In-group as part of the self: In-group favoritism is mediated by medial prefrontal cortex activation

Kirsten G. Volz [a b] , Thomas Kessler [c d] & D. Yves von Cramon [a b]

[a] Max Planck Institute for Neurological Research , Cologne, Germany

[b] Max Planck Institute for Human Cognitive and Brain Sciences , Leipzig, Germany

[c] University of Jena , Jena, Germany

[d] University of Exeter , Exeter, UK
Published online: 07 May 2009.

PLEASE SCROLL DOWN FOR ARTICLE

Ψ Psychology Press
Taylor & Francis Group

In-group as part of the self: In-group favoritism is mediated by medial prefrontal cortex activation

Kirsten G. Volz

Max Planck Institute for Neurological Research, Cologne, and Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

Thomas Kessler

University of Jena, Jena, Germany and University of Exeter, Exeter, UK

D. Yves von Cramon

Max Planck Institute for Neurological Research, Cologne, Germany and Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

Our identity consists of knowledge about our individual attributes (personal identity) as well as knowledge about our shared attributes derived from our membership in certain social groups (social identity). As individuals seek to achieve a positive self-image, they aim at comparing favorably with other individuals or their in-group comparing favorably with referent out-groups. Imaging data suggest a network centered on the medial prefrontal cortex (MPFC) to instantiate functions that are integral to the self, conceived as the personal self. Given that the social self is constituted by the same mechanisms as the personal self, we expect MPFC activation also for situations in which the social self is addressed, for instance when situations permit evaluative intergroup comparisons. Accordingly, participants worked on a modified version of the minimal group paradigm in the present functional magnetic resonance imaging experiment. Imaging data revealed activation within a network centered on the dorsal MPFC specifically for social identity processes. Furthermore, this activation showed correlation with the displayed in-group bias. The present findings show that social and personal identity processes draw on the same cerebral correlates and hence it is concluded that a network centered on the MPFC subserves functions integral to the self.

Keywords: Self-categorization; In-group favoritism; Medial prefrontal cortex; Social comparison; fMRI.

INTRODUCTION

People's sense of who they are comprises individual as well as socially shared characteristics. Thus, people's beliefs and behaviors are shaped not only by their unique characteristics but also by their sense of belonging to a particular group or groups (Tajfel & Turner, 1979; Turner, Hogg, Oakes, Reicher, & Wetherell, 1987). There is vast empirical evidence reliably showing that people hold opinions and engage in behavior that is strongly affected by their membership in groups they belong to and identify with (e.g., Brewer & Brown, 1998; Fiske, 2002; Haslam, 2004; Terry &

Hogg, 1996). For individuals perceiving themselves as members of a particular group, it is a common phenomenon to favor fellow in-group members in evaluations and behavior as well as to neglect or even discriminate against people from various out-groups. Moreover, an additional finding is that group members show a reliable tendency to maximize the difference between in-group and out-group implying a devaluation of out-group members at some cost to the in-group (e.g., Brewer, 1979; Tajfel & Turner, 1986). Both types of behaviors are embraced under the term "social discrimination" or "intergroup bias" (Hewstone, Rubin, & Wills 2002). Importantly, a conflict of interest or previous hostility between the groups is not mandatory for intergroup differentiation and social discrimination to occur (Tajfel & Turner, 1986). For an explanation of intergroup behavior and especially in-group bias, it would be not enough to simply transfer interpersonal theories to the level of intergroup behavior (Mummendey & Otten, 2002). Accordingly, several theories were developed taking into account that behavior at different levels of self-categorization (e.g., personal or group) may be qualitatively different (Brewer & Weber, 1994). According to Social Identity Theory (SIT) and Self Categorization Theory (SCT) (Tajfel & Turner, 1979; Turner et al., 1987), social categorizations *per se* may provide a system of orientation for self-reference: Social categories not only systematize the social world, but for individuals who identify with a particular category they "create and define the individual's place in society" (Tajfel & Turner, 1986, p. 16). Group identification understood as the connection between an individual and a certain social category leads to self-definition in social terms. Accordingly, the self-concept was suggested to comprise two parts: personal identity and social identity. Personal identity refers to the self-knowledge that derives from the individual's unique attributes and hence refers to the conceptualizations that define the individual in relation to or in comparison to other individuals. For example, characterizing oneself as intelligent implies that one is more intelligent than others. Hence, how people see themselves is not at all independent of how they see others. This relational perspective and the idea of positive comparative evaluation have long formed the core mechanism in research on the personal self (e.g., Festinger, 1954; Mussweiler, 2003; Wills, 1981).

The other part of the self-concept, social identity, refers to conceptualizations of the self that derive from memberships in emotionally significant social groups (i.e., in-groups). As individuals tend to maintain or enhance a positive image of themselves, they also aim at a positive social identity, which in turn can be obtained by favorable comparisons of the in-group with relevant out-groups. From this it follows that individuals try to differentiate their in-group positively from a relevant out-group by positively discrepant social comparisons. If social identity gives little satisfaction, individuals will either strive to leave the respective group for a more positive distinct group or the individual will act as a group member and strive to engage in social comparisons making the existing group more positively distinct. Accordingly both constituents of the self-concept, personal identity and social identity, derive largely from favorable comparisons that can be made between the in-group and relevant out-groups. That is, evaluations of the in-group happen by reference to the evaluation of (relevant) out-groups by means of social comparison processes involving the sub-processes (a) standard selection, (b) target-standard comparison, and (c) evaluation (Mussweiler, 2003). In the first stage a standard is selected, either explicitly or implicitly. In the next stage, the critical features that carry weight for the comparison are selected. Then the actual evaluation is made. Whether people compare as individuals with other individuals or as group members with other groups depends on what part of the self is salient. Depending on the social context and an individual readiness (Bruner, 1957; Oakes, 1987), salience of self varies on a continuum from interpersonal to intergroup behavior. For example, lovers won't treat one another as representatives of particular groups, yet arguments between employers and trade unionists will be highly determined by their respective group membership.

Recent research in social neuroscience led to a remarkably rich and varied set of experimental data showing the medial prefrontal cortex (MPFC) to be activated when participants engage in distinctly social cognition (Amodio & Frith, 2006; van Overwalle, in press): The MPFC was shown to be differentially activated when participants form an impression about a person rather than an object (Macrae, Heatherton, & Kelley, 2004), when participants make dispositional inferences to a person (Harris, Todorov, & Fiske,

2005), when participants think about themselves (Macrae et al., 2004), when they think about the content of other minds, i.e., so-called theory of mind tasks (Castelli, Happé, Frith, & Frith, 2001; Gallagher & Frith, 2002; Saxe & Wexler, 2005), or when participants think about other players in trust games (McCabe, Houser, Ryan, Smith, & Trouard, 2001; Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003). Accordingly, the MPFC was shown to be crucial for social judgments. Recent findings suggested a functional subdivision within the MPFC by showing that the more anterior rostral and dorsal part of the MPFC is primarily sensitive to social information, whereas the pregenual anterior cingulate cortex (pACC; according to Vogt, 2005) subserves the evaluation and/or representation of reward information irrespective of the context (Harris, McClure, van den Bos, Cohen, & Fiske, 2007; van den Bos, McClure, Harris, Fiske, & Cohen, 2007). Accordingly, the rostral and dorsal part of the MPFC—which is also referred to as paracingulate cortex (after Amodio & Frith, 2006)—was suggested to subserve more abstract and deliberative forms of social judgments and mentalizing, whereas the ventral and caudal part of the MPFC was suggested to serve a more general affective function, as part of the general evaluation network of the brain.

Regarding the personal self, it has been suggested that a network centered on the MPFC instantiates functions that are integral to the self (e.g., Northoff & Bermpohl, 2004; Ochsner et al., 2004). For example, significant MPFC activation has been reported when participants had to describe themselves concerning personal characteristics (e.g., Johnson et al., 2002; Kelley et al., 2002), when they had to reflect upon their own mental states or feelings (e.g., Gallagher et al., 2001; Gusnard, Akbudak, Shulman, & Raichle, 2001; Ochsner et al., 2004; Vogeley et al., 2001), or when they had to judge a stimulus in terms of morality, beauty, affectivity or coherence, i.e., when they were asked for comparative evaluations (e.g., Ferstl & von Cramon, 2001; Greene & Haidt, 2002; Heekeren, Wartenburger, Schmidt, Schwintowski, & Villringer, 2003; Jacobsen, Schubotz, Hoefel, & von Cramon, 2006; Moll et al., 2002; Zysset, Huber, Ferstl, & von Cramon, 2002). In line with these findings are results from human lesion studies indicating that patients with lesions to the MPFC are described as presenting drastic changes in personality such as high levels of aggressiveness, lack of concern

for social and moral rules and irresponsibility (e.g., Ciaramelli, Muccioli, Làdavas, & di Pellegrino, 2007). At the same time, these patients show preserved intellectual abilities otherwise. Together, imaging and lesion studies have provided ample evidence that the MPFC is crucial for those processes that are considered to be integral for a coherent self-concept derived by social comparison processes as defined above.

