in this space—non-intersection implies significant difference between groups. (A) baseline uncorrected model; (B) baseline corrected model.

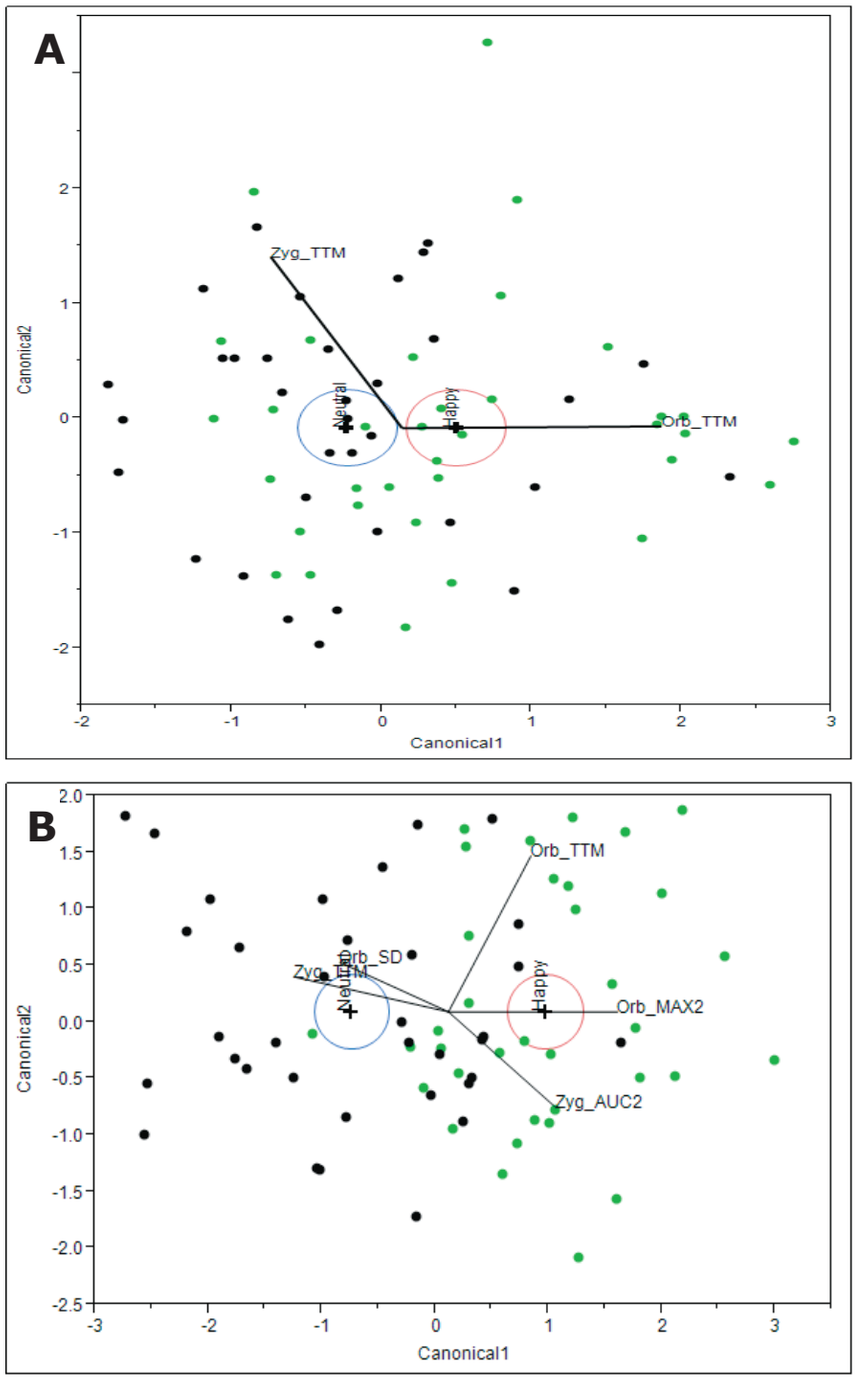

Figure 2. Displays data in two dimensions that best separate the groups (green: Happy, Neutral: black). Circles are confidence intervals for mean in this space—non-intersection implies significant difference between groups. (A) baseline uncorrected model; (B) baseline corrected model.

