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PERCEPTION OF EMOTION-RELATED BODY ODOURS IN HUMANS

ABSTRACT: Many socially living species are able to perceive chemical cues to the emotional state of their conspecifics. The main aim of this paper is to review the current body of evidence about emotion-related odours in humans from the viewpoint of the signalling theory. This approach differentiates between signals and cues, which are assumed to result from different selective pressures. Signals are of adaptive advantage to both the sender and receiver and show a specific design behind such adaptations. On the other hand, traits that were not directly selected for communication purposes but perceivers are nonetheless adapted to be attentive to are called cues. The results of the studies conducted so far indicate that humans are able to distinguish between the odours of other individuals who have been experiencing various affective states to some extent. However, often it is difficult for them to identify the specific affective context in which the odour has been sampled. In other studies it was found that exposure to odour samples collected in a stressful situation changes the perceivers' cognitive functioning and behaviour, even though they may not be aware of what the odour refers to or may not even perceive it on the supraliminal level. For example, exposure to an odour collected in a stressful situation may increase a startle response, greater tendency to risk-taking behaviour or an increase in the level of anxiety or sensory bias in the perception of another person. These changes are more profound in socially anxious individuals. According to the evidence currently available, perception of emotion-related odours indicate the specific adaptive design in the perceiver's olfactory cognition, which allows us to tentatively conclude that human body odour contains cues to affective states to the others. In contrast, the evidence regarding proximate mechanisms behind the production of such odours is missing, which makes it impossible to conclude whether these could be termed signals.

KEY WORDS: Body odour – Smell – Communication – Adaptationism – Emotion – Stress – Competition

INTRODUCTION

Humans have long been regarded as microsmatic because they rely primarily on visual and verbal cues. However, a growing body of evidence suggests that olfaction plays a significant role in various aspects of human social interactions. Recent studies have shown that human body odour provides information about the

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individual's sex, genetic quality, health, reproductive state, and diet (for reviews see, Fialová *et al.* 2013, Havlicek, Lenochova 2008, Havlicek, Roberts 2009, Kippenberger *et al.* 2012).

Several recent studies have also tested whether body odour might provide information about the affective state of an individual. Although many of these studies build their hypothesis on parallels from animal literature, they frequently appear to be theoretically ungrounded. The main aim of this paper is to review the current evidence on this issue and to reconsider it from an evolutionary perspective. Thus, we first introduce the adaptationist theory of communication and show how these concepts fit relevant studies on chemical perception of affective states in various vertebrate taxa. Subsequently, we review the available evidence on emotion-related odours regarding their i) hedonic assessment, ii) recognition, iii) the cognitive and behavioural changes, and iv) changes in brain activity they bring about. In the last section we analyse the results within the signalling theory framework and suggest avenues to be explored by future studies.

ADAPTATIONIST APPROACH TO COMMUNICATION

A wide range of theoretical approaches deal with the definition of communication. In this paper, we employ the adaptationist approach proposed by Maynard Smith and Harper (2003). According to them, communication in the true sense is carried out on the basis of signal transfer. This definition does not fit the perception of cues (see below) and therefore throughout the text it is not considered communication. A signal is not something projected into the world to be captured by a possible recipient, but there would be no communication if either a signaller or a recipient were missing from the equation (Scott-Phillips 2008). In accordance with the adaptationist approach a signal is "any act or structure that i) affects the behaviour of other organisms; ii) evolved because of those effects; and iii) which is effective because the effect (the response) has evolved to be affected by the act or structure". Otherwise specified, a signal must influence the behaviour of another organism and this behaviour has been selected for in order to influence the other organism. Moreover, a signal is expected to consist of complex structure which evolved for a specific purpose and its accidental existence is highly unlikely. Therefore the transferred information mainly appears to be distinct and resistant to confusion. In the majority of cases, the message is also targeted to a specific individual or group of individuals. A signal also differs from a cue; a cue is any act or structure that affects the behaviour of another organism and which is effective because the perception has evolved to be affected by the act or structure but it did not evolve because of those effects. According to this definition of communication, two types of semantic information can be transferred. One type informs about the sender and is often sexually selected for ("self-reporting signals"; signals about physical qualities, status, often represented by sexual displays to the opposite sex), the other type carries information about the environment ("other-reporting signals"; for instance alarm calls and the dance of honey bees) (Maynard Smith, Harper 1995).

It is thought that signals have evolved from cues through the process of ritualization, in which the behaviour originally had another function, but recipients started to use it as a cue and under a selective advantage the cue evolved into a signal and then the original function may or may not have potentially been lost. More specifically, chemical signals are expected to have evolved from compounds which originally had other uses or significance, for example from hormones, chemicals released during injury or waste products. One class of information individuals might signal by means of chemical substances is their internal state which would elicit the appropriate response in the recipient.

PERCEPTION OF CHEMICALS RELATED TO AFFECTIVE STATES IN VERTEBRATES

In a classic study, Karl von Frisch found the fright response in the European minnow (*Phoxinus phoxinus*). When he put a fish with damaged skin back into the water, other fishes swam rapidly away in alarm (Frisch 1938). The skin damage had released a substance and activated anti-predator behaviours such as increased shelter use, shoaling or "freezing". The fright reaction to the substance apparently does not require previous experience, but organisms may learn to associate predator odour and a visual sign with danger when they sense the "alarm" odour. This learning is faster in populations exposed to predation (Levesley, Magurran 1988). Learning gives flexibility because individuals can learn to respond to the predators found in their own habitat.

