COACTION

Assessing facial attractiveness: individual decisions and evolutionary constraints

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Background: Several studies showed that facial attractiveness, as a highly salient social cue, influences behavioral responses. It has also been found that attractive faces evoke distinctive neural activation compared to unattractive or neutral faces.

Objectives: Our aim was to design a face recognition task where individual preferences for facial cues are controlled for, and to create conditions that are more similar to natural circumstances in terms of decision making.

Design: In an event-related functional magnetic resonance imaging (fMRI) experiment, subjects were shown attractive and unattractive faces, categorized on the basis of their own individual ratings.

Results: Statistical analysis of all subjects showed elevated brain activation for attractive opposite-sex faces in contrast to less attractive ones in regions that previously have been reported to show enhanced activation with increasing attractiveness level (e.g. the medial and superior occipital gyri, fusiform gyrus, precentral gyrus, and anterior cingular cortex). Besides these, females showed additional brain activation in areas thought to be involved in basic emotions and desires (insula), detection of facial emotions (superior temporal gyrus), and memory retrieval (hippocampus).

Conclusions: From these data, we speculate that because of the risks involving mate choice faced by women during evolutionary times, selection might have preferred the development of an elaborated neural system in females to assess the attractiveness and social value of male faces.

Keywords: *evolutionary strategies*; *face perception*; *functional magnetic resonance imaging (fMRI)*; *sex differences*; *social behavior*

Introduction

Face perception is underpinned by a distributed neural system in the human brain (Haxby, Hoffman, & Gobbini, 2000, 2002). Several studies showed that facial attractiveness, as a highly salient social cue, influences behavioral responses (e.g. Chen et al., 2012; Eagly, Ashmore, Makhijani, & Longo, 1991). It was also found that attractive faces evoke distinctive neural activation compared to unattractive or neutral faces (for a review, see Little & Jones, 2009). These areas include occipital and occipitotemporal visual regions (e.g. the superior temporal sulcus and fusiform gyrus), frontal regions involved in decision-making tasks [anterior cingulate cortex (ACC)], and parts of the reward system [amygdala, ventral tegmentum, medial orbitofrontal cortex (OFC),

and nucleus accumbens] (Cloutier, Heatherton, Whalen, & Kelley, 2008; Iaria, Fox, Waite, Aharon, & Barton, 2008; Ishai, 2007; O'Doherty et al., 2003; Tsukiura & Cabeza, 2011; Winston, O'Doherty, Kilner, Perrett, & Dolan, 2007).

Some previous studies showed sex differences in brain activation for attractive opposite-sex facial images in contrast with less attractive ones. Winston et al. (2007) found elevated activation in male subjects, but not in females, in the ACC. Cloutier et al. (2008) also revealed sex differences in the recruitment of OFC, which distinguished attractive and unattractive faces only for male participants. O'Doherty et al. (2003) found multiple sex differences: the medial prefrontal cortex showed greater responses to attractive faces of the opposite sex in male subjects, whereas

the right inferior temporal and left middle occipital cortex showed increased activities in female subjects.

The majority of these experiments required explicit attractiveness ratings from subjects during the scanning, which might have recruited different brain regions than passive viewing of the stimuli. A study showed that orbitofrontal cortical activity, for instance, is task dependent (Winston et al., 2007). Distinct patterns of activity were seen across various regions of the OFC when subjects were asked to make a judgment of attractiveness and when they had to estimate the age of the face. The authors suggested that neural responses to facial attractiveness are automatically engaged and are not enhanced as a function of attending to relevant features.

This reasoning is in line with the assumption that evaluation of potential partners under natural conditions does not necessary involve conscious assessment, particularly during the first encounter. In general, aesthetic experience is basically affective which means it elicits immediate and intuitive, sometimes profound response (Thornhill, 2003). Studies on facial attractiveness preferences suggest that genetically prescribed perceptual mechanisms process information about an individual face that may lead to rapid decision-making processes (Maner et al., 2003). This sensory and cognitive equipment enables individuals to perceive fitness-relevant aesthetic traits without conscious attention. Several studies suggest that physically attractive members of the opposite sex can capture people's attention at early stages of visual perception (Duncan et al., 2007; Maner, Rouby, & Gonzaga, 2008). Other studies revealed that attractiveness preferences are present extremely early in life, confirming that they are the result of basic and unconscious processes (Langlois et al., 1987; Rubenstein, Kalakanis, & Langlois, 1999).

Most of the former functional magnetic resonance imaging (fMRI) studies in this field required explicit ratings of attractiveness (Bzdok et al., 2011). Our aim was to design a face recognition task where individual preferences for facial cues are controlled for, and to create conditions that are more similar to natural circumstances in terms of decision making. To this end, in the present experiment, explicit rating of facial attractiveness was not required from the subjects. For the purpose of sustaining the participants' attention, they were asked to push a button on the response grip when they saw a scrambled non-face image. In this manner, it was also possible to decrease movement artifacts during the presentation of opposite-sex faces (see the "Methods" section).

As in the recent research cited in this section, we used a paradigm that differs from former studies in important aspects, and as relatively few subjects were analyzed, it serves mainly exploratory reasons. However, based on previous research, we expected activation in the following brain areas for attractive opposite-sex faces in contrast to unattractive ones:

– occipital and occipitotemporal visual regions (e.g. the superior temporal sulcus and fusiform gyrus)
– frontal regions involved in decision making (e.g. the ACC)
– reward system (the amygdala, ventral tegmentum, mOFC, and nucleus accumbens)

Material and methods

Subjects

For a preliminary experiment, 126 volunteers were recruited, and they were instructed to rate facial images. From this group, 16 individuals volunteered for an event-related fMRI study, for which they were compensated with a small amount of money. A couple of minutes after the start of the scanning procedure, one of the female volunteers said she would not like to participate after all. Thus, seven males (age: $M = 25.00$ years, $SD = 5.53$ years, range: 19–37 years) and eight females (age: $M = 20.13$ years, $SD = 1.96$ years, range: 18–23 years) were included for the final analysis. According to the Hungarian version of the Edinburgh Handedness Inventory (Oldfield, 1971), only one of the female subjects was left-handed; the others were dominantly right-handed. All volunteers had normal or corrected-to-normal vision. All of them were dominantly heterosexual, as concluded from the Epstein Sexual Orientation Inventory filled out after the scanning. Informed written consent was given by all participants in concordance with the Helsinki Declaration, last adopted at the 52nd World Medical Association General Assembly (2000, Edinburgh), and preapproved by the local ethics committee of the Medical School, University of Pécs, Hungary.

