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The human body odor compound androstadienone increases neural conflict coupled to higher behavioral costs during an emotional Stroop task

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ABSTRACT

The androgen derivative androstadienone (AND) is a substance found in human sweat and thus may act as human chemosignal. With the current experiment, we aimed to explore in which way AND affects interference processing during an emotional Stroop task which used human faces as target and emotional words as distractor stimuli. This was complemented by functional magnetic resonance imaging (fMRI) to unravel the neural mechanism of AND-action. Based on previous accounts we expected AND to increase neural activation in areas commonly implicated in evaluation of emotional face processing and to change neural activation in brain regions linked to interference processing.

For this aim, a total of 80 healthy individuals (oral contraceptive users, luteal women, men) were tested twice on two consecutive days with an emotional Stroop task using fMRI.

Our results suggest that AND increases interference processing in brain areas that are heavily recruited during emotional conflict. At the same time, correlation analyses revealed that this neural interference processing was paralleled by higher behavioral costs (response times) with higher interference related brain activation under AND. Furthermore, AND elicited higher activation in regions implicated in emotional face processing including right fusiform gyrus, inferior frontal gyrus and dorsomedial cortex. In this connection, neural activation was not coupled to behavioral outcome. Furthermore, despite previous accounts of increased hypothalamic activation under AND, we were not able to replicate this finding and discuss possible reasons for this discrepancy.

To conclude, AND increased interference processing in regions heavily recruited during emotional conflict which was coupled to higher costs in resolving emotional conflicts with stronger interference-related brain activation under AND. At the moment it remains unclear whether these effects are due to changes in conflict detection or resolution. However, evidence most consistently suggests that AND does not draw attention to the most potent socio-emotional information (human faces) but rather highlights representations of emotional words.

Introduction

Human and animal chemosensory communication. In animal research a wide range of literature exists that addresses the effects of so-called pheromones. These are chemical substances that are released to the outside by a sender organism and induce a specific behavior or developmental process in a second animal of the same species (Karlson and Lüscher, 1959). Pheromones have been found in many species like lobsters, ants, rabbits and rats (Wyatt, 2009), the latter e.g. showing alarm responses and higher levels of aggression when sniffing pheromones secreted by conspecifics (Kiyokawa et al., 2004, 2006).

Yet the question whether human beings are prone to chemosensory communication is largely unexplored. The most important potential carrier of human chemosignals is sweat. Sweat that was secreted by conspecifics in emotional settings has been shown to increase state anxiety in women (Albrecht et al., 2011), induce fearful facial

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expressions in the observer (de Groot et al., 2012) and increase reaction times to anxiety-related words during an emotional Stroop task (Mutic et al., 2016). Though the exact composition of human sweat varies between individuals, it contains a mixture of different compounds including androgens like androstenone, androstenol and androstadienone (4, 16-androstadien-3-one, AND) (Wyatt, 2015). Especially AND was repeatedly identified in male and female axillary hair (Nixon et al., 1988; Gower et al., 1994) that was sampled under neutral, i.e. non-emotional settings, and was found to affect mood states as it reduced nervousness and tension (Grosser et al., 2000) and increased positive mood in women (Grosser et al., 2000; Jacob and McClintock, 2000; Villemure and Bushnell, 2007).

Behavioral effects of AND. Apart from its effects on mood states, AND has also been discussed to affect attentional processes as women stated to feel more focused (Grosser et al., 2000) and reported higher pain intensity under AND exposure (Villemure and Bushnell, 2007). Given its occurrence in human sweat it has furthermore been surmised that AND may especially influence attention in social contexts. Indeed, preliminary research shows that under AND exposure heterosexual women spent more time looking at female faces (Parma et al., 2012) and rated male faces more attractive (Saxton et al., 2008; Ferdenzi et al., 2016). Furthermore, both men and women responded more slowly to social negative and quicker to social positive images (Hummer et al., 2016) only under AND exposure. Furthermore, an emotion-specific facilitation of reactions to angry faces under AND exposure has recently been reported (Frey et al., 2012; Hornung et al., 2017a).

Neural activation under AND. Concerning the level of neural activation, previous studies almost exclusively used passive inhalation of AND and reported enhanced hypothalamic activation under AND exposure (Savic et al., 2005; Berglund et al., 2006; Burke et al., 2012). Apart from this, AND has been probed to affect the stress response in the Montreal Imaging Stress Test (Chung et al., 2016a, 2016b) and led to a sex-specific activation increase (men > women) in visual areas like the fusiform gyrus only during the absence of psychosocial stressors. Another recent study (Hummer et al., 2016) reported enhanced activation of the right orbitofrontal cortex and the right lateral prefrontal cortex during passive viewing of emotional pictures under AND exposure compared to a control odor (Hummer et al., 2016). Additional studies also show a change in skin temperature (Jacob et al., 2001; Bensafi et al., 2004) and an increase in skin conductance (Jacob et al., 2001) giving further evidence that AND exerts central and peripheral nervous effects.

