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Research report

Towards a functional neuroanatomy of self processing: effects of faces and words

Tilo T.J. Kircher[a,e,*], Carl Senior[a], Mary L. Phillips[a], Philip J. Benson[d],
Edward T. Bullmore[b], Mick Brammer[b], Andrew Simmons[c], Steven C.R. Williams[c],
Mathias Bartels[e], Anthony S. David[a]

[a]*Department of Psychological Medicine, Institute of Psychiatry and GKT School of Medicine, De Crespigny Park, London SE5 8AF, UK*
[b]*Department of Biostatistics and Computing, Institute of Psychiatry and GKT School of Medicine, De Crespigny Park, London SE5 8AF, UK*
[c]*Neuroimaging Unit, Institute of Psychiatry and GKT School of Medicine, De Crespigny Park, London SE5 8AF, UK*
[d]*University Laboratory of Physiology, Parks Road, Oxford OX1 3PT, UK*
[e]*Department of Psychiatry, University of Tuebingen, Osianderstr. 24, D-72076 Tübingen, Germany*

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Abstract

We studied the neural correlates of self vs. non-self judgements using functional magnetic resonance imaging (fMRI). Individually tailored faces and personality trait words were used as stimuli in three experiments (exp.). In the first two experiments, brain activation was measured while subjects viewed morphed versions of either their own (self face exp.) or their partner's face (partner's face exp.), alternating in blocks with presentation of an unknown face. In the self face exp. right limbic areas (hippocampal formation, insula, anterior cingulate), the right middle temporal lobe, left inferior parietal and left prefrontal regions showed signal changes. In the partner's face exp., only the right insula was activated. In the third exp., subjects made decisions about psychological trait adjectives previously categorized as describing their own attributes. Activation was present in the precuneus, the left parietal lobe, left insula/inferior frontal gyrus and the left anterior cingulate. A reaction time advantage was present when subjects responded to self-relevant words. The main area with signal changes during self-reference processing, regardless of the type of stimulus, was the left fusiform gyrus. The self-relevant stimuli engaged to a differential extent long term and working memory, semantic and emotional processes. We suggest that regions activated by these stimuli are engaged in self-processing.

Theme: Neural basis of behavior

Topic: Cognition

Keywords: Self; Self-recognition; Self-awareness; Familiar faces; Overlearned faces; Limbic system

1. Introduction

Processing of self relevant information and self knowledge is regarded as distinct from processing 'objective' information [30,56]. Self knowledge is stored in two main memory systems, semantic and episodic memory. Episodic memory [61,68] deals with individual ('narrative') episodes that are definable with respect to time and place, whereas semantic memory contains abstracted facts about the world and who we are, which we need for interaction with our environment. It is assumed that different brain regions contribute to these various forms of memory processing [41,62]. In experiments on memory encoding and retrieval it has been shown that relating information to oneself (self-referent effect) enhances recall [5,33,35,54,63]. This phenomenon is largely independent of access to autobiographical narrative memory [34,37]. There is evidence for the relative independence of semantic and episodic autobiographical memory systems, which can each be accessed independently [13,42,70]. The neural systems involved in modality independent self-knowledge are unknown.

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*Corresponding author. Tel.: +49-7071-298-2311; fax: +49-7071-294-141,.
E-mail address: tilo.kircher@uni-tuebingen.de (T.T.J. Kircher).

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A powerful cue for investigating self-information processing is our own face, which we see regularly in the mirror and in photographs. Mirror recognition does not occur in humans before 18 months [1] or in other primates, except adult great apes [21,48]. Self recognition can therefore be considered a complex neurocognititive function. Several recent studies [29,31,65,66] could demonstrate a unique behavioral response towards the subjects' own face, compared to familiar control faces. It is not known, whether there is a distinct anatomical basis of facial self recognition, although severe deficits in this ability have been found in Alzheimer's Disease [7,49] and a larger P300 response to the subjects' own face compared to familiar faces has been reported [46].

In this study, we wished to shed light on the functional anatomy of processing of self relevant information. We wanted to address whether there are distinct cerebral regions underlying the ability to distinguish between self and non-self, a fundamental capacity of biological systems, and whether such a system is engaged regardless of stimulus material (faces or visually presented words).

We used functional magnetic resonance imaging (fMRI) to delineate significant changes in blood oxygenation level dependent contrast as an index of changes in local neuronal activity in the brains of human volunteers. In 2 experiments, we measured localized MRI signal changes while subjects were presented with photos of their own face, their partner's face and unknown faces. In a further fMRI experiment, we investigated semantic self knowledge by visual presentation of personality trait words.

Based on previous PET studies [14,17] and clinical data [32,36,67], we hypothesized that early sensory input regions are activated by self-referring stimuli irrespective of stimulus modality. We predicted that differential effects would be seen for higher order processing, namely greater right hemispheric activation for one's own face [51] (vs. other face) and greater left sided activation for self-descriptive words (vs. non-self descriptive).

2. Materials and methods

2.1. Subjects

Six male, right handed [4] volunteers in stable heterosexual relationships were recruited. All participants were healthy, native English speakers, on no medication and with no history of neurological or psychiatric illness. Only subjects with a generally positive attitude towards themselves and their partner were selected. The mean estimated IQ [45] was 115 (S.D. 5). Neither the subjects nor their partners wore spectacles and none had facial hair. Subjects knew their partners between 1 and 16 years (median 2.7). Informed written consent for participation in the study was obtained in accordance with the declaration of Helsinki. Ethical permission for the study was obtained from the local research ethics committee.

