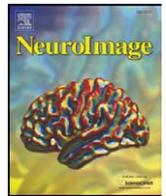




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When I think about me and simulate you: Medial rostral prefrontal cortex and self-referential processes

Roland G. Benoit^{a,b,*}, Sam J. Gilbert^a, Emmanuelle Volle^a, Paul W. Burgess^a

^a Institute of Cognitive Neuroscience and Department of Psychology, University College London, London, UK

^b Medical Research Council, Cognition and Brain Sciences Unit, Cambridge, UK

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ABSTRACT

While neuroimaging studies implicate medial rostral prefrontal cortex (mrPFC) in self-referential processing, simulation accounts of social cognition suggest that this region also supports thinking about other people. This study tested the prediction that mrPFC might be involved in appraising the personality traits of another person to the degree that this person is perceived as similar to oneself. We also examined whether recruiting common processes for thinking about oneself and others might impact on subsequent memory for those judgments. Functional MRI was used while two factors were crossed: (i) the requirement to engage in personality trait or episodic source memory judgments and (ii) the reference for these judgments (i.e., oneself or a friend). The results link haemodynamic changes in mrPFC to both personality judgments about oneself and subsequent episodic memory retrieval of these judgments. The degree to which BOLD signal in this region was also associated with thinking about others correlated with perceived similarity in both tasks, thus corroborating simulation accounts. Moreover, participants who perceived themselves as having similar traits to their friends tended to be poorer at remembering whether they had made trait judgments in reference to themselves or their friend. This behavioral effect was reflected in the BOLD signal in mrPFC: there was a positive correlation between signal change for self versus friend judgments and subsequent memory for the reference of such judgments. The results suggest that investigations of mrPFC activity in the context of self/other judgments should take into account this psychological similarity effect.

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Introduction

An important feature of human experience is to conceive of the self as a more or less coherent entity that persists across time (Gallagher, 2000; Conway and Pleydell-Pearce, 2000). Therefore, one is capable of attributing personality traits to oneself or to identify recollected episodes as memories of one's past. These are examples of self-referential processing. That is, in both cases, the processing subject (i.e., the self) refers to itself.

In recent years, the medial rostral prefrontal cortex (mrPFC; approximating medial aspects of Area 10) has been implicated in a variety of tasks thought to require self-referential processing (Northoff et al., 2006). Some of these asked participants to judge whether personality trait words are descriptive of oneself, and mrPFC activation was stronger when traits were deemed to be more self-relevant (Macrae et al., 2004; Moran et al., 2006). Furthermore, this region tends to be more strongly activated during such judgments

about oneself than about either close friends (D'Argembeau et al., 2007; Heatherton et al., 2006) or famous others (Kelley et al., 2002; D'Argembeau et al., 2005).

Though these studies compellingly link mrPFC with self-referential processing, this region is not exclusively recruited while thinking about oneself. In fact, there is some evidence for comparable activation during trait attributions about either oneself or other people (Ochsner et al., 2005; Schmitz et al., 2004). Therefore, a goal of the present study was to characterize the degree to which mrPFC might also be involved in appraising others. Specifically, predictions from simulation theory were tested: this account posits that one can make inferences about others by referring to knowledge about oneself (Gallese and Goldman, 1998; Frith and Frith, 1999; Mitchell et al., 2005). For example, one could use one's thoughts and feelings to extrapolate what another person might think and feel. Such a strategy, however, is only valid in so far as the self is a good model of the other person. That is, one has to assume that this person is reasonably similar to oneself. In such cases, self-referential processes subserved by mrPFC might also be involved in trait judgments about others (Mitchell et al., 2005). Consistent with this idea, Mitchell et al. (2006) reported more similar activation of this region during mental state inferences about oneself and an unknown person, if this unknown person was thought of as more politically like-minded.

* Corresponding author. MRC Cognition and Brain Sciences Unit, 15 Chaucer Road, Cambridge, CB2 7EF, UK. Fax: +44 1223 359062.

E-mail addresses: r.benoit@ucl.ac.uk, roland.benoit@mrc-cbu.cam.ac.uk (R.G. Benoit).

The present study tested whether mrPFC is also more strongly engaged during trait judgments about personally *known* others in cases of greater perceived similarity. Moreover, we hypothesized that recruiting self-referential processes for similar others may impact on performance on a subsequent episodic source memory task: if trait attributions about the self and a similar friend are subserved by common processes, these shared encoding operations might yield overlapping memory representations for both judgment types (Mashek et al., 2003; Tulving and Thomson, 1973). Hence, remembering the reference of the judgments was expected to be more difficult in case of greater similarity.

The episodic memory task further served the second goal of this study: an integral part of remembering an episode from one's past is the feeling that this memory refers to oneself (Tulving, 2002). Yet, this sense can differ between conditions, and mrPFC has been especially associated with the recollection of memories that entail a pronounced self-referential component (Cabeza et al., 2004; Simons et al., 2008). For example, Hassabis et al. (2007) contrasted recollection of autobiographical experiences and of previously imagined, fictional experiences. Whereas both conditions similarly recruited a widespread network, recollection of autobiographical episodes yielded stronger mrPFC activation. The authors argued that both tasks involved a common process of scene construction. Selective mrPFC recruitment for autobiographical events, in contrast, was proposed to reflect greater self-referential processing of these real-life memories.

To date, the link between activation in this region during episodic memory retrieval and self-referential processing is primarily supported by studies such as those investigating trait judgments (but see also Summerfield et al., 2009). The present study allowed for a more direct test of this account: if mrPFC activation reflects the great self-referential component of recalled memories, this area should also be involved in the successful *retrieval* of trait judgments about oneself. Moreover, consistent with simulation theory, this region should further be recruited during the successful retrieval of trait judgments about others to the degree that the other person is perceived as similar.

The only two previous neuroimaging studies on the retrieval of self-referential trait judgments indeed observed mrPFC activation (Fossati et al., 2004; Lou et al., 2004). In both cases, however, the task used to probe memory did not require any recollection of the actual study episodes (Yonelinas, 2001). Thus, they did not assess whether recruitment of mrPFC was specifically associated with the successful retrieval of self-related information.

Taken together, the present study investigated the contribution of mrPFC to self and other trait judgments and to their subsequent retrieval from memory. Two factors were crossed: (i) the requirement to engage in personality trait or episodic memory judgments and (ii) the reference for these judgments (i.e., oneself or a friend). Specifically, participants alternated between study and test phases, while being scanned by functional magnetic resonance imaging (fMRI). During *study*, they judged the degree to which personality trait words were descriptive of either themselves (*self study* condition) or a close friend (*other study* condition). In a non-semantic control condition, they specified the number of the words' syllables (*syllables study* condition). During *test*, traits were presented that comprised words studied in all conditions plus new words. In the *self test* condition, participants indicated whether they had judged themselves with these traits. Thus, this condition required retrieval of self-referential information. In the *other test* condition, in contrast, they indicated whether they had previously made a judgment with reference to their friend. Accordingly, in the *syllables test* condition participants decided whether they had performed the syllables task. Finally, the perceived similarity to the friend was assessed.

