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Neural activation during anticipation of opposite-sex and same-sex faces in heterosexual men and women

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ABSTRACT

Psychobiological accounts of face processing predict that greater salience is attributed to faces matching a viewer's sexual preference than to faces that do not. However, behaviorally, this effect could only be demonstrated in tasks assessing reward 'wanting' (*e.g.* work-per-view-tasks) but not in tasks assessing 'liking' (*e.g.* facial attractiveness ratings), and has been found to be more pronounced in heterosexual men than women, especially with regard to very attractive faces. Here, we addressed the question if sex differences at the level of 'wanting' persist if participants are uninformed about the attractiveness of an anticipated male or female face. Seventeen heterosexual men and 13 heterosexual women (all single) participated in a social incentive delay task (SID). Participants were required to react on simple graphical cues in order to view a smiling face. Cues provided *a priori* information on the level of smile intensity (low/medium/high) as well as sex of the face (male/ female). A significant interaction of sex-of-face and sex-of-participant was observed in *a priori* defined regions of interest in the brain reward system (including ventral tegmental area, nucleus accumbens and ventromedial prefrontal cortex), reflecting enhanced activation to cues signaling opposite-sex faces relative to same-sex faces in both, men and women. Women additionally recruited the temporo-parietal junction (TPJ) during processing of opposite- *vs.* same-sex cues, suggesting stronger incorporation of social cognition processes in women than men. The findings speak against a general male bias for opposite-sex faces. Instead they provide preliminary evidence that men and women recruit different brain circuits during reward value assessment of facial stimuli.

Introduction

Recent attempts to better understand the neural basis of reward-oriented behavior considerably profited from dissecting reward processing into the two dissociable psychological components of 'liking' and 'wanting' (Berridge and Robinson, 1998). Whereas the liking component describes the hedonic feelings associated with the reward, wanting is closely linked to the psychological concepts of urge and desire, and underlies the motivation to approach a reward. According to the 'incentive salience theory' (Berridge and Robinson, 1998), 'wanting' in its most basic form (as opposed to more cognitive forms of desire) is a very basal mechanism and can be triggered even without a person's conscious awareness (Berridge and Winkielman, 2003). Dissecting reward-processes into 'wanting' and 'liking' proves particularly useful to explain reward-orientation in situations where higher-order goals or social motives differ from initial (maybe even unwanted) desires, so that 'liking' is no longer a synonym of 'wanting', as for example in drug seeking (Robinson and Berridge, 1993), over-eating (Finlayson et al., 2007), or sexual desire (Krishnamurti and Loewenstein, 2012). In the present study, we made use of this concept to address the question if differences in sexual preference shape the reward valuation of pleasant male and female face stimuli, and if these differences emerge at a neural level representative of 'wanting'.

Seminal work by Aharon et al. (2001) provided initial evidence that heterosexual human beings show enhanced activation of brain areas implicated in reward processing, specifically nucleus accumbens (NAcc), ventral tegmental area (VTA) and the amygdala, when viewing faces of beautiful opposite-sex faces as opposed to equally attractive same-sex faces. In addition to their functional neuroimaging study, Aharon et al. (2001) conducted two behavioral experiments in which participants either rated the attractiveness of male and female faces or had to work (*i.e.* repeatedly press a button) in order to extend the viewing time of faces. While the first group made no difference in attractiveness ratings between male and female faces, the second group worked significantly harder to view faces of attractive opposite-sex faces than same-sex faces; hence, replicating the pattern of effects observed in the brain. Though including only male participants, this study provided first evidence that preferred-sex effects might occur at the level of wanting rather than liking. Consecutive imaging studies replicated the finding

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that reward related neural circuitries preferentially respond to faces matching the viewer's sexual preference, but pointed towards a stronger effect in men than women. Kranz and Ishai (2006) found that homo- or heterosexually oriented men as well as homosexually oriented women showed enhanced activation in the mediodorsal thalamus and the (medial) orbitofrontal cortex (OFC), *i.e.* the most ventral part of the ventromedial prefrontal cortex (vmPFC), when rating the attractiveness of persons matching their sexual preference. Studies using other types of reward found mOFC activation to increase with hedonic pleasure ratings, attributing it a general role in reward 'liking' (see Kringelbach, 2005 for a review). Two other studies, exclusively presenting opposite-sex faces of varying attractiveness to heterosexual participants, also reported higher activation in the mOFC for opposite-sex attractive faces in men than women (Cloutier et al., 2008; O'Doherty et al., 2003). However, none of the above studies found differences in behavioral attractiveness ratings between male and female faces or between men and women. In an attempt to further pursue the suggestion by Aharon et al. (2001) that a preferred-sex bias occurs at a level of wanting rather than liking, several research groups (Hayden et al., 2007; Levy et al., 2008) conducted behavioral studies including both, attractiveness ratings and work-per-view-tasks. While men and women showed little difference in attractiveness ratings of opposite-sex faces, men worked significantly harder (Hayden et al., 2007; Levy et al., 2008), and were significantly more willing to exchange money (Hayden et al., 2007) to extend the viewing time of an opposite-sex face than women.