2.2. Construction of stimulus materials

Colored, full face, frontal view photographs were taken of the 6 subjects and their female partners in a photo studio under standardized conditions, 8 weeks prior to the fMRI experiments. The partner's face was chosen as an emotionally salient and overlearned non-self face. A similar looking unknown face, matched for age and sex was paired with each of the self and partner faces. All photos were digitized; the subjects' own faces were mirror-reversed and a black template was applied semi-automatically to remove non-facial attributes such as background, hair and ears. The individual faces were manipulated ('morphed') using a computer warping package with their assigned unknown counterparts in 5% steps [6], resulting in graded blending of facial features between two same-sex identities (see Fig. 1).

In a related behavioral study [75], we could not demonstrate reaction time differences between recognition of unmorphed self and partner faces. The morphing procedure was thus applied, firstly to prevent habituation to the stimuli and secondly to create a slight mismatch between the internal representation of the known faces and the external presentation, ensuring that some attentional processes would be devoted to making the judgements. An alternative to prevent habituation would have been to show the faces from different viewpoint angels. However, Tong and Nakayama [65] as well as Troje and Kersten [66] could show independently, that facial self recognition is viewpoint dependent thus, a manipulated viewpoint would have biased the cognitive processing and presumably cerebral activation.

For the word experiments, subjects judged from a list of 232 adjectives describing personality traits, how well a word described themselves on a 10 point scale ('0' extremely characteristic of me; '9' extremely uncharacteristic), 6 weeks prior to imaging data acquisition. For the rating, the 200 words were taken from Anderson's list [2] which were judged as highly meaningful by their subjects plus an additional 32 words from across the spectrum of likeability were used. Examples were: talented, confident, dishonest, irresponsible, etc. The instructions for the subjects were: 'Does this adjective describe how you typically feel and think about yourself?'

2.3. Experimental tasks and procedures

2.3.1. General setting

The stimuli were arranged in an ABABABABAB design with the known faces or the self describing words in the A condition. The presentation order of the three experiments was counterbalanced across subjects. Each experiment was tailored individually to each subject and consisted of ten

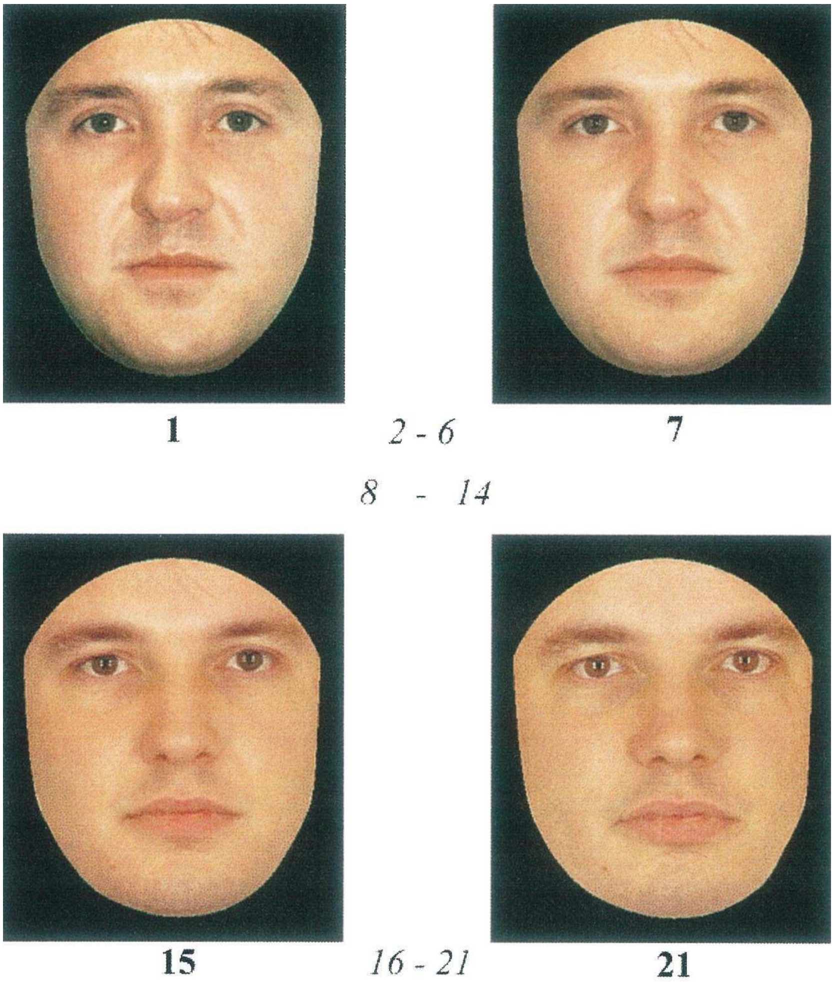

Fig. 1. Examples of a subject's face (No. 1) morphed in 21 steps with an unknown, same sex face (No. 21), resulting in graded blending of facial features between the two identities. Similar pictures were made for the subjects' partner. For experiment 1 and 2, images Nos. 1–7 were used as stimuli for the self resp. partner conditions, and Nos. 15–21 were used for the unknown conditions. Images number 2–6, 8–14 and 16–20 are not displayed here.

separate 30-s presentation phases, alternating between familiar (phase A) and unknown (phase B) stimuli. The stimuli (words or faces) were presented for 2 s each, one at a time, followed by a 1 s blank screen. Subjects indicated their responses to the stimuli by pressing one of two buttons with the right thumb. The accuracy of response and reaction time were recorded for each subject. Stimuli were presented 3.5 m from the subject, subtending visual angles of 10 degrees horizontally and 8 degrees vertically. The tasks were practiced outside as well as inside the scanner with up to six single stimuli for each experiment before data acquisition.

