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Note

Implicit trustworthiness ratings of self-resembling faces activate brain centers involved in reward

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ABSTRACT

On the basis of Hamilton's (Hamilton, W. D. (1964). The genetical evolution of social behavior I, II. *Journal of Theoretical Biology*, 7, 17–52) theory of inclusive fitness, self-facial resemblance is hypothesized as a mechanism for self-referent phenotypic matching by which humans can detect kin. To understand the mechanisms underlying pro-sociality toward self-resembling faces, we investigated the neural correlates of implicit trustworthiness ratings for self-resembling faces. Here we show that idiosyncratic trustworthiness ratings of self-resembling faces predict brain activation in the ventral inferior, middle and medial frontal gyri, substrates involved in reward processing. These findings demonstrate that neural reward centers are implicated in evaluating implicit pro-social behaviors toward self-resembling faces. These findings suggest that humans have evolved to use neurocomputational architecture dedicated to face processing and reward evaluation for the differentiation of kin, which drives implicit idiosyncratic affectively regulated social interactions.

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1. Introduction

Because incorrect assignment of kinship can be dire (inbreeding depression and cuckoldry), neural mechanisms that drive pro-social behavior toward kin are predicted to have evolved (Platek, Keenan, & Mohamed, 2005). Kin discrimination mechanisms allow individuals to modify their behavior with respect to genetic relatedness (Hamilton, 1964) and have been shown to impact social (DeBruine, Jones, Little, & Perrett, 2008; Platek, 2007), sexual (DeBruine, 2005; DeBruine, Jones, & Perrett, 2005), and parental behavior (Daly, 1982, 1998; Platek et al., 2003; Platek, Burch, Panyavin, Wasserman, & Gallup, 2002; Volk and Quinsey, 2002, 2007) in animals (Hain & Neff, 2006) and humans. Impression formation on the basis of facial processing occurs very quickly (Willis & Todorov, 2006) and implicit trustworthiness judgments have been associated with activation in the amygdala (Engell, Haxby, & Todorov, 2007; Winston, Strange, O'Doherty, & Dolan, 2002). Here we investigated activation associated with implicit trustworthiness judgments of faces that expressed varying levels of self-resemblance.

2. Methods

2.1. Participants/stimuli

We transformed 11 (seven female) participants' photographs to resemble them in three ways. Participant faces were: combined with another face of the same sex and ethnicity to create a 50% composite (self-morph), transformed to appear as a member of the opposite sex (self2sex), and transformed to appear as a member of another ethnicity (self2ethnic) (transformed to black face if white participant $n = 9$; transformed to white face if black participant $n = 2$). Facial morphing and transformations was carried out using specialist software (Tiddeman, Burt, & Perrett, 2001). One hundred seventy nine points were delineated on each face. We used these points to calculate the difference between each participant's face and an average composite face of the same race and sex, same sex other race, and same race opposite sex. The resulting difference was then warped onto an average face to create self-resembling morphed and transformed images. All pictures were taken under standard lighting conditions and with the same camera. All participants provided written informed consent and the study was approved by the University of Liverpool Committee on Research Ethics.

2.2. Imaging parameters

Participants were asked to make perceptual discriminations about ethnicity and sex during rapid event-related fMRI (2×300 42 slice (10% gap) full brain coverage volumes; TR = 2.5, TE = 30 (ms), FoV = 19.2 cm, flip angle = 85) at 3 T. Images were presented for 750 ms. Participants were able to respond within a window of 2000 ms, including the face presentation time. A jittered interstimulus interval between 2.5 and 25 s was used by incorporating null events that consisted of a scrambled luminance matched face. Participants were instructed not to respond to the null event. Each face was presented 20 times.