In mammals, communication of internal state through odour was first shown in rats that learned to discriminate

between the odour of stressed and non-stressed individuals (Valenta, Rigby 1968). Similarly, 48-day-old female mice preferred the odour from non-stressed males to that from stressed males (Carr *et al.* 1980). Animals are able to differentiate between these odours but they do not only process the information but change their behaviour accordingly as well (Mackay-Sim, Laing 1980). Stress induces physiological responses such as increased heart rate, perspiration and muscle tension. For example, rodents respond to the odour of stressed individuals with increased defensive and risk-assessment behaviours accompanied by decreased exploratory and grooming behaviours and avoidance of the odour (Kiyokawa *et al.* 2006). Similarly in rats, odour of stressed conspecifics enhances the acoustic startle reflex in recipient individuals (Inagaki *et al.* 2008), perhaps due to increased anxiety level in recipient animals. Another model species for studying "alert" odours are family groups of black-tailed deer (*Odocoileus hemionius columbianus*). Their metatarsal glands are exposed on the hind leg and when disturbed they release a strong garlic-like odour (Müller-Schwarze 1971). Females exposed to the odour from either male or female glands were more likely to show increased alert behaviour and leave.

As we have seen above, various animal species, especially the socially living ones, may communicate their internal state to conspecifics. Evolution of such a signalling system can be exemplified in the case of the so-called alarm odours, which provoke a fight or flight response in the recipients. They appear to have evolved from compounds released by fighting or injured conspecifics. Potential recipients who were sensitive to these compounds and responded appropriately gained a selective advantage. The traditional view expected that defensive compounds gradually gained a signalling function. However, such an explanation of the evolution of alarm signals which can be seen as a form of altruistic signal is questionable because it makes the signallers more conspicuous and at a greater risk of predation than their inconspicuous neighbours. Therefore, it is thought that in most species kin selection was responsible for the evolution of alarm signals (Wyatt 2003). In contrast, the evolution of alarm odours into chemosignals in unrelated individuals is more difficult to explain because there seems to be little benefit to the signaller. Theoretically, an alarm odour could increase the signaller's chance to escape even after being captured (Wyatt 2003). This could happen when an alarm odour acts as a "distress signal" which enables the victim to escape by attracting conspecifics or secondary predators that interfere with the primary predator (Smith 1992). Also, it could be that some responses are adaptive for the responder but that these odours have not evolved as signals on the part of the signaller and should be therefore labelled cues.

One of the alternative explanations suggests that an alert odour by prey may be directed to the predator himself because he is less likely to attack once he has lost the element of surprise (Wyatt 2003). However, conspecifics were selected to be sensitive to such chemicals as they decrease the chance of being attacked by the predator.

The majority of animal studies on reactions to chemicals released by conspecifics experiencing a specific internal state rather indiscriminately refer to communication via chemosensory signals. The evidence is debatable, though. In some cases, the requirements of the adaptationist definition of communication are met, such as in the Japanese honeybees (Ono *et al.* 1995). When a honeybee marks a hornet with the pheromone, it triggers in other honeybees a specific behavioural response with the aim of defeating the hornet. This behaviour is adaptive for both the sender honeybee and other honeybee recipients who are closely related and share their interest of protecting their hive. On the contrary, the release of an alarm odour in minnows may not be adaptive for the injured individual unless it is surrounded by kin. Moreover, it seems that individuals do not release the alarm odour when they see a predator but they are released only in the case when the skin is damaged (Brown *et al.* 2000). The preference for odours of stressed individuals in rats is again adaptive for the perceivers who can obtain some information about another's state or the surrounding environment. However, there is no strong evidence that a stressed individual derives any advantage from informing the conspecifics about its internal state. To sum up, it seems currently premature to unanimously speak about signals in animals but it is important to bear in mind the definition of communication and to carefully examine individual cases. Further, we will focus on the possible communication of affective states in humans where, similarly to other vertebrates, the phrase ‘communication through chemosignals' is used rather indiscriminately.

CHEMOSENSORY CHANNELS INVOLVED IN PERCEPTION OF EMOTION-RELATED CHEMICALS IN HUMANS

Generally it is believed that in humans airborne chemical substances are processed by means of main

olfactory and trigeminal systems. In many other mammals, such as in rodents and ungulates, chemosensation also involves vomeronasal organ (VNO) especially in intraspecies communication (Müller-Schwarze 2006). Although some scholars claimed that humans too might have functional VNO (Monti-Bloch *et al.* 1998), prevailingly it is regarded as vestigial for the following reasons: i) no neural connection of VNO and brain has been found, ii) humans are missing a separated accessory olfactory bulb where sensation from VNO is processed, iii) it does not exhibit functional receptor cells, and iv) most of the genes coding VNO receptors are non-functional (for critical assessment see, Meredith 2001). Most recently another chemosensory system entered the arena, namely the Grueneberg Ganglion. This small cluster of neuronal cells localized in the nasal vestibule was discovered in several mammalian species (Mamasuew *et al.* 2011). Recent studies show that alarm-related chemicals in mice are detected through the activation of olfactory Grueneberg Ganglion neurons (Brechbühl *et al.* 2008). Although a similar effect has not been shown in humans yet we can not exclude the possibility that emotion-related chemicals are analogously perceived via the Grueneberg Ganglion. With this in mind, we conservatively use through the text the term odour as if perception of emotion-related substances would exclusively involve main olfactory and trigeminal systems.