Stimuli

In a study taken 2–12 months prior to the scanning procedure, subjects had to rate 25 black-and-white facial images of the opposite sex. The question 'How attractive do you find this face; how likely would you choose her/him as a mate?' needed to be answered by typing a number from 1 (for 'very unattractive') to 9 (for 'very attractive') on a keyboard. The images were taken under standard conditions and depicted people with a neutral expression, eye gaze, and head position directed forward. The facial images varied across attractiveness, and the judgments of them were not uniform either. Based on each subject's own particular ratings of each individual, one attractive and one relatively unattractive face were selected for each subject in order to present these in the scanner as stimuli. The average rating of the opposite-sex attractive faces was 8.27 ($SD = 0.80$), while the unattractive faces were given 3.20 ($SD = 0.68$) on average. Attractive and unattractive same-sex faces were also selected; these previously had been rated by independent judges.

The average rating of the same-sex attractive faces was 7.75 ($SD = 1.04$), whereas that of the unattractive faces was 3.00 ($SD = 0.91$).

In the brain scanner, visual stimuli were presented to the participants through a headset system with in-built liquid crystal display (LCD) goggles controlled by Presentation software (Neurobehavioral Systems Inc., Albany, CA). Participants lying in the scanner were shown five images (same- and opposite-sex attractive and less attractive faces, and a scrambled non-face image) in a pseudo-randomized order. Facial images were presented for 2000 ms with varying interstimulus intervals, the distribution of which was skewed toward shorter times (range: 1500–10000 ms, mean: 4000 ms) (see Serences, 2004). Because the function of the scrambled images was only to sustain the subjects' attention during the scanning, and neural activation for these was not to be analyzed, these were presented more sparsely than the target stimuli. The subjects were exposed 16 times to each face and eight times to the non-face image during the session (Fig. 1). For the pseudo-randomization of stimuli, MATLAB software was used (Mathworks Inc. Natick, MA).

Including same-sex faces was necessary for several reasons. First, by the use of more than two images, an optimal temporal arrangement of the stimuli in focus could be achieved. Second, with the presence of same-sex images, the sexual identity of opposite-sex faces was emphasized. Third, the greater variety of stimulus images helped to enhance the attention of subjects. As no data were available about the subjects' a priori preference for the same-sex faces used as stimuli, the neural correlates in this context were not analyzed.

Data acquisition

Functional and structural MRI scans were obtained using a 3T Siemens Trio scanner (Siemens, Erlagen, Germany) with a standard head coil. Functional runs were acquired in echo-planar imaging sequences sensitive to BOLD contrast (TR $= 2000$ ms; TE $= 36$ ms; FA $= 76°$; FOV $= 230$ mm^2; in-plane resolution $= 2.5$ mm $\times 2.5$ mm; slice thickness $= 4$ mm). In addition to the functional data, a set of 144 high-resolution axial structural scans was also collected from each participant in the same session using a T1-weighted magnetization-prepared rapid acquisition gradient echo (MP-RAGE) sequence (TR $= 1900$; TE $= 3$ ms; FA $= 9°$; FOV $= 240 \times 240$ mm; in-plane resolution $= 0.89$ mm $\times 0.89$ mm; slice thickness $= 0.9$ mm with no gap).

Image preprocessing and statistics

Standard spatial preprocessing was conducted using SPM5 (Wellcome Trust Centre for Neuroimaging, London, UK; http://www.fil.ion.ucl.ac.uk/spm/). The first three time points were discarded to allow for signal equilibration. All volumes were realigned for motion correction. The time series were corrected for differences in slice acquisition times. The functional images were spatially normalized to conform to the standard MNI-152 stereotaxic space by a 12-parameter affine transformation (three rotations, three translations, three zooms, and three shears). Non-linear normalization was accomplished by a $7 \times 9 \times 7$ discrete cosine transform basis function with 16 iteration steps. After normalization, all scans were re-sampled by a trilinear interpolation method to $2 \times 2 \times 2$ mm isotropic voxels. All reported stereotaxic coordinates refer to the Montreal Neurological Institute (MNI) template and are reported as (x, y, and z). Functional volumes

STIMULUS PRESENTATION TIME: 2000 MS

INTER-STIMULUS INTERVALS: 1500-10000 MS

ATTRACTIVE FEMALE FACE

ATTRACTIVE MALE FACE

SCRAMBLED FACE

UNATTRACTIVE FEMALE FACE
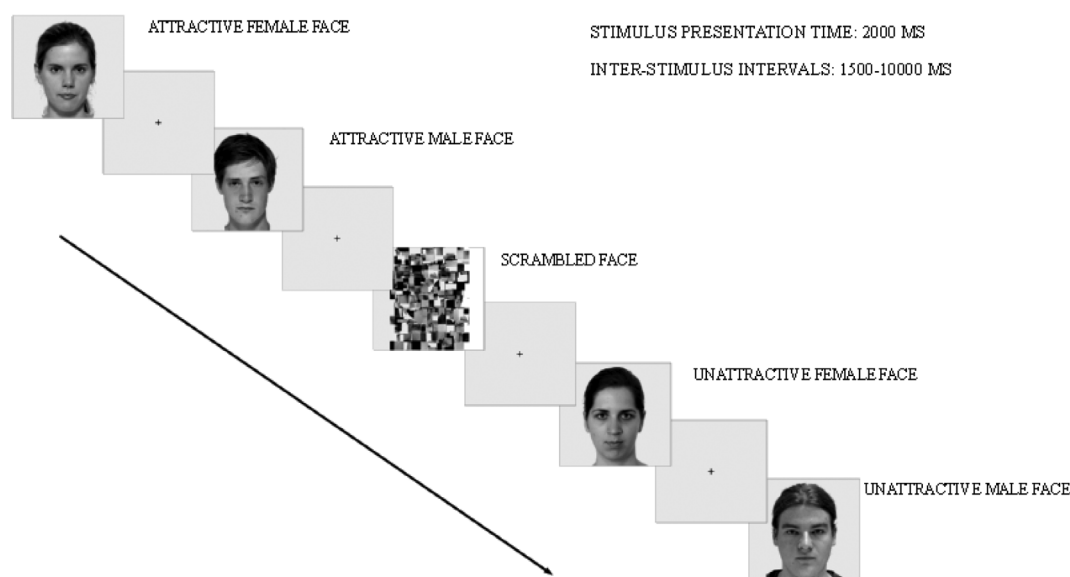
UNATTRACTIVE MALE FACE

Fig. 1. Scheme of the sequence of events in the experimental paradigm. Each face was shown 16 times, and scrambled faces were shown eight times, during the session. The order of the stimuli was pseudo-randomized. Participants were asked to push a button when they saw a non-face stimulus (i.e. a scrambled face).

were spatially smoothed by an 8 mm full width–half maximum (FWHM) isotropic Gaussian kernel. A temporal high-pass filter with a period cutoff of 128 s was also applied. Finally, one-tag autocorrelation was used to correct intrinsic temporal correlations.