A high-resolution structural MP-RAGE (176 1 mm³ voxel sagittal slices, TR = 2040, TE = 5.57, FoV = 256, flip angle = 8) scan was also collected and was used

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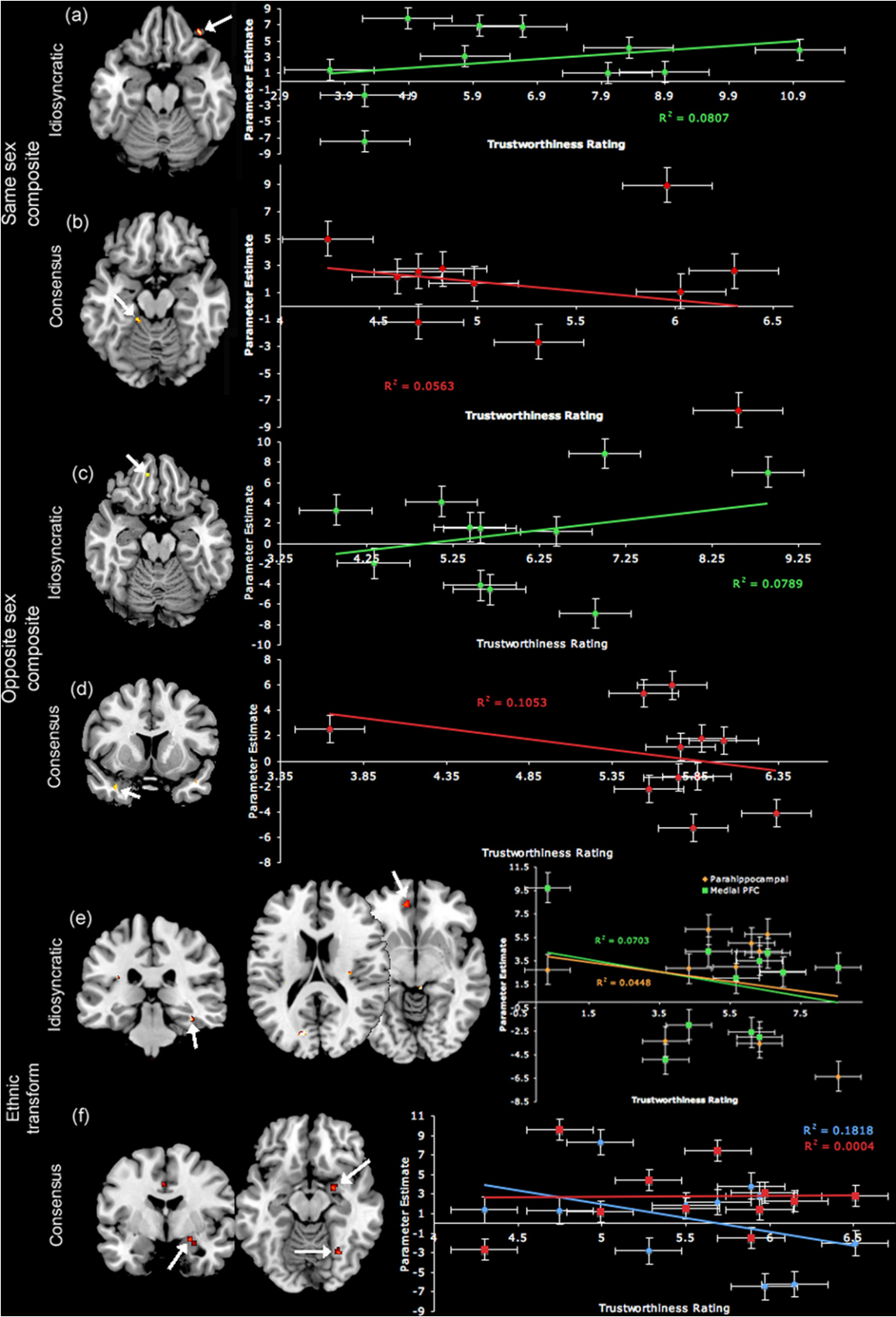
to coregister functional images. Functional images were first realigned using FSL's McFLIRT program. Images were then intensity normalized and smoothed (full width half maximum = 6) using mixed effects modelling in FEAT (Smith et al., 2004).

