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Social and emotional attachment in the neural representation of faces

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To dissociate the role of visual familiarity from the role of social and emotional factors in recognizing familiar individuals, we measured neural activity using functional magnetic resonance imaging (fMRI) while subjects viewed (1) faces of personally familiar individuals (i.e. friends and family), (2) faces of famous individuals, and (3) faces of strangers. Personally familiar faces evoked a stronger response than did famous familiar faces and unfamiliar faces in areas that have been associated with 'theory of mind', and a weaker response in the amygdala. These response modulations may reflect the spontaneous activation of social knowledge about the personality and attitudes of close friends and relatives and the less guarded attitude one has around these people. These results suggest that familiarity causes changes in neural response that extend beyond a visual memory for a face.

Introduction

We have the capacity to recognize an unlimited number of individuals based on the appearance of their faces. Facial appearance, however, is only one aspect of how we recognize a familiar individual. It is common experience to think 'I've seen that face before', but it is only when we associate a face with knowledge about the person, such as his or her name or the circumstances of a previous encounter that we realize that we know that person. Identifying someone we know, therefore, involves other factors in addition to facial appearance, such as one's relationship to an individual and one's representation of that individual's personality and outlook.

Previous neuroimaging studies on familiar face recognition have compared the neural response to faces of strangers to the response to famous faces (Gorno-Tempini et al., 1998; Leveroni et al., 2000; Sergent et al., 1992), to experimentally learned faces (Dubois et al., 1999; Leveroni et al., 2000; Rossion et al., 2001), and to faces of acquaintances (Nakamura et al., 2000). A few areas, such as the temporal poles (Nakamura et al., 2000; Sergent et al., 1992) and the anterior middle temporal gyrus (Gorno-Tempini et al., 1998; Leveroni et al., 2000), responded more strongly to previously familiar faces than to novel faces or to newly learned faces with no associated semantic information. In addition to a stronger response to familiar faces, these areas also responded more strongly to familiar landscapes (Nakamura et al., 2000) and famous names (Gorno-Tempini et al., 1998). These results suggest that these anterior temporal areas are involved in the storage of biographical or autobiographical information.

We were interested in investigating further the role of person knowledge in familiar face recognition. To dissociate the role of visual familiarity from the role of emotional and social factors associated with familiar individuals, we used functional magnetic resonance imaging (fMRI) to measure neural responses to faces with different types of familiarity (Fig. 1). We chose two different categories of faces: faces of people with whom the participants were personally familiar, such as close relatives and friends, and faces of famous individuals whom the participants knew through the media. These two categories of faces were both visually familiar to the participants, but the personally familiar faces differed from the famous familiar faces in terms of stronger emotional attachment and in terms of knowledge about personal traits and associated biographical information. For each subject, the selected famous faces were highly familiar but did not evoke strong emotional reactions, ensuring that the groups of familiar faces differed in social and emotional attachment.

We expected the personally familiar faces, as compared to the famous familiar faces, to evoke a stronger response in areas that are sensitive to emotional and social attributes, such as the amygdala (Breiter et al., 1996; Canli et al., 2002; Morris et al., 1996; Zalla et al., 2000), in anterior temporal areas that are associated with biographical or autobiographical information (Gorno-Tempini et al., 1998; Leveroni et al., 2000; Nakamura et al., 2000; Sergent et al., 1992), and in areas that are associated with the representation of the personal attributes and mental states of others ('theory of mind'), such as the anterior paracingulate cortex (Frith and Frith, 1999; Gallagher and Frith, 2003; Mitchell et al., 2002), and the posterior

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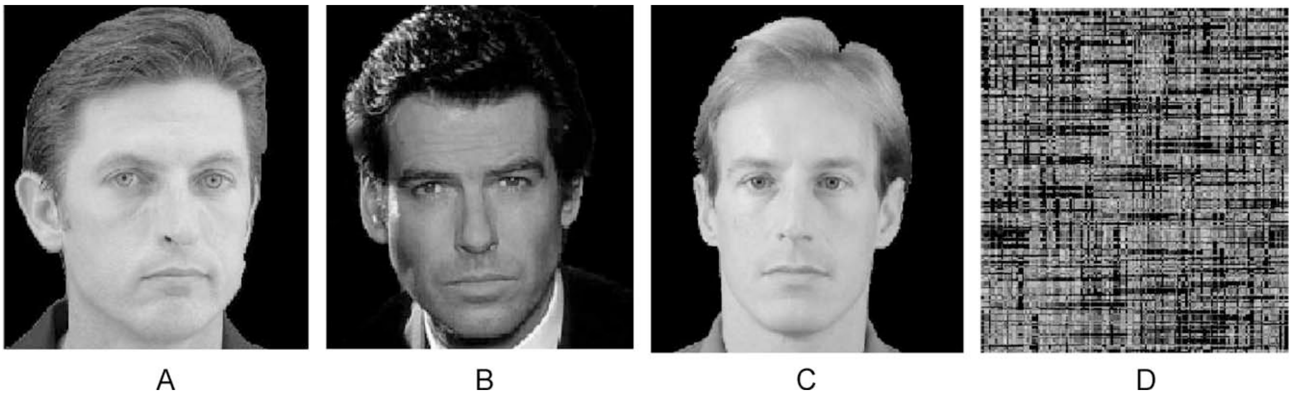

Fig. 1. Examples of stimuli used during the fMRI experiment. (A) Personally familiar faces. (B) Famous familiar faces. (C) Unfamiliar faces, taken from the pool of the photographs of the personally familiar faces for the other subjects and matched for age, race, and gender. (D) Nonsense pattern.

superior temporal sulcus (Frith and Frith, 1999; Gallagher and Frith, 2003).