These findings are in favor of the assumption that faces of the preferred sex are valued over faces not matching the preferred sex, especially if they are very attractive. Moreover, they indicate that men are more likely to show this effect than women. Together, results from behavioral and neuroimaging studies support the notion that sex differences in reward valuation of opposite- or same-sex faces occur at the level of desire and wanting rather than liking. However, all of the above studies included facial beauty as modulating factor, hereby blurring the boundary between sexual preference and aesthetic valuation. Also, previous studies neglected the potential influence of relationship status and steroid hormone levels (except Levy et al., 2008) on mating-related reward processing. Studies on face processing have shown that being in a relationship alters women's preferences for masculinity in a man's face (Little et al., 2002). Reward-related neural function has been found to be modulated by menstrual cycle-dependent changes in gonadal steroid levels (Dreher et al., 2007), especially estrogen levels (see review by Becker et al., 2001), and women's facial preferences have been found to change across the menstrual cycle (Penton-Voak and Perrett, 2000), suggesting that special care should be taken to control for relationship status, and to keep hormone level variation at a minimum when studying social reward processes.

In the present study we used a novel approach to address the question if heterosexual men and women differ in the extend they value opposite-sex faces over same-sex faces. To specifically test the hypothesis, that sex-related neural differences in face valuation occur at the level of *wanting*, we used functional magnetic resonance imaging (fMRI) and a social incentive delay task (SID)(Rademacher et al., 2010; Spreckelmeyer et al., 2009). Over the last decade, incentive delay tasks have been successfully used to trace the neural underpinnings of desire and wanting (see *e.g.* (Knutson and Greer, 2008; Knutson and Peterson, 2005) for reviews). By confronting participants with symbolic cues that announce the value of potential gain, this type of task allows to monitor neural activation related to reward anticipation. Since the outcome of reward trials is uncertain (as it depends on participants' performance), reward cues are assumed to trigger positive arousal, which increases with anticipated reward magnitude (Knutson and Greer, 2008). A plethora of imaging studies, using different types of incentive delay tasks, have identified several key brain regions, including the VTA, NAcc, and the vmPFC to be recruited during reward anticipation (Knutson et al., 2001, 2003; O'Doherty et al., 2002; Spreckelmeyer et al., 2009). While the VTA was found to be implicated in general salience detection (for both, positive and negative events) (Bunzeck and Duzel, 2006), NAcc has been suggested to be exclusively implicated in coding expected reward, and to be the neural correlate of the anticipatory (positive) arousal characteristic for 'wanting' (Knutson and Greer, 2008). Though the vmPFC has also been found to code anticipated reward value, there is evidence that it more strongly incorporates higher-ranking goals and helps to direct appetitive behavior towards appropriate goal objects (Hare et al., 2010; Knutson et al., 2003; O'Doherty, 2011). Also, vmPFC activation patterns have been found to reflect subjective prefence (McClure et al., 2004).

With our study, we try to extend previous findings of sex differences in reward valuation of male and female faces to gain a better understanding of sex differences in social reward processing. We used a previously established social incentive delay task (Rademacher et al., 2010; Spreckelmeyer et al., 2009) to explicitly address the neural correlates of the 'wanting' component of social reward-orientation in heterosexual single men and women.

Material and methods

Participants

Thirty-four right-handed healthy volunteers (16 women) with normal vision and no past neurological or psychiatric history participated in the study. All participants were heterosexual singles (*i.e.* they were not in a relationship at the time of study and had not been for at least 6 months), not taking any medication (including hormonal contraceptives) and all women were nulliparous. Female participants were asked to come into the lab approximately one week after onset of menses (*i.e.* during follicular phase). Cycle phase was confirmed *via* hormone assays conducted on blood samples drawn at the day of scanning. Based on the hormone data, two women were retrospectively excluded because they were in the luteal phase at the time of scanning. Additionally, the data sets of two participants (one man, one woman) were excluded from the study because they were retrospectively found to meet exclusion criteria (one was bisexual, one showed neural anomalies). Thus, data from 30 participants (17 men: mean age = 22.9 years, range = 19–29 years; 13 women: mean age = 22.5 years, range = 20–26 years) were included in the analysis. Female and male participants were comparable with regards to their age ($p = 0.68$) and had similar educational background (all university students, men: mean years of education = 15.6, women: mean = 15.6, $p = 0.98$). The study was approved by the Ethics Committee of the Medical Faculty of the RWTH Aachen University. Subjects gave written informed consent and were paid an allowance for participation in the study.

Stimulus material

The stimulus material consisted of 66 color photographs displaying three different facial expressions of 22 professional actors (11 female, 11 male, NimStim set of Facial Expressions, (Tottenham et al., 2009)). Male and female faces were matched for attractiveness based on a prior rating performed by 10 raters (5 men, 5 women) who did not participate in the present study. To generate control stimuli, 22 portraits were graphically dysmorphed (Adobe PhotoDeluxe Home Edition 3.0, Adobe Systems Incorporated) to eliminate all facial features while keeping size and luminance stable. This procedure resulted in a pool of 22 different control-stimuli which – like the different actors' faces – differed from each other in color and brightness.

Experimental procedure

Task

We used a social incentive delay task (SID) that has previously been found to recruit the brain reward system, including NAcc, during