Receivers: Individual variation in global-local responses

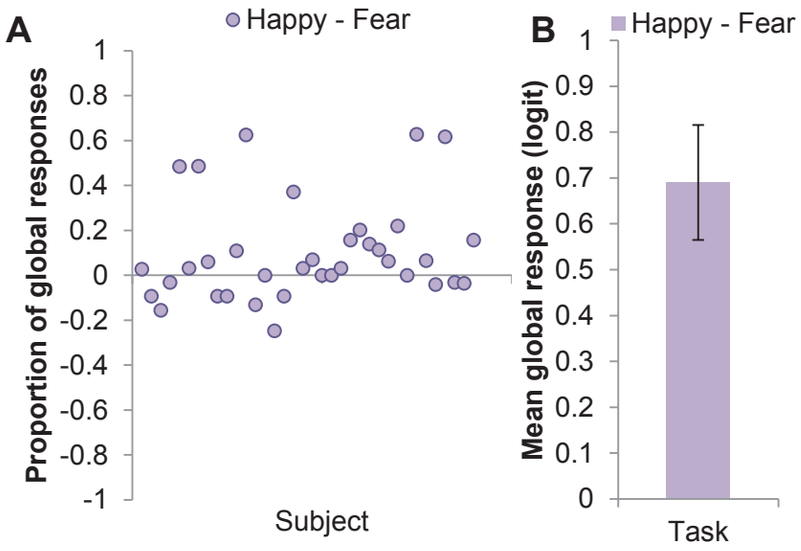

Figure 3. Measure of global-local processing style while receivers were exposed to sweat from individuals induced to be happy and fearful. (A) Distribution of each participant's proportion of global responses in the happy minus the fear condition. A positive (vs. negative) score indicates a greater (vs. smaller) proportion of global responses in the happy compared to the fear condition. (B) Presentation of mean relative differences in global responses in the happy relative to the fear condition on logit scale, excluding participant-to-participant response variability. Error bar, 95% CI.

Multivariate correlations between sweat ratings and facial EMG

Multivariate correlations between sweat ratings (pleasantness, intensity) and facial EMG parameters. Fro = *medial frontalis*; Zyg = *zygomaticus major*; Orb = *Orbicularis Oculi*. TTM = Time to maximum (peak facial muscle activity in mV). SD = Standard deviation. AUC2 = Area under the curve. Max = peak value. We report no p-values for three reasons. First, twenty correlations between sets of random numbers will yield one statistically significant correlation on average (by definition). Second, rejecting the null hypothesis that the true correlation between whatever is being compared is zero is not a particularly strong statement. Third, our data is not based on independent observations.