Interference control and AND-effects. By using an emotional Stroop task, Hummer and McClintock (2009) provided initial evidence that under AND exposure a general attentional bias towards emotional stimuli was present in both men and women. In general, the emotional Stroop task (Etkin et al., 2006; Chechko et al., 2012) creates a response conflict because of the incompatibility of a target and distractor stimulus. This is similar to the classical Stroop task (MacLeod, 1991) where participants are asked to name the ink color of a color-word while ignoring the meaning of the word. In the emotional Stroop task two emotionally conflicting stimuli are presented. That is, participants are e.g. asked to name the emotion expressed by a face while ignoring the meaning of an overlaying emotional word. Typically, participants react faster and more accurately when the emotional expression of the face and the word match (congruent trial) compared to when they do not match (incongruent trial), indicating that participants have to resolve a costly emotional conflict (Etkin et al., 2006; Chechko et al., 2012).

Specifically, in connection with AND exposure, Hummer and McClintock (2009) found increased response times under AND compared to a placebo (PLAC) odor when the color of positive and negative emotional words had to be indicated potentially reflecting an increase in interference by attraction to emotional non-target-stimuli.

Hypotheses. Previous findings implicated AND to draw attention to emotional stimuli (Frey et al., 2012), also suggesting that AND may change interference processing (Hummer and McClintock, 2009). Still, research that addresses task-dependent brain activation to unravel the neural mechanisms of AND action is literally not existent. In this study we therefore used emotional human faces in connection with an emotional Stroop task that taps interference control to address the following odor-related hypotheses.

(i) Emotion hypothesis

Behavioral. Based on previous reports of increased salience of emotional stimuli under AND exposure (Hummer and McClintock, 2009; Frey et al., 2012; Hornung et al., 2017a), we expected faster responses and fewer errors under AND compared to PLAC. Furthermore, to address the question whether AND-action is emotion specific (Frey et al., 2012; Hornung et al., 2017a) or non-specific (Hummer and McClintock, 2009), we incorporated three emotions: happy, angry and fearful facial expressions.

Neural. The increased salience of emotional stimuli under AND should also be visible by increased activation in major regions commonly implicated in emotional face processing including bilateral amygdala, bilateral fusiform gyrus, bilateral inferior frontal cortex, bilateral superior temporal gyrus and dorsomedial frontal gyrus (Dricu and Frühholz, 2016). Specifically, we also expected higher hypothalamic activation under AND based on previous findings (Savic et al., 2005; Berglund et al., 2006; Burke et al., 2012).

(ii) Interference hypothesis

Behavioral. We expected that under AND interference processing should be reduced as attention is more strongly drawn to emotional target faces. Though one previous study using an emotional Stroop task with emotional distractor words and target word color (Hummer and McClintock, 2009) gave evidence that emotional words draw attention under AND, we considered it likely that this attraction was due to the emotional salience of words. Given that human faces convey even stronger socio-emotional information than emotional words, in the present study using target faces and distractor words, we expected reduced interference processing under AND. This should be visible by reduced costs, i.e. lead to a smaller difference between incongruent and congruent trials both for response times and error rates.

Neural. Based on the assumption that stronger brain activation during resolution of conflict indicates higher difficulty (Chechko et al., 2012), we expected reduced activation in brain areas that underlie conflict resolution including preSMA/cingulate cortex, bilateral inferior frontal gyrus, bilateral insula and bilateral intraparietal sulcus (Cieslik et al., 2015; Xu et al., 2016) under AND compared to PLAC.

(iii) Sex/group hypothesis

Behavioral. Since sex differences exist with respect to the behavioral relevance of emotional stimuli suggesting higher saliency for negative emotions in men (Gohier et al., 2013) and positive emotions in women (Donges et al., 2012), plus the fact that mood enhancing effects of AND may be specific to women (Jacob and McClintock, 2000; Bensafi et al., 2004), we further assumed stronger effects of AND in men for fearful and angry faces and stronger effects in women for happy faces. Furthermore, within women one study found AND-effects to depend on the menstrual cycle phase of female participants (Parma et al., 2012). In this study the authors reported that under AND exposure, women during their luteal phase (generally high levels of natural female sex hormones) spent more time looking at female faces than did women in their follicular phase (lower levels of natural female sex hormones).

Thus, under AND we first expected women to display quicker reactions and less errors for positive (happy) faces, while for men the same effects were expected for negative emotions. Furthermore, we expected women during their luteal phase when natural female sex hormones are high to show even stronger effects than women using oral contraceptives who have reduced natural levels of natural female sex hormones.