HEDONIC ASSESSMENT OF EMOTION-RELATED ODOURS

The possibility that in humans, too, odours can provide relevant information about the producer's affective state has recently attracted considerable scientific attention (see, *Appendix 1*). This issue was investigated by employing various paradigms; one of them expects that odours of individuals who have experienced a negative affect will be perceived as less pleasant. However, the results of several studies are ambiguous. Cantafio (2003) sampled body odours in different affective states, namely happiness and fear, and asked a panel of raters to judge their hedonic valence. The results showed that axillary samples which had been collected for a longer period of time (24 minutes) during watching a fearful movie were rated as more intense and also there was a tendency to rate them as more pleasant. Interestingly, the perceived intensity was not associated with the perceived pleasantness of the samples and thus can not solely explain the observed pattern (Cantafio 2003). In a similar experiment, women rated the smell of pads worn while odour donors were watching a terrifying film as significantly stronger and less pleasant than that of pads worn in a neutral situation (Ackerl *et al.* 2002). In contrast, another study did not reveal any significant differences between the anxiety condition, exercise control and an untreated pad (Prehn *et al.* 2006). Also, in several other studies samples collected under anxiety conditions and presented via olfactometer did not differ in their hedonic or intensity ratings (Adolph *et al.* 2010, Albrecht *et al.* 2011, Gelstein *et al.* 2011, Pause *et al.* 2009, Prehn *et al.* 2006, Prehn-Kristensen *et al.* 2009). We can see that the evidence for distinct changes in emotion-related odours detectable in humans is mixed. This could be a result of different methods employed in the individual studies (e.g., sniffing jars vs. using olfactometer) or it may reflect the fact that this approach may not be the most suitable for this kind of research as these changes may not be perceptible on the supraliminal level and thus may be unavailable to the participants for assessment.

RECOGNIZING EMOTIONS IN HUMAN BODY ODOUR

Another line of research has focused on the ability of humans to recognize various emotional states based solely on odour cues. In the first study on this topic, the authors asked the odour donors to watch a funny and a frightening movie to induce a happy or a fearful state (Chen, Haviland-Jones 2000). Subsequently, when a panel of participants was asked to choose "the odour of people when they are afraid", both men and women chose above the chance level the congruent body odours of men who had watched the frightening movie, but this was not the case with female body odours. Women also correctly chose "the odour of people when they are happy", collected from both men and women, however men were only successful in the case of "happy women", but not in the case of men. Women generally recognized odours better than men which could be the result of their higher smell sensitivity and they also may be better at perceiving differences associated with an emotionally significant stimulus (Chen, Haviland-Jones 2000). In a similarly designed experiment, participants watched either a terrifying or an emotionally neutral (control condition) movie while their axillary odours were being collected. Results of a triple forced-choice test showed that participants were able to discriminate between the fear and non-fear axillary pads (Ackerl *et al.* 2002). Moreover,

a successful recognition of odours is not restricted to axillary odours but people are also able to differentiate between mood odours collected from the forehead (Cantafio 2003) where sebaceous glands are found in higher densities than in the axillae (Johnson *et al.* 1997). Although forehead odours collected in different moods are distinguishable, participants labelled them incongruently. In particular, raters significantly misidentified the happy samples when asked for the smell of fear, but selected the sterile control when asked for the smell of the happy. Another study demonstrated that evaluators are able to distinguish between fear-related axillary odours that have been collected for different lengths of time (sampling duration: 6, 12, and 24 minutes), independent of their perceived intensity (Cantafio 2003). Thus, these studies argue against the assumption that subjects use the intensity of the donor's odour as a cue for identification of the fear and happy samples. Mood odours collected for a longer period of time are not simply considered more fearful than odours collected for a shorter length of time (6 minutes) and these odours are not simply thought to indicate the donors were more happy at the time of sampling than the donors of the samples that have been collected for a longer period of time (24 minutes). The above-mentioned studies suggest that humans are to some extent able to differentiate between experienced emotions based solely on the body odour. However, they might misidentify the emotional context. Recognition rate also depends on both the perceiver's and the body odour donor's sex, however, it is rather independent of the intensity of the odour, suggesting that odours might indeed differ in their quality.

COGNITIVE AND BEHAVIOURAL CHANGES AS A CONSEQUENCE OF EXPOSURE TO THE ODOUR OF STRESSED INDIVIDUALS

The above-mentioned studies show that some emotional states affect human body odour and that other individuals are able to perceive such changes. However, in some cases they might not be consciously aware of the odour and thus may not be able to evaluate it. Therefore, the following studies have focused on this issue. In particular, they have tested whether exposure to odours collected during stressful situations (including competition) may affect behaviour or cognitive performance.