2.3.2. Experiment 1 — 'own face'

For the self vs. unknown experiment, the 7 faces closest to the 'self' endpoint in each series were presented one at a time on a computer screen in a randomized order. This was followed by presentation of 7 faces from the unknown endpoint (non-self) in a similar way. As distracters, 2 faces of the opposite end of the morph spectrum were randomly intermingled into each block to ensure that subjects were attending. They had to indicate by button pressing, whether the identity was self or unknown.

2.3.3. Experiment 2 — 'partner's face'

This experiment was intended to control for overlearning — an aspect known to influence face-recognition. The design was the same as experiment 1, but instead of the own face, the morphed partner's face was shown and instead of the unknown male, the unknown female face was presented. To prevent subjects being surprised by the stimuli, they viewed the endpoints of each morphed series for 15 s in the scanner before the experiment began.

2.3.4. Experiment 3 — 'self descriptors'

The neural correlates of explicit self knowledge of personality traits were investigated. For the verbal self descriptiveness judgement tasks, the words which were previously rated by the subjects were categorized into self describing and non self describing. If a word was given an intermediate value of 4 or 5 on a scale between 0 and 9, it was not used. Each word was only presented once. The stimuli comprised 8 self descriptive personality trait adjectives which were followed by 8 non self descriptive adjectives. Two words of the opposite category were added randomly into each block as distracters to prevent response habituation (i.e. 10 words in total in each block). The words in the two blocks were of approximately similar frequency ($P=0.2$, $z=-1.3$) [38], 'likability' ($P=0.03$, $z=-2.2$) and 'meaningfulness' ($P=0.04$, $z=-2.1$) [2]. It was not possible to match self and non-self words on all of these parameters completely since they reflected the individuals' choice. The subjects had to indicate whether a word was self descriptive or not by means of a button press as in the face experiments.

2.4. Image acquisition

Gradient-echo echoplanar MR images were acquired using a 1.5 Tesla GE Signa System (General Electric, Milwaukee, WI, USA) fitted with Advanced NMR hardware and software (ANMR, Woburn, MA, USA) at the Maudsley Hospital, London. Daily quality assurance was carried out to ensure high signal to ghost ratio, high signal to noise ratio and excellent temporal stability using an automated quality control procedure [60]. A quadrature birdcage head coil was used for RF transmission and reception. In each of 14 non-contiguous planes parallel to the inter-commissural (AC–PC) plane, 100 T_2^*-weighted MR images depicting BOLD contrast [47] were acquired with TE=40 ms, TR=3000 ms, $\theta=90$ degrees, in-plane resolution=3.1 mm, slice thickness=7 mm, slice skip=0.7 mm. Head movement was limited by foam padding within the head coil and a restraining band across the forehead. At the same session, a 43 slice, high resolution inversion recovery echoplanar image of the whole brain was acquired in the AC–PC plane with TE=73 ms, TI=180 ms, TR=16,000 ms, in-plane resolution=1.5 mm, slice thickness=3 mm, slice gap=0.3 mm.

2.5. Image analysis

Rigid body motion in 3 spatial dimensions during fMRI data acquisition was estimated and corrected by a two stage procedure, realignment followed by regression [10]. Periodic change in MR signal intensity at the frequency of the periodic AB input function was estimated by pseudo-generalised least squares (PGLS) fit of a sinusoidal regression model to the movement corrected time series observed at each voxel [11]. PGLS fitting involved modeling the residuals of an ordinary least squares (OLS) fit of the sinusoidal regression model by a first order auto-regressive AR (1) process, transforming the terms of the regression model by the estimated AR (1) coefficient, and refitting the transformed model by OLS. The model included sine and cosine waves at the fundamental frequency of the input function, parameterised by coefficients χ and δ. The sign of χ indicates the timing of signal increase relative to the input function [12]. If $\chi>0$ then the modeled response to the experimental input function will be relatively increased during the first condition. The power of periodic response was estimated by $\chi^2+\delta^2$, and divided by its standard error to yield a standardized test statistic, the fundamental power quotient (FPQ). In order to sample the distribution under the null hypothesis that observed values were not determined by experimental design (with few theoretical assumptions), the 99 images observed in each anatomical plane were randomly permuted and FPQ was estimated exactly as above in each permuted time series. This process was repeated 10 times, resulting in 10 permuted maps of FPQ at each plane for each subject. Observed and permuted FPQ maps were transformed into the standard space of Talairach and Tournoux [64] and smoothed by a 2D Gaussian filter with full width at half maximum (FWHM)=7 mm. The median observed FPQ at each intracerebral voxel in standard space was then tested against a critical value of the permutation distribution for median FPQ ascertained from the permuted maps. For a one-tailed test of size $P<0.002$, the critical value is simply the 100*(1–P)th percentile of the permutation distribution. Generically activated voxels were color coded according to the sign of median χ and superimposed on an inversion recovery EPI dataset to form a generic brain activation map (GBAM) [8].

We used repeated measures analysis of variance to estimate task-related differences in power of functional response at each voxel. The main effect of task was tested for significance by permutation at voxels which demonstrated significant activation by one task or both [10,16].

Subsequently, FPQ data from experiments 1 and 3 were combined and analysed using a linear model to detect effects that were dependent on and independent of the nature of the unimodal components of each contrast.