This design addressed the two hypotheses. First, if self-referential processes are more strongly engaged for trait judgments about more

similar others, three findings were predicted: foremost, any difference in mrPFC activation between the self and other study condition should be smaller for those participants who perceive their respective friend as more alike. Furthermore, due to shared encoding operations, it should be more difficult to correctly remember the reference of trait judgments about oneself and a more similar other person. Finally, areas specifically implicated in retrieving self-referential information should be more strongly recruited while retrieving judgments about others in cases of greater similarity. This prediction is further specified by the second hypothesis: mrPFC activation is expected for successful retrieval of self-referential information.

Methods

Participants

Sixteen volunteers participated in this experiment. They were all right-handed, had normal or corrected-to-normal vision and reported good health with no known history of neurological or psychiatric illness. Prior to the experimental session, they gave written informed consent. All participants received £15 reimbursement as approved by the local research ethics committee. Three participants had to be excluded from further analysis either due to chance performance (2) or technical problems (1). Thus, data from 13 participants (5 females; age: mean = 24.2, range = 19.4–31 years) are reported.

Task and procedure

Participants alternated between study and test phases (see Fig. 1). *Study phases* required judgments about visually presented personality trait words. Particularly, in the *self study* condition, participants indicated the degree to which the traits were descriptive of themselves (i.e., "Judge the extent to which you are well characterized by the personality trait words."). They specified their responses by pressing one of four keys with their right hand ("sure yes", "unsure yes", "unsure no", "sure no"). In the *other study* condition, participants made similar judgments about trait words. However, rather than having to relate the words to themselves, they had to judge whether their best friend would be well characterized by these traits. A control condition asked participants to judge the number of *syllables* of the trait words (i.e., two, three, four, or five syllables).

Test phases also consisted of *self*, *other*, and *syllables* conditions. For each condition, participants were presented with a series of traits. Half of these had previously been encountered in the corresponding study condition (subsequently referred to as *old/same* words), whereas the other half had either been shown in the two other study conditions (*old/different* words) or were not yet presented (*new* words). Participants engaged in an exclusion task, giving their response as a confidence judgment on the same four-choice scale as during study. That is, the correct response was "yes" only for *old/same* words, but "no" for both *old/different* and *new* words (see Fig. 1), i.e., participants only had to respond "old", if the word was previously seen in the specified task. For example, they might have encountered "educated" during a *self study* and "modest" during an *other study* phase, before seeing both words again during a *self test* phase. In this case, they would have had to respond "yes" to the *old/same* word "educated" but "no" to the *old/different* word "modest".

A total of 240 words was selected from a list of normed personality trait words (Anderson, 1968), which were randomly allocated to three lists. These were matched for average desirability of the traits and included the same distribution of 2, 3, 4, and 5 syllables words. Pseudo-randomized across participants, each list was assigned to a condition (i.e., self, other, and syllables). At the outset, participants were told to think of someone of the same sex whom they would consider their best friend, and asked for how long

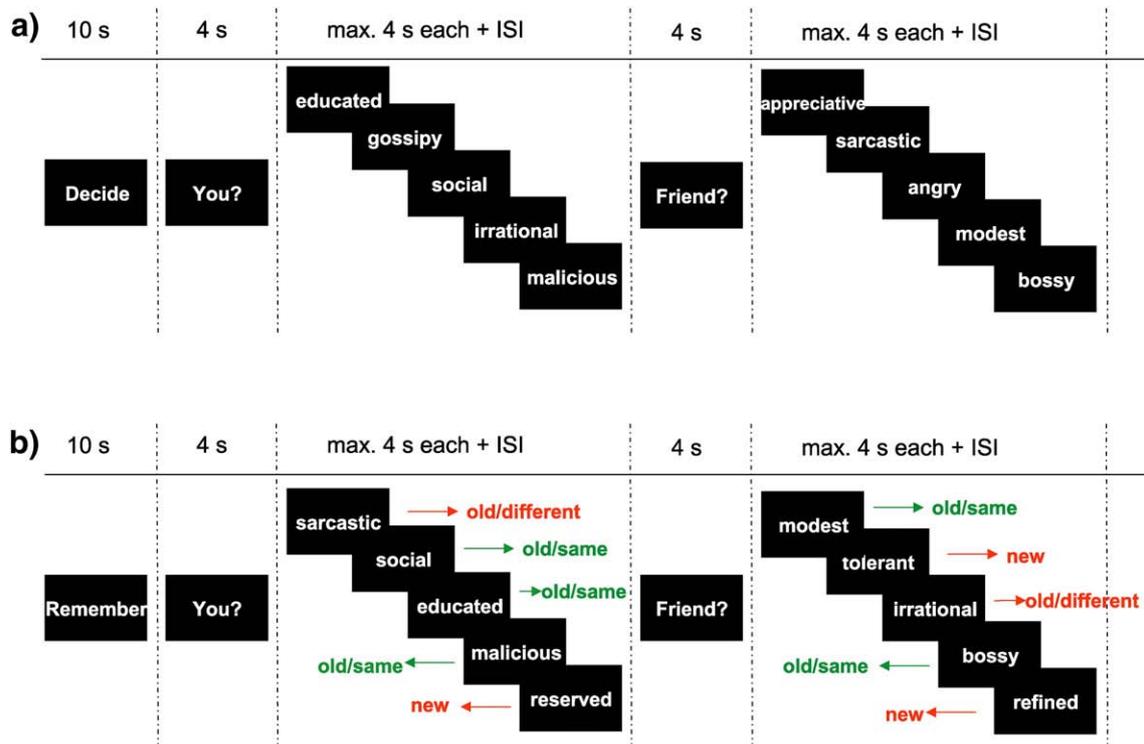


Fig. 1. Illustration of the task design: (a) During study, personality trait words were presented and participants had to indicate the degree to which the respective word was descriptive of either themselves (self study) or a friend (other study). The syllables study condition (not shown) required counting the syllables of the words. (b) For each condition of the test phase (i.e., self; other; syllables (not shown)), words were presented that were either previously encountered in the respective study condition (old/same words) or in the other two study conditions (old/different words) or were not shown before (new words). Participants had to accept only old/same words but reject both old/different and new words. Responses were always given on a four-point scale (sure yes, unsure yes, unsure no, sure no).

they already knew that person. The chosen friend served as the reference for trait judgments in the *other study* condition. Participants then read task instructions and practiced one block of each study and test condition.