Prehn *et al.* (2006) tested the effect of stress-related odours on pre-attentative functioning. Samples of axillary odour were collected before an oral academic examination and during ergometric training (control condition). These chemosensory stimuli from pooled sweat samples and from unused cotton pads were presented by means of a constant-flow olfactometer and acoustic startle probes were delivered during and between the presentations of the chemosensory stimuli. The startle reflex amplitude recorded in the context of chemosensory anxiety stimuli increased as compared to the contexts in which either an exercise or an untreated pad from the same donors served as stimuli. This could mean that anxiety odours pre-attentively prime defensive behaviour (Prehn *et al.* 2006). A follow-up study showed a similar effect and further examined whether chemosensory perception of social stress is modulated by the degree of social anxiety, with social anxiety being characterized by abnormal processing of the social threat information. Indeed, the startle reflex was more augmented in socially anxious individuals than in non-anxious participants during exposure to axillary sweat collected under the stress condition compared to startle responses obtained in the context of sport sweat (Pause *et al.* 2009). Here we can draw a parallel to the animal studies. As shown above, the odour from stressed conspecifics in rats induces startle reflex (Inagaki *et al.* 2008). Similarly in humans, the reaction to such odour can be interpreted as part of defensive behaviour (increase startle reflex) and the response thus resembles the producer's behaviour. For this reason we might conclude that the odours contain some markers to affective states of other individuals and might contribute to the predictive processes in social interactions.

Another study focused on a significant aspect of cognitive functioning – decision making – which partly depends on the appropriate interpretation of emotional processes of interacting individuals. It was shown that risk-taking behaviour in an experimental game was significantly higher in participants who were exposed to the anxiety odour (collected during a high rope course) compared to the exercise (ergometer workout) and control conditions. Moreover, participants showed a higher latency before making a decision in the most risky choices during the anxiety condition (Haegler *et al.* 2010). The following study investigated cognitive performance in a word-association task while smelling fear-related body odour, neutral body odour and control odour. Participants exposed to the fear condition performed more accurately with no sacrifice for speed than those under either the neutral or the control condition. But they performed slower on tasks containing ambiguous content. Results suggest that humans exposed to fear-related odour are more cautious and that their cognitive strategies change slightly (Chen *et al.* 2006).

Whether emotion-related markers transferred by one sense (olfaction) modulate how the same emotion-related cue is perceived in another sense (vision) has been repeatedly investigated. Pause *et al.* (2004) focused on changes in face perception due to exposure to anxiety-related odour. Happy, fearful, and sad facial expressions were used as primes and neutral faces as targets and odour samples were presented before and during picture presentation. Target faces were judged more positive when primed by happy faces and exposed to control body odour samples than when they were primed by the negative facial expression. In contrast, the priming effect of the happy faces decreased in female (but not in male) participants in the context of anxiety odour. A similar effect was not observed when participants were primed by negative facial emotions. In another study odour samples collected in a fearful context biased women toward interpreting ambiguous facial expressions as more fearful. No effect appeared when the facial expression was more discernible (Zhou, Chen 2009). A similarly designed study showed that individuals exposed to stress-related odours elicited heightened electrocortical activity (measured by late positive potentials; LPP) across all facial expression, while LPP response under the control condition was larger for threatened than neutral facial stimuli (Rubin *et al.* 2012).

Other studies have focused on changes in affective states in individuals perceiving emotion-related odours. It was found that male anxiety-related body odour increases an anxious state in women compared to sweat collected during the neutral condition (Albrecht *et al.* 2011). Another study showed that odours collected in the fearful context evoke facial expressions of fear and sensory acquisition (increased sniff magnitude and an increase in the visual scanning process). On the other hand, odours from people exposed to disgusting stimuli elicited disgusted facial expressions and sensory rejection (decreased first sniff magnitude and a lower number of visual fixations) (de Groot *et al.* 2012). Remarkably, unlike in the majority of other studies which sampled odours from the axillary region, one recent study employed tears as stimuli instead. After sniffing negative emotion-related odourless tears, men attributed lower sexual appeal to pictures of women's faces. Moreover, they experienced reduced self-rated sexual arousal, and exhibited reduced physiological measures of arousal and a decreased level of testosterone. The effect was also accompanied by reduced activity in the brain substrates of sexual arousal in men as revealed by functional magnetic resonance imaging (Gelstein *et al.* 2011).

As shown above, axillary odours could carry cues to an emotional state of an individual, e.g., stress and anxiety. Therefore, other studies have tested whether a similar effect could be found in different emotions accompanying the competitive context, such as aggression. Aggression is thought to have developed as an evolutionary adaptation which should act as one of the possible way of resolving a conflict between two individuals. Individuals tend to become the most dominant when it comes to securing survival and limited resources for themselves (Buss 2007). Previous studies have shown that axillary odour could serve as a cue to dominance status. Women in the fertile phase of their menstrual cycle prefer body odour of dominant males. This preference is stronger in fertile women in a stable relationship than in fertile single women (Havlicek *et al.* 2005). Dominance and aggressiveness might manifest themselves in a competitive context. Therefore it was tested whether odour samples collected during a competition (badminton match) induce a different reaction compared to a sport control condition (running) (Adolph *et al.* 2010). The donors' testosterone level, which is an indicator of a competitive situation, indeed rose higher during the competition condition. The chemosensory stimuli were presented through a constant-flow olfactometer while skin conductance was measured. Skin conductance is a marker of sympathetic autonomic activity, associated with arousal and orienting towards a meaningful stimulus and emotionally significant stimuli usually elicit a larger skin conductance response. Results revealed that the skin conductance response was larger during exposure to stimuli collected during the competition condition as compared to those collected during the sport control condition. The effect was again stronger in participants who scored higher on a trait social anxiety scale (Adolph *et al.* 2010). Odour changes of competitive origin could serve as a warning of threat for other individuals.