Table 7

Multivariate correlations

	Pleasant	**intensity**	**Fro_TTM**	**Orb_TTM**	**Zyg_TTM**	**Fro__SD**	**Orb__SD**	**Zyg__SD**	**Fro__AUC2**	**Orb__AC2**	**Zyg_AUC2**	**Fro_MAX2**	**Orb_MAX2**	**Zyg_MAX2**
pleasantness	1.0000	-0.4107	-0.1613	0.0790	-0.0659	0.1565	-0.0489	0.1472	-0.1454	-0.1363	-0.0298	0.1219	-0.1631	0.0560
intensity	-0.4107	1.0000	-0.2585	0.1646	0.0250	0.0072	0.0053	-0.1054	-0.0543	0.1440	0.1092	-0.0256	0.1987	-0.0165
Fro_TTM	-0.1613	-0.2585	1.0000	0.0508	0.3193	0.0365	0.0847	0.0988	0.3923	0.1023	0.0153	0.1369	0.0524	0.0461
Orb_TTM	0.0790	0.1646	0.0508	1.0000	0.3955	-0.0678	-0.0051	0.0852	-0.0168	0.3769	0.4319	-0.0094	0.2518	0.2416
Zyg_TTM	-0.0659	0.0250	0.3193	0.3955	1.0000	-0.0036	0.1082	0.1560	0.1622	0.3871	0.4637	0.0127	0.3779	0.3762
Fro_SD	0.1565	0.0072	0.0365	-0.0678	-0.0036	1.0000	0.0493	0.2152	0.3585	-0.0377	0.0162	0.8756	-0.1198	0.1272
Orb_SD	-0.0489	0.0053	0.0847	-0.0051	0.1082	0.0493	1.0000	0.7764	0.1154	-0.0490	0.0719	0.0615	0.6051	0.5848
Zyg_SD	0.1472	-0.1054	0.0988	0.0852	0.1560	0.2152	0.7764	1.0000	0.1375	0.1010	0.2292	0.2385	0.4189	0.8293
Fro_AUC2	-0.1454	-0.0543	0.3923	-0.0168	0.1622	0.3585	0.1154	0.1375	1.0000	0.0986	0.1208	0.5748	0.0967	0.1688
Orb_AUC2	-0.1363	0.1440	0.1023	0.3769	0.3871	-0.0377	-0.0490	0.1010	0.0986	1.0000	0.5336	0.0041	0.5967	0.3081
Zyg_AUC2	-0.0298	0.1092	0.0153	0.4319	0.4637	0.0162	0.0719	0.2292	0.1208	0.5336	1.0000	0.1699	0.4421	0.6369
Fro_MAX2	0.1219	-0.0256	0.1369	-0.0094	0.0127	0.8756	0.0615	0.2385	0.5748	0.0041	0.1699	1.0000	-0.0386	0.2518
Orb_MAX2	-0.1631	0.1987	0.0524	0.2518	0.3779	-0.1198	0.6051	0.4189	0.0967	0.5967	0.4421	-0.0386	1.0000	0.5311
Zyg_MAX2	0.0560	-0.0165	0.0461	0.2416	0.3762	0.1272	0.5848	0.8293	0.1688	0.3081	0.6369	0.2518	0.5311	1.0000