The model can be expressed as

$$\mathrm{FPQ}_{ij} = \alpha_{0i} + \alpha_{1i}G + \epsilon_{ij}$$

where FPQ_{ij} is the FPQ in the jth individual (i.e. exp. 1 or 3) at the ith voxel in standard (Talairach) space, a_{1i} and a_{0i} are the parameters estimated from the model at the ith voxel and e_{ij} voxel-wise residual error. In the above model, the contrast between experiments 1 and 3 using a group classification variable G is parameterised by a_{1i} at the ith voxel and contrast-independent effects (common to exp. 1 and 3) by $a_{0i.}$ Significant effects were identified by testing the voxel-wise estimates of α_1 and α_0 against null distributions obtained by fitting the above model to the randomized FPQ data (see above). Model parameters with a voxel-wise probability under the null hypothesis of less than 0.001 were identified after computing the appropriate critical threshold values from the null distributions. In identifying effects common to exp. 1 and 3, we discarded any voxels from the activation maps that also exhibited significant contrast-dependent effects (α_{1i}) as these could clearly lead to a significant value of α_{0i} due solely to a strong response in one of the two experiments.

3. Results

3.1. Behavioral data

The behavioral data obtained during scanning are shown in Table 1. Accuracy judgements for both of the face experiments was 99.2%. Reaction time showed delayed response for the known (self, partner) vs. the unknown faces. There was no significant reaction time difference when judgement for the self face was compared with judgement for partner faces or the reaction times for the unknown faces between both experiments.

In exp. 3, the self descriptive traits were judged significantly faster than the non self descriptive traits, accuracy was 85% according to the subjects own ratings 6 weeks previously.

3.2. Generic brain activation mapping

3.2.1. Experiment 1: recognition of own face vs. unknown face

Comparing the presentation of the subjects' own face vs. a morphed unknown face resulted in activation of the right sided expanded limbic system [44], including hippocampal formation (Brodmann area, BA 27), insula, anterior cingulate (BA 24/32), as well as the junction between the right superior/middle temporal (BA 21), left inferior parietal (BA 40) and left middle (BA 8/9) and superior frontal gyrus (45/46). In addition, the right precuneus, the right subthalamic nucleus and the cerebellum, more extensively on the left side, were activated. The results are summarized in Table 2 and Fig. 2, row 1.

3.2.2. Experiment 2: recognition of partner's face vs. unknown face

The comparison of the partner's face versus an unknown woman's face demonstrated significant activation in the right anterior insula only (Table 2 and Fig. 2, row 2) during the partner face condition.

3.2.3. Experiment 3: self descriptions

Table 3 summarizes the areas activated in association with the judgement of self descriptive personality traits (see also Fig. 2, row 3). There are predominantly left sided activations in the precuneus (BA 7), the superior parietal lobe (BA 7), anterior cingulate gyrus (BA 23), cingulum (BA 31) and a region between the junction of the left anterior insula and the inferior frontal gyrus (BA 44). In addition, the left postcentral gyrus (BA 40), putamen and medial geniculate body were activated.

3.3. Common areas activated in the own-face (exp. 1) and self-descriptions (exp. 3) experiments

The own-face minus other-face (exp. 1) and the self-descriptors minus non-self descriptors (exp. 3) experiments were compared (see methods). The resulting activation pattern delineates the areas for self-relevant information processing irrespective of stimulus material. The region most extensively activated was the left fusiform gyrus (BA 19). Also significantly activated were the left precuneus (BA 7), the right lingual gyrus (BA 18/19) and right insula (Table 4; Fig. 3 row A).

3.4. Between experiment differences in power of response

We aimed to compare the two experiments involving explicit judgements of self (exp. 1 and 3) on the basis of their differences in activation pattern. Above we have described areas of common activation. Below we provide a more formal test of the null hypothesis of zero between-experiment difference in mean FPQ by an analysis of variance at each voxel.

3.4.1. Differences between own-face (exp. 1) and partner's-face (exp. 2)

The null hypothesis was tested at the 503 voxels that were significantly activated in one or both of the GBAMs, with the probability of Type I error for each test $a = 0.05$. For this size of test, no more than 25 false positive voxels

Table 1

The mean reaction time from the onset of stimulus presentation to pressing one of 2 buttons is shown. The test of significance refers to the self (exp. 1 and 3) or partner (exp. 2) reaction time versus non-self or non-partner. Accuracy judgement refers to the percentage of correct responses in judging the identity of a face (exp. 1 and 2) and the categorisation of the personality trait words into self or non-self descriptors according to the subjects own judgement 6 weeks prior to the scanning experiment (exp. 3)

	Experiment		
	Own face (exp. 1)	Partner's face (exp. 2)	Self descriptors (exp. 3)
Reaction time (ms); mean (S.D.)	Self: 1069 (100) Non-self: 1000 (80)	Partner: 1092 (97) Non-partner: 1025 (65)	self: 1218 (296) non-self: 1394 (317)
P-value (*t*-value)	0.08 (5.0)	0.02 (3.2)	.05 (2.4)
Accuracy judgement (mean, range, S.D.)	99.2% (98.3–100%, S.D. 0.6%)	99.2% (98.3–100%, S.D. 0.6%)	85% (66–97%, S.D. 13.3%)

Table 2
Areas of significant signal changes during the judgement for self- and partner recognition. The Talairach coordinates of the voxel within each cluster with the largest fundamental power quotient (FPQ) in phase with the 'known' condition are given. Probability of false activation is less than 0.001. The number of voxels refers to the number of contiguous pixels within a cluster