BRAIN ACTIVITY AND EMOTION-RELATED ODOURS

Previous studies have shown that exposure to odours collected during emotionally valenced situations elicit cognitive and behavioural changes. Thus one may also expect specific changes in the brain neurophysiology. The primary area associated with emotion processing is the amygdala. It was shown that amygdala activation occurs after the presentation of sweat collected during an acute emotional, but not physical, stress situation

(collection during a first-time tandem skydive) without the conscious perception of a distinct odour (Mujica-Parodi *et al.* 2009). Smelling anxiety-related odours (i.e., collected while waiting to sit an academic examination) activated brain areas involved in the processing of social emotional stimuli (fusiform gyrus), and in the regulation of empathic feelings (insula, precuneus, cingulated cortex). Neuronal activity within the attentional (thalamus, dorsomedial prefrontal cortex) and emotional (cerebellum, vermis) control systems was also observed. The chemosensory perception of human anxiety-related odours thus seems to recruit empathy-related resources (Prehn-Kristensen *et al.* 2009). An analogous study investigated how anxiety odours donated by humans awaiting an academic examination are processed by the human brain by analysing chemosensory event-related potentials (CSERPs). It was shown that processing anxiety or stress-related odours requires more neuronal activity during early pre-attentive stimulus processing than the processing of body odour sampled in a non-emotional control condition. The neocortical sources of this activity were located within the medial and lateral frontal brain areas. Neuronal response was stronger in females than in males. However, socially anxious males processed chemosensory anxiety stimuli earlier than the control stimuli collected during an ergometer training (Pause *et al.* 2010).

ARE EMOTION-RELATED BODY ODOURS SIGNALS?

The aim of this paper was to summarize the current knowledge about the effect of emotion-related odours in humans and to interpret the findings of the relevant studies in the view of the signalling theory. Human studies in this area are apparently inspired by previous work in other vertebrates (see, for instance, Ackerl *et al.* 2002, Prehn-Kristensen *et al.* 2009) and commonly deal with what they refer to as chemosignals (although none of the studies explicitly states how a signal should be defined or to which theory of signals they refer to). Animal researchers use the term "chemosignals" or "alarm pheromones" all too widely, which, by definition, would equal a signal. However, it has been repeatedly pointed out that affective state-related odours could only evolve into signals under a specific condition such as kin selection and that in most vertebrates in which this phenomenon has been studied the conditions either have not been satisfied or the evidence has been missing (Wyatt 2003). In humans, to decide whether emotion-related odours might be labelled chemosignals we face similar difficulties. In this case we must identify ultimate (evolutionary) functions, specific receivers and proximate mechanisms underlying such adaptations (e.g., specific design, physiologic processes regulating such design both in sender and receiver).

ULTIMATE FUNCTION AND ITS EVOLUTION

The evolutionary analysis of communication systems considers signals as adaptation and asks therefore what reproductive advantage this communication of information brings to the producer and what advantage it brings to receivers who are being attentive to such information. From this perspective, producers might**,** via emotion-related odours**,** communicate to the conspecifics their likely future behaviour in order to synchronize group action. More specifically, in the case of anxiety-related odours, they might communicate potential danger and their reactions to it in form of flee/fight response.

In theory, such a system might have evolved in humans who have lived in small, often closely related groups for most of their evolutionary history (Barrett *et al.* 2002). However, this might not be restricted solely to related individuals as humans cross-culturally show high level**s** of cooperation, reciprocity and synchronized action. Further, evolutionary analysis gives us not only a functional but also a phylogenetical perspective. More specifically, such communication systems might not have evolved in human lineage but have been inherited from our ancestors. Unfortunately, our current knowledge about the role of olfaction in the social realms of apes is highly limited and awaits future investigations.

PROXIMATE MECHANISMS FOR THE PRODUCTION OF EMOTION-RELATED ODOURS

If emotion-related odours are signals, we should be able to identify the design in the sender that has evolved specifically for the signalling purposes. More specifically, the production of such odours would involve a specific mechanism and/or production of special substances or a specific mixture of substances. However, if differences in the body odour are simply a by-product of physiological processes related to stress or competition we might conclude that they have not evolved for the purpose of information transfer and they should be rather referred to as cues.

In studies in which samples have been collected in the anxious condition and the control sport condition, the effects of secretions of two different gland types of the human skin could have been compared. Sweat collected during the exercise or neutral condition (high in physical activity, low in emotion) might be predominantly produced by the eccrine glands that serve mainly for thermoregulation. Body odour sampled in the anxiety context (high in emotion but low in physical activity) is presumably produced by the apocrine glands which secret a complex mixture of compounds and may react to psychological stimuli. Thus it is questionable whether these two kinds of samples are comparable. However, we do not know exactly whether emotion-related odour changes are caused by the eccrine or apocrine production or their combinations. Other possible mechanisms involve indirect effects through the sympathetic nervous system and induction of the more intense eccrine secretion in an emotionally valenced situation, subsequent increase in humidity in the axilla and the proliferation of different bacteria species which consequently could lead to qualitative odour changes. This potential problem is addressed in the study of Adolph *et al.* (2010) in which they compared stimuli collected within the sport competitive context and the control sport condition. Therefore, the collected samples vary only in the tested variable and exclude alternative explanations as was the case in the above-reviewed studies.

So far, none of the studies focused on physiology of emotion-related odours, also we do not know the chemical composition of the sweat collected under such conditions. Thus, future studies should explore in detail which skin glands are involved in the production of the chemicals and whether it involves specific compounds or a specific mixture of the volatiles. Consequently, the lack of such data makes it difficult to decide whether the emotion-related odours might be coined signals.