Arguably, as the social self (i.e., social identity based on membership of a particular group) is derived by the same cognitive mechanisms as the personal self (i.e., comparative evaluation processes), we expect significant MPFC activation particularly for situations in which the social self is addressed, i.e., when situations permit evaluative intergroup comparisons as compared to situations that do not access such favorable ingroup–outgroup comparisons. According to SIT and SCT, and according to our assumption of MPFC activation, social identity processes should only come into play when social identity is salient and people thereby act in terms of their shared social identity. To be anatomically more precise, for social identity processes, we expect activation within the anterior dorsal part of the MPFC ($z > 0$), as descriptive meta-analytic data on studies investigating aspects of the personal self revealed this area as a focus (Ochsner et al., 2004).

As outlined above, functions instantiating the self are associated with a network centered around the MPFC, i.e., activation within the MPFC is almost always accompanied by activation within posterior medial areas, i.e., within the precuneus and adjacent areas within the posterior cingulate cortex (e.g., Gallagher et al., 2000; Kelley et al., 2002; Ochsner et al., 2004; Zysset et al., 2002). Connectivity data showed the precuneus to be strongly interconnected with medial prefrontal areas (Cavanna & Trimble, 2006). Based on imaging findings, associating the precuneus with successful episodic memory retrieval, the network of medial prefrontal and medial parietal regions has been suggested to serve as a network through which personal identity and past personal experiences are interlinked, thereby assigning a first person perspective (e.g., Vogeley & Fink, 2003). Based on these findings, we expect activation also within the precuneus for social identity processes.

According to Tajfel and Turner (1986), there are three classes of variables that influence intergroup differentiation and therewith, social

identity processes to occur: People must be categorized and subjectively identified with their in-group, the situation should permit evaluative intergroup comparisons, and the out-group must be sufficiently comparable (e.g. similar or proximal). Since the ''minimal group paradigm'', originally designed by Tajfel and colleagues (Tajfel, Billig, Bundy, & Flament, 1971) to investigate the effects of social categorization on behavior, realized all these issues and reliably triggered intergroup behavior (Brewer, 1979; Brewer & Brown, 1998), we used a modified version of this paradigm in the present functional magnetic resonance imaging (fMRI) study: Participants were categorized as members of two non-overlapping groups on the basis of a trivial performance criterion. Their task was to make decisions by awarding amounts of money to pairs of other subjects, excluding the participants themselves. In each trial, participants could select from a given matrix the column of numbers that represented how they would like to distribute the points—representing real money—between the two subjects. The two subjects could both belong to participants' in-group (denoted as in-group trials), to an out-group (denoted as out-group trials), or the pair was made up of a member of the in-group and a member of the out-group (denoted as mixed trials) (see Figure 1). The recipients were anonymous except for their group membership. As the participants were only referred to by their group membership, as well as all other in-group and out-group members, this
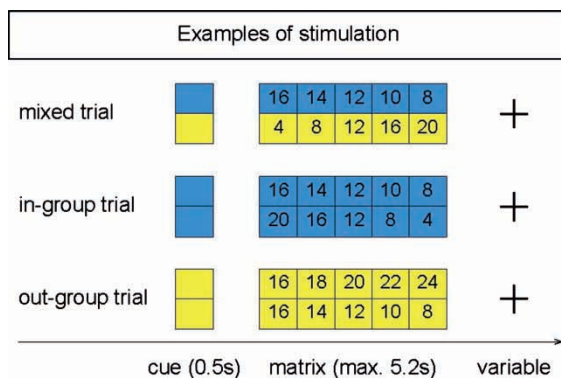
Figure 1. Examples of the various trial types are shown for a subject who was assigned to the blue group (blue = in-group). Within one trial a cue was presented for 0.5 s indicating which matrix would be presented next. The matrix was presented for a maximum of 5.2 s, during which participants' response was recorded. Once a choice was made, the matrix disappeared and a fixation cross was presented until the next trial started.

experimental procedure is designed to make group membership the most salient feature in this context. Participants, who certainly knew their own group membership, awarded the amounts of money to each subject-pair individually and anonymously whereby no decision criterion how to divide the amounts was given. In the instruction it was pointed out to the participants that their behavior had significant consequences in the form of effective payments for the target subjects who participated in a different experiment and whom they would never meet. To rule out expectations of indirect reciprocity (e.g., Yamagishi & Kiyonari, 2000), the amount of money for participating in the actual experiment was fixed (see Gaertner & Insko, 2000; Sassenberg, Kessler, & Mummendey, 2003 for a similar procedure). As the two groups were generated ad-hoc, conflict of interests or a history of conflicts between the two groups is not likely, nor was there any rational link between economic self-interest and the strategy of in-group favoritism. Thus, the groups were purely cognitive and hence are denoted as ''minimal''.

A reliable finding of experiments using the minimal group paradigm is that the trivial intergroup categorization leads to in-group favoritism. Moreover, group members not only favor their fellow in-group members but also tend to maximize the difference between in-group and out-group (Tajfel & Turner, 1986; Bourhis, Sachdev, & Gagnon, 1994). Hence, group members prefer to forgo a larger profit for their in-group in order to maximize the difference between the groups. This finding suggests that intergroup differentiation can be more important than superiority in terms of economic payoff: Participants rather compete with the out-group than simply following the strategy of maximizing the economic gain for the in-group members. Although it may seem intuitive that group members might use in-group favoring behavior as a heuristic, Forgas and Fiedler (1996) showed that superficial or heuristic as well as more systematic cognitive processing can lead to in-group favoritism. Their results reveal that sometimes group members differentiate more between in-group and out-group with increasing information processing depth. This supports the assumption that group members can be motivated to favor their in-group over an out-group.

Accordingly, in the present fMRI study we expected dorsomedial prefrontal cortex (dMPFC) and precuneus activation especially for intergroup

behavior, i.e. for the following contrast: for (a) mixed trials in which the absolute in-group profit was sacrificed in favor of a high relative profit as compared to a fair division, (b) for mixed trials showing in-group maximization as compared to a fair division, and (c) for mixed trials showing an out-group minimization as compared to a fair division. Accordingly, depending on the individuals' performance, only mixed trials on which participants acted with more bias were compared to those mixed trials in which participants did not show such an intergroup bias (performance-dependent analyses). Beyond, medial prefrontal and medial parietal activation was exclusively expected on mixed trials where participants had to divide the money between an in-group member and an out-group member, and hence where intergroup differentiation is feasible, as compared to same-group trials (stimulus-dependent analysis: contrast "mixed trials vs. in-group/out-group trials"). This is because only in mixed-group trials can participants build social comparisons with the out-group, allowing the in-group to be positively distinct. In contrast, activation within frontal and posterior medial structures was not expected on same-group trials, since in these trials there is neither a need nor the possibility to establish a positive social identity by means of comparative evaluation processes (stimulus-dependent analysis: contrast "in-group trials vs. out-group trials"). Based on the findings by Harris and Fiske (2006), one could assume MPFC activation for the latter contrast when participants may perceive out-group members as less than human (dehumanized). Yet, since we did not give any individuating information about the out-group members, we did not expect differential activation within MPFC when comparing same-group trials. Regarding our behavioral hypotheses, we expected a pattern of intergroup behavior that consists of a tendency to maximize in-group members' pay-off and a tendency to maximize the difference in pay-off between in-group and out-group members.

SUBJECTS AND METHODS

Participants

Twenty right-handed healthy volunteers (10 female, mean age 25.3, SD 2.5, range 21–29 years) with no history of neurological or psychiatric symptoms participated in the fMRI experiment. Informed consent was obtained from each participant according to the Declaration of Helsinki. The experimental standards were approved by the local ethics committee of the University of Leipzig. Data were handled anonymously.

Materials: Stimuli, task, and, experimental session

Stimuli consisted of a 2×5 matrix centrally depicted on a black screen. The matrix was 9 cm wide and 3 cm high, resulting in a horizontal visual angle of $5.15°$ and a vertical visual angle of $1.72°$. Participants could choose one of the five columns, each consisting of two cells, by pressing one of the five designated response buttons which were distributed across both hands. Half of the participants were instructed to use their left middle and index fingers to choose the two left outermost columns, the right middle and ring finger to choose the two right outermost columns, and the right index finger to choose the middle column of the matrix. The other half of the participants received an inverted response assignment.

Within each trial a cue was presented for 500 ms indicating what kind of matrix was to be presented next. Subsequently, a fixation cross was presented for 500 ms, which was followed by the presentation of the matrix (see Figure 1). The matrix was presented for a maximum of 5200 ms, during which participants' response was recorded. Once participants made their choice the matrix disappeared and a fixation cross was presented until the next trial started. The matrix itself was either monochrome blue or yellow, or it was two-colored in such a way that the upper row was blue and the lower row was yellow or vice versa. In each cell of the matrix numbers were presented and participants were told that these numbers represented amounts in euro cents. Thirty matrices differing in their distribution of euro cents were used (examples are presented in Figure 1).