Cerebral region	BA	Side	Tal. *x* (mm)	Tal.*y* (mm)	Tal. *z* (mm)	No. activated voxels	Max. FPQ
Experiment 1: own face versus unknown face							
Anterior and mid posterior Insula	–	R	49	−3	4	50	1.7
	–	R	46	−3	−2	23	1.7
Fusiform gyrus	19	L	−20	−83	−13	34	1.6
Lenticular/subthalamic nucleus	–	R	12	−11	−2	23	1.7
Superior/middle temporal gyrus	21/22	R	49	−3	−7	23	1.7
Inferior frontal gyrus	45/46	L	−32	31	20	18	1.5
		L	−38	31	4	11	1.6
Cerebellum	–	R	9	−47	−18	18	1.6
Anterior Cingulate	24/32		0	6	37	14	1.6
		R	3	36	4	12	1.6
		R	6	42	−2	10	1.6
Supramarginal gyrus/inferior parietal lobe	40	L	−49	−42	31	11	1.6
Precuneus	31	R	6	−64	20	9	1.7
		R	9	−61	26	8	1.6
Middle frontal gyrus	8/9	L	−26	31	37	9	1.6
Hippocampal formation	27/30	R	11	−45	4	7	1.6
		R	12	−36	−2	6	1.6
Experiment 2: partner's face versus unknown face							
Anterior Insula	–	R	26	14	15	5	1.6

are expected over the search volume under the null hypothesis. There were 148 suprathreshold voxels. All the voxels with significantly different FPQ values (Table 4 and Fig. 3, row B) originated from the own-face experiment. These were located in the right insula, hippocampal formation (BA 27/30), lenticular/subthalamic nucleus, middle temporal gyrus (BA 21), and the left sided inferior frontal gyrus (BA 45/46), middle frontal gyrus (BA 8/9), supramarginal gyrus/inferior parietal lobe (BA 40), cerebellum and lingual gyrus (BA 18).

3.4.2. Differences between the own-face (exp. 1) and the self descriptions (exp. 3) experiments

The reason for testing differences in power of activation between these two experiments stems from the hypothesized differences in stimulus processing. The null hypothesis was tested at the 659 voxels that were significantly activated in one or both of the GBAMs, with the probability of Type I error for each test $a = 0.05$. For this size of test, no more than 32 false positive voxels over the search volume are expected under the null hypothesis. There were 164 suprathreshold voxels. Most of the regions with a significant difference in mean FPQ could be demonstrated in the own face experiment (Table 5 and Fig. 3, row C). They comprised the right insula, middle temporal gyrus (BA 21) and cerebellum and left sided inferior frontal gyrus (BA 45/46), middle frontal gyrus (BA 8/9) and the supramarginal gyrus/inferior parietal lobe (BA 40). A greater response for the self descriptors experiment occurred only in the right precuneus (BA 7) (Table 6).

4. Discussion

In the present study, we attempted to map out the neural system involved in self-information processing. In two separate, individually tailored experiments, the subjects' own face and self describing personality trait adjectives were used as stimuli. Irrespective of modality, (face or words) the left fusiform gyrus was activated. Differential signal changes for the own face experiment involved the right limbic system and left prefrontal areas. The regions specialized for analysis of verbal self descriptions are the left superior parietal lobe, anterior cingulate and putamen. Recognition of the partners' face was used in a third experiment, thus controlling for emotional salience and overlearning of a highly familiar face. Activation was only present in the left insula.

In a PET study by Craik et al. [14] subjects had to judge personality trait words according to self-descriptiveness. However, the authors did not tailor their stimuli specifically to each subject. No differences in activation were found when they directly contrasted 'self' with 'other' or 'general' judgements.

Several previous PET and fMRI studies have investigated the brain regions engaged in recognition memory of faces [25–28,59]. However, in these studies subjects had to acquire new information just before or while being scanned. In other related studies, recognition of a number of different famous or unfamiliar faces [24] or objects [22] were contrasted with each other. In our experiments, it is assumed that subjects see their own and their partner's face