Materials and methods

Subjects

Ten healthy right-handed volunteers, five males and five females, participated in the experiment (mean age 26.8, range 22–39). All participants gave written informed consent. Data from one subject were not analyzed because of movement.

Stimuli

Stimuli were grayscale pictures of faces and nonsense patterns (Fig. 1). Nonsense pictures were scrambled images of faces and thus had equivalent luminance and contrast.

Three different categories of faces were presented: famous familiar faces (actors, singers, public leaders), personally familiar faces (relatives and friends), and strangers.

Each subject was asked to provide several photographs of each of six living individuals with whom they were personally familiar, namely, parents, siblings, other relatives with whom they had a close personal relationship, and close friends whom they had known for more than 1 year. From these photographs, two different pictures of each individual were selected. These photographs were scanned into digital form. Each face was isolated and superimposed on a black background using Adobe Photoshop (San Jose, CA).

Famous face stimuli for each subject were selected from a set of 100 public figures to ensure that the faces used for each subject were well known to that subject and did not evoke strong emotions. Each subject completed a computerized test of familiarity with all famous faces before stimulus selection. The test consisted of presentations of each stimulus followed by (1) rating the subject's familiarity with the famous face, (2) writing down the name of the face, (3) selecting the name of the face from a multiple choice list, (4) rating one's feelings while viewing the image (positive/negative), and (5) rating how aroused one was while viewing the image (high/low). Ratings were completed using nine-point scales with each level of valence and arousal illustrated by a word and an image using a computerized version of the Self-Assessment Manikin (SAM, Lang, 1980). Two pictures of six famous familiar individuals were selected for each subject. The famous faces selected were those that were recognized by name, rated as neutral or slightly positive, and matched to the personally familiar faces on age, race, and gender.

Each subject's pictures of strangers were selected from the pool of the photographs of other subjects' personally familiar faces to standardize stimulus quality (Fig. 1). For each subject, strangers' faces were selected to match personally familiar and famous faces on age, race, and gender.

Task

Subjects performed a one-back repetition detection task. Stimuli were blocked by condition (personally familiar faces, famous familiar faces, unfamiliar faces, scrambled control images). Each block consisted of 30 stimuli. Stimuli were presented for 1 s with a 1-s interstimulus interval. A visual cue alerted the subject at the beginning of each block. Subjects indicated whether each stimulus matched the previous stimulus by pressing either a button with their right (match) or left thumb (nonmatch). Accuracy and reaction times were collected.

Before and after the scans, the participants rated the valence and the level of arousal of all the stimuli using the computerized version of the SAM scale. The SAM is a self-administered scale with icons that indicate graphically how arousing and pleasant stimuli are. Each picture used during the fMRI session appeared on a computer screen, and participants evaluated arousal and pleasantness by choosing the icon, or a level of intermediate intensity between two icons, that best reflected their reaction to each stimulus.

Imaging

Responses to different faces and scrambled pictures were measured using blood oxygen level dependent (BOLD) contrast fMRI with the acquisition of T2*-weighted gradient echo echo-planar images. Scanning was accomplished with a 1.5T GE scanner (General Electric, Milwaukee, WI). One hundred ten whole brain volumes were acquired in each time series. Each volume consisted of 22 contiguous 5-mm-thick slices [TR = 3 s, TE = 40 ms, flip angle = 90°, field of view (FOV) = 24 cm].

High-resolution T1-weighted spoiled gradient recall (SPGR) anatomical images also were obtained for each subject (124 1.2-mm-thick sagittal images, FOV = 24 cm, 256 × 256 matrix).

Twelve time series were obtained in each subject in a single fMRI session. The order of the series was randomized for each subject. Each time series began and ended with 12 s of rest. In each time series, four blocks of 30 stimuli were presented, one for each of the four stimulus conditions separated by 12 s intervals of rest. The order of blocks was counterbalanced across time series.

Statistics

Image data were analyzed with multiple regression (Haxby et al., 1997). An omnibus test of the significance of differences among responses to faces of varying familiarity and nonsense pictures (unfamiliar faces, personally familiar faces, famous familiar faces, nonsense pictures) was calculated to identify voxels that were face-responsive.

A group analysis was performed to test the significance of the following three contrasts using *t* tests: (1) personally familiar versus famous familiar faces, (2) personally familiar versus strangers, and (3) famous familiar versus strangers. The magnitude of response to each category of faces relative to a no stimulus baseline was calculated for each subject individually based on the β-weights from the multiple regression analysis. The maps of response magnitudes for each subject were converted to Talairach space (Talairach and Tournoux, 1988). Conversion to Talairach space and *t* tests were calculated using the Analysis of Functional Neuroimages software package (AFNI; http://afni.nimh.nih.gov/afni/). *T* tests are random effects tests in which each subject accounts for a single degree of freedom.

Significant clusters were defined as contiguous voxels with $P < 0.025$ (uncorrected for multiple comparisons) and a minimum volume of 250 μl. The maximum *Z* score for each cluster is reported in the tables. In the amygdala, smaller clusters of voxels were defined as significant because of the small volume of this structure and previous hypotheses about its role in face perception.