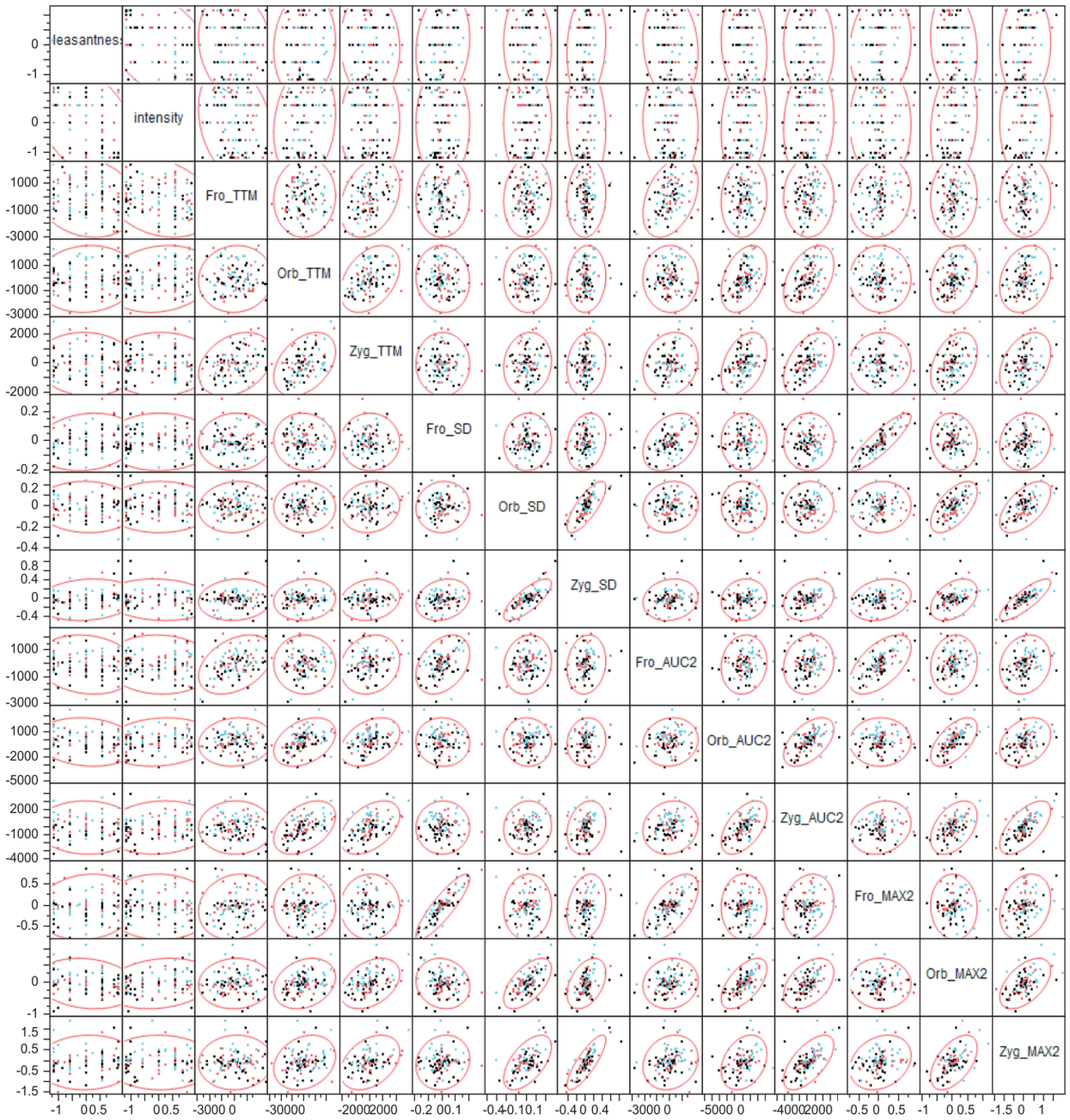

Figure 4. Scatterplox matrix depicting multivariate correlations.

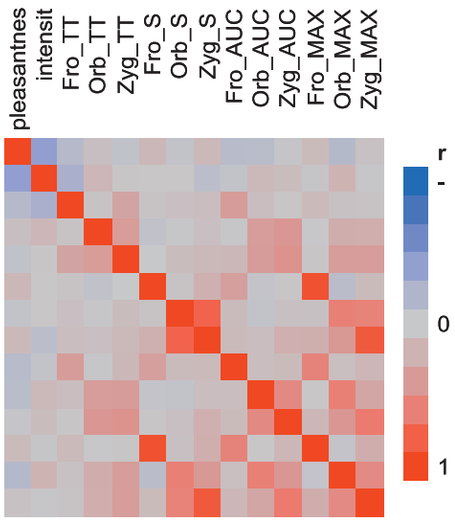

Figure 5. Color map depicting multivariate correlations.

Acknowledgment

(Dankwoord)

Promoveren binnen drie jaar is een uitdaging (understatement). Mijn dank gaat uit naar degenen die zorgden voor een leuke (werk)sfeer en/of welkome afleiding, zij die hebben bijgedragen aan dit proefschrift en zij die mij op één of andere manier hebben geïnspireerd. Dit dankwoord is opgeschreven met inachtneming van het volgende (nogal subjectief op te vatten en voor de kenners ironische) principe: "Wat zich überhaupt laat zeggen, laat zich helder zeggen; en waarvan men niet kan spreken, daarover moet men zwijgen." (Wittgenstein)

In de eerste plaats wil ik Monique bedanken. Ik herinner me nog goed hoe ik als ambitieus knaapje tijdens de research master stage bij je deed. Naast een uitstekend wetenschapper heb ik je leren kennen als een zeer prettig en onbaatzuchtig mens. Tevens heb je me enthousiast gemaakt voor geuronderzoek; daarvoor ben ik je zeer erkentelijk. Ik leerde al snel dat dit type onderzoek complex en tijdsintensief is, waarbij op obsessief-compulsieve wijze alle mogelijke verstorende factoren moeten worden gecontroleerd. Je inspireerde me om deze uitdagingen samen met jou (en later ook met Gün) aan te gaan en ik heb er allerminst spijt van. Tijdens dit project werd ik bij het uitvoeren van experimenten meermaals bijgestaan door twee competente onderzoeksassistenten. Dank hiervoor, Annemarie en Evi-Anne!

Then to my other esteemed promotor. Gün, I would like to thank you for the many opportunities you gave me, both before and during my PhD project. You have put a royal (no pun intended) amount of attention into this research project and I thank you for that. I admire your creativity, cleverness, sense of humor, and also your connections and political skills. You continuously challenged me to stay sharp and productive. It has been a great learning experience.