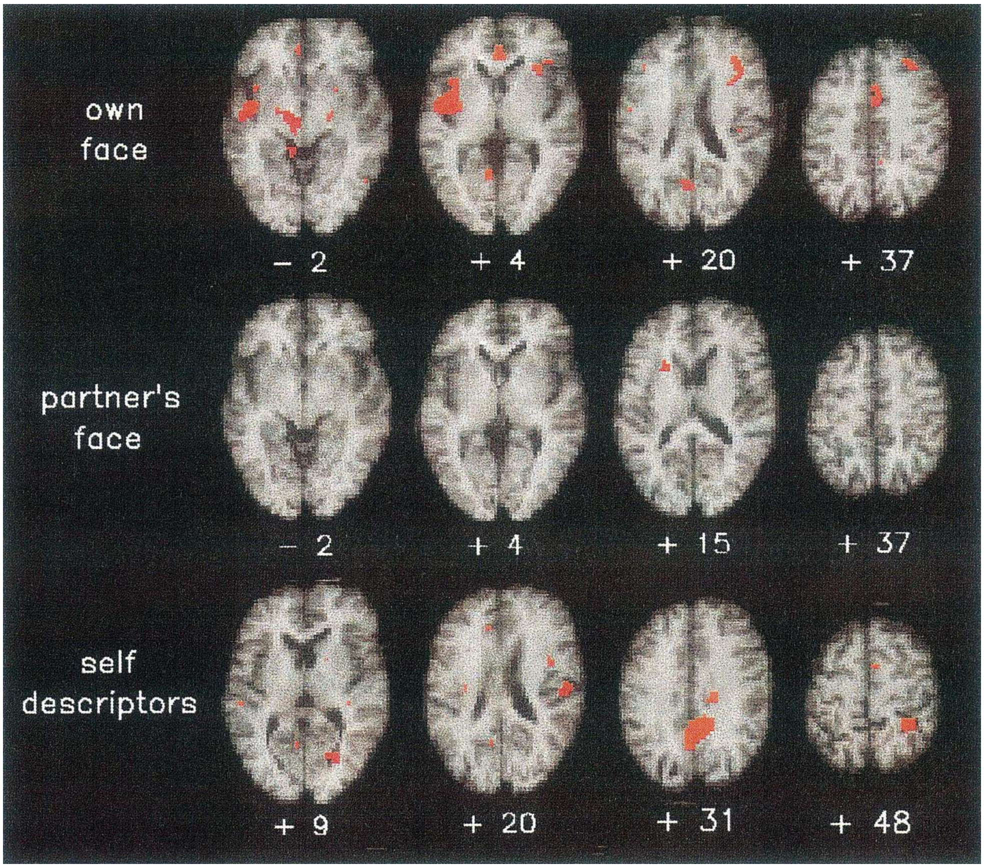

Fig. 2. Generic Brain Activation Maps of the three experiments in 6 right handed normal subjects during judgements for self- (top row) and partner-recognition (middle row) and semantic self knowledge (bottom row). Main regions of signal changes in phase with the self (partner) conditions (probability of false positive activation less than 0.001) are shown superimposed on a high resolution SPGR (Spoiled Grass) image, warped into Talairach space. The numbers below the slices indicate z-axis Talairach coordinates.

on a daily basis. Our interest was not in mere familiarity but rather self-recognition or awareness.

Individuals are assumed to have an abstract and stable self concept over time. This semantic autonoetic ('self-knowing') awareness [71,74] entails a capacity for awareness of knowledge derived from familiarity or other implicit information that can occur in the absence of mentally re-experiencing the encoding episode [40]. Our finding of left fusiform gyral activity modulation in response to both types of self-relevant stimuli (exp. 1 and

Table 3

Regions of significant signal changes as subjects make judgements about personality traits (exp. 3). The Talairach coordinates of the voxel within each cluster with the largest fundamental power quotient (FPQ) in phase with the 'self' condition are given. Probability of false activation is less than 0.001. The number of voxels refers to the number of contiguous voxels within a cluster

Cerebral region	BA	Side	Tal. *x* (mm)	Tal. *y* (mm)	Tal. *z* (mm)	No. activated voxels	Max. FPQ
Experiment 3: judgement of personality traits							
Precuneus	7	L	−6	−53	31	51	1.6
		R	6	−53	37	15	1.6
Superior parietal lobule	7	L	−26	−47	48	13	1.6
Putamen	–	L	−20	0	−7	13	1.6
	–	L	−17	0	4	13	1.6
Postcentral gyrus	40	L	−49	−17	20	12	1.6
Medial geniculate body	–	L	−17	−25	−2	10	1.5
Cingulum	31	L	−23	−67	9	10	1.5
Cingulate Gyrus	23	L	−12	−22	31	7	1.6
Insula/inferior frontal gyrus		L	−38	0	20	5	1.5
Fusiform gyrus	19	L	−24	−75	−13	4	1.6

Table 4
Regions of common signal changes during processing of one's own face (exp. 1) and self referant personality trait adjectives (exp. 3). Talairach co-ordinates refer to the voxel with the maximum FPQ (fundamental power quotient) in each regional cluster. The probability of false activation of each voxel over all six subjects was <0.001

Cerebral region	BA	Side	Tal. *x* (mm)	Tal. *y* (mm)	Tal. *z* (mm)	No. activated voxels	Max. FPQ
Fusiform gyrus	19	L	−26	−69	−13	75	1.7
Precuneus	7	L	−3	−47	31	19	1.6
		L	−6	−44	37	12	1.6
			0	−67	37	9	1.5
		R	9	−64	20	9	1.5
Fornix			0	−11	15	14	1.6
Lingual gyrus	18/19	R	12	−56	4	13	1.6
		R	9	−58	−2	10	1.5
		R	17	−64	−7	12	1.6
Cerebellum		R	32	−56	−18	10	1.5
Insula		R	38	−3	4	8	1.5