2.3. Behavioral procedures

Four weeks after scanning, participants rated each face they saw during scanning on trustworthiness (*idiosyncratic* ratings) (see Engell et al., 2007; Winston et al., 2002). Additionally, we asked an independent group of 40 participants (20 female) to rate all the faces on trustworthiness to obtain *consensus* trustworthiness ratings (see Engell et al., 2007; Winston et al., 2002). Idiosyncratic and consensus trustworthiness ratings were entered as separate regressors into a parametric analysis used to model brain activation using FSL-FEAT (Smith et al., 2004). For each face transformation condition, we used mixed effects general linear models (Beckmann, Jenkinson, & Smith, 2003; Woolrich, Behrens, Beckmann, Jenkinson, & Smith, 2004; Worsley, Evans, Marrett, & Neelin, 1992) for activation as a function of both idiosyncratic and consensus trustworthiness ratings. Statistical parametric threshold was set to uncorrected $p < .005$.

3. Results

Consensus ratings for self-morph faces were negatively associated with activation in the left parahippocampal gyrus, whereas idiosyncratic ratings showed a positive association with activation in right ventral middle frontal gyrus (Fig. 1a and b; Table 1).

Consensus ratings for self2sex faces were associated with activation in right superior temporal sulcus, right insula, and right parahippocampal gyrus, where as idiosyncratic ratings of self2sex were associated with activation in left ventral superior frontal gyrus, right ventral inferior frontal gyrus, and left medial frontal gyrus. Consensus ratings were negatively associated with activation in a region of interest (ROI) at the parahippocampal/uncus/amygdala, while idiosyncratic ratings were positively associated with activation in an ROI at the ventral medial prefrontal cortex (Fig. 1c and d; Table 1).

Consensus ratings for self2black transformed face were associated with activation in the left thalamus, let cingulate gyrus, left medial frontal gyrus, right lingual gyrus, right postcentral gyrus, right anterior parahippocampal gyrus/uncus, left middle frontal gyrus, and right amygdala, whereas idiosyncratic ratings were associated with activation in the right inferior temporal gyrus, left anterior cingulate, and right parahippocampal gyrus. Consensus trustworthiness ratings were negatively associated with activation in an ROI at the right parahippocampal/uncus/amygdala and fusiform gyrus ROI. Idiosyncratic ratings were negatively associated with activation in the right parahippocampal gyrus and medial prefrontal cortex (Fig. 1e and f; Table 1).

Consensus ratings for white distracter faces were associated with activation in right superior temporal sulcus, right insula, left cingulate gyrus, right parahippocampal gyrus, left lingual gyrus, and left inferior frontal gyrus, whereas idiosyncratic ratings of white faces were associated with activation in left middle occipital gyrus, right middle temporal gyrus, right superior frontal gyrus, right fusiform gyrus, right cuneus, left inferior occipital gyrus, and left cingulate gyrus (Table 1).

Consensus ratings for black faces were associated with activation in left precuneus, left inferior parietal lobe, left fusiform gyrus, left superior frontal gyrus, right cingulate gyrus, and left inferior frontal gyrus, whereas idiosyncratic rating of black faces showed activation only in the left middle and superior occipital gyrus (Table 1).

Collapsing across all other distractor faces (white and black) revealed activation associated with trust rating in left inferior occipital gyrus and right middle frontal gyrus, whereas idiosyncratic ratings of faces collapsing across white and black were associated with activation in left lingual gyrus, right precuneus, left superior temporal gyrus, right posterior cingulate, and left cuneus (Table 1).

4. Discussion

Important social judgments about faces can be made quickly (Willis & Todorov, 2006) and without need to deeply process or act on the judgments (Bargh & Chartland, 2005). Several studies have demonstrated negative associations between trustworthiness ratings and activation in the medial temporal lobe (amygdala, uncus and parahippocampal gyrus) (Engell et al., 2007; Winston et al., 2002). The amygdala appears to be involved in automatic face coding with respect to impression management and is predicted to drive social responses toward individuals. Similarly, several studies have demonstrated that attractive faces activate neural substrates implicated in reward processing (O'Doherty et al., 2003; Winston, O'Doherty, Kilner, Perrett, & Dolan, 2007) and that amygdala activation to faces based on attractiveness indicates the social value of the face (Winston et al., 2007).