The actual session comprised four study-test cycles, which participants performed while being scanned by fMRI. Each study phase started with an instruction for 10 s and comprised three blocks of each condition. These alternated randomly, with the constraint that two blocks of the same condition were not in immediate succession. Each block lasted for 27 s and was preceded by an instruction for 4 s that indicated the current condition. Within each block, 5 trait words were presented for a maximum of 4 s each until a response had been given. At the time of response, the word was replaced by a fixation cross for the remainder of the 4 s. The subsequent inter-stimulus-interval was jittered (mean = 1.4 s; sd = 1.2 s) to maximize the efficiency of event-related analyses of the fMRI data. In total, there were 60 trials in each condition.

Each test phase was preceded by an instruction for 10 s and consisted of four blocks of each condition. The block and trial structure was identical to the study phases. In total, 80 traits were presented in each condition, 50% of which had been encoded in the respective condition, 25% in the two other conditions, and 25% of which had not previously been presented (i.e., 40 old/same, 20 old/different, and 20 new words). Thus, the probability that “yes” is the correct response was 0.5. The mapping of the keys to the order of responses (from “sure yes” to “sure no”) was counterbalanced across subjects. After the scanning session, participants made trait judgments about their friends with all words previously encountered in the *self study* condition. Similarly, they applied all traits from the *other study* condition to themselves. Thus, participants provided both a self- and an other-rating for each trait word. Pearson correlation coefficients between these self and friend judgments served as a measure of the perceived similarity.

fMRI recordings

A 1.5 T Siemens Avanto MRI scanner was used for interleaved acquisition of T2*-weighted echoplanar images sensitive to BOLD contrast (64 × 64; 3.5 × 3.5 mm pixels; TR: 2.5 s; TE: 40 ms; flip angle 90°). The brain was covered by volumes that comprised 33 axial slices (3.5 mm thick, oriented to the AC–PC plane), omitting the cerebellum and inferior aspects of the occipital lobes. For each of the four study-test cycles a separate functional scan of 274 volumes was acquired, of which the first 4 volumes were discarded to allow for T1 equilibration effects. Stimuli were projected on a mirror in view of the participant. Additionally, T1-weighted structural images were acquired (256 × 224; 1 mm³ cubic voxels; 160 slices; TR: 12 ms; TE: 5.6 ms; flip angle 19°).

Data analysis

Behavioral analysis

For study phases, response times were analyzed for all conditions (i.e., self, other, syllables); for the syllables task also the accuracy was assessed. For test phases, response times and percentage of correctly identified words were analyzed as a function of condition and separately for old/same, old/different, and new words (Fig. 1). Statistical analyses used repeated-measures analyses of variances (ANOVA), applying Greenhouse–Geisser adjustments for non-sphericity when appropriate.

fMRI analysis

fMRI data were analyzed using SPM5 (<http://www.fil.ion.ucl.ac.uk/spm/software/spm5/>). The four sessions were concatenated, and the volumes were corrected for different slice acquisition times, realigned, and co-registered with the structural images. These were spatially normalized and the resulting parameters served to

normalize the functional images into 2 mm³ cubic voxels by 4th-degree B-spline interpolation (using the Montreal Neurological Institute reference brain). The images were then smoothed by an isotropic 8 mm FWHM Gaussian kernel.

The variance in BOLD signal of the time series was decomposed in a general linear model (Friston et al., 1995). Transient activation associated with correctly-responded words was modeled by delta functions (coding for word onsets). This was done separately for the three conditions during study (i.e., self study, other study, syllables study), and separately for the nine combinations of condition (i.e., self test, other test, syllables test) and word type (i.e., old/same, old/different, new) during test. In addition to these 12 regressors of interest, further delta functions coded for trials of incorrect or missing responses during study or test. Furthermore, a nuisance regressor was included to model the transitions between sessions in the concatenated data. Moreover, boxcar regressors coded separately for the instruction periods of the study and test phases and for the block instructions. These regressors were all convolved with a canonical haemodynamic response function. Finally, to control for different session means of the concatenated data, three of the four sessions were modeled by individual boxcar regressors. The full model additionally comprised regressors representing the mean over scans and residual movement artifacts. A 1/128 Hz high-pass filter was applied to the data and the model.

Parameters for each regressor were estimated from the least-mean-squares fit of the model to the data. Effects of interest were assessed in a random effects analysis as follows. For study phases, three contrasts were performed, each individually assessing the variance explained by the regressors representing each of the three conditions of interest (*self_study*, *other_study*, *syllables_study*). Similarly, for test phases also separate contrasts were performed for each condition. To specifically assess variance explained by the successful retrieval of old/same words, parameter estimates for this word type were contrasted with the respective estimates for correctly-rejected new words (i.e., old/same > new) (Rugg and Wilding, 2000), yielding three contrasts (*self_test*, *other_test*, *syllables_test*).

For second level analyses, the six contrasts from each individual were entered into a repeated-measures ANOVA using non-sphericity correction (Friston et al., 2002). In addition, to assess the influence of perceived similarity between participants and their respective friends on brain activation, two *t*-tests were calculated. One of these was based on the individual contrasts comparing *self_study* and *other_study*. The second one was performed with the *other_test* (i.e., old/same > new) contrasts of each subject. Both of these tests included the similarity measures as a covariate. This allowed to investigate the modulation (i.e., the interaction) of the particular contrast (i.e., [self_study > other study] or *other_test*) by the perceived similarity.

Finally, a separate GLM examined whether brain activation was parametrically modulated by response type. Therefore, responses (i.e., “sure no”, “unsure no”, “unsure yes”, “sure yes”) were recoded to numerical values (i.e., -1.5, -0.5, 0.5, 1.5). These values were used to specify additional regressors that coded for linear effects of a response type in each of the 12 conditions. One subject had to be excluded from this analysis, since she gave only high confident responses for old/same words in the self condition. All statistical parametric maps (SPM) were thresholded at an uncorrected α of 0.001 with a minimum cluster size of 10 contiguous voxels.

Results

Behavioral results

Self–other similarity

The duration that participants knew each other was variable, ranging from 9 months to 23 years (median: 84 months). Pearson correlation coefficients between self and other judgments were

positive except for two participants (median r : 0.43, range: -0.33–0.76). This similarity measure was not significantly correlated with the duration of the friendship (Spearman's ρ : -0.33, $p = 0.271$).