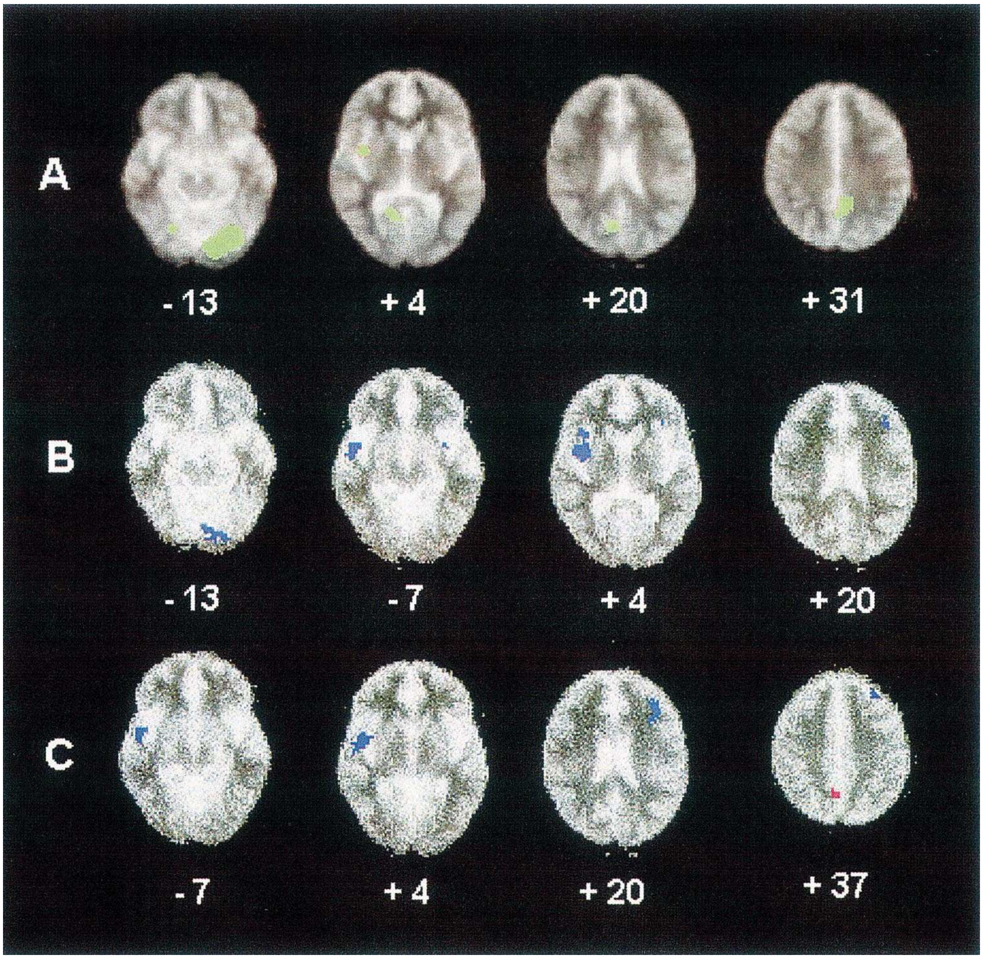

Fig. 3. Row A shows a conjunction analysis of the regions commonly activated during self-referent processing in exp. 1 (own face) and exp. 3 (self-descriptors). Voxelwise probability of Type I error <0.001. Rows B and C show ANCOVA maps with areas of significant response between experiments. Row B shows differences between exp. 1 (own face) and exp. 2 (partner's face). Blue voxels have a greater power of response in exp. 1 (own face). Row C shows differences between exp. 1 (own face) and exp. 3 (self descriptors). Blue voxels have a greater power of response in exp. 1 (own face), red voxels have a greater power of response in exp. 3 (self descriptors). Voxelwise probability of Type I error <0.05.

Table 5
Comparison (ANCOVA) of significant differences in activation during the 'own face' (exp. 1) and 'partner's face' (exp. 2) conditions. Talairach co-ordinates refer to the voxel with the maximum FPQ (fundamental power quotient) in each regional cluster. The probability of false activation of each voxel over all six subjects was <0.001

Cerebral region	BA	Side	Tal. *x* (mm)	Tal. *y* (mm)	Tal. *z* (mm)	No. activated voxels	Max. FPQ
Response: own face>partner's face							
Lingual gyrus	–	L	−14	−81	−13	29	0.7
Cerebellum	18	L	−6	−78	−13	26	0.7
Lenticular/subthalamic nucleus	–	R	12	−11	−2	17	0.9
Middle temporal gyrus	21	R	46	−3	−7	16	0.7
Anterior and mid posterior Insula	–	R	40	−3	4	10	0.7
	–	R	52	−6	−2	8	0.5
Inferior frontal gyrus	45	L	−38	25	20	6	0.6
Middle frontal gyrus	8/9	L	−32	28	37	6	0.6
Supramarginal gyrus/inferior parietal lobe	40	L	−49	−39	31	6	0.5
Hippocampal formation	30	R	9	−36	−2	4	0.5

3) is consistent with this. We suggest that information matching the internal self concept is being implicitly recognized as such, at an early processing level. Thus the modality independent signal changes in the left fusiform gyrus for self referent information. This area was not activated in the partner-face experiment, as we showed in a formal comparison between the self- and partner-face experiments. The internal semantic representation of oneself serves as a facilitator for a self referent stimulus if it matches the stored representation. Evidence for this self-referent facilitation effect comes from several sources. In psychological studies related to ours, subjects were asked to make upper-lower case, semantic and self reference judgements about words. In a later retrieval experiment, the words encoded for judgement of self reference were remembered better [33,35,54,63]. In our testing session 6 weeks prior to the imaging experiment, subjects might have encoded the self descriptive traits better than the non self descriptive ones and therefore were able to recall them faster in the study. On the other hand, we would argue that subjects have an elaborate and stable self-concept, and this serves as an 'internal prime', regardless of previous testing. In our experiments, the reaction times during the scanning procedure showed that subjects responded faster to the self descriptive words. In a recent related experiment, we could demonstrate a reaction time advantage for the perception of one's own face [75], suggesting this facilitation effect. In PET studies of repetition priming, in which participants respond faster to a second presentation of a stimulus, a corresponding modulation in blood flow occurs in the dorsolateral prefrontal cortex and left occipital lobe [9,15,52,57], which is interpreted as reflecting more efficient processing of the previously presented stimuli [20]. Self reference leads to more efficient processing of self as opposed to non-self. This is reflected, we suggest, in the left fusiform signal changes. In line with this interpretation is evidence, that the fusiform gyrus is recruited by expertise in differentiating similar looking objects, which do not have to be faces [22].

Besides common regions for self processing, stimulus dependent signal changes for self-face and self-descriptive words was also revealed. Extensive signal changes in the right limbic system was demonstrated for the self-face experiment. Such lateralised regions are known to be engaged in emotional responses [23,39,50] and a study of autobiographical memory has shown the engagement of

Table 6
Comparison (ANCOVA) of significant differences in activation during the 'own face' (exp. 1) and 'self descriptions' (exp. 3) conditions. Talairach co-ordinates refer to the voxel with the maximum FPQ (fundamental power quotient) in each regional cluster. The probability of false activation of each voxel over all six subjects was <0.001