Our findings show that idiosyncratic ratings of trustworthiness in self-resembling faces, a hypothesized cue to kinship, are associated parametrically with increased activation in neural substrates implicated in reward. Self-face resemblance has been shown to increase ratings of attractiveness and trust. The current findings ratify these behavioral studies by showing that the affectively regulated pro-social behavior toward self-resembling faces is caused by parametrically activated neural reward circuitry. This effect is marked in same ethnicity faces regardless of sex, but is not upheld in differing ethnic faces. These results are consistent with studies showing increased activation in the amygdala and fusiform gyrus in response to ethnically different faces and extend these previous findings by showing that ethnically different faces also exaggerate amygdala-related activation associated with implicit trustworthiness ratings. That same and opposite sex same ethnicity self-resembling faces activate reward centers suggests that appetitive responses would be directed toward kin of either sex (i.e., brothers/sisters, nieces/nephews).

Because these reward regions are also activated in response to facial attractiveness, our findings extend the KI_i model (Lieberman, 2007), which hypothesizes the presence of dedicated neurocomputational architecture for kin detection. Our findings suggest that humans use existing neurocomputational architecture involved

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Fig. 1. Activation maps for idiosyncratic and consensus parametric ratings of trustworthiness in self-morph, self2sex, and self2ethnic faces. (a) Activation in the ventral middle frontal gyrus associated with idiosyncratic ratings of trustworthiness in self-morph faces and plot of parameter estimates showing positive association between trustworthiness ratings and activation in this region. (b) Activation in the parahippocampal gyrus associated with consensus ratings of trustworthiness and plot of parameter estimates showing negative association between trustworthiness ratings and activation in this region. (c) Activation in the ventral medial frontal gyrus associated with idiosyncratic ratings of trustworthiness in self2sex faces and plot of parameter estimates showing positive association between trustworthiness ratings and activation in this region. (d) Activation in the parahippocampal gyrus/uncus associated with consensus ratings of trustworthiness in self2sex faces and plot of parameter estimates showing positive negative association between trustworthiness ratings and activation in this region. (e) Activation in the parahippocampal gyrus (yellow) and medial prefrontal gyrus (green) associated with idiosyncratic ratings of trustworthiness in self2ethnic faces and plot of parameter estimates showing negative association between trustworthiness ratings and activation in this region. (f) Activation in the parahippocampal gyrus/uncus/amygdala (red) and fusiform gyrus (red) associated with consensus ratings of trustworthiness in self2ethnic faces and plot of parameter estimates showing negative association between trustworthiness ratings and activation in the parahippocampal gyrus/uncus/amygdala and no relationship, but heightened activation in the fusiform gyrus.

Table 1
List of parametrically activated substrates and Z scores for statistical parametric maps