Study phase

Response times appeared to be shorter for trait than for syllable judgments (Table 1), though the effect was only significant for the comparison of self and syllables judgments ($t(12) = -2.62$, $p < 0.05$; other versus syllables: $t(12) = -1.85$, $p < 0.09$; self versus other: $t(12) = -0.72$, $p = 0.49$). Visual inspection of the frequency of the responses types for the trait judgments suggested a tendency for choosing the two middle (“unsure”) options. This was corroborated by an ANOVA with the factors reference (self, other) and response type (“sure yes”, “unsure yes”, “unsure no”, “sure no”) that yielded a main effect of response type ($F(3,36) = 8.72$, $p < 0.001$). Follow-up tests revealed a lower frequency of “sure” than of “unsure” responses in the self-reference condition (all $|t| > 2.2$, all $p < 0.05$). For the other-reference, only the comparison of “sure yes” and “unsure yes” was significant ($t(12) = -2.9$, $p < 0.05$). Finally, participants' responses in the syllables task were consistently above chance (mean: 78.14%, SD: 16.9; $t(12) = -11.33$, $p < 0.001$).

Test phase

Results for the test phases are summarized in Table 2. The data suggest more accurate performance in the self than in the other condition, which, in turn, yielded higher percent correct values than the syllables condition. Moreover, across conditions, participants responded correctly more often to new than to both old/same and old/different words. These impressions were supported by statistical analyses: an initial ANOVA with the factors reference and word type (old/same, old/difference, new) revealed both main effects (reference: $F(2,24) = 39.77$, $p < 0.001$; word type: $F(2,24) = 19.02$, $p < 0.001$). Following up the former main effect yielded significant differences between all reference conditions (self versus other: $F(1,12) = 4.88$, $p < 0.05$; self versus syllables: $F(1,12) = 59.16$, $p < 0.001$; other versus syllables: $F(1,12) = 49.54$, $p < 0.001$). Comparing the different word types indicated a greater percentage of correct responses for new words than for both old/same ($F(1,12) = 33.74$, $p < 0.001$) and old/different ($F(1,12) = 36.31$, $p < 0.001$) words.

Interestingly, there was indeed a strong trend for a negative correlation between the similarity measure and the percentage of correctly identified old/same words in both the self ($r = -0.55$, $p = 0.05$) and the other ($r = -0.54$, $p = 0.06$) condition. Thus, participants who perceived their friends as more similar were likely to be worse at retrieving the reference of the trait judgments. In contrast, there was no such association for the syllables condition ($r = 0.01$, $p = 0.98$).

An ANOVA on the response times revealed main effects for both reference ($F(2,24) = 10.29$, $p < 0.001$) and word type ($F(2,24) = 22.59$, $p < 0.001$). The interaction was also significant ($F(4,48) = 5.88$, $p < 0.005$). As indicated by follow-up analyses, this reflected an effect of reference for old/same words only ($F(2,24) = 59.16$, $p < 0.001$). For this word type, responses were faster in the self than in both the other

Table 1

Mean and standard error of the mean (SEM) for response times, and frequency of the responses “sure yes” (s yes), “unsure yes” (u yes), “unsure no” (u no), and “sure no” (s no) during study.

	Response times		Frequency							
	Mean	SEM	s yes		u yes		u no		s no	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
Self	1966	79	11.5	1.6	18.8	1.9	19.4	2.0	9.3	1.5
Other	1997	102	10.8	1.5	16.8	0.8	17.5	1.8	13.6	1.5
Syllables	2169	92	n/a							

Table 2

Mean and standard error of the mean (SEM) for percent correct values and response times (ms) during test.

		Percent correct		Response times	
		Mean	SEM	Mean	SEM
Self	Old/same	82.2	2.5	1627	55
	Old/different	72.7	3.1	1891	74
	New	93.5	1.3	1695	88
Other	Old/same	74.2	3.2	1821	92
	Old/different	76.2	3.4	1951	93
	New	89.4	2.5	1680	96
Syllables	Old/same	63.5	3.1	2004	93
	Old/different	64.8	3.8	1983	79
	New	85.6	3.1	1753	99

($t(12) = -4.59$, $p < 0.001$) and the syllables ($t(12) = -6.02$, $p < 0.001$) condition. Response times in the other condition were also shorter than in the syllables condition ($t(12) = -2.89$, $p < 0.05$).

fMRI results

Study phase

Common activation for self and other trait judgments. The aim of the study phase was to examine whether self-referential trait judgments are associated with activation in mrPFC, and whether this region might also be involved in judging similar friends. Contrasting both trait judgment conditions (i.e., self and other) with the syllables task revealed a largely overlapping, left-lateralized network of brain regions (see Table 3, Fig. 2). These included extensive aspects of the medial surface of the prefrontal cortex, bilateral inferior frontal cortices, and both anterior and posterior cingulate. Bilateral inferior temporal cortices and more superior aspects of the temporal lobes and of the left occipital cortex were also more strongly activated during trait judgments. The other-reference condition additionally recruited the medial temporal lobes bilaterally.

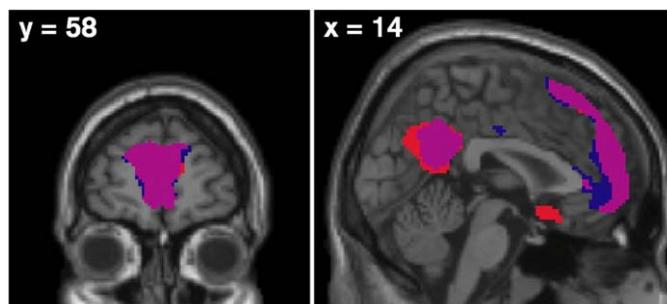


Fig. 2. Regions showing greater BOLD signal increase during trait judgments about the self (blue) or about the other person (red) than during syllables judgments. The two contrasts (i.e., self study>syllables study and other study>syllables study) yielded BOLD signal increases in extensively overlapping areas as indicated in purple. The SPM is thresholded at $p < 0.001$, uncorrected, with a minimum cluster size of 10 contiguous voxels. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Differential activation for self versus other judgments. Although both trait judgment tasks were associated with activation in a common cluster of brain regions, the two conditions differed in the strength of the activation in some of these areas (see Table 4). Compared with the self-reference condition, trait judgments about a friend were associated with stronger activation of the posterior cingulate/precuneus, and inferior lateral aspects of bilateral temporal lobes. This contrast also revealed stronger activation around the ventral anterior cingulate, which was not part of the commonly recruited network. The reverse contrast (i.e., self>other) indicated that some parts of this network were more strongly activated for self than for other judgments. In particular, judgments about oneself were associated with stronger activation of the anterior cingulate, bilateral inferior frontal cortices, and superior and medial aspects of the right inferior temporal lobe. Additionally, self compared to other judgments recruited parts of right rostrolateral PFC, bilateral inferior parietal lobes, and the right insula.

Table 3

Regions showing significant differences in BOLD signal between conditions ($p < 0.001$, uncorrected, cluster size min. 10 contiguous voxels). Brodmann areas (BA) are approximate.

