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Brain systems for assessing facial attractiveness

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Abstract

Attractiveness is a facial attribute that shapes human affiliative behaviours. In a previous study we reported a linear response to facial attractiveness in orbitofrontal cortex (OFC), a region involved in reward processing. There are strong theoretical grounds for the hypothesis that coding stimulus reward value also involves the amygdala. The aim of the present investigation is to address whether the amygdala is also sensitive to reward value in faces, indexed as facial attractiveness. We hypothesized that contrary to the linear effects reported previously in OFC, the amygdala would show a non-linear effect of attractiveness by responding to both high and low attractive faces relative to middle attractive faces. Such a non-linear response would explain previous failures to report an amygdala response to attractiveness. Human subjects underwent fMRI while they were presented with faces that varied in facial attractiveness where the task was either to rate faces for facial attractiveness or for age. Consistent with our hypothesis, right amygdala showed a predicted non-linear response profile with greater responses to highly attractive and unattractive faces compared to middle-ranked faces, independent of task. Distinct patterns of activity were seen across different regions of OFC, with some sectors showing linear effects of attractiveness, others exhibiting a non-linear response profile and still others demonstrating activation only during age judgments. Significant effects were also seen in medial prefrontal and paracingulate cortices, posterior OFC, insula, and superior temporal sulcus during explicit attractiveness judgments. The non-linear response profile of the amygdala is consistent with a role in sensing the value of social stimuli, a function that may also involve specific sectors of the OFC.

Keywords: Amygdala; Orbitofrontal cortex; Reward; Face processing; Social judgment

1. Introduction

Human attractiveness conveys significant biological advantages as expressed in mating success (Pashos & Niemitz, 2003; Thornhill, Gangestad, & Comer, 1995), earning potential (Frieze, lson, & Russell, 1991) and longevity (Henderson & Anglin, 2003). It can be conjectured that facial attractiveness is an important variable in mate choice (Fink & Penton-Voak, 2002; Thornhill & Gangestad, 1999) and that evolved brain systems show sensitivity to this aspect of the sensory environment. The idea that the human brain possesses regions responsive to attractiveness is supported by data from brain imaging studies. Aharon et al. (2001) showed that attractive female faces activate reward regions in men more than attractive males or unattractive faces of either gender. O'Doherty et al. (2003) showed dissociable regions of prefrontal cortex responded to attractive and unattractive faces; specifically showing that medial prefrontal regions, including medial orbitofrontal cortex, responded to attractive faces and lateral regions respond more to unattractive faces. The theoretical approach in both these studies was to treat viewing of attractive faces as akin to reward, an approach vindicated by behavioural data showing that men work to observe attractive female faces, but not unattractive females or any male face (Aharon et al., 2001). In addition, behavioural evidence demonstrates that an attractive female face will lead men to discount higher future rewards against smaller immediate rewards (Wilson & Daly, 2004), consistent with this construal of attractive faces as rewards.

While these previous studies have implicated the orbitofrontal cortex in facial attractiveness, another region thought to have an important role in coding stimulus reward-value as well as in evaluating social stimuli is the amygdala (for a review see e.g. Baxter & Murray, 2002). However, previous neuroimaging studies of attractiveness have failed to demonstrate activation in this region which we conjecture reflects an assumption that the amygdala responds linearly across "valence space". How-

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ever, evidence that the amygdala may show a response to a broad range of emotions relative to stimuli of neutral valence (Garavan, Pendergrass, Ross, Stein, & Risinger, 2001; Hamann, Ely, Grafton, & Kilts, 1999; Winston, O'Doherty, & Dolan, 2003) predicts non-linear responses to facial attractiveness, responding to both high and low attractiveness stimuli compared to those of average attractiveness. In other words, we predict that the amygdala may respond maximally to stimuli at both extremes of valence.

In previous studies, responses to attractive faces were measured while subjects performed an unrelated task in which subjects did not directly assess stimuli for attractiveness (Aharon et al., 2001; O'Doherty et al., 2003). The fact that robust reward-related responses were found in these studies suggests that neural responses to facial attractiveness are automatically engaged even if subjects are performing an unrelated task. In the present study we aimed to investigate this phenomenon in more detail by exploring the degree to which responses to facial attractiveness were modulated as a function of task. Specifically, we aimed to compare neural responses to facial attractiveness while subjects performed an explicit judgment of facial attractiveness compared to neural responses elicited during performance of an implicit task in involving an relatively unrelated facial judgment (age). We hypothesized that explicit judgments of attractiveness might enhance responses in reward-related regions, in a manner analogous to the effect of attentional modulation on neural responses to other visual stimulus properties such as colour or motion (e.g. Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991).

