



Ventromedial prefrontal volume predicts understanding of others and social network size

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ABSTRACT

Cognitive abilities such as Theory of Mind (ToM), and more generally mentalizing competences, are central to human sociality. Neuroimaging has associated these abilities with specific brain regions including temporoparietal junction, superior temporal sulcus, frontal pole, and ventromedial prefrontal cortex. Previous studies have shown both that mentalizing competence, indexed as the ability to correctly understand others' belief states, is associated with social network size and that social group size is correlated with frontal lobe volume across primate species (the social brain hypothesis). Given this, we predicted that both mentalizing competences and the number of social relationships a person can maintain simultaneously will be a function of gray matter volume in these regions associated with conventional Theory of Mind. We used voxel-based morphometry of Magnetic Resonance Images (MRIs) to test this hypothesis in humans. Specifically, we regressed individuals' mentalizing competences and social network sizes against gray matter volume. This revealed that gray matter volume in bilateral posterior frontal pole and left temporoparietal junction and superior temporal sulcus varies parametrically with mentalizing competence. Furthermore, gray matter volume in the medial orbitofrontal cortex and the ventral portion of medial frontal gyrus, varied parametrically with *both* mentalizing competence and social network size, demonstrating a shared neural basis for these very different facets of sociality. These findings provide the first fine-grained anatomical support for the social brain hypothesis. As such, they have important implications for our understanding of the constraints limiting social cognition and social network size in humans, as well as for our understanding of how such abilities evolved across primates.

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Introduction

The ability to infer the mental states of other individuals, commonly known as Theory of Mind, is widely accepted as a crucial cognitive basis for sociality in humans (Frith and Frith, 2003; Leslie, 1987, 1994; Wimmer and Perner, 1983). The neural basis of Theory of Mind (ToM) has received considerable attention in recent years and a number of core brain structures have been implicated in solving false belief tasks, the generally accepted benchmark for Theory of Mind (Wimmer and Perner, 1983). These include regions of the medial prefrontal cortex (mPFC) (Gallagher and Frith, 2003), temporo-parietal junction (TPJ) (Saxe and Kanwisher, 2003), superior temporal sulcus (STS) (Frith and Frith, 2003), and frontal pole (FP) (Decety and Lamm, 2007; Gallagher et al., 2000; Saxe, 2006;

Saxe et al., 2004; Spreng et al., 2009). ToM is functionally equivalent to second order intentionality ("I believe that you suppose..."), and is acquired by the age of about 4–5 years (Astington, 1993; Leslie, 1987). As such, ToM poses no challenges for normal adult humans, who are usually able to cope with mentalizing tasks up to 4th or 5th order intentionality (Kinderman et al., 1998; Stiller and Dunbar, 2007), with only rare individuals performing well at 6th order. Performance at these higher orders of intentionality has recently been shown to predict prefrontal volume (Powell et al., 2010). However, this work used large regions of interest encompassing the entire dorsal and orbital prefrontal cortices and thus provides little information as to the specific subregions in which these quantitative differences in neurobiology may occur (Dunbar, 2009; 2011).

At the other end of the scale, the well-documented cross-species positive correlation between social group size and neocortex volume in primates, otherwise known as the social brain hypothesis (Dunbar, 1998; Dunbar and Shultz, 2007; Pérez-Barbería et al., 2007; Shultz and Dunbar, 2007, 2010), implies that the social cognitive skills

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underpinning this relationship must have some kind of neurophysiological representation (Shultz and Dunbar, 2010). To date, it has proved difficult to integrate the social brain hypothesis with any underlying cognitive and neurophysiological substrates, and this weakness has attracted some criticism (Healy and Rowe, 2007). Nonetheless, at least in humans, individual competences on high order intentionality tasks correlate positively with the size of personal social networks (Stiller and Dunbar, 2007), and there is strong circumstantial evidence to suggest that social cognitive competences might correlate positively with some aspects of brain size (notably frontal lobe volume) across primate species (Dunbar, 2003).

These observations raise two obvious questions. First, do those who can compute higher levels of intentionality have access to greater processing power in the brain networks required for mentalizing? In other words, is there a quantitative relationship between the level of intentionality at which a healthy individual can habitually work and the volume of neural matter in the classic Theory of Mind regions that the individual can bring to bear on the problem? Second, do either of these correlate with the size of the person's social network (i.e. the number of individuals they list as personal friends)?