Study contrasts	Region	Side	BA	MNI (peak)			Cluster size	z	
				x	y	z			
Self>syllables	Superior and medial frontal gyri	b	8/9/10	-8	36	52	5901	>8	
	Inferior frontal cortex	r	45/47	50	30	-8	286	5.12	
		l	47	-48	28	-8	4009	>8	
	Inferior and middle temporal cortex	l	20	-50	-2	-32		>8	
	Inferior and middle temporal cortex	r	20/21	68	-10	-20	485	5.05	
	Cingulate cortex	b	23/24	-2	-12	36	56	4.41	
	Posterior cingulate cortex/precuneus	b	23/30/31	-6	-50	24	1679	6.28	
	Superior temporal lobe	l	39	-44	-56	26	2040	7.53	
		r	39	58	-64	24	434	5.34	
	Superior occipital lobe	l	19	-10	-92	24	12	3.36	
	Other>syllables	Medial frontal gyrus	b	10	0	60	14	4654	6.83
		Superior and medial frontal gyri	b	9	-12	56	28		6.89
			b	8	-8	36	52		7.76
Anterior cingulate cortex		b	24/23	6	38	4	31	3.32	
Inferior frontal cortex		r	47	46	30	-16	139	4.84	
		r	47	30	22	-22		3.42	
		r	45	58	26	4	14	3.61	
		l	47	-48	28	-8	3260	8.22	
Middle and superior temporal cortex		l	21/38	-46	10	-30		>8	
Anterior cingulate cortex/subcallosal gyrus		b	25	0	12	-12	136	4.85	
Middle and inferior temporal cortex		r	21/20	48	2	-32	847	4.85	
		r	21	64	-2	-16		5.98	
Medial temporal lobe		r		26	-14	-16	32	3.66	
		l		-20	-10	-14	13	3.49	
Posterior cingulate cortex/precuneus		b	23/31	-4	-52	24	2200	7.68	
Superior temporal lobe	l	39/40	-48	-58	26	2009	>8		
Superior and middle temporal cortex	r	39	58	-64	24	703	6.11		
Superior occipital lobe	l	19	-12	-94	22	14	3.42		

Table 4
Regions showing significant differences in BOLD signal between conditions ($p < 0.001$, uncorrected, cluster size min. 10 contiguous voxels). Brodmann areas (BA) are approximate.

Study contrasts	Region	Side	BA	MNI (voxels)			Cluster size	z
				x	y	z		
Self > other	Middle and superior frontal cortex	r	10	26	50	26	16	3.32
	Anterior cingulate cortex	b	32	-12	34	26	127	4.02
	Inferior frontal cortex	l	46	-42	32	10	29	3.87
		r	45/47	46	28	4	33	3.79
	Superior temporal lobe	r	22/38	52	10	-6	11	3.82
	Inferior frontal lobe	r	9	42	4	24	81	4.00
	Insula	r	13	34	4	6	17	3.57
	Middle temporal lobe	r	21	38	-4	-34	11	3.39
	Basal ganglia	b		-32	0	2	31	3.57
	Diencephalon	b		0	-2	18	16	3.82
	Inferior parietal lobule	r	40	62	-36	40	177	4.12
		l						
	Other > self	Anterior cingulate cortex	b	25	0	14	-12	30
Middle and superior temporal cortex		l	21	-48	12	-32	18	3.57
Middle and inferior temporal cortex		r	21	66	-2	-14	83	3.97
		r	21	60	-4	-24		3.64
Posterior cingulate cortex/precuneus		b	31	2	-54	28	586	4.85

Taken together, trait judgments in both reference conditions were subserved by a largely common cluster of brain regions that did include the medial PFC. Though self and other judgments differed in the strength of activation in some of these areas, there was no evidence for selective recruitment of mrPFC for the self-reference condition.

Differences for self versus other judgments modulated by similarity.

As a next step, we examined whether any activation varied between the two reference conditions with the degree of perceived self-other

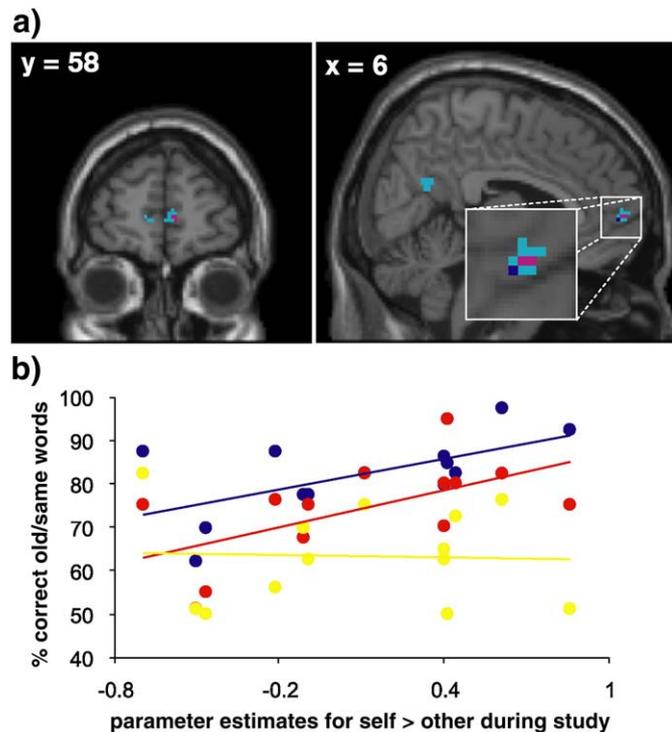


Fig. 3. (a) Regions showing less BOLD signal increase for the contrast of self and other trait judgments in case of greater perceived self-other similarity (blue), and regions yielding greater BOLD signal increase during self judgments in case of greater self-relevance of the trait word (cyan). The overlap between both contrasts is depicted in purple. The SPM is thresholded at $p < 0.001$, uncorrected, with a minimum cluster size of 10 contiguous voxels. (b) Across participants, the BOLD signal difference between self and other trait judgments in mrPFC was predictive of the percentage of correctly identified old/same words for both the self (blue) and other (red) but not for the syllables (yellow) test condition. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

similarity (Mitchell et al., 2005, 2006). Specifically, the prediction was tested that a difference in mrPFC activation is greater for participants who perceive themselves as less similar to their friends. To identify any brain regions that would show such an effect, a SPM was computed based on the negative interaction between (i) the contrast of self versus other-reference and (ii) the similarity measure. As expected, this analysis revealed activation in mrPFC ($x, y, z: 6, 58, 4; z = 3.48; BA10; Fig. 3a$). This effect was not significant for any other brain region apart from a cluster in right lateral PFC ($50, 20, 24; z = 3.58; BA46/9$). Thus, these areas showed less activity for contrasting self with other judgments to the extent that the other was perceived as more similar.