Contrast	Substrate	Z score	MNI Coordinates (x, y, z)
Self-morph			
Consensus	Left parahippocampal gyrus	2.8	−24, −40, −16
Idiosyncratic	Right ventral middle frontal gyrus	2.48	36, 40, −19
Self2sex			
Consensus	Right superior temporal sulcus	2.98	58, −54, 20
	Right insula	2.54	34, 18, 10
	Right parahippocampal gyrus	2.76	34, 10, −28
Idiosyncratic	Left ventral superior frontal gyrus	2.6	−18, 50, −18
	Right ventral inferior frontal gyrus	2.58	26, 32, −14
	Left medial frontal gyrus	2.64	−6, 50, 8
Self2ethnic			
Consensus	Left thalamus	3.61	−14, −18, 16
	left cingulate gyrus	4.67	−8, −8, 48
	Left medial frontal gyrus	3.7	−6, 8, 52
	Right lingual gyrus	4.67	−8, −8, 48
	Right postcentral gyrus	3.21	24, −34, 50
	Right ant. parahippocampal gyrus	2.61	24, −2, −14
	Left middle frontal gyrus	3.32	−30, 58, 12
	Right amygdala	2.61	28, −4, −18
Idiosyncratic	Right inferior temporal sulcus	3.28	52, 0, −36
	Left anterior cingulate	2.69	−8, 44, −4
	Right parahippocampal gyrus	2.67	32, −10, −32
Non-self-resembling faces			
Distracter white faces			
Consensus	Right superior temporal sulcus	2.83	62, 12, −2
	Right insula	2.67	40, −6, 8
	Left cingulate gyrus	3.01	−12, −4, 50
	Right parahippocampal gyrus	2.78	30, −28, −26
	Left lingual gyrus	2.74	−18, −84, −4
	Left inferior frontal gyrus	2.34	−36, 22, 6
Idiosyncratic	Left middle occipital gyrus	2.87	−28, −84, 18
	Right middle temporal gyrus	2.79	34, −76, 16
	Right superior frontal gyrus	2.79	20, 62, 14
	Right fusiform	2.95	28, −58, −14
	Right cuneus	2.51	20, −90, 18
	Left inferior occipital gyrus	2.82	−28, −86, −8
	Left cingulate gyrus	2.58	0, −28, 30
Distractor black faces			
Consensus	Left precuneus	3.02	−30, −68, 46
	Left inferior parietal lobe	2.75	−56, −44, 46
	Left fusiform gyrus	3.14	−46, −38, −22
	Left superior frontal gyrus	2.79	−24, 14, 56
	Right cingulate gyrus and left inferior frontal gyrus	2.66	2, 10, 44
		2.84	−40, 32, 14
Idiosyncratic	Left middle	2.89	−26, −80, 12
	Superior occipital gyrus	2.83	−36, −90, 22
Collapsing across white and black distracter faces			
Consensus	Left inferior occipital gyrus	2.45	−36, −94, −8
	Right middle frontal gyrus	2.66	48, 22, 30
Idiosyncratic	Left lingual gyrus	2.81	−12, −60, 0
	Right precuneus	2.98	4, −72, 18
	Left superior temporal gyrus	2.93	−54, −28, 2
	Right posterior cingulate and left cuneus	2.71	18, −58, 12
		2.83	−14, −76, 10

in face processing (Gobbini & Haxby, 2007), reward evaluation (Aharon et al., 2001; Breiter & Rosen, 1999; O'Doherty, Kringelbach, Rolls, Hornack, & Andrews, 2001), and prediction (Berns, McClure, Pagnoni, & Mantague, 2001; Hsu, Bhatt, Adolphs, Tranel, & Camerer, 2005) in a combinatorial fashion to make adaptive decisions about faces that may represent members of their kin group (see Platek et al., 2005, 2004, 2008). It seems more plausible that evaluation of kinship would recruit several neural systems because the consequences of incorrect kin assignment can be dire (e.g., inbreeding depression and cuckoldry). Recent evidence suggests dopamine D2

receptor density in the medial prefrontal cortex is associated with differences in learning from one's own errors (Klein et al., 2007). If the findings of Klein et al. can be extended (from their investigation of addictive behaviors/tendencies) to interpersonal based social behaviors, then one might speculate that this neurogenetic loci is also involved in monitoring behavioral outcomes between social group members, specifically those outcomes that bear on kin-appetitive/aversive outcomes. Our findings suggest that part of the neural network involved in differentiating kin from non-kin members of one's social group involves recruitment of several

substrates involved in generalized face (Gobbini and Haxby, 2006, 2007; Gobinni, Leibenluft, Satiago, & Haxby, 2004; Golby, Gabrieli, Chiao, & Eberhardt, 2001; Gusnard, Akbudak, Shulman, & Raichle, 2001; Leveroni et al., 2000) (and other social sensory, e.g., olfactory) processing circuitry as a recursively monitored sub-circuitry which feeds a kinship estimator.

This process may not be limited simply to differentiation of kin from non-kin and same race from other race faces, but may form the basis for a neural substrate associated with identification of group membership more broadly speaking. As such, this could represent a hierarchical mechanism involved in selection acting at various levels of group membership including such characteristics as ethnic, cultural and even possibly linguistic similarities. This suggestion demands further research.

Acknowledgement

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