Results

Behavioral results

Reaction times recorded during the performance of the one-back repetition detection task during the fMRI experiment were slower for the personally familiar faces as compared to faces of strangers (613 ms, SD = 63, versus 594 ms, SD = 68, $P < 0.05$). Reaction times for famous faces (602 ms, SD = 61) did not differ significantly from the reaction times for either personally familiar faces or for the faces of strangers. Accuracy was 99% in all conditions. The ratings of the stimuli (Self-Assessment Manikin, Lang, 1980) recorded before and after the fMRI experiment (see Table 1 for details) showed that the personally familiar faces were judged as significantly more ‘positive’ and ‘arousing’ than were the famous familiar faces ($P < 0.001$ in both cases) and the faces of strangers ($P < 0.001$ in both cases) and the famous familiar faces were evaluated as more ‘positive’ and ‘arousing’ than were the faces of strangers ($P < 0.001$ in both cases).

Neuroimaging results

The neuroimaging results showed differential responses in visual and nonvisual cortical areas based on the degree and type of familiarity associated with faces.

Table 1
Means of valence and arousal across categories measured pre- and post-scanning

Stimuli	Pre-scan		Post-scan	
	Mean	SD	Mean	SD
Valence				
Family and friends	2.95	1.43	3.01	1.56
Celebrities	3.57	1.35	3.67	1.18
Strangers	5.23	0.92	5.43	1.29
Arousal				
Family and friends	3.75	1.59	3.76	1.54
Celebrities	4.48	1.45	4.56	1.51
Strangers	5.6	1.26	5.6	1.29

Personally familiar faces versus famous familiar faces

Personally familiar faces evoked a significantly stronger response than did famous familiar faces in the anterior paracingulate cortex bilaterally ($P < 0.001$), the posterior cingulate and precuneus bilaterally ($P < 0.001$), the posterior superior temporal sulcus bilaterally ($P < 0.001$), the fusiform gyrus bilaterally ($P < 0.01$ on the left and $P < 0.001$ on the right), and the left lingual gyrus ($P < 0.001$) (Fig. 2) (see Table 2 for all cortical and subcortical loci that showed a response difference). The response evoked in the posterior cingulate and the precuneus included the dorsal portion of the posterior cingulate and the inferior portion of the precuneus; this region will be referred to as ‘posterior cingulate/precuneus’. A stronger response for the famous familiar faces was recorded in the right amygdala ($P < 0.01$) (Fig. 3).

Personally familiar faces versus strangers

The analysis of the contrast between familiar and unfamiliar faces revealed a stronger response to personally familiar faces than to the faces of strangers in the anterior paracingulate cortex ($P < 0.001$ in the left and $P < 0.01$ on the right) and in the left posterior cingulate ($P < 0.01$). A stronger response to the faces of strangers was detected in the right amygdala ($P < 0.001$). For a more detailed report of the areas activated in this contrast, see Table 3.

Famous familiar faces versus strangers

A stronger response to famous familiar faces as compared to unfamiliar faces was detected in the left anterior paracingulate cortex ($P < 0.001$). A stronger response for faces of strangers was detected in the right amygdala (Fig. 3) and in the left fusiform gyrus ($P < 0.01$). For a more detailed report of the areas activated in this contrast, see Table 4.

Discussion

In this study of familiar face perception, we attempted to dissociate the role of social and emotional attachment from the role of visual appearance. For this purpose, we selected two groups of familiar faces that were both visually familiar but differed from each other in social and emotional attributes: personally familiar faces and famous faces. The personally familiar faces were chosen from relatives and close friends, and the famous faces were selected from individuals who were well known to the participants but did not evoke strong emotions. Viewing familiar faces mod-

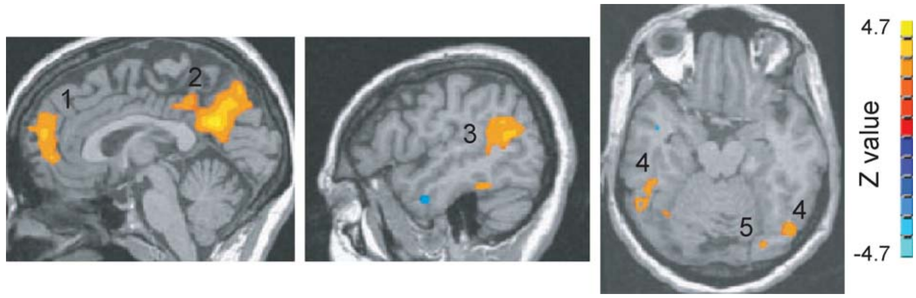

Fig. 2. Areas that showed stronger activation in the contrast personally familiar faces versus famous familiar faces. Regions showing differences: 1. Anterior paracingulate cortex (maximum at *x* −4; *y* 53; *z* 19); 2. Posterior cingulate/precuneus (*x* −6; *y* −68; *z* 28); 3. Posterior superior temporal sulcus (*x* 49; *y* −55; *z* 19); 4. Fusiform gyrus (*x* −44; *y* −65; *z* −17); 5. Lingual gyrus (*x* −23; *y* −78; *z* −19).

ulated activity in areas that have been associated with the representation of the personal attributes and mental states of others, in areas that are associated with emotional response, such as the amygdala, and in face-responsive regions in the ventral occipito-temporal cortex. The results of this study suggest that recognition of a familiar individual involves more than the representation of that person's appearance.

Areas associated with person knowledge

Personally familiar faces evoked a stronger response than did famous familiar faces in the anterior paracingulate cortex, in the posterior superior temporal sulcus, and in the posterior cingulate/precuneus.