Participants were categorized as members of two non-overlapping groups on the basis of a trivial performance criterion described below. Group membership was represented by color, i.e., either yellow or blue. Accordingly, monochrome matrices in the color of the in-group were termed *in-group trials*, monochrome matrices in the color of the out-group were termed *out-group trials*, and two-colored matrices were denoted as *mixed trials*. The task of the participants was to

make decisions by awarding amounts of money to pairs of other subjects, excluding the self. Depending on the color of the matrix, the money had to be assigned to a pair of in-group members, to a pair of out-group members, or to a mixed pair. Recipients were anonymous except for their group membership. Participants, who of course knew their own group membership, awarded the amounts of money to each subject-pair individually and anonymously whereby no decision criterion as to how to divide the amounts was given. It was pointed out to the participants that their behavior would have significant consequences in the form of effective payment for other subjects, who would participate in another experiment on group membership, but that they would never meet these other subjects. The amount of money paid to the actual participants was fixed and hence in-group favoritism did not pay off.

Before the functional session, participants were requested to accomplish a perceptual task so as to determine their individual group membership, which in turn defined what instruction they received for the functional session. In the perceptual task, participants were briefly (3 s) presented with black-and-white bi-stable phenomena, such as the Rubin vase–face illusion, and ambiguous figures; they had to indicate what they perceived first. The possible answers were given on the screen and participants had to choose among them. The fake evaluation revealed for all participants that they could be categorized as individuals who firstly analyze the foreground information and only later analyze the background and context information ("figure perceivers"). Group-membership was then assigned by a color (yellow or blue). Participants were informed that another way to apprehend bi-stable phenomena could be to firstly analyze the background and context information and only later the foreground information ("ground perceivers"). This group-membership was assigned the remaining color (yellow or blue). To make group-membership salient, participants were told that this very perceptual ability correlates with several other important personality characteristics. Apparently, psychology students were excluded from participation because of their potential knowledge about psychology of perception and the minimal group categorization procedure.

In the fMRI experiment, 195 trials (60 trials per condition, 15 null-events) were presented in a pseudorandom order. Response assignment was balanced between participants as described above. All trials lasted for 8 s, i.e., four scans of repetition time (TR = 2 s). To allow for measurements to be taken at numerous time points along the BOLD signal curve, the onset of each stimulus presentation relative to the beginning of the first of the three scans was varied randomly in four time steps (0, 500, 1000, and 1500 ms). The purpose of this procedure was to enhance the temporal resolution of the image acquisition (Birn, Cox, & Bandettini, 2002; Miezin, Maccotta, Ollinger, Petersen, & Buckner, 2000). After the experimental session, participants filled out a questionnaire assessing their social identification with their in-group. Subsequently, they were thanked and debriefed.

MRI scanning procedure

Imaging

Imaging was performed on a 3 T scanner (Siemens TRIO, Erlangen, Germany). Twenty-two axial slices (4 mm thickness, 20% spacing, field of view (FOV) 19.2 cm, data matrix of 64×64 voxels, and in-plane resolution of 3 mm $\times$ 3 mm) parallel to the bi-commissural plane (AC–PC) covering the whole brain were acquired using a single-shot echo-planar imaging (EPI) sequence (TR 2 s, echo time [TE] 30 ms, flip angle 90°). Prior to functional runs, 22 anatomical T1-weighted modified driven equilibrium Fourier transform (MDEFT; Norris, 2000; Ugurbil et al., 1993) images (data matrix 256×256, TR 1.3 s, TE 10 ms) were acquired as well as 22 T1-weighted EPI images with the same spatial orientation as the functional data. The latter were used to co-register the functional scans with previously acquired high-resolution full-brain 3-D brain scans.

Data analysis

The MRI data were processed using the software package LIPSIA (Lohmann et al., 2001). Functional data were motion-corrected offline with the Siemens motion correction protocol (Siemens, Erlangen, Germany). To correct for the temporal offset between the slices acquired in one scan, a cubic-spline-interpolation was applied. A temporal highpass filter with a cut-off frequency of 1/96 Hz was used for baseline correction of the signal and a spatial Gaussian filter with 5.65 mm FWHM was applied. The

anatomical slices were co-registered with the full brain scan that resided in the stereotactic coordinate system and then transformed by linear scaling to a standard size (Talairach & Tournoux, 1988). The transformation parameters obtained from this step were subsequently applied to the functional slices so that the latter were also registered into the stereotactic space. This linear normalization process was improved by a subsequent processing step that performed an additional nonlinear normalization (Thirion, 1998). Slice-gaps were scaled using a trilinear interpolation, generating output data with a spatial resolution of $3 \times 3 \times 3$ mm (27 mm^3).

The statistical evaluation was based on a least-squares estimation using the general linear model (GLM) for serially autocorrelated observations (random effects model; Friston, 1994; Friston, Frith, Turner, & Frackowiak, 1995; Worsley & Friston, 1995). An event-related design was implemented, i.e., the hemodynamic response function was modeled by means of the experimental conditions for each stimulus (event = onset of matrix presentation). The design matrix was generated utilizing a synthetic hemodynamic response function and its first and second derivative (Friston et al., 1998) and a response delay of 6 s. The model equation including the observation data, the design matrix, and the error term was convolved with a Gaussian kernel of dispersion of 4 s FWHM to deal with the temporal autocorrelation (Worsley & Friston, 1998). Contrast images, i.e., estimates of the raw-score differences between specified conditions, were generated for each subject. The single-subject contrast images entered into a second-level analysis based on Bayesian statistics (Neumann & Lohmann, 2003). In the approach by Neumann and Lohmann (2003), posterior probability maps and maps of the effect size for the effects of interest in groups of subjects are calculated on the basis of the resulting least-squares estimates of parameters for the GLM. The output of the Bayesian second-level analysis is a probability map showing the probability for the contrast to be larger than zero. For visualization, a threshold of 99.9% was applied to the probability maps. Reasons to use Bayesian second-level analysis for fMRI data are many: A comparison between the established analysis based on t statistics and Bayesian second-level analysis showed that the latter is more robust against outliers. Furthermore, the Bayesian approach overcomes some problems of null hypothesis significance testing such as the need to correct for multiple comparisons, and this approach provides estimates for the size of an effect of interest as well as for the probability that the effect occurs in the population (Neumann & Lohmann, 2003).

RESULTS

Behavioral results

Reaction times (RT) between in-group trials (mean: 2161 ms; *SE*: 117), out-group trials (mean: 2052 ms; *SE*: 121), and mixed trials (mean: 1976 ms; *SE*: 122) differed significantly on the 5% level, such that participants were fastest in awarding amounts of money in the mixed trials, $F(2, 18) = 4.28$; $p = .044$. According to our hypotheses, overall, participants awarded significantly more money to their in-group members (€2.609, *SE*: 34) than to out-group members, (€2.301, *SE*: 45), $t(19) = 4.62$; $p < .0001$. Across all trials, the difference in money between the two other subjects differed significantly between the three trial types such that the difference was largest in the mixed trials and, hence, the in-group subject was favored, $F(2, 18) = 16.63$; $p < .0001$; in-group trials: mean, €1.02 (*SE*, 8.9); out-group trials: mean, €0.87 (*SE*, 8.9); mixed trials: mean, €2.06 (*SE* 24.5). On the trial level, this corresponds to a difference of €0.017 (*SE*: 0.15) in in-group trials; €0.014 (*SE*: 0.15) in out-group trials; and €0.034 (*SE*: 0.49) for in-group members in mixed trials. In the mixed trials, since no response specifications were made, participants could either try to be as fair as possible (i.e., they award approximately the same amount of money to both other subjects) or aim at maximizing the outcome between the two groups (i.e., they differentiate between in-group and out-group). Other strategies are to focus on the maximization of the profit of the in-group member or on the minimization of the profit of the out-group member.

In mixed trials, participants showed equitable distributions in 45% (*SE*: 6.1), of the trials in which fair behavior was possible. In contrast, when it was possible to differentiate, participants showed differentiation in 44% (*SE*: 0.04) of the cases. When it was possible to maximize the profit of the in-group member, participants applied this strategy in 47% (*SE*: 0.07) of the cases, and when it was possible to minimize the profit of the out-group member, participants applied this strategy in 29% (*SE*: 0.6) of the cases. Together, when

discriminating behavior could be applied, participants showed an in-group bias in 40% (*SE*: 5.7) of the cases. On the group level, neither the means, $t(19) = 0.67$; $p = .51$, nor reaction times differed significantly between fair and discriminating trials, $t(19) = -1.04$; $p = .313$ (discriminating behavior: mean, 2072 ms; *SE*: 184; fair behavior: mean, 2201 ms; *SE*: 153). Yet a closer look revealed two types of responders: those who showed fair behavior in the majority of cases and did not much engage in discriminating behavior, and the opposite. These two response patterns correlated significantly negative ($r = -.54$; $p = .014$), indicating a clear tendency for either fair behavior or competitive behavior.