Subsequent statistical analysis to model fMRI time series was performed on the first and second levels using the general linear model. On the single participant's level, individual task-related activation was evaluated and event-related responses to experimental stimuli were modeled using the canonical hemodynamic response function (HRF), and linear contrasts were generated. Only clusters with more than 10 voxels were accepted in all statistical analyses to avoid type II statistical errors.

As the first step of the second-level analysis, a two-sample t-test was used in order to detect differences in signal intensities of the 'attractive > unattractive' and 'unattractive > attractive' contrasts between male and female subgroups. 'Male > female' and 'female > male' comparisons were generated. Next, for within-group analysis, the attractive versus unattractive contrasts were tested against zero using a one-sample t-test in the female subgroup and the male subgroup. The alpha level was set at 0.001, uncorrected in every case.

Results

Analysis of demographic data of subjects showed that the age of males ($M = 25.000$, $SD = 5.529$) was slightly higher than that of females ($M = 20.125$, $SD = 1.959$, $t_{14} = -2.351$, $p = 0.034$), although all were members of the same age group.

All of the participants responded with 100% accuracy in the behavioral task. They pressed the button on the response grip every time when the scrambled face was presented, and they never made false responses to facial stimuli. This indicates that their attention could be sustained during the duration of the scanning.

The second-level statistical analysis of all subjects showed increased hemodynamic activities for attractive opposite-sex faces in contrast to less attractive faces. The most significant activation with the largest clusters was found in the left and right middle occipital gyri and the right superior gyrus. In addition, in the left hemisphere, elevated BOLD signals were observed in the fusiform gyrus, lingual gyrus, precentral gyrus, and anterior cingular gyrus. In the right hemisphere, besides the middle occipital gyrus, activation was found in the middle inferior frontal gyrus (Table 1).

The comparison between the male cohort and female cohort, using a two-sample t-test, did not yield significant results. However, besides the activation in the left middle occipital, left inferior frontal, and left precentral gyri – which was also observed in the whole-group analysis – the second-level female subgroup analysis showed additional brain activation in the insular lobes bilaterally (Fig. 2), as well as the left hippocampus (Fig. 3), left superior temporal gyrus (STG) (Fig. 4), left middle frontal gyrus, right superior frontal gyrus, and left and right cerebellum (Table 2). The analysis of the male group did not show any significant neural activation.

Discussion

Activation related to attractive opposite-sex faces in the whole group
The areas in which elevated activation was observed in response to attractive opposite-sex faces, in contrast to unattractive faces, include the occipital and occipitotem-

Table 1. BOLD effects of facial attractiveness of the whole group ($n = 15$)[a]

Regions	Peak t-scores	Peak Z-scores	Peak cluster extents	Montreal Neurological Institute (x, y, and z)		
Left middle occipital gyrus	5.40	4.02	437	−26	−76	24
	5.19	*3.92*		*−46*	*−82*	*20*
	4.90	*3.78*		*−26*	*−66*	*42*
Right middle occipital gyrus	4.93	3.79	277	36	−84	18
	4.77	*3.71*		*28*	*−74*	*28*
Right superior occipital gyrus	*4.76*	*3.71*		*28*	*−84*	*26*
Left fusiform gyrus	4.88	3.77	168	−28	−60	−8
	4.05	*3.31*		*−32*	*−54*	*−14*
Left anterior cingulate gyrus	4.82	3.73		−16	40	10
Left lingual gyrus	4.80	3.72	14	−16	−74	4
Right inferior frontal gyrus	4.32	3.47	10	42	32	16
Left precentral gyrus	4.17	3.38	25	−34	−2	48
	3.71	*3.11*		*−40*	*−6*	*44*

The significance level was set at $p < 0.001$, uncorrected, k = 10. Secondary peaks are in italics.
[a]Significantly larger hemodynamic responses were found during an experimental task in the 'attractive > non-attractive' condition.
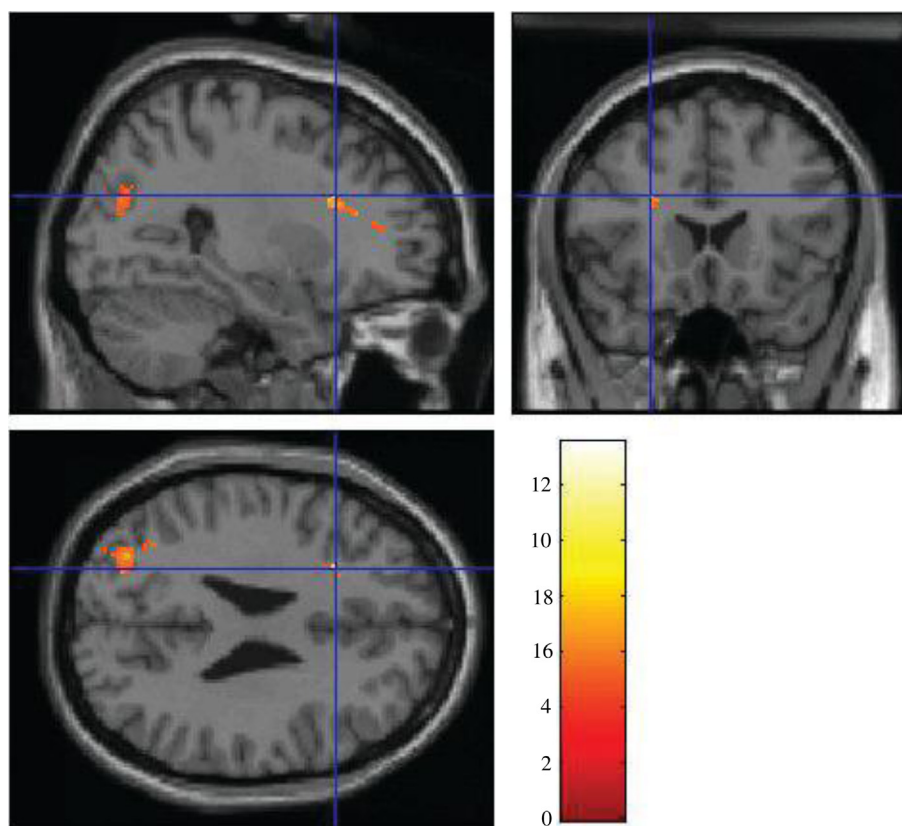
Fig. 2. Neural activity in females' left insula to attractive in contrast to unattractive male faces (*p* <0.001).