Table 2
Areas of significant activity for the contrast personally familiar faces as compared to famous familiar faces (*Z* score is reported for the maximum in each cluster)

Area	Hemisphere	BA	*x*	*y*	*z*	*Z* score
Anterior paracingulate cortex	L	9	−4	53	19	4
Anterior paracingulate cortex	R	9	2	52	17	3.3
Middle frontal gyrus	L	6	−22	12	44	2.6
Middle frontal gyrus	R	6	38	4	31	3
Middle frontal gyrus	R	6	28	−4	53	3.6
Superior temporal sulcus	L	39	−36	−63	30	3.5
Superior temporal sulcus	R	39	49	−55	19	3.8
Middle temporal gyrus	L	21	−46	−38	−6	3.4
Middle temporal gyrus	R	21	44	−1	−23	−3.8
Posterior cingulate/ precuneus	L	31	−6	−68	28	4.6
Posterior cingulate/ precuneus	R	31	4	−59	28	3.7
Fusiform gyrus	L	19	−44	−65	−17	2.9
Fusiform gyrus	R	37	30	−28	−13	4.5
Fusiform gyrus	R	37	52	−51	−14	3.5
Lingual gyrus	L	18	−23	−78	−19	3.7
Amygdala	R	NA	22	−11	−12	−2.8
Postcentral gyrus	L	40	−63	−22	17	4.5
Inferior parietal lobule	L	41	−46	−22	16	−2.6
Cerebellum	L		−24	−77	−20	3.7
Cerebellum	R		18	−38	−24	3.8
Cerebellum	R		37	−60	−21	2.8
Thalamus	L	Th	−6	−9	14	3.1
Thalamus	R	Th	6	−13	16	2.9
Globus pallidus	R	GP	11	−1	1	3.6

Personal familiarity with immediate family and long-term friends differs from impersonal familiarity with celebrities on many factors, such as the amount of exposure, social knowledge about personal traits, and emotional response. Although the increased neural responses in these areas to personally familiar faces could be due to any combination of these factors, previous research on the anterior paracingulate, the posterior superior temporal sulcus, and the posterior cingulate/precuneus has linked these areas to the representation of the personal attributes and mental states of others, or "theory of mind" (Frith and Frith, 1999; Gallagher and Frith, 2003; Gallagher et al., 2000; Mitchell et al., 2002). These areas have also been associated with the retrieval of episodic autobiographical memory (Maguire, 2001). The stronger neural responses in these areas, therefore, may be due to the spontaneous activation of semantic knowledge of the personal traits, attitudes, and intentions of very familiar individuals. Because we studied the type of familiarity that accrues naturally with years of social interaction, in the case of family and friends, or media exposure, in the case of celebrities, other accounts for this result cannot be ruled out definitively. For example, the faces that evoke stronger responses in "theory of mind" areas are all associated with greater exposure and presumably stronger familiarity, and presumably a richer store of associated semantic and episodic knowledge. These faces may also be of greater interest, and consequently may get more attention. The stronger emotional response to these faces, as demonstrated by the behavioral ratings, may also affect the strength of responses in these areas. Ruling out these alternative explanations will probably require study of the effect of experimentally induced and controlled

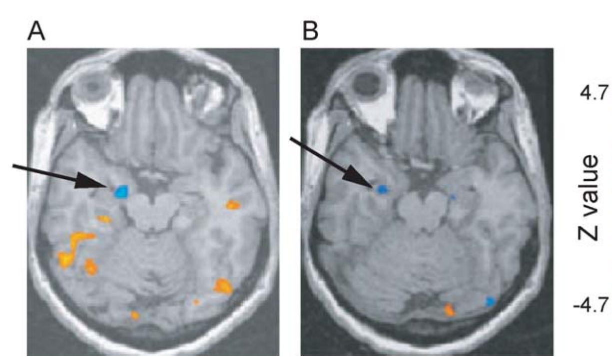

Fig. 3. (A) Weaker response to personally familiar faces as compared to famous faces in the amygdala (maximum at *x* 22; *y* −11; *z* −12). (B) Weaker response to famous familiar faces as compared to the faces of strangers in the amygdala (*x* 27; *y* −9; *z* −16).

Table 3
Areas of significant activity for the contrast personally familiar faces as compared to faces of strangers (*Z* score is reported for the maximum of activation in each cluster)

Area	Hemisphere	BA	*x*	*y*	*z*	*Z* score
Anterior paracingulate cortex	L	9	− 12	43	12	4.1
Anterior paracingulate cortex	R	9	2	47	12	2.6
Superior frontal gyrus	L	6	− 7	− 11	52	− 3.3
Superior frontal gyrus	R	6	8	6	62	3.3
Middle frontal gyrus	R	9	44	37	31	− 2.8
Cingulate gyrus	L	24	− 4	3	32	− 2.8
Superior temporal gyrus	L	38	− 32	7	− 27	− 3.5
Superior temporal gyrus	L	22	− 57	9	− 9	3.4
Superior temporal gyrus	R	22	46	− 8	0	− 2.7
Posterior cingulate	L	31	− 2	− 50	26	2.6
Posterior orbital gyrus	L	11	− 18	36	− 2	− 2.7
Insula	L	Ins	− 37	4	0	− 2.8
Insula	R	Ins	42	− 6	14	− 2.9
Lingual gyrus	L	18	− 15	− 82	− 17	3
Amygdala	R	NA	26	− 11	− 17	− 3.1
Cerebellum	R		15	− 60	− 20	3
Thalamus	L	Th	− 26	− 26	5	− 3.3
Globus pallidus	L	GP	− 30	− 8	2	− 4
Globus pallidus	R	GP	27	− 6	− 4	− 4.9

familiarity. Such studies, of course, will never be able to simulate fully the effect of true familiarity that develops over years of varied interpersonal experiences.