After the functional session, participants were asked to fill in a questionnaire inquiring, among other things, their social identification with their in-group. Social identity was assessed by three items, e.g., "I identify myself with the 'blue' group". All questions were answered on a five-point scale ranging from (1) "I do not agree at all" to (5) "I agree entirely". The mean of the three social identity items was 3.95, normally distributed (Kolmogorov-Smirnov test: $Z = .93$; $p = .36$), and significantly above the midpoint of the scale, $t(19) = 2.23$; $p = .04$. Although this finding clearly indicates that our identity manipulation worked, there were four participants showing an identification value below the scale mean. Since identification with the in-group is a prerequisite for social identity processes to occur and therewith crucial for the interpretation of our data, we excluded the four low identifiers from all fMRI analyses.

To test whether identification with the in-group differed between the two types of responders described above, we compared, in a post-hoc analysis, the identification values of participants who predominantly showed discriminating behavior (mean: 3.6, *SE*: 0.21) and those who predominantly showed fair behavior (mean: 3.7, *SE*: 0.25, excluded the low identifiers). Results revealed no significant difference between the groups with regard to identification with the in-group, $t(14) = -0.37$; $p = .84$.

Imaging results

According to our hypothesis, activation within a network centered on the MPFC should only occur when social comparison processes between the in-group and out-group are possible. Thus, contrasting mixed trials with in-group trials, out-group trials, or both sorts of trials were the analyses of interest. All three contrasts revealed the same activation pattern: A significantly higher hemodynamic activity for mixed trials was revealed within the dMPFC, the pregenual anterior cingulate cortex (pACC, according to the nomenclature of Vogt, 2005), within the precuneus, and bilaterally within the temporoparietal junction area (TPJ; see Figure 2A and Table 1). For the inverse contrast significant activation was observed within the left inferior middle frontal gyrus ($x = -50$, $y = 36$, $z = 15$) and bilaterally within the cuneus/occipital lobe ($x = 10$, $y = -69$, $z = 15$).

To test whether the activation pattern was specific for comparative evaluation processes also when participants had to divide money in same-group trials (e.g., between two in-group members), we contrasted purely in-group trials with purely out-group trials. Significant activation was observed bilaterally within the superior portion of the anterior insula and the anterior calcarine sulcus but not in frontal and posterior medial structures (see Figure 2B and Table 1). Hence, the activation pattern observed for the contrasts mixed trials versus in-group and out-group trials indeed seems to be specific for comparative evaluation processes.

To test for the specific neural correlates of discriminating intergroup behavior, and therewith for the relationship between behavior and brain activity, we investigated in a performance-dependent analysis the hemodynamic response elicited by all trials in which in-group maximization, out-group minimization or differentiating occurred and contrasted each of these conditions with those trials in which participants engaged in fair behavior. Additionally, since the three contrasts differed with respect to sample size, we pooled the three conditions and contrasted them with fair behavior trials. In all three contrasts and in the combined contrast a significantly higher hemodynamic activity for discriminating intergroup behavior was revealed within the left dMPFC, pACC, and left TPJ (see Figure 2C and Table 1). Except for out-group minimization, significant activation also was revealed within posterior MPFC (BA 8).

Given these results and the behaviorally determined two types of responders, we expect activation within the medial structures for the contrast "mixed-group trials compared to same-group trials", especially for those participants that
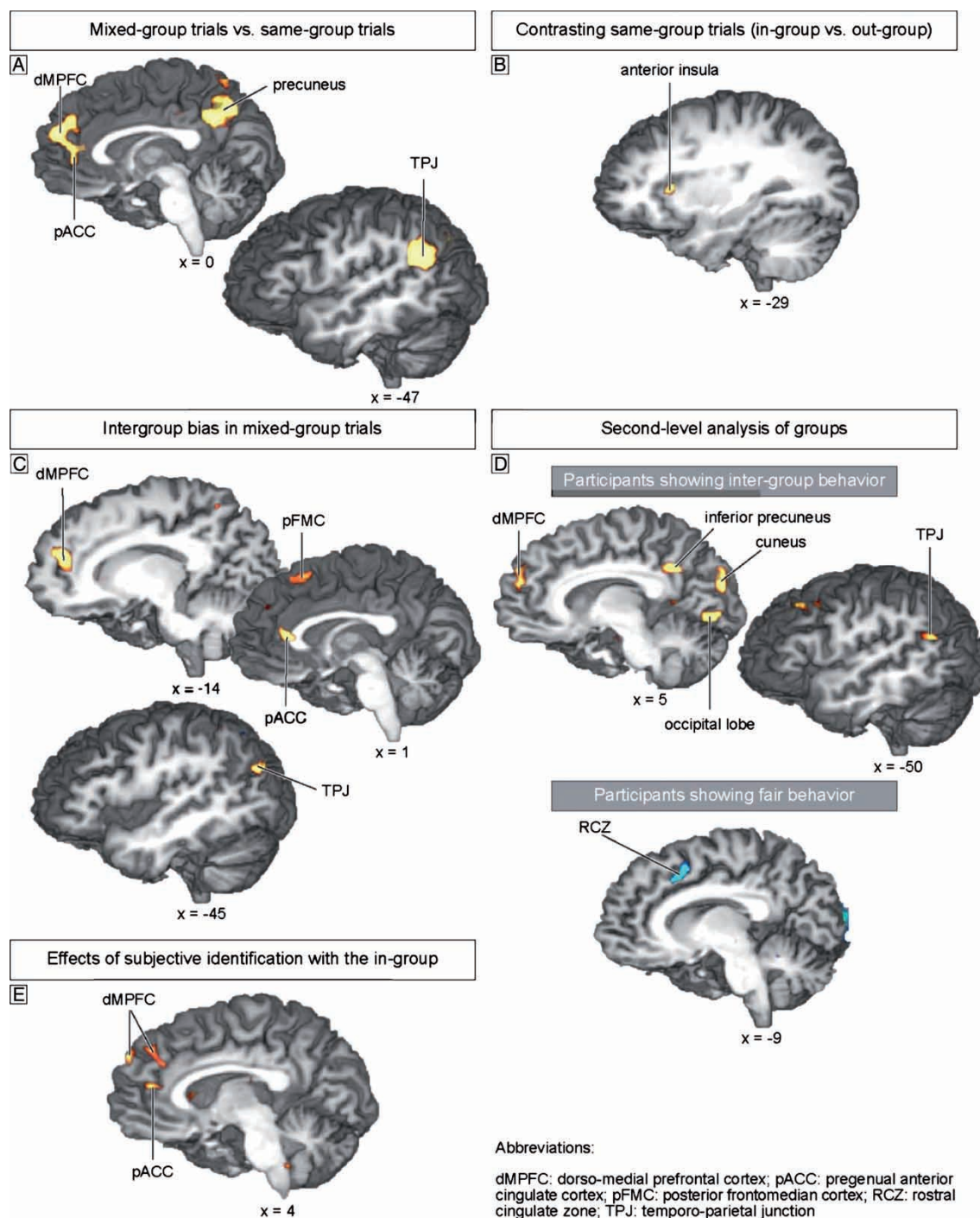
Figure 2. Group averaged activations are shown on sagittal slices taken from an individual brain normalized and aligned to the Talairach stereotactic space. For visualization, a threshold of 99.9% was applied to all probability maps, except for the contrast shown in (E). Here, because of the small sample size ($n = 8$), a threshold of 96% was applied. (A) The direct contrast between mixed-group trials and same-group trials, i.e., in-group trials and out-group trials. (B) The direct contrast between same-group trials, i.e., between purely in-group trials and purely out-group trials. (C) The performance-dependent contrast (on mixed-group trials only) between trials in which participants showed discriminating behavior and trials in which they showed fair behavior. (D) Results of the post-hoc second-level analysis of groups for the contrast mixed trials versus in-group trials. The upper panel in D shows the result for the group that engaged considerably in discriminating behavior; the lower panel depicts the results for the group that substantially showed fair behavior. (E) The effect of subjective identification with the in-group: Four randomly chosen participants that identified with their in-group were contrasted against the four participants that did not identify with their in-group (contrast mixed-group trials vs. in-group trials).

TABLE 1

Laterality, anatomical specification, and Talairach coordinates (*x, y, z*) for activation according to Bayesian analysis are shown for the direct contrasts, the parametric contrast, and the conjunction analysis. All activation foci were set to posterior probabilities of 99.9%.