poral visual regions (the bilateral middle occipital gyri, left fusiform gyrus, and left lingual gyrus), parietal areas (the precentral gyrus), and frontal areas (the ACC and right inferior frontal gyrus). It was shown that the fusiform gyrus – which is involved in the categorization of objects and the recognition of temporally invariant facial structures (Haxby et al., 2000; McCarthy, Puce, Gore, & Allison, 1997) – is more active for attractive than for unattractive faces (Chatterjee, Thomas, Smith, & Aguirre, 2009). Furthermore, its role in processing attractiveness proved to be more pronounced than that of the superior temporal sulcus (Iaria et al., 2008). The left precentral gyrus in the premotor area is responsible for the motoric representation of the face (Hanakawa, Parikh, Bruno, & Hallett, 2005) and for visual selective attention (de Fockert, Rees, Frith, & Lavie, 2001), whereas the middle occipital gyrus was identified as a face-sensitive visual region (Puce, Allison, Gore, & McCarthy, 1995). In this study, frontal regions were also sensitive to the attractiveness of opposite-sex faces. Consistent with our results, the ACC was formerly found to be active while responding to sexually arousing stimuli in both men and women (Karama et al., 2002), and it responded to positively evaluated (i.e. attractive or trustworthy) faces (Mende-Siedlecki, Said, & Todorov, 2012), but it is also involved in reward-based decision-making tasks (Bush et al., 2002). The right inferior

frontal gyrus processes emotional communicative signals; hence, it plays a role in the assessment of facial emotions (e.g. Kitada et al., 2013; Nakamura et al., 1999). In this experiment, faces with neutral expressions were used as stimuli; however, attractiveness is usually associated with positive social value (Eagly et al., 1991). It was proposed that face evaluation involves an overgeneralization from invariable facial features in order to effectively predict the intentions of others (Oosterhof & Todorov, 2008). This adaptive mechanism can be considered as a potential explanation for the enhanced activation in the inferior frontal gyrus despite the fact that no apparent emotional expressions were present.

To date, about a dozen fMRI studies have been published showing that sexually attractive faces activate a subset of those brain regions that are part of the distributed face recognition system (for a review, see Little & Jones, 2009). The enhanced activation in the regions mentioned in this article is consistent with previous findings on perception of facial attractiveness. Crucial divergence from this pattern was found only in the reward system, to be discussed later in this section.

Activation related to attractive opposite-sex faces in females
Although the direct comparison of male and female brain activation did not indicate that sex-dependent processes
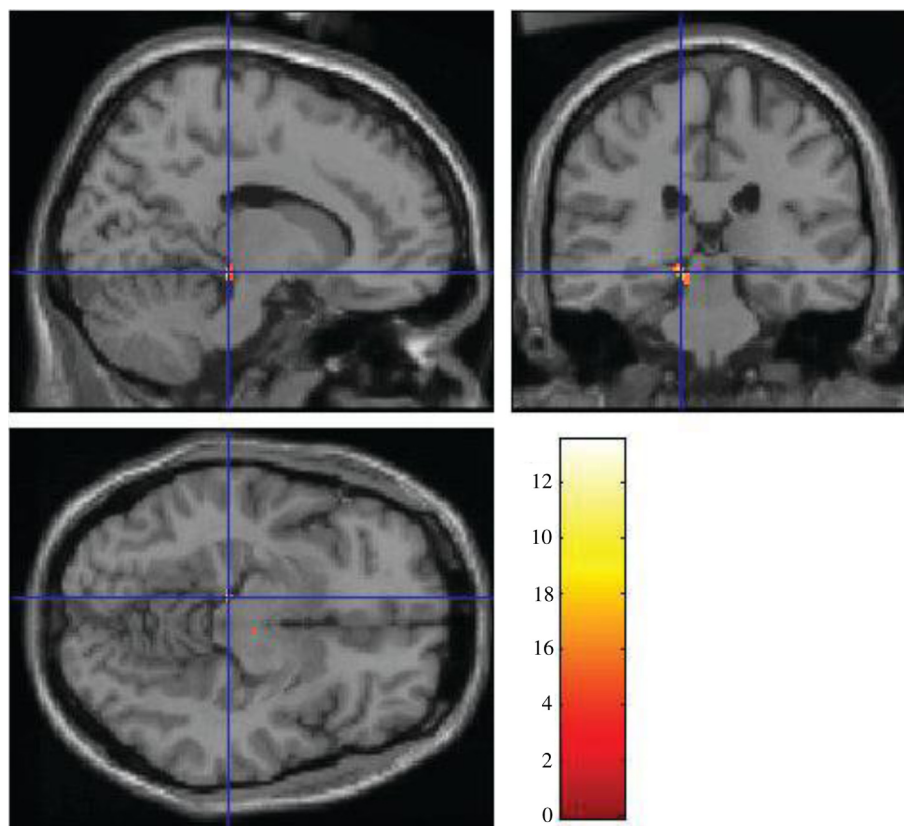
Fig. 3. Neural activity in females' left hippocampus to attractive in contrast to unattractive male faces ($p < 0.001$).

are at work during observation of faces, the fact that the group-level analysis of the eight female subjects revealed significant activation for increased attractiveness in some additional brain areas could be of crucial importance and worthy of attention.

The insula, in particular, is involved in processes connected with basic emotions and desires (Nieuwenhuys, 2012); it is also activated by disgusting behaviors (Calder, Lawrence, & Young, 2001; Phillips, Drevets, Rauch, & Lane, 2003), and it enables the representation of the current autonomic state. This is essential in the perception of one's own emotional response to different stimuli (Adolphs, 2002; Cunningham & Zelazo, 2007; Damasio, 1999; all cited in Doallo et al., 2011). In this relation, attractive faces can be considered as more arousing than non-attractive ones. Based on an event-related electro-encephalography experiment, Marzi and Viggiano (2010) also pointed out that attractiveness yields responses typical of emotionally charged stimuli, even when faces with neutral expressions are used. Thus, affective responses are triggered by the attractive features of the presented face. As the group-level analysis in the recent study showed, females might be more sensitive to, or emotionally more affected by, these cues with high reproductive relevance.

In addition to the issue discussed here, it is important to mention that higher insula activation to unattractive faces was found by O'Doherty et al. (2003); to untrustworthy faces, by Winston, Strange, O'Doherty, and Dolan (2002); and to attractive faces, by Winston et al. (2007). Taken all together with our finding that insula activation in female subjects is associated with attractive faces, rather than with less attractive ones, it can be suggested that the insula responds to emotionally salient social stimuli, irrespective of its valence. Winston et al. (2002) suggested that this non-linear activation is mediated by the amygdala. However, the analysis in the recent study did not reveal amygdala activation.