Functional imaging studies have found consistently that the anterior paracingulate cortex and the posterior superior temporal sulcus are activated during the performance of tasks that require interpreting and predicting other people's behavior (Castelli et al., 2000; Frith, 2001; Gallagher et al., 2000). Perceiving eye gaze, an important clue for assessing the mental states and intentions of others, also modulates activity in the posterior superior temporal sulcus (Hoffman and Haxby, 2000; Puce et al., 1998) and the anterior paracingulate cortex (Calder et al., 2002).

The anterior paracingulate cortex, the posterior superior temporal sulcus, and the posterior cingulate/precuneus appear to play different roles in the representation of person knowledge. The anterior paracingulate cortex seems to be involved particularly in the representation of knowledge about the personal traits (Mitchell et al., 2002) and mental states of others (Calder et al., 2002; Frith and Frith, 1999; McCabe et al., 2001 but see also Ferstl and von Cramon, 2002; Gusnard and Raichle, 2001; Kelley et al., 2002). By contrast, the posterior superior temporal sulcus appears to play a general role in social cognition that is related more to the representation of the intentions of others (Allison et al., 2000; Hoffman and Haxby, 2000; Perrett et al., 1985; Puce and Perrett, 2003; Winston et al., 2002) and less to the representation of personal traits (Mitchell et al., 2002). The posterior cingulate/precuneus is involved in the retrieval of images and other long-term memories (Burgess et al., 2001; Fletcher et al., 1995; Gorno-Tempini et al., 1998; Ishai et al., 2000; Leveroni et al., 2000; Nakamura et al., 2001; Shah et al., 2001). Activity in the posterior cingulate also is elicited by perception of emotionally salient stimuli (Maddock, 1999) and by self-generated emotions (Damasio et al., 2000), suggesting that the stronger response to familiar stimuli in this region might be related to their higher emotional content.

Behavioral studies of social cognition show evidence for the spontaneous activation of traits and attitudes associated with perceived individuals (Bargh et al., 1996; Greenwald and Banaji, 1995; Todorov and Uleman, 2002). Viewing a personally familiar face, therefore, probably is associated with the spontaneous activation of an elaborate representation of personal knowledge about that person. The one-back repetition detection task that we chose for this experiment did not explicitly call for retrieval of information about the personal traits or attitudes of familiar people. Our results suggest, therefore, that this information is retrieved spontaneously. This information could be about personal traits (is that person kind or malicious, funny or serious, suspicious or trusting, cautious or reckless?), intentions (what is that person up to?), attitudes (what are that person's likes and dislikes?), mental states (is that person happy or distressed, in the know or in the dark?), and relationships to oneself and others. Activation of this information would prepare one to interact appropriately and effectively with that person. We propose that the stronger responses to familiar faces in areas that are associated with social cognition, personal traits, and "theory of mind" may reflect the spontaneous activation of this kind of person knowledge.

In a related study of the neural response in mothers viewing pictures of their own child, their children's friends, and unfamiliar children, we found similar effects of familiarity on the responses in these areas (Leibenluft et al., under review). Responses in the anterior paracingulate, the posterior superior temporal sulcus, and the posterior cingulate/precuneus were strongest while viewing one's own child, were of intermediate strength while viewing familiar children, and were weakest while viewing unfamiliar children. The consistency of this result in our two studies indicates that the participation of these areas in the representation of familiar people is not specific to attitudes toward celebrity or to maternal attitudes toward children.

Anterior temporal areas

Others have shown that the recognition of familiar stimuli (faces, names, landscapes) elicits activity in the anterior temporal cortex (Gorno-Tempini et al., 1998; Leveroni et al., 2000; Nakamura et al., 2000; Sergent et al., 1992). Our results do not replicate

Table 4
Areas of significant activity for the contrast famous familiar faces versus strangers (*Z* score is reported for the maximum of activation in each cluster)

Area	Hemisphere	BA	*x*	*y*	*z*	*Z* score
Anterior paracingulate cortex	L	9	− 10	44	11	3.1
Superior frontal gyrus	L	6	− 14	− 10	65	2.8
Superior frontal gyrus	L	6	− 9	− 11	51	− 2.8
Middle frontal gyrus	L	6	− 33	− 1	20	− 3.6
Posterior orbital gyrus	L	11	− 21	36	− 2	− 2.6
Superior temporal gyrus	R	22	54	− 14	1	− 2.7
Fusiform gyrus	L	37	− 37	− 58	− 4	− 2.6
Inferior occipital gyrus	L	18	− 23	94	− 5	− 3.3
Lingual gyrus	L	18	− 13	− 83	− 17	2.9
Postcentral gyrus	L	2	− 15	− 46	72	− 3.1
Amygdala	R	NA	27	− 9	− 16	− 2.5
Cerebellum	R		4	− 43	− 24	− 2.6
Thalamus	L	Th	− 26	− 27	5	− 3.3
Globus pallidus	L	Gp	− 19	− 3	0	− 3.7
Globus pallidus	R	Gp	26	− 7	− 4	− 3.8

the findings of others in this regard. This could be due to the fact that we presented the same pictures of different individuals repeatedly in our fMRI experiment. Because of the limited number of personally familiar individuals for each subject, repeated presentation of these faces might have produced an adaptation effect that obscured a stronger response to the familiar faces in these regions (Sugiura et al., 2001).