mrPFC and episodic memory performance. Since participants who perceived themselves as more similar to their friends (i) recruited mrPFC to a more similar degree for both self and other judgments and (ii) tended to be worse at attributing the reference of previous trait judgments, we examined whether mrPFC activation for self versus other judgments was correlated with subsequent memory performance. For each subject, parameter estimates for the contrast of self and other judgments were extracted from a region-of-interest (ROI; 5 mm radius sphere). This ROI was centered on the mrPFC peak activation from the interaction between the contrast of the two trait judgment tasks and the similarity measure. The mean estimate was then correlated with the percentage of correctly identified old/same words for each of the three test conditions (i.e., self, other, syllables). This analysis revealed significant positive correlations between (i) mrPFC activation at study for self versus other judgments and (ii) successful retrieval of both types of trait judgments (self: $r = 0.61, p < 0.05$; other: $r = 0.59, p < 0.05$) but not of syllable judgments ($r = -0.04, p > 0.89$) (Fig. 3b).¹ Thus, the more mrPFC was selectively associated with self judgments, the better was the subsequent memory for the actual reference of the trait judgments.

Parametric modulation by the degree of self-relevance. Finally, we tested whether mrPFC activation during self judgments is modulated by the degree of self-relevance of the particular personality traits. Therefore, estimates of the parametric regressor were analyzed that coded for a linear effect of response type (from “sure no” to “sure yes”). Amongst others, this analysis identified two clusters in mrPFC

¹ Note that the ROI was defined by a contrast that did not examine memory performance data. However, as expected, there were trends for negative correlations between the similarity measure and memory performance in the self and other conditions. Thus, the respective correlations with mrPFC activation might reflect this shared variance.

(6, 58, 4; $z=3.7$; $-6, 60, 2$; $z=3.42$; both BA10). Intriguingly, the peak of the bigger cluster was identical to the one shown to be more strongly activated for self than for other judgments in case of less perceived similarity (Fig. 3a). An analogous analysis of the other judgments, in contrast, did not reveal any mrPFC activation.

To summarize, mrPFC seems to be involved in making trait judgments both about the self and a close friend. However, the lesser the other person was perceived as similar on these personality traits, the more this region was selectively recruited during “self” judgments. Activation in the same subregion of mrPFC also increased within individuals to the degree that the words were considered self-descriptive.

Test phase

The aim of the test phase was to examine whether medial PFC is particularly involved in the successful retrieval of self-referential information. Analyses therefore focused on the contrasts of old/same and new words, since these contrasts reveal brain regions associated with successful retrieval (Rugg and Wilding, 2000). These contrasts (old/same>new) were compared between the three reference conditions (self, other, syllables) to examine brain activation specific to the retrieval of the respective reference.

Successful retrieval of self judgments. The self compared with the syllables condition was associated with greater activation in two clusters within medial PFC. As predicted, one of these was located in rostral aspects of ventromedial PFC (14, 50, -8 ; $z=4.01$; BA10). The other one was situated more caudally in orbitofrontal PFC (0, 28, -12 ; $z=3.72$; BA11) (see Fig. 4a). In contrast, the other compared with the syllables condition was associated with greater activation in the basal ganglia only ($-22, 14, 12$; $z=3.79$). Thus, only retrieval of self-referential judgments yielded activation in mrPFC.

Contrasting the other with the self condition revealed stronger activation in the right medial temporal lobe, the left inferior frontal cortex (BA46), and aspects of the left middle frontal gyrus. The reverse contrast was associated with a number of regions including the right inferior frontal cortex (BA47), left medial temporal lobe, midbrain structures, and dorsal medial PFC. However, this direct comparison did not yield greater mrPFC activation for the self condition.

As a post hoc test, we assessed whether the self compared with the other condition was associated with greater activation in the area that was more active for the successful retrieval of self than of syllables judgments. A small-volume-correction around this region (5 mm radius sphere) was applied for the self versus other contrast. Family-wise-error corrected, this analysis was significant (peak: 18, 48, -10 ; $z=3.3$, $p<0.02$), suggesting that mrPFC was particularly involved in the retrieval of self judgments.²

Taken together, successful retrieval of self-referential information was selectively associated with recruitment of mrPFC. That is, only during the retrieval of self judgments was activation in this region greater than during the retrieval of syllables judgments. Moreover, small-volume-corrected, mrPFC activation was also observed for the direct contrast of the self and other condition.

Successful retrieval of other judgments as modulated by similarity.

Next, the prediction was tested that mrPFC activation associated with the successful retrieval of other judgments is greater for those participants who perceive their respective friend as more alike. Two approaches were taken: first, for each subject, estimates of the other

² One might object that the contrast under investigation (i.e., self_test>other_test) is not independent from the one used to derive the ROI (i.e., self_test>syllables_test). Therefore, we repeated the analysis using the orthogonal comparison of the averaged self and other conditions against the syllables condition to construct the ROI (i.e., self_test and other_test>syllables_test). This approach led to the same result. That is, the effect was still found, even when the ROI was defined independently of the contrast under investigation.

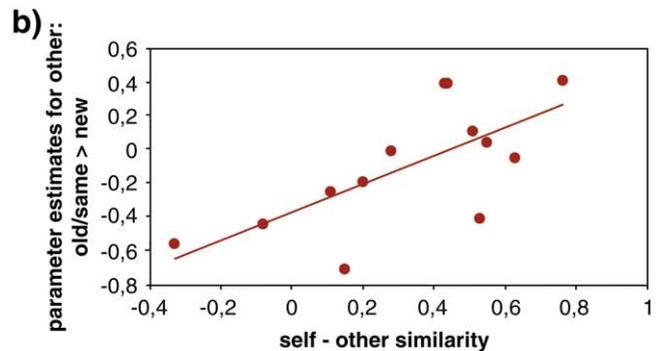
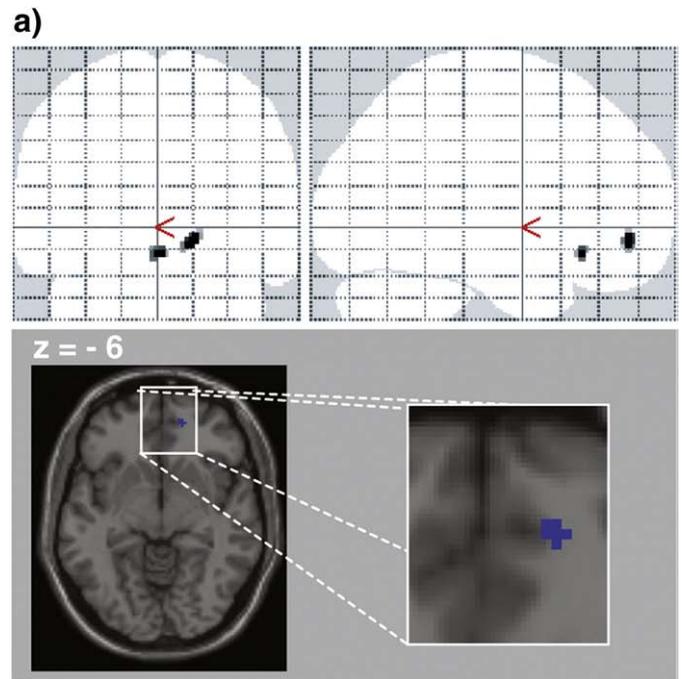