Area	*x*	*y*	*z*
Mixed trials >in- and out-group trials			
R dorso-medial prefrontal cortex (dMPFC)	1	51	21
R pregenual anterior cingulate cortex (pACC)	1	39	12
R precuneus	4	−54	33
L temporo-parietal junction (TPJ)	−53	−54	25
R	43	−60	30
L middle temporal gyrus	−53	−30	0
Mixed trials >in-group trials			
L dMPFC	7	51	24
L pACC	−2	39	15
R precuneus	4	−51	36
L TPJ	−44	−57	24
R	52	−53	30
Mixed trials >out-group trials			
R dMPFC	4	51	21
R pACC	1	33	18
R precuneus	1	−60	42
L TPJ	−59	−48	27
R	52	−54	33
In-group >out-group trials			
L anterior insula	−29	18	9
R	25	18	6
L anterior calcarine sulcus	−20	−54	9
In-group-bias >fair behavior (pooled across strategies)			
L dMPFC	−11	45	24
R pACC	1	30	12
R posterior MPFC (BA 8)	7	18	51
L TPJ	−59	−48	21
R	7	−60	57
L anterior insula	−35	24	12
Participants showing inter-group behavior (contrast mixed trials vs. in-group trials)			
R dMPFC	8	52	31
L pACC	−5	45	15
R inferior precuneus/posterior cingulate cortex	4	−48	33
L TPJ	−50	−58	24
R cuneus	7	−84	21
R occipital lobe	7	−81	0
Participants showing fair behavior (contrast mixed trials vs. in-group trials)			
L rostral cingulate zone (RCZ)	−8	12	42
L occipital gyrus	−35	−72	−3
R	40	−78	−4
Group analysis on in-group identification (n =8, threshold 96%)			
R dMPFC	7	42	39
	16	51	30
R pACC	4	42	15

rarely engaged in fair behavior as compared to those participants that, in the majority of cases, showed fair behavior (median-split). Accordingly, we conducted a post-hoc second-level analysis of groups for the contrast "mixed trials versus in-group trials". For those participants that engaged a good deal in discriminating behavior and less so in fair behavior, we found significant activation within the right dMPFC, left pACC, the right precuneus extending into the posterior cingulate cortex, right cuneus, and within the TPJ bilaterally. In contrast, for participants that predominantly engaged in fair behavior, significant activation was observed within the left rostral cingulate zone and the occipital gyri (see Figure 2D and Table 1). That is, participants who acted with more bias on mixed trials showed greater activation within the regions putatively involved in social identity.[1]

As outlined above, there are several classes of variables that influence intergroup differentiation in concrete social situations. One of the critical variables is that individuals must have internalized their group membership as an aspect of their self-concept. Since this issue is a prerequisite for social identity processes to occur, in the present study we excluded four participants from the analyses who did not identify with their in-group.[2] According to our results hitherto, activation within the medial-frontal-medial-parietal network should only be observed for mixed-group trials for those participants that identified with their in-group, as compared to the four participants that did not identify with their in-group (and that were excluded from all reported analyses so far). Thus, we conducted a post-hoc second-level analysis of groups comparing the four participants that did not identify with their in-group to four randomly selected individuals that identified with their in-group. Results revealed significant activation within the dMPFC and pACC (precuneus activation was close to the threshold) for individuals that subjectively

identified with their in-group (see Figure 2E and Table 1).[3]

DISCUSSION

In the present study we set out to investigate the cerebral implementation of social identity. Social identity is understood as the individual's self-concept that derives from perceived memberships in significant social groups (Hogg & Vaughan, 2002). As individuals have a need for positive social identity, generating a positively valued distinctiveness for their own group compared to other groups is fundamental. This is achieved by positively discrepant social comparisons between in-group and out-group (Brewer, 1979). In the present study we used a modified version of the minimal group paradigm by Tajfel and colleagues (Tajfel et al., 1971), originally designed to investigate the effects of social categorization on behavior, while participants' neurovascular activity was measured. As expected, the present imaging results revealed activation within a network centered on the dMPFC specifically for social identity processes.

Comparison processes in social judgment and the dMPFC

Substantial evidence from social psychology suggests that social identity is derived largely by favorable comparisons between the in-group and relevant out-groups, i.e., the group identifications define the individual as "better" or "worse" than members of other groups (Brewer & Brown, 1998). Thus, the processes by which social identity is derived are supposed to be similar to the ones by which personal identity is derived: comparative evaluation processes. Imaging data suggested a network of medial prefrontal and medial parietal areas to support the mental representation of the personal self. Given that the social self is derived by the same cognitive mechanisms as the personal self, similar activation within the medial-prefrontal-medial-parietal network was expected. The present results reinforce this claim. We found that four regions of the human brain— dMPFC, pACC, TPJ, and precuneus—were recruited selectively when participants were offered

---

[1] One may wonder why we did not calculate a correlational analysis between behavior and brain activity. Since we used second-level analyses of groups of subjects based on Bayesian statistics providing probability maps, a correlational analysis between a probability and a performance index is, in our opinion, difficult to interpret. Nevertheless, a correlational analysis of probability and intergroup behavior revealed basically the same activation pattern as observed with the median-split.

[2] Mean identification value of the four low-identifiers: 2.25 vs. 3.7 for the 16 high-identifiers, $t(18) = -7.22$; $p < .001$.

[3] Due to the small sample size a more liberal threshold of 96.8% was applied.

the opportunity for competitive intergroup behavior and when they actually showed intergroup discrimination favoring the in-group. In particular, when participants were maximizing the profit of the in-group member compared to the out-group member, minimizing the profit of the out-group member compared to the in-group member, or maximizing the difference in payoffs between the in-group and the out-group members, significant activation was observed within the medial-prefrontal-medial-parietal network. Thus, positively discrepant social comparisons between in-group and out-group appeared to be crucial for activation within dMPFC, pACC, precuneus, and TPJ. Yet activation within this network was not observed for same-group trials. We assume this is because in same-group trials, where the money is divided between two members of the same group, comparative evaluation processes are neither indicated nor enabled. Accordingly, only in situations when the social self was addressed, i.e., when situations allowed for evaluative intergroup comparisons, was activation within the medial-prefrontal-medial-parietal network observed. Moreover, supporting evidence that the observed activation pattern seems to be specific for comparative evaluation processes comes from a post-hoc group analysis showing greater activity in the target regions (dMPFC, pACC, TPJ, and precuneus) for those participants that acted with more bias (on mixed trials) compared to those participants that predominantly showed fair behavior. Finally, the group analysis between participants that identified with their in-group and participants that did not identify with their in-group revealed activation within the observed network only for those that incorporated their group membership as an aspect of their self-concept. Hence, we conclude that the observed pattern of brain activity is specifically related to social identity processes.

Recently, activation within dMPFC has been suggested as the neural correlate for understanding triadic social relations, i.e., the representation of relations between Me, You, and This (Saxe, 2006). This conception includes situations in which individuals (Me and You) share attention to an object (This) or collaborate on a shared goal (e.g., Tomasello, Carpenter, Call, Behne, & Moll, 2005). This interpretation partially fits with our suggestion that dMPFC reflects comparison processes in social judgments encompassing the subprocesses standard selection, target–standard comparison/featural focus, and evaluation. Particularly, in

order to arrive at a statement such as "I am highly athletic", I have to establish triadic relations between Me, the Standard I would like to compare with, and the Object of Evaluation (This), in this example athletic skills. Thus, first I have to determine an appropriate judgmental standard (Mussweiler, 2003). The level of standard selection is followed by the so-called featural focus, i.e., determining the particular features, on which the target–standard comparison has to be based. Thus, in our example, I would have to determine which particular sporting skills (speediness, muscular endurance, flexibility, etc.) have to be included in the comparison. Notably, in social judgments featural guidelines are usually lacking and hence the judge himself is required to identify the critical features that carry weight to the comparison. In a next step the actual evaluation is carried out, e.g., comparing my standing in terms of sportiness with that of the selected standard. With regard to social identity and intergroup behavior, the representation of the triadic relation is suggested to correspond to In-group, Out-group, and Monetary Difference. Our outlined functional interpretation of dMPFC activation subserving comparative evaluation processes (in social judgments) underlines the component of *relating* these different constituents subject to the context and not just representing the component parts (e.g., Saxe, 2006). Thus, we would emphasize the active role of the judge during comparative evaluation processes. Especially in social judgments the relevant constituents are rarely given. Thus, judges have to identify appropriate standards as well as critical features that carry weight to the comparison. That is, comparative evaluations regarding social stimuli cannot be based directly on sensory input, but have to be based on the accessible target knowledge. For example, to compare and assess whether psychologists or physicists are better scientists one has to derive knowledge about the standards of science as well as one's stereotypes, events, and other knowledge related to psychologists and physicists.

Regardless of whether the representational component or the processing component is stressed, it allows for a coherent interpretation of the so far disparate observations: The assessment of beauty (Jacobsen et al., 2006), morality (Heekeren et al., 2003; Moll et al., 2002), coherence (Ferstl & von Cramon, 2001; Sieboerger, Ferstl, & von Cramon, 2007), other individuals' mental states (Gallagher et al., 2000; Saxe & Wexler, 2005) and emotions (Ochsner et al., 2004) all require comparative evaluations with regard to

social matters. That is, to which standard should the target in question be compared, and on which particular features should the comparison should be based? The distinctiveness of comparative evaluations with regard to social matters is that comparisons cannot be based directly on sensory input (as experiential ones; Strack, 1992), but have to be based on accessible target knowledge. In the present study, the accessible target knowledge was primed by the explicit reference to the group membership, i.e., the social categorization per se.