CUES TO EMOTIONS

To label emotion-related odour cues to emotions we should identify the ultimate function of the responsiveness to such odours and be able to demonstrate specific design (i.e., proximate mechanism) on the side of the perceiver. From the ultimate perspective, such changes in the perceiver's behaviour might present a source of selective advantage, for example predict the conspecifics' future behaviour or identify danger (in the case of anxiety-related odours). From the proximate perspective, the emotion-related odours should induce specific behavioural or cognitive responses in the recipient that have evolved for this particular purpose.

The above-reviewed studies suggest that people are able to distinguish between the odours of individuals who have been experiencing various affective states. Several studies have also revealed that individuals who perceive such odours exhibit increased startle response (Prehn *et al.* 2006), greater tendency towards risk-taking behaviour (Haegler *et al.* 2010), changes in evaluations of own sexual arousal (Gelstein *et al.* 2011) and bias in the perception of others (Zhou, Chen 2009).

Interestingly, the majority of the studies employed similar conditions (watching a horror film, sitting an academic examination, taking part in a high rope course, undergoing a first-time tandem skydive) to induce an affective state, which different authors label as stress (Mujica-Parodi *et al.* 2009), anxiety (Albrecht *et al.* 2011, Haegler *et al.* 2010, Pause *et al.* 2004, 2010, Prehn-Kristensen *et al.* 2009) or fear (Ackerl *et al.* 2002, Chen *et al.* 2006, Zhou, Chen 2009). However, each of these affective states relates to a slightly different concept. Fear is often defined as an emotional response to a specific stimulus of threat and danger. Fear should be distinguished from anxiety which typically occurs without any external threat. In other words, fear is related to the specific behaviours of escape and avoidance whereas anxiety is the result of threats which are perceived to be uncontrollable or unavoidable. Further, anxiety is frequently considered as part of the reaction to stress which may help a person deal with a difficult situation (Lewis, Haviland-Jones 2004). Stress is generally defined as factors causing an organism's condition to deviate from homeostasis. According to Koolhaas *et al.* (2011) the term stress should be restricted to conditions where an individual believes that an environmental demand has exceeded his natural regulatory capacity, in particular situations that include unpredictability and uncontrollability.

On a related issue, during an induced affective state the participants might be experiencing other affects such as relief and/or thrill, for instance during or after the freefall (Mujica-Parodi *et al.* 2009) and in a high rope course (Haegler *et al.* 2010), or they could have gained more confidence during the course since they have not fallen or made mistakes, which were, however not assessed in the subsequent psychometric session. Therefore, the effects may not be exclusively anxiety-related. As the odour samples have been collected during the whole procedure, we currently do not know whether

such temporal affective changes could manifest themselves in the body odour.

Thus, the specificity of the observed effects is not clear at this point. In other words, changes in cognitive performance might either be specific to the perception of odours related to particular affective states or might show a similar pattern when smelling odours taken under similarly valenced conditions. In the second case, the similarity might arise from two sources. Firstly, the cognitive system of the perceiver may not be specifically sensitive to subtle differences in body odour collected under specific affective conditions. Or, secondly, body odours may be a product of non-specific arousal related to stressful situations rather than to specific affective states. The issue of specificity is substantial in relation to the concept of cues as it should show specific response. Future studies should thus compare responses to odours collected under different emotionally valenced conditions.

On the other hand, the above reviewed brain imaging studies show that odours collected under affective states cause specific changes in the neurophysiology of perceivers. It seems that perceiver's neurophysiological response mirrors the affective state of the producer as activation occurs in areas connected with emotion processing, empathic feelings and processing of social emotional stimuli. Such specific proximate mechanisms are suggestive of the past selective pressure on the perciever's brain neurophysiology and selection on the perceiver's side. Therefore, although we clearly need more refined and theoretically well grounded studies we may tentatively conclude that emotion-related odours can be termed cues.

CONCLUSIONS

The review intended to summarize current evidence about possible communicative function of emotion-related odours in humans. Above-reviewed studies use various approaches to investigate the effect of odours collected under emotionally-valenced conditions and demonstrated changes in some aspects of psychological functioning (hedonic rating, recognizing emotions, cognitive and behavioural changes, brain activity) due to exposure to such odours. Here we aimed to theoretically ground this research within signalling theory. This approach focuses on functional aspects of communication and differentiates between signal and cues as a result of different selective pressures which are responsible for their origin. To label emotion-related odours signals we should be able to show the adaptive advantage it brings to both sender and receiver and the specific design behind such adaptations. On the other hand, traits which were not directly selected to be produced for communication purposes, however perceivers are adapted to be attentive to them are called cues. In such cases, they are often by-products of the producer's metabolism. The results of the above-reviewed studies are suggestive of the specific adaptive design in perceiver's olfactory cognition and thus enable us to tentatively conclude that human odour contain cues to affective states of the others individuals.

To make firm conclusions regarding the emotion-related odours as signals would be currently premature as available evidence is in many respects missing. The future research should thus focus on mechanisms involved in emotion-related odour production, for example to perform chemical analysis of the body odour of stressed individuals and investigate how such a profile is produced. Another line of research should examine possible effect of emotion-related odours in apes. Such results would allow us to perform phylogenetic analysis which might elucidate the evolutionary origin of the phenomena and reveal specific conditions favourable for evolution of such a signalling system.