Being a member of the Cratylus research group was also an interesting experience. I want to thank its (other) members/alumni: Margarida, Catarina, Ana Rita, Francesco, Hande, Stephanie, and Xiaoqian. Another member of Cratylus deserves additional appreciation, in my opinion. Tomás, thanks for the wonderful time in the office we shared together with Baran. It's unfortunate that we were separated because of the Van Unnik move, but that's life. Tomás, you are an extremely friendly, warm-hearted, smart, and funny guy. We laughed about the Journal of Universal Rejection and its hilarious blog (which stream of nonsense contributions, by the way, has kind of dried up, unfortunately), each other, and ourselves. Baran, your presence and unlimited appetite for coffee are hilarious in itself. You are a very friendly, funny, intelligent, and

social person—not at all the jealous type. Thank you for inviting me to various social events, including your Pizza Friday (although many were in fact cancelled) with Mike and Katharina. M & K, you are very kind people and I enjoy your gezelligheid. Hetzelfde geldt voor huidig kantoorgenootje Florien. Ik heb me erg vermaakt met je genuanceerde opmerkingen over van alles en nog wat! Marloes en Daniël, jullie waren ook heel fijn gezelschap en het is jammer dat ik jullie maar kort heb kunnen meemaken. Pier-Eric, I want to thank you for the hilarious and memorable "situations" you "produced".

Hans, tof dat je me hebt vergezeld tijdens het SPSP-congres in New Orleans. Je spitsvondigheid leidt nogal eens tot hilariteit, zo ook in het zuidelijke deel van de VS: "W'all having a good time". Erik, bedankt dat je me hebt geleerd dat je af en toe van je af moet bijten in de academische wereld. Natuurlijk ook bedankt voor je gezelligheid. Datzelfde geldt voor Anouk en Claire. Myrthel, tevens bedankt voor je grenzeloze optimisme en in hetzelfde straatje, Peter, bedankt voor je nimmer aflatende stroom sarcastische humor. Robert, jij ook bedankt voor je fijne aanwezigheid, hulp en humor. Toch bijzonder om te zien hoe twee mensen van één middelbare school uiteindelijk op één afdeling zijn beland. Ik hoop dat je kennis en kundigheid behouden blijft voor de wetenschap!

Henk, bedankt voor je "deur die altijd open staat" en je (soms bizarre) humor. Kees, ik heb veel waardering voor het feit dat je wetenschappelijke vaardigheden combineert met "menselijke" eigenschappen zoals hartelijkheid en vriendelijkheid. Esther P. and Larry, you are fantastic; thanks for helping me understand your at times complex and always fascinating research ideas. Toon, Esther K., Madelijn, Michael, Veerle, Maria, Richta, Elianne en Jan Fekke, bedankt voor jullie hulp, aardigheid en/of het feit dat jullie mijn praatjes tijdens de LOSP en/of SOP research meeting(s) wilden aanschouwen. Tom 40, Belle en mensen van het "Nijmeegse uitwisselingsproject": Tom 30, Ron en Reine, dank voor jullie aanhoudende gezelligheid tijdens lunches en borrels. Hetzelfde geldt voor de mensen die nu (grotendeels) uit zicht zijn: Liesbeth, Hagar, Gerdientje, Chantal en Michelle. Het ga jullie goed!

Dan de mensen buiten werk. Allereerst Alexander. Niemand heeft veel vrienden nodig als je één beste vriend hebt zoals Alexander. Ik ken je al vanaf de eerste klas van de middelbare school. Daar stond ik al versteld van je fenomenale geheugen en aandacht voor details. We raken nooit uitgepraat en delen veel interesses en je bent immer geïnteresseerd in hoe het gaat. Samen trokken we veel op met een Rus. Evgeni, ook al woon je tegenwoordig op grote afstand, je blijft een vriend aan wie ik vele goede herinneringen koester. Je bent een slim, ambitieus en inspirerend mens, maar het meest waardeer ik je warme persoonlijkheid. Tom, ook jij bent

(tijdelijk) niet meer in de buurt vanwege je studie aan de University of Bradford. Ik vind je een fantastische kerel en we houden contact.