The BOLD signal in females' STG can also be interpreted as a consequence of stronger emotional reaction to attractive male faces. STG is especially active in regard to eyes with a fearful expression in both sexes (Radua et al., 2010), as well as masculinized male faces in females (Rupp et al., 2009). Affective scenes with humans in contrast to scenes without humans evoke stronger event-related potential (ERP) signals in this region in female subjects (Proverbio, Adorni, Zani, & Trestianu, 2009). Studies demonstrated that STG may also play an important role in decision making (Paulus, Feinstein, Leland, & Simmons, 2005) and social cognition (Baron-Cohen et al., 1999). Therefore, higher activation in female subjects' insula and STG during observation of attractive males is possibly the result of an evaluation process of potential partners, which involves risk assessment based
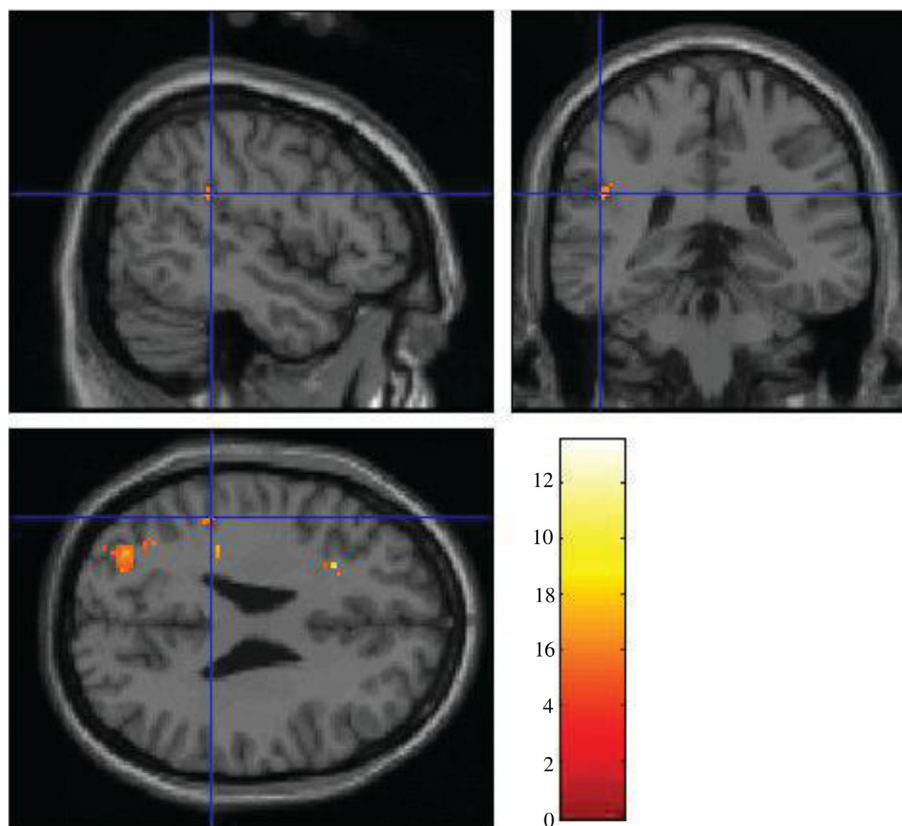
Fig. 4. Neural activity in females' right superior temporal gyrus to attractive in contrast to unattractive male faces (*p* <0.001).

Table 2. BOLD effects of facial attractiveness in the female subgroup (*n* =8)[a]

Regions	Peak *t*-scores	Peak Z-scores	Peak cluster extents	Montreal Neurological Institute coordinates (*x*, *y*, and *z*)		
Left precentral gyrus	10.28	4.29	31	−34	−6	48
Left hippocampus	9.32	4.14	16	−14	−28	−10
Left middle occipital gyrus	9.20	4.13	249	−36	−80	20
	8.90	*4.08*		*−36*	*−64*	*24*
	6.46	*3.58*		*−26*	*−76*	*26*
Left insula	8.46	4.00	39	−28	20	26
Left inferior frontal gyrus (p. triangularis)	*6.54*	*3.60*		*−32*	*32*	*14*
Right superior frontal gyrus	8.09	3.93	14	12	38	34
Left insula	7.43	3.80	14	−36	−32	26
	5.25	*3.24*		*−44*	*−32*	*34*
Left superior temporal gyrus	7.19	3.75	11	−50	−36	26
Right thalamus	6.98	3.70	86	2	−22	2
Left middle frontal gyrus	6.94	3.69	17	−30	40	12
Left inferior frontal gyrus	*5.89*	*3.43*		*−30*	*36*	*2*
Left cerebellum	6.83	3.67	21	−2	−56	−28
Right cerebellum	*4.93*	*3.14*		*6*	*−58*	*−24*
Right insula	6.02	3.46	13	36	−4	14
Left insula	5.88	3.43	28	−34	−20	14

The significance level was set at *p* <0.001, uncorrected, k =10. Secondary peaks are in italics.
[a]Significantly larger hemodynamic responses were found during an experimental task in the 'attractive >non-attractive' condition.

on invariable facial cues and on detection of the male's intentions. In addition to this, the recent experimental task also evoked an elevated BOLD signal in frontal areas associated with cognitive control, task preparation, and selection of action (Amodio & Frith, 2006; Brass, 2002; Rushworth, Walton, Kennerley, & Bannerman, 2004), such as the left middle, left inferior, and right superior frontal gyri.

It has been suggested that memory processes interact with facial attractiveness throughout all stages from encoding to retrieval (Shepherd & Ellis, 1973); hence, activities in corresponding brain regions are expected to be modulated by the facial cues in question. In accord with this assumption, attractive faces seen in the first block of an experimental paradigm elicited enhanced ERP responses compared to unattractive ones during a recognition task (Marzi & Viggiano, 2010). Although in the recent experiment no OFC activation was found – for a couple of reasons, detailed in this chapter – another fMRI study revealed functional connectivity between the OFC and hippocampal regions, which was the strongest during the encoding of attractive faces (Tsukiura & Cabeza, 2011). The authors explain this as a neural process to integrate aesthetic judgments of novel faces into one's prior knowledge of the social world. The recent finding that there is a significant BOLD activation in females' hippocampus during exposure to attractive opposite-sex faces may point indirectly to the possibility that females have an enhanced tendency – compared to males – for this bias during the observation of attractive opposite-sex faces.

Evolutionary constraints in mate choice decisions

Sex differences in behavior are explained in evolutionary terms by Trivers' (1972) parental investment theory. Because of their higher investment in offspring, females face higher risks during reproduction. Choosing a mate whose genetic quality is low – which may result in decreased survival chances of the child – or whose willingness to support his mate and her offspring during infancy is low will largely reduce females' reproductive success. These evolutionary constraints provided selective advantage to those females who followed cautious, risk-avoiding mate choice strategies (Fetchenhauer & Rohde, 2002; Gangestad & Simpson, 2000; Wang, Kruger, & Wilke, 2009). This implies a higher rejection rate of potential partners, the need for more emotional commitment from the partner's side, and a more comprehensive evaluation of the mate's personality traits and social status (Brase, 2006; Gonzaga, Haselton, Smurda, Davies, & Poore, 2008; Hald & Høgh-Olesen, 2010; Hill, Donovan, & Koyama, 2005).