In summary, we find investigations into the social aspects of emotion-related odours a highly promising research avenue which is certain to bear fruit by yielding many interesting insights. However, we urge scholars to employ appropriate theories and terminology to sharpen our understanding instead of blurring it.

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APPENDIX 1. Summary of studies testing the effect of exposure to emotionally-valenced odours according to the (neuro)psychological effect tested (hedonic assessment, recognizing of emotions, cognitive and behavioural changes, and brain activity). It presents the authors of the studies, induced affective state (i.e., fear, happy, anxiety, stress, competition-related, negative-emotion), targets' sex and sample size (F indicates women, M indicates men), procedure to induce the affective state (i.e., watching film, high rope course, oral academic examination, first-time tandem skydive, sport competition), and control (i.e., watching film, running, ergometer workout, saline, unused pad, clean air), raters' sex and sample size, exposure method (i.e., sniffing jars, olfactometer, pads placed under the nose), and length, measurement method (i.e., ratings of the samples, VAS – visual analogue scale, ordering the samples, identification, forced-choice test, questionnaire, reaction time, risk-taking behaviour, startle response, fMRI – functional magnetic resonance imaging, EEG – electroencephalography; EMG – electromyography; SCR – skin conductance response), and the main findings (↑/↓, increase/decrease in tested variable, NS – no significant effect, LPP – late positive potential).

Authors	Affective state	Donors	Induction of affective state (control)	Raters	Exposure method (length)	Measure	Result
Hedonic assessment							
Ackerl *et al.* 2002	Fear	42F	Watching frightening film (neutral film)	62F	Sniffing jars with odours (time not restricted)	Ratings of intensity, pleasantness, "smells like sex", "smells like aggression", and "smells like fear" on VAS	↑ intense, ↓ pleasant, ↑ aggression, sex: NS, fear: NS
Adolph *et al.* 2010	Competition-related	6M	Badminton match (running/clean room air)	9F, 9M	Constant flow olfactometer (0.5 s)	Ratings of intensity, pleasantness, unpleasantness, familiarity on VAS	NS
Albrecht *et al.* 2011	Anxiety	13M	High rope course (ergometer workout)	20F	Pads placed under the nose (20 min)	Ratings of pleasantness, intensity, familiarity, masculinity/femininity, and sexual attractiveness on VAS	NS
Cantafio 2003[1]	Fear, happy	7F, 7M	Watching frightening/ funny film	84F	Sniffing jars with odours (max 2 min)	Ordering the samples according to intensity (pleasantness, masculinity)	Fear samples ↑ intense, tendency ↑ pleasant, ↓ masculine than happy samples
Chen *et al.* 2006	Fear	3F, 4M	Watching frightening film (neutral film/unused pads)	68F	Pads placed under the nose (time not specified)	Ratings of intensity, and pleasantness on 7-point scale	NS
Gelstein *et al.* 2011	Negative-emotion	3F	Watching sad film (saline)	24M	Sniffing jars with tears (time not specified)	Ratings of intensity, pleasantness, and familiarity on VAS	NS
Haegler *et al.* 2010	Anxiety	21M	High rope course (ergometer training/unused pads)	16F, 14M	Pads placed under the nose (15 min)	Ratings of pleasantness, intensity, familiarity, masculinity, and sexual attractiveness on VAS	Fear ↓ pleasant, ↑ intensity

APPENDIX 1. Continued.

Authors	Affective state	Donors	Induction of affective state (control)	Raters	Exposure method (length)	Measure	Result
Pause *et al.* 2009[2]	Anxiety	21F, 28M	Before oral academic examination (during ergometric training/unused pads)	16F, 16M	Constant flow olfactometer (3 s)	Ratings of intensity, pleasantness, unpleasantness, and familiarity on VAS	NS
Prehn *et al.* 2006[3]	Anxiety	12M	Before oral academic examination (during ergometric training/unused pads)	3F, 4M	Constant flow olfactometer (3 s)	Ratings of intensity, pleasantness, unpleasantness, and familiarity on 7-point scale	NS
Prehn-Kristensen *et al.* 2009[2]	Anxiety	21F, 29M	Before oral academic examination (during ergometric training)	14F, 14M	Continuous airflow olfactometer (0.5 s)	Ratings of intensity, pleasantness, unpleasantness, and familiarity on 9-point scale	NS
Zhou, Chen 2009	Fear, happy	8M	Watching frightening/happy film (unused pads)	64F	Pads placed under the nose (time not specified)	Ratings of intensity, and pleasantness on 7-point scale	Fear ↓ pleasant, intensity: NS, happy: NS
Recognizing emotions							
Ackerl *et al.* 2002	Fear	42F	Watching frightening film (neutral film)	62F	Sniffing jars with odours (time not restricted)	Triple forced-choice discrimination test	Above chance discrimination
Cantafio 2003[1]	Fear, happy	14F, 14M	Watching frightening/funny film (unused pads)	54F	Sniffing jars with odours (time not specified)	Triple forced-choice discrimination and identification test	F discriminate fear and happy, correct identification only with M odours; forehead odours discrimination but not correct labelling
Chen, Haviland-Jones 2000	Fear, happy	14F, 11M	Watching frightening/ funny film (unused pads)	40F, 37M	Sniffing jars with odours (time not specified)	Three and six choice identification test	F correctly choose happy and afraid odours, M only afraid M and happy F
Cognitive and behavioural changes							
Adolph *et al.* 2010	Competition-related	6M	Badminton match (running/clean room air)	9F, 9M	Continuous airflow olfactometer (0.5 s)	SCR	↑ SCR response

APPENDIX 1. Continued.