Fig. 4. (a) Regions showing greater BOLD signal during the successful retrieval of self trait judgments than of syllables judgments. The SPM is thresholded at $p<0.001$, uncorrected, with a minimum cluster size of 10 contiguous voxels. (b) The more similar the other person was perceived of, the greater was the BOLD signal in mrPFC also during the successful retrieval of other trait judgments.

test contrast (i.e., old/same>new) were extracted from a ROI (5 mm radius sphere) within mrPFC. The ROI was centered on the peak of the orthogonal contrast that compared successful retrieval of self and syllables judgments (see above). These data were then correlated with the similarity measure, which indeed resulted in a positive correlation ($r=0.692$, $p<0.01$) (see Fig. 4b). Thus, the area specifically involved in remembering self judgments was more strongly activated during the successful retrieval of other judgments, if the other person is thought of as more similar. Secondly, the prediction was also tested by calculating an unbiased SPM of the positive interaction between (i) the successful retrieval contrast for the other condition (i.e., old/same>new) and (ii) the similarity measure. This map reveals any regions that are more strongly activated while retrieving judgments about more similar others. The analysis identified two significant clusters, both of which were part of rostral PFC. One of these was situated in lateral aspects of rostral PFC (28, 48, 24; $z=4.3$; BA10). As predicted, the other one was located in mrPFC (8, 54, -6 ; $z=3.49$; BA10).

Parametric modulation of mrPFC activation by confidence. Finally, if mrPFC is associated with the recollection of memories that entail more self-referential information, one might expect greater activation

for high-confidence (i.e., sure) responses to old/same words in the self condition. That is, these responses are likely to be associated with recollection of more self-referential details than the unsure responses. To test this prediction, we examined whether activation was parametrically modulated by the degree of confidence in the judgments. Amongst others, this analysis revealed slightly more caudal aspects of ventromedial PFC (0, 46, -4, $z = 3.73$). In contrast, no such effect was found in mrPFC for the other test condition.

Discussion

Two issues were addressed in this study. First, we examined whether mrPFC is differentially engaged during judgments about personality characteristics of similar versus dissimilar others (Mitchell et al., 2006). Importantly, this study additionally investigated whether recruiting self-referential processes for thinking about others might influence subsequent source memory performance. Second, we investigated whether mrPFC is also activated during the successful retrieval of self-referential information. Thus, the hypothesis was tested that recruitment of this region during episodic retrieval reflects the self-referential component of the memories (e.g., Cabeza and St Jacques, 2007). The discussion will first focus on those brain regions associated with personality trait judgments before concentrating on the involvement of mrPFC in successful episodic memory retrieval.

Common and dissociable brain regions for self and other trait judgments

Making personality trait judgments about oneself and a close friend was associated with recruitment of a largely overlapping cluster of brain regions. These included areas thought to be generally involved in semantic retrieval (i.e., ventral temporal cortices) and in the selection of semantic knowledge (i.e., left inferior frontal cortex) (Thompson-Schill, 2003). Moreover, both types of trait judgments recruited the posterior cingulate/precuneus as well as extensive aspects of medial PFC (including mrPFC, see below). These are all regions that have previously been implicated in self-reflection (e.g., Gusnard et al., 2001; Johnson et al., 2006) and in mental state inferences about others (Amodio and Frith, 2006).

Though recruiting this common cluster of brain areas, the two trait judgment tasks activated its components to different degrees. Trait judgments about friends were associated with, for instance, greater activation of the posterior cingulate/precuneus. Previous evidence has linked this region with taking the perspective of another person (Jackson et al., 2006), and adopting a more externally-directed focus (Johnson et al., 2006). This condition was also associated with recruitment of bilateral medial temporal lobes, which have been implicated in evidence-based (as compared to intuition-based) trait judgments (Lieberman et al., 2004).

When, on the other hand, participants made judgments about themselves, activation was stronger in the right insula, thought to be involved in introspecting on one's feelings (Fossati et al., 2003; Silani et al., 2008). Self judgments were also associated with greater activation of right lateral rostral PFC. This region has previously been implicated in the recognition of one's face (Platek et al., 2006) and in self-reflection (Ochsner et al., 2005; Schmitz et al., 2004). More generally, lateral rostral PFC has been suggested to bias attention towards internally-generated information (Burgess et al., 2001, 2007a; Christoff et al., 2001).

mrPFC and trait judgments: similar others and self-descriptiveness

The first goal of this study was to examine whether self-referential processes subserved by mrPFC are involved in judging similar others. The current study provides support for this simulation account (Mitchell et al., 2006). Though there was no overall difference in

mrPFC activation for trait judgments about the self and another person, this region was associated with an interaction between this contrast and the similarity measure. Specifically, the more the other was perceived as similar to oneself, the stronger recruited was mrPFC during judging this person. An analogue pattern *within* subjects has previously been reported: Mitchell et al. (2006) observed comparable mrPFC activation for inferences about the self and an unknown person who was thought of as having similar political attitudes. In contrast, inferences about another unknown, who was perceived as having opposing political views, were associated with less activation. Moreover, a recent study examined cultural differences in the neural correlates of judgments about oneself and one's mother (Zhu et al., 2007). Whereas Westerners showed greater mrPFC activation for self than for mother judgments, there was no such difference in the Chinese sample (who were argued to more strongly include their mothers in their self concept). Thus, there has been support for the simulation prediction both within individuals (Mitchell et al., 2005, 2006) and between cultural groups (Zhu et al., 2007). The current study complements this pattern by revealing that mrPFC recruitment for self versus other judgments can also vary as a function of perceived similarity across members of a relatively homogenous cultural group (i.e., first language English; London university students). Therefore, simulation theory could potentially reconcile the findings of those studies that reported stronger mrPFC activation for self than for other judgments (D'Argembeau et al., 2005, 2007; Kelley et al., 2002; Pfeifer et al., 2007; Heatherton et al., 2006), and of those that did not find any such difference (Schmitz et al., 2004; Ochsner et al., 2005). That is, the latter studies might have tested a sample that, on average, perceived the respective others as very similar, resulting in comparable mrPFC recruitment for self and other judgments.