Cerebral region	BA	Side	Tal. *x* (mm)	Tal. *y* (mm)	Tal. *z* (mm)	No. activated voxels	Max. FPQ
Response: own face>self descriptions							
Anterior and mid posterior Insula	–	R	38	−3	4	17	0.3
Inferior frontal gyrus	45/46	L	−35	22	20	15	0.2
Middle temporal gyrus	21	R	46	−3	−7	14	0.3
Middle frontal gyrus	8/9	L	−32	28	37	6	0.3
Supramarginal gyrus/inferior parietal lobe	40	L	−46	−36	31	6	0.2
Cerebellum	–	R	32	−56	−18	6	0.2
Response: own face<self descriptions							
Precuneus	7	R	9	−50	37	7	

right limbic regions in the recollection of personal memories [17]. Memory retrieval seems unlikely to be solely responsible for the signal changes in of the hippocampal formation or the limbic system in the own-face experiment, since there was little activation present in the partner-face experiment. Moreover, the reaction times for recognizing one's own (1069±100 ms) or the partner's face (1092±97 ms) are not significantly different, the processing effort is thus likely to be similar in the 2 experiments. In a PET study by Tulving et al. [69], right limbic activation was found during encoding of novel stimuli. However, if 'novelty' would be responsible for the signal changes in our experiment, we would see them in both, the 'non-self' and 'non-partner' conditions because also the 'non-partner' face would be novel and the signal changes would be more prominent in the 'non-self' and 'non-partner' condition. However, the modulation of activation we found that in part overlap with the novelty encoding network, were only found during the 'self-face' condition, but not in any of the others. Furthermore, subjects were familiarized with all the stimulus material extensively 6 weeks prior to and through repeated presentation during scanning, thus all the faces were to an extend familiar. We suggest that a rather unique emotional response is evoked by seeing one's own face. Further evidence for this interpretation stems from studies with split brain patients and healthy controls. Both groups showed an increased skin conductance to their own face presented to the right hemisphere than to any other stimulus-visual field combination [51]. The signal changes in the anterior insula in the partner-face experiment could reflect an emotional response to the familiar partner's face. One might speculate that the apparently small activity modulation in the partner's face condition is due to large interindividual associations towards the partner.

The signal changes during the verbal self description experiment in the left parietal lobe and precuneus are in line with the left hemispheric processing of verbal material. We suggest long term memory [19,55,72], and more specifically personal semantic memory [3] processes to be responsible for these signal changes in the precuneus. It should be noted that verbal descriptions are not individual-specific in the same way as the face is. Further work with proper names and more specific personal information would be valuable.

Left lateral inferior and superior frontal regions only showed activity modulation in the self-face experiment, but not in the partner-face experiment. These areas have been characterized as being involved in executive processes such as the integration of information to build up a coherent whole from multi-modal inputs [43,73]. In this case, they might serve to integrate or 'bind' emotional responses and associations about oneself.

This is the first study to date on self recognition using fMRI. Although the group size was small, the careful selection of only male, healthy subjects reduced possible confounding heterogeneity, and facilitated the use of individually tailored stimuli. A morphing procedure was applied to all facial stimuli to reduce habituation. Whether the differences between the self- and partner-face experiments was to some extent heightened by the morphing procedure remains unclear. In fact, some of the subjects reported a slight feeling of depersonalization when confronted with their own but not with the partner's or the unknown morphed face. However even if this was the case, the self reference component is the crucial factor distinguishing the 2 experiments and not the morphing procedure. We cannot rule out the possibility that there are gender differences in the perception of one's partner. However, we know of no data suggesting male and female faces are processed in distinct anatomical regions and a recent study did not show gender differences in self- and parter recognition [75]. Replication with other close persons would nonetheless be desirable. Furthermore, comparative neuroanatomical studies in great apes and humans in light of their ability of mirror self recognition would be interesting. The phylogenetically evolving brain areas could be compared with the findings of our study.

4.1. Clinical implications

The process of autobiographical trait knowledge is of particular interest in patients with retrograde amnesia. It has been hypothesized, that episodic and semantic autobiographical memory can be accessed independently from each other [13,70]. In fact, patients with brain damage [67], concussion [36] or in fugue states [58] have been described, who have lost their memory for past episodes, but who nevertheless can judge their personality accurately. Such judgements about self traits must have been made without explicit reference to trait relevant autobiographical episodes. Further, signal changes in the right fronto-temporal region in the partner face experiment may provide clues towards understanding disorders of misidentification of close associates, such as the Kahlbaum–Capgras and the Fregoli Syndrome, where damage to this structure could be involved [18,53]. The neurobiology of such phenomena will only be understood once the brain regions involved in self- and other-information processing in normal volunteers are more fully mapped out. The current study constitutes a first step in this direction.

4.2. Conclusions

In principle, two different types of neural representation for self relevant information are possible. One of them would be an anatomically and functionally circumscribed 'self-module', supported by generic processes. The alternative is a complex neural integrative process, in which self-relevant information is represented as a specific pattern of signal changes in anatomically distant neuron assemblies.

The anatomical area activated in the self- but not in the partner conditions was the left fusiform gyrus. We argue, that a stable self concept (semantic autonoesis) serves as an internal facilitator for self relevant stimuli. A matching of internal representation and external stimulus may underlie the signal changes in the fusiform gyrus. We demonstrated differential activation, depending on the modality of processing, suggesting the contribution of different cerebral areas in dealing with self referent information, although the stimuli differed in terms of their degree of individual specificity. We propose a tentative framework model based on our findings, for self relevant information processing. Three components are involved, sensory input, memory and emotion, which are capable of processing information on a self-non-self dimension. To evoke explicit self recognition, the same dimensions in all 3 modules have to be activated within a time window. We speculate that long term episodic and semantic memory retrieval processes are important for a continuous representation of oneself over longer periods of time. Self relevant information via sensory input continually refreshes and updates this representation and working memory provides the continuity essential to a feeling of self. A specific emotional component underlies all such processing and may provide the feeling of familiarity and coherence to the sense of self.

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