Authors	Affective state	Donors	Induction of affective state (control)	Raters	Exposure method (length)	Measure	Result
Albrecht *et al.* 2011	Anxiety	13M	High rope course (ergometer training)	20F	Pads placed under the nose (20 min)	Anxiety questionnaire (STAI X1)	↑ anxiety after 5 min and 20 min odour exposure
Chen *et al.* 2006	Fear	3F, 4M	Watching frightening film (neutral film/unused pads)	68F	Pads placed under the nose (time not specified)	Reaction time test and correct responses in word-association task, self-ratings of happiness, sadness, anger, anxiety, fear, disgust, and neutral on VAS	↑ performance in word-association task, reaction time test: NS, ↓ performance on tasks with ambiguous content, ↑ fear, anxiety, disgust; happiness, sadness, anger, neutral: NS
Gelstein *et al.* 2011	Negative-emotion	3F	Watching sad film	24M	Pads placed under the nose (time not specified)	Ratings of sadness and sexual attraction in emotionally ambiguous faces on VAS, self-ratings of mood on VAS, salivary levels of testosterone, GSR	↓ sexual appeal attributed to faces, ↓ self-rated sexual arousal, ↓ physiological measure of arousal, ↓ level of testosterone, ↑ GSR for tears
de Groot *et al.* 2012	Fear, disgust	10M	Watching fear film/film with disgusting content (unused pads)	36F	Sniffing jars with odours (time not specified)	EMG, nasal-pressure-monitoring cannula, infrared stereo camera for visual task	Fear: ↑ medial frontalis activity, fear expression, disgust: ↑ levator labii muscles, disgust expression, fear: ↓ first sniff magnitude, disgust: ↓ second sniff magnitude, fear: ↑ visual quick scan, disgust: ↓ visual fixations
Haegler *et al.* 2010	Anxiety	21M	High rope course (ergometer training/unused pads)	16F, 14M	Pads placed under the nose (time not specified)	Risk-taking behaviour in computerized card game (Haegler's Risk Game)	↑ risk-taking behaviour
Mujica-Parodi *et al.* 2009	Stress	32F, 32M	First-time tandem skydive (running on a treadmill/air)	5F, 9M	Continuous airflow olfactometer (5.7 s)	Emotion identification in ambiguous faces	Stress samples ↑ emotion-perception of ambiguous facial stimuli

APPENDIX 1. Continued.

Authors	Affective state	Donors	Induction of affective state (control)	Raters	Exposure method (length)	Measure	Result
Pause *et al.* 2004[3]	Anxiety	12M	Before oral examination (during ergometric training)	8F, 8M	Constant airflow olfactometer (920 ms)	Priming and emotion identification in ambiguous faces	F: ↓ positive happy faces, sad or fearful faces: NS
Pause *et al.* 2009[2]	Anxiety	21F, 28M	Before oral academic examination (during ergometric training/unused pads)	16F, 16M	Constant flow olfactometer (3 s)	Eye blink startle response recorded by EMG	↑ startle reflex in all, ↑ in highly socially anxious individuals
Prehn *et al.* 2006[3]	Anxiety	12M	Before oral examination (during ergometric training/unused pads)	3F, 4M	Constant flow olfactometer (3 s)	Eye blink startle response recorded by EMG	↑ startle reflex
Zhou, Chen 2009	Fear, happy	8M	Watching frightening /happy film (neutral film/unused pads)	64F	Pads placed under the nose (time not specified)	Emotion identification task in ambiguous faces, anxiety questionnaire (STAI X1)	↑ interpreting ambiguous expressions as fearful, more discernible facial emotions: NS, anxiety: NS
Brain activity							
Gelstein *et al.* 2011	Negative-emotion	3F	Watching sad film (saline)	24M	Pads placed under the nose (time not specified)	fMRI	Selectively ↓ activity in brain substrates of sexual arousal (hypothalamus, left fusiform gyrus)
Mujica-Parodi *et al.* 2009	Stress	40M	First-time tandem skydive (running on a treadmill/air)	8F, 8M	Continuous airflow olfactometer (5 s)	fMRI	↑ amygdala activation
Pause *et al.* 2010[2]	Anxiety	21F, 28M	Before oral academic examination (during ergometric training/unused pads)	20F, 24M	Continuous airflow olfactometer (0.5 s)	EEG	↑ neuronal resources during early pre-attentive stimulus processing (lateral frontal brain areas), social anxious males process earlier

APPENDIX 1. Continued.

Authors	Affective state	Donors	Induction of affective state (control)	Raters	Exposure method (length)	Measure	Result
Prehn-Kristensen *et al.* 2009[2]	Anxiety	21F, 28M	Before oral examination (during ergometer training)	14F, 14M	Continuous airflow olfactometer (3 s)	fMRI	↑ activity in brain areas involved in the processing of social emotional stimuli (fusiform gyrus), regulation of empathic feelings (insula, precuneus, cingulated cortex), neuronal activity within attentional (thalamus, dorsomedial prefrontal cortex) and emotional control systems (cerebellum, vermis)
Rubin *et al.* 2012	Stress	64M	First-time tandem skydive (running on a treadmill)	8F, 6M	Nebulizing olfactometer (2.5 s)	EEG	Stress samples ↑ LPP all faces, control samples ↑ LPP threatened faces

Note: Superscript marks studies using same body odour sample.

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