Amygdala

Whereas activation in areas associated with 'theory of mind' was stronger for personally familiar faces, the response in the amygdala, a structure involved in the processing of emotional stimuli, especially threat stimuli (Breiter et al., 1996; Morris et al., 1996) was weaker for the personally familiar faces. Personally familiar faces evoked a weaker response in the amygdala than did famous familiar faces, and both personally familiar and famous familiar faces evoked weaker responses in this structure than did strangers' faces. The modulation of activity in the amygdala based on the degree of familiarity was one of the most surprising findings of this study. The direction of response modulation in this region was not in the expected direction. Functional imaging studies have shown that the amygdala responds preferentially to stimuli with emotional significance, both positive and negative (Breiter et al., 1996; Canli et al., 2002; Morris et al., 1996; Zalla et al., 2000). Therefore, we expected that the personally familiar faces would elicit the strongest response in this anatomical structure.

In a related study, we found a similar effect when comparing the neural responses when viewing familiar children as compared to viewing unfamiliar children, with a weaker amygdala response to familiar children (Leibenluft et al., under review).

Behavioral ratings were collected before and after the scan session to assess how the participants evaluated the stimuli presented during the fMRI experiment. Personally familiar faces were judged as more pleasant and arousing compared to famous familiar faces or strangers' faces, but the functional imaging data showed the weakest response in the amygdala during viewing of personally familiar faces and the strongest response during viewing of strangers' faces.

These results suggest that the amygdala is engaged during the appraisal of unfamiliar individuals, perhaps reflecting an increased state of vigilance or wariness when encountering someone new. This finding is consistent with the hypothesis that the amygdala plays a role in evoking a state of alertness (Davis and Whalen, 2001) and with the hypothesis that it functions as a "social brake" when evaluating sources of potential threats (Adolphs et al., 1998; Amaral, 2002; Winston et al., 2002). Moreover, faces that are deemed untrustworthy evoke a stronger response in the amygdala, even when the subject is not explicitly evaluating trustworthiness (Winston et al., 2002). Therefore, reduced activity in the right amygdala while viewing personally familiar faces, as compared to famous faces and faces of strangers, may reflect a lower level of vigilance. When among friends and family, people tend to relax and let their guard down. We propose that increased amygdala activity when viewing faces of strangers reflects a role for this structure in mediating a cautious or wary attitude in social situations.

Ventral occipito-temporal regions

Activation in face-responsive regions in the ventral occipito-temporal cortex did not show a simple modulation by familiarity. The response to famous familiar faces in the fusiform gyrus was weaker than the response to either personally familiar faces or strangers' faces. If the response in the fusiform cortex was modulated simply by visual familiarity, the magnitude of the response to famous faces should be intermediate between the response to the personally familiar faces of friends and family and the response to strangers' faces. These results suggest that the response in these perceptual areas is affected by multiple factors that may be mediated by other cortical regions.

Previous imaging studies have explored the effect of familiarity in the extrastriate cortex, but the results have not been consistent. Some studies have reported a stronger response to familiar faces (Henson et al., 2000; Leveroni et al., 2000), whereas other studies have reported a weaker response (Dubois et al., 1999; Rossion et al., 2001) or no modulation at all (Gorno-Tempini et al., 1998; Shah et al., 2001). The inconsistency of these results may be due to different demands on memory or attention (Henson et al., 2002) and differences in the social and emotional attributes associated with different kinds of familiar faces.

In our experiment, the modulation of the neural response to faces in ventral occipito-temporal cortex based on familiarity may reflect feedback from other areas. ERP studies in humans (Bentin et al., 1999; Eimer, 2000; Puce et al., 1999) have shown that the initial response to faces, the N170 potential, is not modulated by familiarity or stimulus repetition, but later responses to faces (between 200 and 500 ms) are sensitive to familiarity (these later responses are located over parietal and frontal cortex). Whereas the early responses appear to reflect a rapid feed-forward process that does not reflect familiarity, the later responses occur in a time window that allows interactions among multiple face-responsive regions (Haxby et al., 2000).

Other differences between famous and personally familiar faces

We selected our stimulus sets to vary social and emotional attachment of familiar faces. Famous faces and personally familiar faces vary on multiple dimensions, such as attractiveness, picture quality, and celebrity. Our selection of famous faces that were rated as neutral or only slightly positive was intended to minimize the effect of the celebrity factor. Most of the differences between responses to personally familiar and famous faces, however, extended to contrasts with unfamiliar faces, which were not confounded with the effects of attractiveness, picture quality, and celebrity. Moreover, in a related study, we found remarkably similar effects of familiarity on the responses in the 'theory of mind' areas and the amygdala in mothers viewing pictures of familiar and unfamiliar children (Leibenluft et al., submitted for publication). The stronger responses in the 'theory of mind' areas and the weaker response in the amygdala while viewing personally familiar faces, therefore, are probably not attributable to factors that are unique to famous faces.

We are proposing a novel hypothesis for the functional role played by the rostral paracingulate and the superior temporal sulcus in person recognition, namely, the spontaneous activation of person knowledge. Because of other differences between personally familiar and famous familiar faces, such as episodic knowledge, attractiveness, and relevance, the current results, while consistent with our hypothesis, do not definitively rule out alternative explanations related to these other factors. Converging evidence from multiple studies, which vary person knowledge, semantic and episodic knowledge, and relevance independently, will be necessary to confirm our hypothesis.

Conclusion

The results of the present experiment suggest that familiarity causes changes in the neural response to faces that extend beyond developing a visual memory for the appearance of a face. Perceiving a familiar face activates a distributed network of brain structures related not only to visual familiarity but also to knowledge about a person's personality, attitudes, and intentions; to episodic memories associated with that person; and to the emotional response to that person. The 'knowledge' about the other person is retrieved spontaneously and appears to play an integral role in the recognition of familiar individuals.