Psychological studies based on the above theory revealed different strategies between men and women during mate choice. Women's ratings of facial attractiveness

of men appear to be more variable than men's ratings of women, given that women's ratings reflect personal circumstances more than men's do (Thornhill & Gangestad, 1999). Numerous studies found that women's mating psychology and behavior change across their menstrual cycle (Gangestad, Thornhill, & Garver-Apgar, 2010; Penton-Voak et al., 1999; Rosen & López, 2010). They also show a strategic pluralism in their sexual interest and commitment: if the benefits (e.g. genetic advantage to offspring) outweigh the costs of short-term mating (unwanted pregnancy, partner loss, etc.), then women may take advantage of short-term mating opportunities (Gangestad & Simpson, 2000; Provost, Troje, & Quinsey, 2008). Facial attractiveness is a reliable source of information for assessing traits linked to the reproductive value of potential mates, such as developmental stability (Gangestad, Thornhill, & Yeo, 1994) and health, which indicate resistance to pathogens (Grammer & Thornhill, 1994), or semen quality (Soler et al., 2003), which is predictive of fertility. However, women generally engage in long-term mating strategies and tend to be more cautious before being committed in a romantic relationship. Therefore, it is not surprising that facial cues provide sufficient information for female – but not male – observers to accurately assess the sociosexual orientation of men (Boothroyd, Jones, Burt, DeBruine, & Perrett, 2008).

Taking these considerations of evolutionarily informed research into account, it is possible that brain functioning also reflects this cognitively demanding strategy. The specific brain activities of female subjects during the observation of attractive male faces might indicate that they are equipped with a wider set of cognitive processes than males for estimating the mate value of their potential partner.

Lack of activation in the reward system

Considering former studies, the lack of significant activation in regions of the reward system is somewhat unexpected. Attractive faces usually evoke neural activation in parts of the reward system, such as the amygdala (Cloutier et al., 2008; Iaria et al., 2008; O'Doherty et al., 2003), the OFC (Cloutier et al., 2008; Iaria et al., 2008; Ishai, 2007; O'Doherty et al., 2003; Tsukiura & Cabeza, 2011; Winston et al., 2007), and the nucleus accumbens (Cloutier et al., 2008). However, if the experimental paradigm is examined in more detail, crucial differences can be found that could explain the discrepancy. In this section, we focus on these differences.

First, random presentation of male and female faces diminished the effect of reward anticipation, which could have contributed to the activation of the nucleus accumbens observed by Aharon et al. (2001) – and, more recently, by Cloutier et al. (2008) – and also highlighted by O'Doherty et al. (2003).

Second, since attractiveness is not a monolithic trait, it is a hard task to find out exactly what particular features people's judgments are based on when asking them to rate different faces. Is it symmetry, texture, expression, hormone markers, or a combination of these? There could be more emphasis on certain parts of the face, such as the eyes or lips, than on others. Usually, no data are available on individual preferences and priorities; therefore, when a wide range of facial images is shown to subjects, it could be erroneous to merge similarly rated faces into a single category during statistical analysis, even with the use of standardized photos. The fact that, in the recent study, the same face (judged by the subjects themselves) was presented 16 times in each category eliminates the possibility – at least on the subject-level analysis – that the detected brain activation resulted from the subject's attraction to diverse aspects of the various stimuli. People, however, may have individual priorities to focus on different facial features when judging others; thus, the above-mentioned possible fallacy could not be ruled out entirely during group-level analysis. This means that the activation can be interpreted as a response to attractiveness defined as 'subject's rating of the particular face as a potential mate', irrespective of what particular traits the subjects tend to focus on.

Furthermore, in contrast to familiar stimuli, novel ones can evoke enhanced activation in the anterior OFC, which is related to reward processing, as also shown by Rolls, Browning, Inoue, and Hernadi (2005) in a single cell measurement experiment in rhesus macaques. The exposure to and repeated presentation of only one face per attractiveness category probably led to the devaluation of the opposite-sex images in the recent experiment. This could explain the discrepancy between the former's ratings and the rewarding properties of attractive faces.

Third, using just two attractiveness categories (i.e. attractive vs. less attractive) makes the detection of non-linear responses impossible. The amygdala, for instance, is known to respond equally to emotionally intense stimuli, irrespective of valence (e.g. Dolan, 2002; Sander, Grafman, & Zalla, 2003; for a review, see Bzdok et al., 2011). Winston et al. (2007), in contrast to the four faces in our experiment, used 72 male and female images as stimuli, representing a broad range of attractiveness, and found non-linear responses in the medial OFC and the amygdala. Although such responses might be typical of the reward system, it remained unrevealed in this study.

Limitations

A possible limitation of our study is that the activation for same-sex and opposite-sex faces cannot be compared. The reason for this is because there was a crucial difference in the procedure of the selection of the two types of stimuli. While the participants were asked to rate a set of opposite-sex faces, and hence the ratings of the faces used during the scanning reflect individual differences in face preferences, for the selection of attractive and unattractive same-sex faces the average ratings of independent judges were used. Because of this difference, opposite-sex faces reflect much more genuinely the individual taste of the subjects. This, unfortunately, causes a potential difficulty regarding the interpretation of our findings: It is possible that the activation found here is not specific to the attractiveness of the potential mate but to the attractiveness of a face overall, irrespective of its sex. This could be tested only if the design had been the same for both sexes.

Although the data presented here are not robust enough to support the assumption about the cognitive differences between men and women in the context of mate choice, investigating sex differences in the neural correlates of attractiveness perception can be a promising direction for future research.

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References

Adolphs, R. (2002). Trust in the brain. *Nature Neuroscience*, *5*, 192–193.

Aharon, I., Etcoff, N., Ariely, D., Chabris, F., O'Connor, E., & Breiter, H.C. (2001). Beautiful faces have variable reward value: fMRI and behavioral evidence. *Neuron*, *32*, 537–551.

Amodio, D.M., & Frith, C.D. (2006). Meeting of minds: The medial frontal cortex and social cognition. *Nature Reviews Neuroscience*, *7*(4), 268–277.

Baron-Cohen, S., Ring, H.A., Wheelwright, S., Bullmore, E.T., Brammer, M.J., Simmons, A., et al. (1999). Social intelligence in the normal and autistic brain: An fMRI study. *European Journal of Neuroscience*, *11*(6), 1891–1898.

Boothroyd, L.G., Jones, B.C., Burt, J.D., DeBruine, L.M., & Perrett, D.I. (2008). Facial correlates of sociosexuality. *Evolution of Human Behavior*, *29*, 211–218.

Brase, G.L. (2006). Cues of parental investment as a factor in attractiveness. *Evolution of Human Behavior*, *27*, 145–157.