Contribution of precuneus to comparative evaluation processes

As expected, social identity processes activated medial prefrontal areas as well as a medial parietal region, the precuneus. The precuneus' involvement (together with the PCC and the retrosplenial cortex) in episodic memory retrieval processes has repeatedly been shown in imaging studies in humans (Krause et al., 1999; Maguire, Frith, & Morris, 1999; Squire et al., 1992). For example, the precuneus was shown to be sensitive to successful retrieval (old/new effects; Henson, Rugg, Shallice, Josephs, & Dolan, 1999; Fletcher et al., 1995), autobiographical memory retrieval (Addis, McIntosh, Moscovitch, Crawley, & McAndrews, 2004; Gilboa, Winocur, Grady, Hevenor, & Moscovitch, 2004), retrieval orientation (Dobbins, Rice, Wagner, & Schacter, 2003)) and to the subjective perception that information is old (perceived recognition; Kahn, Davachi, & Wagner, 2004; Wheeler & Buckner, 2003). These findings and interpretations only apply to the posterior part of the precuneus; whereas the anterior part is suggested to subserve self-centered mental imagery strategies (Cavanna & Trimble, 2006). The activations in the present study fall within the posterior part of the precuneus and hence validate our assumption that the contribution of the precuneus activation consists of successful episodic retrieval. This interpretation is supported by the data of the post-session questionnaire: Participants reported retrieving the episodes of discriminating and fair behavior in mixed trials so as to adapt their current response. Also in in-group and out-group trials episodic retrieval was indicated, so as to use the range of variation within the applied strategy.

The corticocortical connections of the posterior medial cortex support the assumption of episodic retrieval influencing the current re-

sponse pattern. Besides connections with adjacent posteriomedial areas, the principal extraparietal corticocortical connections of the precuneus are with the frontal lobes concentrating at the level of BA 9 (dMPFC), 8, and 46, and with ACC (Cavanna & Trimble, 2006). It is assumed that past experiences and social identity are interlinked with one another in this way.

Contribution of pACC and TPJ to comparative evaluation processes

When participants showed intergroup discrimination favoring the in-group, activation was not observed exclusively within dMPFC and precuneus, but also within the pACC and TPJ. We did not formulate hypotheses on these areas, yet, based on the available imaging data, we infer pACC activation to reflect the emotional coloring to the uncertain social judgments, and TPJ activation to subserve abstract spatial relations between the social self and counterparts as outlined briefly in the following.

Activation observed within the ACC in the present study was consistently located in a rostral position, anterior to the genu of the corpus callosum, and is according to Vogt (2005) referred to as pregenual ACC (pACC; other authors also refer to this area as para-anterior cingulate cortex; e.g., Harris et al., 2007; van den Bos et al., 2007). The pregenual part of the ACC together with its subgenual division has repeatedly been shown to be involved in assessing the salience of emotional information and the regulation of emotional responses in normal individuals (Bush, Luu, & Posner, 2000; Vogt, 2005). Correspondingly, in psychiatric disorders such as obsessive-compulsive disorder or social phobia, this part of the ACC showed an increase with symptom provocation as well as increased activation as compared to controls in affect-related tasks (Amir et al., 2005; Fitzgerald et al., 2005). Whereas the sACC is suggested to be involved in autonomic and classical conditioning functions, the pACC was shown to be mainly engaged in positively valenced events (Harris et al., 2007; Rogers et al., 2004; van den Bos et al., 2007; Vogt, 2005). Moreover, van den Bos and colleagues (2007) showed that pACC activation in social judgments is not specifically socially tuned but rather serves a more general affective function as part of the evaluation network of the brain. Accordingly, we suggest pACC activation during

social comparison processes to provide emotional coloring, probably leading to (modulatory) adjustments in behavior. Interestingly, this positive emotional coloring was not observed when participants made monetary allocations to in-group versus out-group members.

The contribution of activation within the TPJ is less clear-cut. Due to the area's contribution in a variety of very different tasks, the function of the TPJ is still debated (Decety & Lamm, 2007). The recourse to macaque data of the posterior parietal cortex does not help in defining the TPJ's function: Comparative anatomy suggested that the inferior parietal lobe has expanded greatly in humans compared with monkeys, particularly the angular gyrus and the TPJ (Orban, van Essen, & Vanduffel, 2004; Zilles & Palomero-Gallagher, 2001; for a review see Husain & Nachev, 2006). At present it is not clear whether this expansion reflects the evolution of new areas or simply the enlargement of old ones. Hence we have to stick to the imaging literature: A number of imaging studies showed the TPJ to be part of a network mediating theory of mind processes, i.e., the representation of specific contents of mental states such as beliefs (e.g., Frith & Frith, 2006; Saxe & Kanwisher, 2003; Saxe & Wexler, 2005). Furthermore, TPJ activation has repeatedly been reported when participants (a) had to shift their egocentric viewpoint to that of another person, i.e., when they had to determine how spatial relations between two objects would appear from a character's point of view opposed to their own position (Vogeley et al., 2004) or (b) had to imagine themselves occupying a different space from the body's actual location (Arzy, Thut, Mohr, Michel, & Blanke, 2006). These findings on the sense of self-embodiment, together with the findings of the present study on social identity, suggest the TPJ to subserve more abstract (spatial) representations of the self (Abraham, Werning, Rakoczy, von Cramon, & Schubotz, 2008). This suggestion is supported by the finding of TPJ activation exclusively for situations in which participants had to divide money between an in-group and an out-group member (in mixed trials), and not when they had to allocate money in same-group trials.

CONCLUSION

All in all, by investigating the social self, the findings of the present study suggest the dMPFC to subserve comparative evaluation processes,

which lie at the core of any judgment. That is, each judgment requires the comparison of the target against a pertinent norm or standard, which in social matters cannot directly be based on sensory input but has to be determined *ad hoc*. In this way, the standard selection, the retrieved target knowledge, and the comparison mechanism are susceptible to a number of moderators such as context, recency, frequency, intensity, or ego-involvement. An interesting next issue with regard to the neural correlates of social identity would be to investigate individuals who tend to construe their self primarily as related to or separate from others (Markus & Kitayama, 1991, 1998).

The present research shows that the assessment of the social self involves similar brain structures as the assessment of the personal self. These results shed some light on the debate about the relation between personal and social selves (e.g., Gaertner & Insko, 2000). As the personal self consists in all the attributes and processes traditionally subsumed under the notion of self concept, we now have neurophysiological evidence that the social self represents also basic aspects of an individual's self concept. This implies that our selves ("what we are") extend psychologically well beyond the borders of our physical body and involve belonging to particular other individuals (i.e., the in-group) and differentiating from others (i.e., the out-group). Moreover, regardless of the actual level of self-categorization, the same psychological processes may regulate the judgments and behavior of individuals. Thus, for instance, motivational processes effectively working on a personal level of identity may similarly regulate intergroup behavior when a social identity is salient (Sassenberg et al., 2003). As all these aspects of the self (personal and social identities) are based on common processes, it is important to examine when and how these identities influence and shape each other.

REFERENCES

Abraham, A., Werning, M., Rakoczy, H., von Cramon, D. Y., & Schubotz, R. I. (2008). Minds, persons, and space: An fMRI investigation into the relational complexity of higher-order intentionality. *Conscious Cognition*, *17*, 438–450.

Addis, D. R., McIntosh, A. R., Moscovitch, M., Crawley, A. P., & McAndrews, M. P. (2004). Characterizing spatial and temporal features of autobiographical memory retrieval networks: A partial least squares approach. *NeuroImage, 23,* 1460–1471.

Allman, J. M., Watson, K. K., Tetreault, N. A., & Hakeem, A. Y. (2005). Intuition and autism: A possible role for Von Economo neurons. *Trends in Cognitive Science, 9,* 367–373.

Amir, N., Klumpp, H., Elias, J., Bedwell, J. S., Yanasak, N., & Miller, L. S. (2005). Increased activation of the anterior cingulate cortex during processing of disgust faces in individuals with social phobia. *Biological Psychiatry, 57,* 975–981.

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

Arzy, S., Thut, G., Mohr, C., Michel, C. M., & Blanke, O. (2006). Neural basis of embodiment: Distinct contributions of temporoparietal junction and extrastriate body area. *Journal of Neuroscience, 26,* 8074–8081.

Birn, R. M., Cox, R. W., & Bandettini, P. A. (2002). Detection versus estimation in event-related fMRI: Choosing the optimal stimulus timing. *NeuroImage, 15,* 252–264.

Bourhis, R. Y., Sachdev, I., & Gagnon, A. (1994). Intergroup research with the Tajfel matrices: Methodological notes. In M. P. Zanna & J. M. Olson (Eds.), *The psychology of prejudice: Ontario symposium on personality and social psychology* (Vol. 7, pp. 209–232). Hillsdale, NJ: Lawrence Erlbaum.