Intriguingly, the same subregion shown to be more strongly activated for other judgments in case of greater perceived similarity, was also more active for decisions about highly self-relevant traits. That is, consistent with previous findings (Moran et al., 2006; Macrae et al., 2004), activation in this region was modulated *within* individuals by the degree of judged self-descriptiveness. However, what functional processes might be subserved by mrPFC that are common to these effects? One similarity between judgments about more similar others and more self-relevant traits is that both might be based on what has been coined intuition-based self knowledge (Lieberman et al., 2004). This mode of accessing information about the self has been suggested to rely, amongst others, on the mrPFC (see also Ochsner et al., 2005). Scanning professionals from different domains, Lieberman et al. demonstrated that this region was specifically involved in judgments about traits relevant to the respective field of expertise, which were accordingly accessed with greater ease. Another study observed greater activation in mrPFC when participants made trait judgments about their current self than when they had to reflect about their traits 5 years ago (D'Argembeau et al., 2008). A role for this region in intuitive self judgments is also consistent with recent evidence that its activation implicitly tracks the self-relevance of previously presented pictures, i.e., when attention was not directed towards this feature (Schneider et al., 2008). Anatomically, mrPFC would be well suited to subserve such judgments, since it receives projections from regions such as anterior insular, amygdala, and ventral striatum (Ongur et al., 2003; Ongur and Price, 2000; Price, 2005). These are involved in interoception and the representation of the current feeling state (Critchley, 2005), which has been proposed to serve as a benchmark for interactions with the environment (Critchley, 2005; Damasio, 1994). Thus, if there is a close link between the self-relevance of presented trait words and accompanying changes of this state, this alteration might be exploited for self judgments. Moreover, such a mechanism of intuitive self-reflection might also be applied to similar others.

Perceived similarity and mrPFC activation: prediction of subsequent memory

This study also tested the novel hypothesis that recruiting similar processes for appraising oneself and similar others might impact on the subsequent retrieval of these judgments. The results support this idea: first, there was a strong tendency for the similarity measure to be *negatively* correlated with the percentage of correctly identified old/same words in both the self and other but not in the syllables condition. Thus, those participants who were more likely to engage similar processes for self and other judgments also tended to be worse at successfully retrieving the reference of these judgments. Secondly, the difference in mrPFC activation for self and other trait judgments might be taken as an index of the differential processing of these two judgment types. This activation difference was *positively* correlated with the rate of successful retrieval of both self and other judgments. Consistently, greater mrPFC activation has previously been observed for self-referential trait judgments that were remembered rather than forgotten in an incidental recognition test (Macrae et al., 2004). The present findings provide complementary evidence for simulation theory by demonstrating that subsequent behavior might reflect previous engagement of similar processes for appraising oneself and similar others.

mrPFC and the retrieval of self-referential information

The second goal of this study was to examine the involvement of mrPFC in the retrieval of self-referential information. To identify neural correlates of successfully retrieving the encoding conditions, activation associated with correctly identified old/same words was contrasted with activation accompanying correctly-rejected new words. Compared with the syllables condition, only successful retrieval of self judgments recruited this region. After small-volume-correction, activation in this area was also observed for the direct contrast of the self and other conditions. Thus, as predicted, mrPFC was primarily associated with the successful retrieval of self-referential information.

Because the current study employed an exclusion paradigm, i.e., only old/same but not old/different words required a “yes” response, correct performance was likely to be based on recollection of the study episode rather than just on familiarity of the test cue (Henson et al., 1999). Moreover, a caudal aspect of mrPFC was more strongly activated for previously self-referenced traits that were remembered with high rather than low confidence. Assuming that high-confidence decisions are especially associated with actual recollection of the study episode (Yonelinas, 2002), this region might have been specifically involved in the recollection of self-referential processes.

In recent years, this region has been implicated in the recollection of contextual details that were internally generated (e.g., thoughts and feelings during an event) rather than externally derived (e.g., where and when that event happened) (Simons et al., 2005a,b). For instance, Simons et al. (2006) demonstrated greater mrPFC activation for retrieving whether a particular item had been perceived or imagined during study than for remembering its previous location on a screen. Similarly, this region is more strongly engaged when participants reported having imagined compared to having perceived an object during study (Kensinger and Schacter, 2006; Vinogradov et al., 2006; Turner et al., 2008). It has been suggested that recollection of internally-generated details relies on retrieval of endogenously controlled cognitive operations. In contrast, recollection of more externally-derived details is thought to be predominantly supported by the retrieval of perceptual information (Johnson et al., 1993; Burgess and Shallice, 1996; Schacter et al., 1998). Thus, memories of internally-generated details arguably entail a stronger component of self agency, and mrPFC might accordingly be implicated in attributing this self-reference (c.f., Simons et al., 2008).

mrPFC and the retrieval of trait judgments about similar others

The present study extended previous tests of simulation accounts by examining mrPFC activation associated with *memory* for thinking about others: if similar processes subserve judgments about oneself and similar others, also the retrieval of these two judgment types might involve similar processes. In line with this prediction, mrPFC activation for the successful retrieval of other judgments correlated positively with the similarity measure. That is, the region shown to be selectively involved in the retrieval of self-referential memories was more strongly engaged for the retrieval of judgments about others in case of greater similarity. Thus, shared processes for appraising oneself and similar others were also reflected by common recruitment of mrPFC for the retrieval of these judgments.

Functional specialization within mrPFC?

Both trait and episodic judgments recruited mrPFC in the self conditions. However, the former were associated with more anterior activation than the latter. Though this pattern needs to be replicated, it might be consistent with recent observations by Gilbert et al. (2007). They showed that rostral aspects of this region are involved in attending towards the external world, whereas caudal mrPFC is engaged for mentalising (which requires the integration of external cues and one's internal mental states) (see also Gilbert et al., 2006). Thus, recruitment of distinct mrPFC subregions for trait and episodic memory judgments might reflect differences in the relative contribution of externally- and internally-directed processes (cf., Burgess et al., 2007b). In particular, *intuitive* trait judgments might be more directly triggered by the externally presented words, compared with episodic memory judgments that might require more elaborative integration of the words and the internally represented memory trace.

Summary and conclusions

MrPFC was activated during appraisal of one's personality traits as well as during subsequent retrieval of those judgments. Crucially, the degree to which this area was also activated while processing others correlated with the degree of perceived similarity. Thus, the data support simulation accounts which posit that self-referential processes are also employed for thinking about another person, if one assumes oneself to be a good model of this person. Moreover, recruiting similar processes for appraising oneself and others was associated with impaired source memory for these judgments, which suggests an impact of extrapolating self-referential processes on subsequent behavior. The activation of caudal mrPFC for successful retrieval of self-referential information sheds light on the often-reported recruitment of this area for the recollection of highly self-relevant memories, such as autobiographical events (Cabeza and St Jacques, 2007).

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