Brass, M. (2002). The role of the frontal cortex in task preparation. *Cerebral Cortex*, *12*(9), 908–914.

Bush, G., Vogt, B.A., Holmes, J., Dale, A.M., Greve, D., Jenike, M.A., et al. (2002). Dorsal anterior cingulate cortex: A role in reward-based decision making. *Proceedings of the National Academy of Sciences*, *99*(1), 523–528.

Bzdok, D., Langner, R., Caspers, S., Kurth, F., Habel, U., Zilles, K., et al. (2011). ALE meta-analysis on facial judgments of trustworthiness and attractiveness. *Brain Structure and Function*, *215*(3–4), 209–223.

Calder, A.J., Lawrence, A.D., & Young, A.W. (2001). Neuropsychology of fear and loathing. *Nature Reviews Neuroscience*, *2*(5), 352–363.

Chatterjee, A., Thomas, A., Smith, S.E., & Aguirre, G.K. (2009). The neural response to facial attractiveness. *Neuropsychology*, *23*(2), 135–143.

Chen, J., Zhong, J., Zhang, Y., Li, P., Zhang, A., Tan, Q., et al. (2012). Electrophysiological correlates of processing facial

attractiveness and its influence on cooperative behavior. *Neuroscience Letters*, *517*(2), 65–70.

Cloutier, J., Heatherton, T.F., Whalen, P.J., & Kelley, W.M. (2008). Are attractive people rewarding? Sex differences in the neural substrates of facial attractiveness. *Journal of Cognitive Neuroscience*, *20*(6), 941–951.

Cunningham, W.A., & Zelazo, P.D. (2007). Attitudes and evaluations: A social cognitive neuroscience perspective. *Trends in Cognitive Sciences*, *11*(3), 97–104.

Damasio, A. (1999). *The feeling of what happens: Body and emotion in the making of consciousness*. New York: Harcourt Brace.

Dolan, R.J. (2002). Emotion, cognition, and behavior. *Science*, *298*(5596), 1191–1194.

Doallo, S., Raymond, J.E., Shapiro, K.L., Kiss, M., Eimer, M., & Nobre, A.C. (2011). Response inhibition results in the emotional devaluation of faces: Neural correlates as revealed by fMRI. *Social Cognitive and Affective Neuroscience*, *7*(6), 649–659.

Duncan, L.A., Park, J.H., Faulkner, J., Schaller, M., Neuberg, S.L., & Kenrick, D.T. (2007). Adaptive allocation of attention: Effects of sex and sociosexuality on visual attention to attractive opposite-sex faces. *Evolution and Human Behavior*, *28*, 359–364.

Eagly, A.H., Ashmore, R.D., Makhijani, M.G., & Longo, L.C. (1991). What is beautiful is good, but…: A meta-analytic review of research on the physical attractiveness stereotype. *Psychological Bulletin*, *110*(1), 109–128.

Fetchenhauer, D., & Rohde, P.A. (2002). Evolutionary personality psychology and victimology: Sex differences in risk attitudes and short-term orientation and their relation to sex differences in victimizations. *Evolution and Human Behavior*, *23*(4), 233–244.

de Fockert, J.W., Rees, G., Frith, C.D., & Lavie, N. (2001). The role of working memory in visual selective attention. *Science*, *291*(5509), 1803–1806.

Gangestad, S.W., & Simpson, J.A. (2000). The evolution of human mating: Trade-offs and strategic pluralism. *Behavioral and Brain Sciences*, *23*(4), 573–587.

Gangestad, S.W., Thornhill, R., & Garver-Apgar, C.E. (2010). Fertility in the cycle predicts women's interest in sexual opportunism. *Evolution and Human Behavior*, *31*(6), 400–411.

Gangestad, S.W., Thornhill, R., & Yeo, R.A. (1994). Facial attractiveness, developmental stability, and fluctuating asymmetry. *Ethology and Sociobiology*, *15*(2), 73–85.

Gonzaga, G.C., Haselton, M.G., Smurda, J., Davies, M.S., & Poore, J.C. (2008). Love, desire, and the suppression of thoughts of romantic alternatives. *Evolution and Human Behavior*, *29*(2), 119–126.

Grammer, K., & Thornhill, R. (1994). Human (*Homo sapiens*) facial attractiveness and sexual selection: The role of symmetry and averageness. *Journal of Comparative Psychology*, *108*(3), 233–242.

Hald, G.M., & Høgh-Olesen, H. (2010). Receptivity to sexual invitations from strangers of the opposite gender. *Evolution and Human Behavior*, *31*(6), 453–458.

Hanakawa, T., Parikh, S., Bruno, M.K., & Hallett, M. (2005). Finger and face representations in the ipsilateral precentral motor areas in humans. *Journal of Neurophysiology*, *93*(5), 2950–2958.

Haxby, J.V., Hoffman, E.A., & Gobbini, M.I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, *4*(6), 223–233.

Haxby, J.V., Hoffman, E.A., & Gobbini, M.I. (2002). Human neural systems for face recognition and social communication. *Biological Psychiatry*, *51*(1), 59–67.

Hill, R.A., Donovan, S., & Koyama, N.F. (2005). Female sexual advertisement reflects resource availability in twentieth-century UK society. *Human Nature*, *16*(3), 266–277.

Iaria, G., Fox, C.J., Waite, C.T., Aharon, I., & Barton, J.J.S. (2008). The contribution of the fusiform gyrus and superior temporal sulcus in processing facial attractiveness: Neuropsychological and neuroimaging evidence. *Neuroscience*, *155*(2), 409–422.

Ishai, A. (2007). Sex, beauty and the orbitofrontal cortex. *International Journal of Psychophysiology*, *63*(2), 181–185.

Karama, S., Lecours, A.R., Leroux, J.-M., Bourgouin, P., Beaudoin, G., Joubert, S., et al. (2002). Areas of brain activation in males and females during viewing of erotic film excerpts. *Human Brain Mapping*, *16*(1), 1–13.

Kitada, R., Okamoto, Y., Sasaki, A.T., Kochiyama, T., Miyahara, M., Lederman, S.J. et al. (2013). Early visual experience and the recognition of basic facial expressions: Involvement of the middle temporal and inferior frontal gyri during haptic identification by the early blind. *Frontiers in Human Neuroscience*, *7*. doi:10.3389/fnhum.2013.00007.

Langlois, J.H., Roggman, L.A., Casey, R.J., Ritter, J.M., Rieser-Danner, L.A., & Jenkins, V.Y. (1987). Infant preferences for attractive faces: Rudiments of a stereotype? *Developmental Psychology*, *23*, 363–369.

Little, A.C., & Jones, B.C. (2009). The evolutionary cognitive neuropsychology of face preferences. In S.M. Platek, & T.K. Shackelford (Eds.), *Foundations in evolutionary cognitive neuroscience*. Cambridge, UK: Cambridge University Press.