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Tot slot, mijn lieve Natalie: ik ben ontzettend blij dat ik je zes jaar geleden in Lyon heb ontmoet! Tijdens mijn AiO-periode heb ik veel gehad aan je steun. Niets was tevens relativerender dan wanneer ik aankwam met een geaccepteerd artikel in een bepaald tijdschrift en jouw reactie was: “Is dat goed, dan?”. Bovenal benadrukte je dat het belangrijk is om tijd en energie te steken in dingen buiten werk, zaken die ook écht belangrijk zijn in het leven, zoals vriendschap, liefde, en “fun”. Daar ben ik je heel dankbaar voor, want zelf verloor ik nogal eens de balans uit het oog. Dank ook voor de gezelligheid en hartelijkheid die ik heb ervaren bij je ouders Fred en Lisa en je zusje Isabelle. Natalie, rest me nog datgene helder te zeggen, wat zich überhaupt laat zeggen (en tevens zien): ik houd van je. Op naar 25-09!

Curriculum Vitae

Biography

Jasper de Groot was born on the 25th of May 1989 in the peaceful medieval town of Harderwijk. Once home to the infamous Guelders Academy, Harderwijk witnessed the closure of its university's doors by the French in 1811. What started was an exodus of prospective students to cities such as Utrecht, the place chosen by Jasper to study Psychology. After finishing his bachelor's degree in June 2009, he went on to obtain his research master's degree (cum laude) in Social & Health Psychology. He then wrote a research talent grant proposal under the supervision of professor Semin and Smeets. In April 2012, NWO funded the proposal and this enabled Jasper to undertake a 3-year PhD project at Utrecht University. He finished his dissertation in February 2015. Currently, Jasper is a postdoctoral researcher at Utrecht University.

Publications

*Included in this dissertation

*__de Groot, J. H. B.__, Smeets, M. A. M., Rowson, M. J., Bulsing, P. J., Blonk, C. G., Wilkinson, J. E., & Semin, G. R. (2015). A sniff of happiness. *Psychological Science.* Advance online publication. doi: 10.1177/0956797614566318

*__de Groot, J. H. B.__, Smeets, M. A. M., & Semin, G. R. (2015). Rapid stress system drives chemical transfer of fear from sender to receiver. *PLoS One*, 10, e0118211. doi: 10.1371/journal.pone.0118211

*__de Groot, J. H. B.__, Semin, G. R., & Smeets, M. A. M. (2014). Chemical communication of fear: A case of male-female asymmetry. *Journal of Experimental Psychology: General*, *143*, 1515–1525. doi: 10.1037/a0035950

*__de Groot, J. H. B.__, Semin, G. R., & Smeets, M. A. M. (2014). I can see, hear, and smell your fear: Comparing olfactory and audiovisual media in fear communication. *Journal of Experimental Psychology: General*, *143*, 825–834. doi: 10.1037/a0033731

*Semin, G. R., & __de Groot, J. H. B.__ (2013). The chemical bases of human sociality. *Trends in Cognitive Sciences*, *17*, 427–429. doi: 10.1016/j.tics.2013.05.008

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Aarts, H., Ruys, K. I., Veling, H., Renes, R. A., __de Groot, J. H. B.__, van Nunen, A. M., &

Geertjes, S. (2010). The art of anger: Reward context turns avoidance responses to anger-related objects into approach. *Psychological Science*, *21,* 1406–1410. doi: 10.1177/0956797610384152

Grants and Awards

- **Travel Award** (2015). Association for Chemoreception Sciences (AChemS).
- **Travel Award** (2015). Society for Personality and Social Psychology (SPSP).
- **Housing Award** (2014). Association for Chemoreception Sciences (AChemS).
- **Research Talent Grant** (2012). Nederlandse Organisatie voor Wetenschappelijk Onderzoek (NWO) [the Netherlands Organization for Scientific Research].
- **P. G. Swanborn Thesis Prize** (2011). Award for best master's thesis written within the Faculty of Social and Behavioral Sciences, Utrecht University.
- **Best Presentation Prize** (2010). Social & Health Psychology research master, Utrecht University.

Media appearances

Radio interviews: BNR Nieuwsradio; Radio M; Fun X; RTV Utrecht

Television interviews: VRT (Flemish Radio & Television): "Ook getest op mensen" (2015); RTV Utrecht (Radio & Television Utrecht): "Westbroek! (2014)

The "Kurt Lewin Institute Dissertation Series" started in 1997. Since 2013 the following dissertations have been published in this series:

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