The results of this study also suggest that the amygdala plays a role as a social brake in the appraisal of new individuals, mediating the wariness or reserve that most experience when meeting new people.

In visual areas that respond preferentially to faces, the complex modulation of response by familiarity indicates that the representation of familiar faces in these areas is influenced by feedback from other areas.

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References

Adolphs, R., Tranel, D., Damasio, A.R., 1998. The human amygdala in social judgment. Nature 393, 470–474.

Allison, T., Puce, A., McCarthy, G., 2000. Social perception from visual cues: role of the STS region. Trends Cogn. Sci. 4, 267–278.

Amaral, D.G., 2002. The primate amygdala and the neurobiology of social behavior: implications for understanding social anxiety. Biol. Psychiatry 51, 11–17.

Bargh, J.A., Chen, M., Burrows, L., 1996. Automaticity of social behavior: direct effects of trait construct and stereotype-activation on action. J. Pers. Soc. Psychol. 71, 230–244.

Bentin, S., Deouell, L.Y., Soroker, N., 1999. Selective visual streaming in face recognition: evidence from developmental prosopagnosia. Neuroreport 10, 823–827.

Breiter, H.C., Etcoff, N.L., Whalen, P.J., Kennedy, W.A., Rauch, S.L., Buckner, R.L., Strauss, M.M., Hyman, S.E., Rosen, B.R., 1996. Response and habituation of the human amygdala during visual processing of facial expression. Neuron 17, 875–887.

Burgess, N., Maguire, E.A., Spiers, H.J., O'Keefe, J., 2001. A temporoparietal and prefrontal network for retrieving the spatial context of lifelike events. Neuroimage 14, 439–453.

Calder, A.J., Lawrence, A.D., Keane, J., Scott, S.K., Owen, A.M., Christoffels, I., Young, A.W., 2002. Reading the mind from eye gaze. Neuropsychologia 40, 1129–1138.

Canli, T., Sivers, H., Whitfield, S.L., Gotlib, I.H., Gabrieli, J.D., 2002. Amygdala response to happy faces as a function of extraversion. Science 296, 2191.

Castelli, F., Happe, F., Frith, U., Frith, C., 2000. Movement and mind: a functional imaging study of perception and interpretation of complex intentional movement patterns. Neuroimage 12, 314–325.

Damasio, A.R., Grabowski, T.J., Bechara, A., Damasio, H., Ponto, L.L., Parvizi, J., Hichwa, R.D., 2000. Subcortical and cortical brain activity during the feeling of self-generated emotions. Nat. Neurosci. 3, 1049–1056.

Davis, M., Whalen, P.J., 2001. The amygdala: vigilance and emotion. Mol. Psychiatry 1, 13–34.

Dubois, S., Rossion, B., Schiltz, C., Bodart, J.M., Michel, C., Bruyer, R., Crommelinck, M., 1999. Effect of familiarity on the processing of human faces. Neuroimage 9, 278–289.

Eimer, M., 2000. The face-specific N170 component reflects late stages in the structural encoding of faces. Neuroreport 11, 2319–2324.

Ferstl, E.C., von Cramon, D.Y., 2002. What does the frontomedian cortex contribute to language processing: coherence or theory of mind? Neuroimage 17, 1599–1612.

Fletcher, P.C., Frith, C.D., Baker, S.C., Shallice, T., Frackowiak, R.S., Dolan, R.J., 1995. The mind's eye—precuneus activation in memory-related imagery. Neuroimage 2, 195–200.

Frith, U., 2001. Mind blindness and the brain in autism. Neuron 32, 969–979.

Frith, C.D., Frith, U., 1999. Interacting minds—a biological basis. Science 286, 1692–1695.

Gallagher, H.L., Frith, C.D., 2003. Functional imaging of 'theory of mind'. Trends Cogn. Sci. 7, 77–83.

Gallagher, H.L., Happe, F., Brunswick, N., Fletcher, P.C., Frith, U., Frith, C.D., 2000. Reading the mind in cartoons and stories: an fMRI study of 'theory of mind' in verbal and nonverbal tasks. Neuropsychologia 38, 11–21.

Gorno-Tempini, M.L., Price, C.J., Josephs, O., Vandenberghe, R., Cappa, S.F., Kapur, N., Frackowiak, R.S., 1998. The neural systems sustaining face and proper-name processing. Brain 121, 2103–2118.

Greenwald, A.G., Banaji, M.R., 1995. Implicit social cognition: attitudes, self-esteem, and stereotypes. Psychol. Rev. 102, 4–27.

Gusnard, D.A., Raichle, M.E., 2001. Searching for a baseline: functional imaging and the resting human brain. Nat. Rev. Neurosci. 2, 685–694.

Haxby, J.V., Maisog, J.M., Courtney, S.M., 1997. Multiple regression analysis of effects of interest in fMRI time series (online). http://nimh.nih.gov/pubs.html.

Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2000. The distributed human neural system for face perception. Trends Cogn. Sci. 4, 223–233.

Henson, R., Shallice, T., Dolan, R., 2000. Neuroimaging evidence for dissociable forms of repetition priming. Science 287, 1269–1272.

Henson, R.N., Shallice, T., Gorno-Tempini, M.L., Dolan, R.J., 2002. Face repetition effects in implicit and explicit memory tests as measured by fMRI. Cereb. Cortex 12, 178–186.