Brewer, M. B. (1979). In-group bias in the minimal intergroup situation: A cognitive motivational analysis. *Psychological Bulletin, 86,* 307–324.

Brewer, M. B., & Brown, R. (1998). Intergroup relations. In D. T. Gilbert, S. T. Fiske, & G. Lindzey (Eds.), *The handbook of social psychology, Vol. 2* (4th ed., pp. 554–594). New York: McGraw-Hill.

Brewer, M. B., & Weber, J. G. (1994). Self-evaluation effects of interpersonal and intergroup social comparisons. *Journal of Personality and Social Psychology, 66,* 268–275.

Bruner, J. S. (1957). On perceptual readiness. *Psychological Review, 64,* 257–263.

Bush, G., Luu, P., & Posner, M. I. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in Cognitive Science, 4,* 215–222.

Castelli, F., Happé, F., Frith, U., & Frith, C. D. (2000). Movement and mind: A functional imaging study of perception and interpretation of complex intentional movement patterns. *NeuroImage, 12,* 314–325.

Cavanna, A. E., & Trimble, M. R. (2006). The precuneus: A review of its functional anatomy and behavioral correlates. *Brain, 129,* 564–583.

Ciaramelli, E., Muccioli, M., Làdavas, E., & di Pellegrino, G. (2007). Selective deficit in personal moral judgment following damage to ventromedial prefrontal cortex. *Social Cognitive and Affective Neuroscience, 2,* 84–92.

Decety, J., & Lamm, C. (2007). The role of the right temporoparietal junction in social interaction: How low-level computational processes contribute to meta-cognition. *Neuroscientist, 13,* 580–593.

Dobbins, I. G., Rice, H. J., Wagner, A. D., & Schacter, D. L. (2003). Memory orientation succcess: Separable neurocognitive components underlying episodic recognition. *Neuropsychologia, 41,* 318–333.

Ferstl, E. C., & von Cramon, D. Y. (2001). The role of coherence and cohesion in text comprehension: An event-related fMRI study. *Cognitive Brain Research, 11,* 325–340.

Festinger, L. (1954). A theory of social comparison processes. *Human Relations, 7,* 117–140.

Fiske, S. T. (1998). Stereotyping, prejudice, and discrimination. In D. T. Gilbert, S. T. Fiske, & G. Lindzey (Eds.), *Handbook of social psychology, Vol. 2* (4th ed., pp. 357–411). New York: McGraw-Hill.

Fiske, S. T. (2002). What we know now about bias and intergroup conflict, the problem of the century. *Current Directions in Psychological Science, 11,* 123–128.

Fitzgerald, K. D., Welsh, R. C., Gehring, W. J., Abelson, J. L., Himle, J. A., Liberzon, I., et al. (2005). Error-related hyperactivity of the anterior cingulate cortex in obsessive-compulsive disorder. *Biological Psychiatry, 57,* 287–294.

Fletcher, P. C., Frith, C. D., Grasby, P. M., Shallice, T., Frackowiak, R. S., & Dolan, R. J. (1995). Brain systems for encoding and retrieval of auditory-verbal memory. An in vivo study in humans. *Brain, 118,* 401–416.

Forgas, J. P., & Fiedler, K. (1996). Us and Them: Mood effects on intergroup discrimination. *Journal of Personality and Social Psychology, 70,* 28–40.

Friston, K. (1994). Functional and effective connectivity in neuroimaging: A synthesis. *Human Brain Mapping, 2,* 56–78.

Friston, K. J., Frith, C. D., Turner, R., & Frackowiak, R. S. (1995). Characterizing evoked hemodynamics with fMRI. *NeuroImage, 2,* 157–165.

Friston, K. J., Fletcher, P., Josephs, O., Holmes, A., Rugg, M. D., & Turner, R. (1998). Event-related fMRI: Characterizing differential responses. *NeuroImage, 7,* 30–40.

Frith, U., & Frith, C. D. (2001). The biological basis of social interaction. *Current Directions in Psychological Science, 10,* 151–155.

Frith, C. D., & Frith, U. (2006). The neural basis of mentalizing. *Neuron, 50,* 531–534.

Gaertner, L., & Insko, C. A. (2000). Intergroup discrimination in the minimal group paradigm: Categorization, reciprocation, or fear? *Journal of Personal and Social Psychology, 79,* 77–94.

Gallagher, H. L., & Frith, C. D. (2002). Functional imaging of "theory of mind". *Trends in Cognitive Science, 7,* 77–83.

Gallagher, H. L., Happé, F., Brunswick, N., Fletcher, P.C., Frith, U., & Frith, C. D. (2000). Reading the mind in cartoons and stories: An fMRI study of "theory of mind" in verbal and nonverbal tasks. *Neuropsychologia, 38,* 11–21.

Gilboa, A., Winocur, G., Grady, C. L., Hevenor, S. J., & Moscovitch, M. (2004). Remembering our past: Functional neuroanatomy of recollection of recent

and very remote personal events. *Cerebral Cortex*, *14*, 1214–1225.

Greene, J., & Haidt, J. (2002). How (and where) does moral judgment work? *Trends in Cognitive Science*, *6*, 517–523.

Gusnard, D. A., Akbudak, E., Shulman, G. L., & Raichle, M. E. (2001). Medial prefrontal cortex and self-referential mental activity: Relation to a default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America*, *98*, 4259–4264.

Harris, L. T., & Fiske, S. T. (2006). Dehumanizing the lowest of the low. Neuroimaging responses to extreme out-groups. *Psychological Science*, *17*, 847–853.

Harris, L. T., McClure, S. M., van den Bos, W., Cohen, J. D., & Fiske, S. T. (2007). Regions of the MPFC differentially tuned to social and nonsocial affective evaluation. *Cognitive, Affective and Behavioral Neuroscience*, *7*, 309–16.

Harris, L. T., Todorov, A., & Fiske, S. T. (2005). Attribution on the brain: Neuro-imaging dispositional inferences, beyond theory of mind. *Neuro-Image*, *28*, 763–769.

Haslam, S. A. (2004). *Psychology in organizations: The social identity approach* (2nd ed.). London: Sage.

Heekeren, H. R., Wartenburger, I., Schmidt, H., Schwintowski, H. P., & Villringer, A. (2003). An fMRI study of simple ethical decision-making. *NeuroReport*, *14*, 1215–1219.

Henson, R. N. A., Rugg, M. D., Shallice, T., Josephs, O., & Dolan, R. J. (1999). Recollection and familiarity in recognition memory: An event-related functional magnetic resonance imaging study. *Journal of Neuroscience*, *19*, 3962–3972.

Hewstone, M., Rubin, M., & Willis, H. (2002). Intergroup bias. *Annual Review of Psychology*, *53*, 575–604.

Hinkle, S., & Brown, R. J. (1990). Intergroup comparisons and social identity: Some links and lacunae. In D. Abrams & M. A. Hogg (Eds.), *Social identity theory: Constructive and critical advances* (pp. 48–70). London: Harvester Wheatsheaf.

Hogg, M. A., & Vaughan, G. M. (2002). *Social psychology* (3rd ed.). London: Prentice Hall.

Husain, M., & Nachev, P. (2006). Space and the parietal cortex. *Trends in Cognitive Science*, *11*, 30–36.

Jacobsen, T., Schubotz, R. I., Hoefel, L., & von Cramon, D. Y. (2006). Brain correlates of aesthetic judgment of beauty. *NeuroImage*, *29*, 276–285.

Johnson, S. C., Baxter, L. C., Wilder, L. S., Pipe, J. G., Heiserman, J. E., & Prigatano, G. P. (2002). Neural correlates of self-reflection. *Brain*, *125*, 1808–1814.

Kahn, I., Davachi, L., & Wagner, A. D. (2004). Functional-neuroanatomic correlates of recollection: Implications for models of recognition memory. *Journal of Neuroscience*, *24*, 4172–4180.

Kelley, W. M., Macrae, C. N., Wyland, C. L., Caglar, S., Inati, S., & Heatherton, T. F. (2002). Finding the self? An event-related fMRI study. *Journal of Cognitive Neuroscience*, *14*, 785–794.

Krause, B. J., Schmidt, D., Mottaghy, F. M., Taylor, J., Halsband, U., Herzog, H., et al. (1999). Episodic retrieval activates the precuneus irrespective of the imagery content of word pair associates. A PET study. *Brain*, *122*, 255–263.

Lohmann, G., Muller, K., Bosch, V., Mentzel, H., Hessler, S., Chen, L., et al. (2001). LIPSIA—a new software system for the evaluation of functional magnetic resonance imaging of the human brain. *Computerized Medical Imaging and Graphics*, *25*, 449–457.

Macrae, C. N., Heatherton, T. F., & Kelley, W. M. (2004). A self less than ordinary: The medial prefrontal cortex and you. In M. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 1067–1075). Cambridge, MA: MIT Press.