Maner, J.K., Kenrick, D.T., Becker, D.V., Delton, A.W., Hofer, B., Wilbur, C.J., et al. (2003). Sexually selective cognition: Beauty captures the mind of the beholder. *Journal of Personality and Social Psychology*, *85*(6), 1107–1120.

Maner, J.K., Rouby, D.A., & Gonzaga, G.C. (2008). Automatic inattention to attractive alternatives: The evolved psychology of relationship maintenance. *Evolution and Human Behavior*, *29*(5), 343–349.

Marzi, T., & Viggiano, M.P. (2010). When memory meets beauty: Insights from event-related potentials. *Biological Psychology*, *84*(2), 192–205.

McCarthy, G., Puce, A., Gore, J.C., & Allison, T. (1997). Face-specific processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience*, *9*(5), 605–610.

Mende-Siedlecki, P., Said, C.P., & Todorov, A. (2012). The social evaluation of faces: A meta-analysis of functional neuroimaging studies. *Social Cognitive and Affective Neuroscience*, nsr090. doi:10.1093/scan/nsr090.

Nakamura, K., Kawashima, R., Ito, K., Sugiura, M., Kato, T., Nakamura, A. et al. (1999). Activation of the right inferior frontal cortex during assessment of facial emotion. *Journal of Neuropsychology*, *82*.

Nieuwenhuys, R. (2012). The insular cortex: A review. In *Evolution of the primate brain (Progress in Brain Research* Vol. 195, pp. 123–163). Amsterdam: Elsevier.

O'Doherty, J., Winston, J., Critchley, H., Perrett, D., Burt, D., & Dolan, R. (2003). Beauty in a smile: The role of medial orbitofrontal cortex in facial attractiveness. *Neuropsychologia*, *41*(2), 147–155.

Oldfield, R.C. (1971). The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia*, *9*(1), 97–113.

Oosterhof, N.N., & Todorov, A. (2008). The functional basis of face evaluation. *Proceedings of the National Academy of Sciences*, *105*(32), 11087–11092.

Paulus, M.P., Feinstein, J.S., Leland, D., & Simmons, A.N. (2005). Superior temporal gyrus and insula provide response and outcome-dependent information during assessment and action selection in a decision-making situation. *NeuroImage*, *25*(2), 607–615.

Penton-Voak, I.S., Perrett, D.I., Castles, D.L., Kobayashi, T., Burt, D.M., Murray, R.K., et al. (1999). Menstrual cycle alters face preference. *Nature*, *399*, 741–742.

Phillips, M.L., Drevets, W.C., Rauch, S.L., & Lane, R. (2003). Neurobiology of emotion perception I: The neural basis of normal emotion perception. *Biological Psychiatry*, *54*(5), 504–514.

Proverbio, A.M., Adorni, R., Zani, A., & Trestianu, L. (2009). Sex differences in the brain response to affective scenes with or without humans. *Neuropsychologia*, *47*(12), 2374–2388.

Provost, M., Troje, N., & Quinsey, V. (2008). Short-term mating strategies and attraction to masculinity in point-light walkers. *Evolution and Human Behavior*, *29*(1), 65–69.

Puce, A., Allison, T., Gore, J.C., & McCarthy, G. (1995). Face-sensitive regions in human extrastriate cortex studied by functional MRI. *Journal of Neurophysiology*, *74*(3), 1192–1199.

Radua, J., Phillips, M.L., Russell, T., Lawrence, N., Marshall, N., Kalidindi, S., et al. (2010). Neural response to specific components of fearful faces in healthy and schizophrenic adults. *NeuroImage*, *49*(1), 939–946.

Rolls, E.T., Browning, A.S., Inoue, K., & Hernadi, I. (2005). Novel visual stimuli activate a population of neurons in the primate orbitofrontal cortex. *Neurobiology of Learning and Memory*, *84*(2), 111–123.

Rosen, M.L., & López, H.H. (2009). Menstrual cycle shifts in attentional bias for courtship language. *Evolution and Human Behavior*, *30*(2), 131–140.

Rubenstein, A.J., Kalakanis, L., & Langlois, J.H. (1999). Infant preferences for attractive faces: A cognitive explanation. *Developmental Psychology*, *35*(3), 848–855.

Rupp, H.A., James, T.W., Ketterson, E.D., Sengelaub, D.R., Janssen, E., & Heiman, J.R. (2009). Neural activation in women in response to masculinized male faces: Mediation by hormones and psychosexual factors. *Evolution and Human Behavior*, *30*(1), 1–10.

Rushworth, M.F.S., Walton, M.E., Kennerley, S.W., & Bannerman, D.M. (2004). Action sets and decisions in the medial frontal cortex. *Trends in Cognitive Sciences*, *8*(9), 410–417.

Sander, D., Grafman, J., & Zalla, T. (2003). The human amygdala: An evolved system for relevance detection. *Reviews in the Neurosciences*, *14*(4), 303–316.

Serences, J.T. (2004). A comparison of methods for characterizing the event-related BOLD timeseries in rapid fMRI. *NeuroImage*, *21*(4), 1690–1700.

Shepherd, J.W., & Ellis, H.D. (1973). The effect of attractiveness on recognition memory for faces. *American Journal of Psychology*, *86*, 627–633.

Soler, C., Núñez, M., Gutiérrez, R., Núñez, J., Medina, P., Sancho, M., et al. (2003). Facial attractiveness in men provides clues to semen quality. *Evolution and Human Behavior*, *24*(3), 199–207.

Thornhill, R. (2003). Darwinian aesthetics informs traditional aesthetics. In E. Voland, & K. Grammer (Eds.), *Evolutionary aesthetics* (pp. 9–38). Berlin: Springer.

Thornhill, R., & Gangestad, S.W. (1999). Facial attractiveness. *Trends in Cognitive Sciences*, *3*(12), 452–460.

Trivers, R.L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man* (pp. 139–179). Chicago, IL: Aldine de Gruyter.

Tsukiura, T., & Cabeza, R. (2011). Remembering beauty: Roles of orbitofrontal and hippocampal regions in successful memory encoding of attractive faces. *NeuroImage*, *54*(1), 653–660.

Wang, X.T., Kruger, D.J., & Wilke, A. (2009). Life history variables and risk-taking propensity. *Evolution and Human Behavior*, *30*(2), 77–84.

Winston, J.S., O'Doherty, J., Kilner, J.M., Perrett, D.I., & Dolan, R.J. (2007). Brain systems for assessing facial attractiveness. *Neuropsychologia*, *45*(1), 195–206.

Winston, J.S., Strange, B.A., O'Doherty, J., & Dolan, R.J. (2002). Automatic and intentional brain responses during evaluation of trustworthiness of faces. *Nature Neuroscience*, *5*(3), 277–283.

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