Hoffman, E.A., Haxby, J.V., 2000. Distinct representations of eye gaze and identity in the distributed human neural system for face perception. Nat. Neurosci. 3, 80–84.

Ishai, A., Ungerleider, L.G., Haxby, J.V., 2000. Distributed neural systems for the generation of visual images. Neuron 28, 979–990.

Kelley, W.M., Macrae, C.N., Wyland, C.L., Caglar, S., Inati, S., Heatherton, T.F., 2002. Finding the self? An event-related fMRI study. J. Cogn. Neurosci. 14, 785–794.

Lang, P.J., 1980. Behavioral treatment and bio-behavioral assessment: computer applications. In: Sidowski, J.B., Johnson, J.H., Williams, E.A. (Eds.), Technology in Mental Health Care Delivery Systems. Ablex, Norwood, NJ, pp. 119–137.

Leveroni, C.L., Seidenberg, M., Mayer, A.R., Mead, L.A., Binder, J.R., Rao, S.M., 2000. Neural systems underlying the recognition of familiar and newly learned faces. J. Neurosci. 20, 878–886.

Maddock, R.J., 1999. The retrosplenial cortex and emotion: new insights from functional neuroimaging of the human brain. Trends Neurosci. 22, 310–316.

Maguire, E.A., 2001. Neuroimaging studies of autobiographical event memory. Philos. Trans. R. Soc. Lond., B Biol. Sci. 356, 1441–1451.

McCabe, K., Houser, D., Ryan, L., Smith, V., Trouard, T., 2001. A functional imaging study of cooperation in two-person reciprocal exchange. Proc. Natl. Acad. Sci. U. S. A. 98, 11832–11835.

Mitchell, J.P., Heatherton, T.F., Macrae, C.N., 2002. Distinct neural systems subserve person and object knowledge. Proc. Natl. Acad. Sci. U. S. A. 99, 15238–15243.

Morris, J.S., Frith, C.D., Perrett, D.I., Rowland, D., Young, A.W., Calder, A.J., Dolan, R.J., 1996. A differential neural response in the human amygdala to fearful and happy facial expressions. Nature 383, 812–815.

Nakamura, K., Kawashima, R., Sato, N., Nakamura, A., Sugiura, M., Kato, K., Hatano, K., Ito, K., Fukuda, H., Schormann, T., Zilles, K., 2000. Functional delineation of the human occipito-temporal areas related to face and scene processing. A PET study. Brain 123, 1903–1912.

Nakamura, K., Kawashima, R., Sugiura, M., Kato, T., Nakamura, A., Hatano, K., Nagumo, S., Kubota, K., Fukuda, H., Ito, K., Kojima, S., 2001. Neural substrates for recognition of familiar voices: a PET study. Neuropsychologia 39, 1047–1054.

Perrett, D.I., Smith, P.A., Mistlin, A.J., Chitty, A.J., Head, A.S., Potter, D.D., Broennimann, R., Milner, A.D., Jeeves, M.A., 1985. Visual analysis of body movements by neurones in the temporal cortex of the macaque monkey: a preliminary report. Behav. Brain Res. 16, 153–170.

Puce, A., Perrett, D., 2003. Electrophysiology and brain imaging of biological motion. Philos. Trans. R. Soc. Lond., B Biol. Sci. 358, 435–445.

Puce, A., Allison, T., Bentin, S., Gore, J.C., McCarthy, G., 1998. Temporal cortex activation in humans viewing eye and mouth movements. J. Neurosci. 18, 2188–2199.

Puce, A., Allison, T., McCarthy, G., 1999. Electrophysiological studies of human face perception: III. Effects of top-down processing on face-specific potentials. Cereb. Cortex 9, 445–458.

Rossion, B., Schiltz, C., Robaye, L., Pirenne, D., Crommelinck, M., 2001. How does the brain discriminate familiar and unfamiliar faces?: a PET study of face categorical perception. J. Cogn. Neurosci. 13, 1019–1034.

Sergent, J., Ohta, S., MacDonald, B., 1992. Functional neuroanatomy of face and object processing. A positron emission tomography study. Brain 115, 15–36.

Shah, N.J., Marshall, J.C., Zafiris, O., Schwab, A., Zilles, K., Markowitsch, H.J., Fink, G.R., 2001. The neural correlates of person familiarity. A functional magnetic resonance imaging study with clinical implications. Brain 124, 804–815.

Sugiura, M., Kawashima, R., Nakamura, K., Sato, N., Nakamura, A., Kato, T., Hatano, K., Schormann, T., Zilles, K., Sato, K., Ito, K., Fukuda, H., 2001. Activation reduction in anterior temporal cortices during repeated recognition of faces of personal acquaintances. Neuroimage 13, 877–890.

Talairach, J., Tournoux, P., 1988. Co-planar Stereotaxic Atlas of the Human Brain. 3-Dimensional Proportional System: An Approach to Cerebral Imaging. Thieme, Stuttgart.

Todorov, A., Uleman, J.S., 2002. Spontaneous trait inferences are bound to actors' faces: evidence from a false recognition paradigm. J. Pers. Soc. Psychol. 83, 1051–1065.

Winston, J.S., Strange, B.A., O'Doherty, J., Dolan, R.J., 2002. Automatic and intentional brain responses during evaluation of trustworthiness of faces. Nat. Neurosci. 5, 277–283.

Zalla, T., Koechlin, E., Pietrini, P., Basso, G., Aquino, P., Sirigu, A., Grafman, J., 2000. Differential amygdala responses to winning and losing: a functional magnetic resonance imaging study in humans. Eur. J. Neurosci. 12, 1764–1770.