Maguire, E. A., Frith, C. D., & Morris, R. G. (1999). The functional neuroanatomy of comprehension and memory: The importance of prior knowledge. *Brain*, *122*, 1839–1850.

Markus, H., & Kitayama, S. (1991). Culture and the self: Implications for cognition, emotion, and motivation. *Psychological Review*, *98*, 224–253.

Markus, H., & Kitayama, S. (1998). The cultural psychology of personality. *Journal of Cross-Cultural Psychology*, *29*, 63–87.

McCabe, K., Houser, D., Ryan, L., Smith, V., & Trouard, T. (2001). A functional imaging study of cooperation in a two-person reciprocal exchange. *Proceedings of the National Academy of Sciences of the United States of America*, *98*, 11832–11835.

Miezin, F. M., Maccotta, L., Ollinger, J. M., Petersen, S. E., & Buckner, R. L. (2000). Characterizing the hemodynamic response: Effects of presentation rate, sampling procedure, and the possibility of ordering brain activity based on relative timing. *NeuroImage*, *11*, 735–759.

Moll, J., de Oliveira-Souza, R., Eslinger, P. J., Bramati, I. E., Mourao-Miranda, J., Andreiuolo, P. A., et al. (2002). The neural correlates of moral sensitivity: A functional magnetic resonance imaging investigation of basic and moral emotions. *Journal of Neuroscience*, *22*, 2730–2736.

Mummendey, A., & Otten, S. (2002). Theorien intergruppalen Verhaltens. In D. Frey & M. Irle (Eds.), *Theorien der Sozialpsychologie*, Vol II (pp. 95–199). Berne, Switzerland: Huber.

Mussweiler, T. (2003). "Everything is relative": Comparison processes in social judgment. The 2002 Jaspars Lecture. *European Journal of Social Psychology*, *33*, 719–733.

Neumann, J., & Lohmann, G. (2003). Bayesian second-level analysis of functional magnetic resonance images. *NeuroImage*, *20*, 1346–1355.

Norris, D. G. (2000). Reduced power multislice MDEFT imaging. *Journal of Magnetic Resonance Imaging*, *11*, 445–451.

Northoff, G., & Bermpohl, F. (2004). Cortical midline structures and the self. *Trends in Cognitive Science*, *8*, 102–107.

Oakes, P. J. (1987). The salience of social categories. In J. C. Turner, M. A. Hogg, P. J. Oakes, S. Reicher, & M. Wetherwell (Eds.), *Rediscovering the social group: A self-categorization theory* (pp. 117–141). Oxford: Blackwell.

Ochsner, K. N., Knierim, K., Ludlow, D. H., Hanelin, J., Ramachandran, T., Glover, G., et al. (2004). Reflect-

ing upon feelings: An fMRI study of neural systems supporting the attribution of emotion to self and other. *Journal of Cognitive Neuroscience, 16*, 1746–1772.

Orban, G. A., van Essen, D., & Vanduffel, W. (2004). Comparative mapping of higher visual areas in monkeys and humans. *Trends in Cognitive Science, 8*, 315–324.

Rogers, R. D., Ramnani, N., Mackay, C., Wilson, J. L., Jezzard, P., Carter, C. S., et al. (2004). Distinct portions of anterior cingulate cortex and medial prefrontal cortex are activated by reward processing in separable phases of decision-making cognition. *Biological Psychiatry, 55*, 594–602.

Sanfey, A. G., Rilling, J. K., Aronson, J. A., Nystrom, L. E., & Cohen, J. D. (2003). The neural basis of economic decision-making in the Ultimatum Game. *Science, 300*, 1755–1758.

Sassenberg, K., Kessler, T., & Mummendey, A. (2003). Less negative = more positive? Social discrimination as avoidance and approach. *Journal of Experimental Social Psychology, 39*, 48–58.

Saxe, R. (2006). Uniquely human social cognition. *Current Opinion Neurobiology, 16*, 235–239.

Saxe, R., & Kanwisher, N. (2003). People thinking about thinking people. The role of the temporo-parietal junction in "theory of mind". *NeuroImage, 19*, 1835–1842.

Saxe, R., & Wexler, A. (2005). Making sense of another mind: The role of the right temporo-parietal junction. *Neuropsychologia, 43*, 1391–1399.

Sieboerger, F. T., Ferstl, E. C., & von Cramon, D. Y. (2007). Making sense of nonsense: An fMRI study of task induced inference processes during discourse comprehension. *Brain Research, 29*, 77–91.

Squire, L. R., Ojemann, J. G., Miezin, F. M., Petersen, F. E., Videen, T. O., & Raichle, M. E. (1992). Activation of the hippocampus in normal humans: A functional anatomical study of memory. *Proceedings of the National Academy of Sciences of the United States of America, 89*, 1837–1841.

Strack, F. (1992). The different routes to social judgments: Experiential versus informational strategies. In L. L. Martin & A. Tesser (Eds.), *The construction of social judgment* (pp. 249–275). Hillsdale, NJ: Lawrence Erlbaum.

Tajfel, H., Billig, M. G., Bundy, R. F., & Flament, C. (1971). Social categorization and intergroup behavior. *European Journal of Social Psychology, 1*, 149–177.

Tajfel, H., & Turner, J. C. (1979). An integrative theory of intergroup conflict. In W. G. Austin & S. Worchel (Eds.), *The social psychology of intergroup relations* (pp. 33–47). Monterey, CA: Brooks/Cole.

Tajfel, H., & Turner, J. C. (1986). The social identity theory of intergroup behavior. In S. Worchel & W. G. Austing (Eds.), *Psychology of intergroup relations* (2nd ed., pp. 7–24). Chicago: Nelson-Hall.

Talairach, P., & Tournoux, J. (1998). *Co-planar stereotactic atlas of the human brain*. Stuttgart, Germany: Thieme.

Terry, D. J., & Hogg, M. A. (1996). Group norms and the attitude–behavior relationship: A role for group identification. *Personal and Social Psychology Bulletin, 22*, 776–793.

Thirion, J. P. (1998). Image matching as a diffusion process: An analogy with Maxwell's demons. *Medical Image Analysis, 2*, 243–260.

Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences, 28*, 675–691.

Turner, J. C., Hogg, M. A., Oakes, P. J., Reicher, S. D., & Wetherell, M. S. (1987). *Rediscovering the social group: A self-categorization theory*. Oxford, UK: Basil Blackwell.

Turner, J. C., & Reynolds, K. J. (2004). The social identity perspective in intergroup relations: Theories, themes, and controversies. In M. B. Brewer & M. Hewstone (Eds.), *Self and social identity* (pp. 259–277). Oxford, UK: Blackwell Publishing.

Ugurbil, K., Garwood, M., Ellermann, J., Hendrich, K., Hinke, R., Hu, X., et al. (1993). Imaging at high magnetic fields: Initial experiences at 4 T. *Magnetic Resonance Quarterly, 9*, 259–277.

Van den Bos, W., McClure, S. M., Harris, L. T., Fiske, S. T., & Cohen, J. D. (2007). Dissociating affective evaluation and social cognitive processes in the ventral medial prefrontal cortex. *Cognitive, Affective and Behavioral Neuroscience, 7*, 337–346.

Van Overwalle, F. (in press). Social cognition and the brain: A meta-analysis. *Human Brain Mapping*.

Vogeley, K., Bussfeld, P., Newen, A., Herrmann, S., Happé, F., Falkai, P., et al. (2001). Mind reading: Neural mechanisms of theory of mind and self-perspective. *NeuroImage, 14*, 170–181.

Vogeley, K., & Fink, G. R. (2003). Neural correlates of the first-person-perspective. *Trends in Cognitive Science, 7*, 38–42.

Vogeley, K., May, M., Ritzl, A., Falkai, P., Zilles, K., & Fink, G. R. (2004). Neural correlates of first-person perspective as one constituent of human self-consciousness. *Journal of Cognitive Neuroscience, 16*, 817–827.

Vogt, B. A. (2005). Pain and emotion interactions in subregions of the cingulate gyrus. *Nature Reviews Neuroscience, 6*, 533–544.

Wheeler, M. E., & Buckner, R. L. (2003). Functional dissociation among components of remembering: Control, perceived oldness and content. *Journal of Neuroscience, 23*, 3869–3880.

Wills, T. A. (1981). Downward comparison principles in social psychology. *Psychological Bulletin, 90*, 245–271.

Worsley, K. J., & Friston, K. J. (1995). Analysis of fMRI time-series revisited—again. *NeuroImage, 2*, 173–181.

Yamagishi, T., & Kiyonari, T. (2000). The group as the container of generalized reciprocity. *Social Psychology Quarterly, 63*, 116–132.

Zilles, K., & Palomero-Gallagher, N. (2001). Cyto-, myelo-, and receptor architectonics of the human parietal cortex. *NeuroImage, 14*, S8–S20.

Zysset, S., Huber, O., Ferstl, E. C., & von Cramon, D. Y. (2002). The anterior frontomedian cortex and evaluative judgment: An fMRI study. *NeuroImage, 15*, 983–991.