To address these questions we used a factorial fMRI experimental design with a parametric factor of attractiveness, and categorical factors of task, stimulus (face) gender and subject gender. Stimulus and subject gender have been shown to be important in processing of facial attractiveness (e.g. Aharon et al., 2001; O'Doherty et al., 2003), and were therefore included as experimental variables. Aside from the amygdala and OFC the key regions of interest in this report are the core components of the distributed system for face perception (Haxby, Hoffman, & Gobbini, 2000), namely fusiform and superior temporal sulcus (STS).

2. Methods

2.1. Stimuli

Insufficient stimuli were available in our original set, as our previous aim was to examine effects of extreme attractiveness rather than characterising responses across an "attractiveness space". Consequently, we supplemented the stimuli from O'Doherty et al. (2003b) with additional faces from similar sources. The additional stimuli were picked by the authors primarily to be of average attractiveness. Stimuli, which were colour image files, were cropped similarly to the originals with little hair visible and adjusted to have equal mean luminance. Faces had direct eye-gaze and head direction and were approximately coregistered for eye-position. As in the previous study, images showed expressions between neutral and mild smiles. Seventy-two images were used (36 women).

2.2. Subjects

fMRI data was obtained from 28 healthy subjects (13 women) with normal or corrected-to-normal vision who gave informed consent to take part in the study which had been approved by the local ethics committee. Data from two subjects (both males) were excluded after a debriefing questionnaire revealed non-hetrosexual preferences (self-rated sexuality < 5 on scale where $1 =$ exclusively homosexual and $7 =$ exclusively heterosexual). The age range of the remaining subjects was 18–35 (mean = 25.5), with no significant difference between the ages of males and females ($p = 0.12$).

2.3. Experimental paradigm

Subjects performed one of two tasks on the face stimuli, with task alternating in a blocked fashion. In the *attractiveness* task subjects made a judgment of attractiveness with one of three buttons ("highly attractive", "medium", "low attractiveness"). In the *age* task subjects judged the age of the face as being young, medium or old, with three buttons to represent the response. Blocks of each task were preceded by an instruction and a summary instruction remained onscreen during each block. Stimuli were presented for 1000 ms and interstimulus interval (ISI) was 1900 ms. Blocks consisted of nine stimuli giving an overall block length of 26 s. In total, there were 16 blocks for each task and each stimulus was presented twice in the context of each task. The starting block was counterbalanced across-subjects.

2.4. fMRI data

Data were collected on a 1.5 T MRI scanner (Siemens, Erlangen, Germany) using gradient echo T2*-weighted echo-planar images, with blood oxygenation level dependent (BOLD) contrast. Volumes consisted of 36 slices angled at $-30°$ to the horizontal. Tilting of slices in this manner improves image quality in the ventral prefrontal cortex (Deichmann, Gottfried, Hutton, & Turner, 2003). The effective repetition time (TR) was 3.2 s, and 295 volumes were collected, with the first five subsequently discarded. Slice thickness was 2 mm with a 1 mm gap between slices and in-plane resolution was 3 mm × 3 mm. The use of low field strength MRI, tilted axial acquisition, thin slice thickness, and fine in-plane resolution all aid signal quality in amygdala (Chen, Dickey, Yoo, Guttmann, & Panych, 2003; Robinson, Windischberger, Rauscher, & Moser, 2004). A T1-weighted structural image was acquired for each subject for detailed anatomical information.

2.5. Debriefing

Participants undertook two debriefing tasks outside the scanner. They first rated all the faces on attractiveness, using a computerised visual analogue scale. The scale was marked with extremes as "highly unattractive" and "highly attractive", with the mid-point marked; participants could leave the cursor at any point in between the two extremes. Ratings were scaled between -10 and $+10$ with $+10$ representing ratings of high attractiveness, though numbers were not apparent to the participant. Subsequently they rated the faces on happiness on a similar scale with the extremes labelled "happy" and "unhappy", and the mid-point indicated. Participants also provided information concerning their sexual orientation on an ordinal scale.

2.6. Data analysis

Imaging data were pre-processed and analysed using SPM2 (Wellcome Department of Imaging Neuroscience, London; http://www.fil.ion.ucl.ac.uk/spm). Preprocessing consisted of determining and applying rigid affine transformations to the image series to realign the scans (Friston et al., 1995a), slice timing correction (Henson, Buchel, Josephs, & Friston, 1999), normalisation (Friston et al., 1995a) to a standard EPI template in MNI space and smoothing with a three-dimensional 8 mm Gaussian kernel to account for residual inter-subject anatomical differences.

Because the factor of task was blocked, but the order, gender and perceived attractiveness of face stimuli were randomised, the experimental design conforms to a mixed block/event-related paradigm. Task was blocked in order to minimise the number of task switches required of subjects. However, in an experimental design such as the one adopted here, with parametric interpretation of events based upon *post hoc* ratings, it is impossible to block the stimulus type