Here, we used voxel-based morphometry (VBM) of high resolution magnetic resonance imaging (MRI) brain scans to test these hypotheses. On the basis of several recent meta-analyses (Frith and Frith, 2003; Spreng et al., 2009; Van Overwalle, 2009), we identified four principal regions of the brain that are commonly associated with conventional Theory of Mind: mPFC, TPJ, STS, and FP. We first tested for a quantitative relationship between individuals' social cognitive competences (indexed as the intentionality fail level) and the volume of gray matter in these four regions. We then tested for a relationship between the size of each individual's personal social network and gray matter volume in these same regions. Finally, we tested for areas correlating with *both* high order intentionality abilities and social network size. We chose the fine-grained analysis offered by VBM in order to determine whether or not those regions known to be involved in Theory of Mind (i.e. conventional second order intentionality) exhibit a parametric relationship with individual differences in mentalizing competences (higher order intentional competences) and/or network size. Such a relationship would imply that higher order intentionality is computationally more demanding, and that social competence is linked to neural recruitment within quite tightly defined brain regions. Since we aimed to test the role of information processing, rather than information exchange between processing units, we focus explicitly on gray matter volume rather than white matter volume.

Materials and methods

We sampled 45 individuals, 26 females and 19 males aged between 18 and 50 years (mean 25.6 years for both females and males, SEM 2 and 1 years respectively). We used subjects who: (1) reported no history of neurological problems, (2) were native English speakers, and (3) had not previously been involved in research on Theory of Mind. All subjects gave written fully informed consent of their willingness to participate. The study was approved by the appropriate local ethics committee.

We determined competence on intentionality and memory tasks using a written questionnaire. This consisted of a series of five short stories, based on revised versions of those used by Stiller and Dunbar (2007), and identical to those used in Powell et al. (2010) (see Supplementary materials) which were designed to test subjects' ability to correctly infer the mind states, i.e. the beliefs, of the characters in the story. Each story was approximately 200 words in length and described a social interaction involving several individuals. Subjects answered 20 questions immediately after reading each story, 10 mentalizing questions varying from 2nd to 6th order intentionality and 10 factual (memory) questions varying from 2 to 6 facts. The

original stories were revised to a standard length, composition, and number of questions at each complexity level. The subject's own mind state was defined as first order intentionality, and the mind state of each protagonist from the story included in a question added successive levels of intentionality. A 6th order intentionality question thus involved tracking the mind states of five individuals in the story, as well as the subject's own mind state. The number of words used and the number of people mentioned were balanced across intentionality and memory questions (t -test $P > 0.05$ in both cases). Participants were asked to read the stories to themselves twice and then proceed to the questions which they answered by specifying T or F. Subjects were not cued as to which were mentalizing and which memory questions, and the two kinds of questions were randomly interspersed. Performance was assessed in an identical manner for both intentionality and memory for facts. In both cases, following Stiller and Dunbar (2007), we calculated the mean 'fail point' by using a re-scaled weighted mean of performance at the 5 levels of complexity examined (levels 2–6).

Personal social networks consist of a series of concentric layers that include progressively more individuals, with the size of the layers scaling with each other with a constant scaling ratio of about 3 (Hill & Dunbar 2003; Zhou et al. 2005; Hamilton et al. 2007). Because the layers scale so closely with each other, which layer is used as an index of an individual's social engagement is largely a matter of convenience. For present purposes, we have focused on the second layer, sometimes known as the sympathy group (Buys and Larson, 1979) because it maximizes the range of variation across individuals while at the same time minimizing the time and effort required to complete the questionnaire, as well as reducing the risk of individuals being overlooked (Roberts et al. 2009). We derived information about social network size using a second written questionnaire completed immediately after the IMT (see Online supplementary material). Here, following prior reports (Dunbar and Spoor, 1995; Stiller and Dunbar, 2007; Powell et al. 2010), participants were asked to list the initials of every individual with whom they had had personal contact or communication over the previous 30 days. The instructions were: 'In the spaces below, please list the **INITIALS** of everyone with whom you had some kind of social contact (a) **during the last 7 days** and (b) **during the rest of the last month** (i.e. approx. 30 days). Contact means some form of interaction, including face-to-face, phone call, email or text-messaging, or a letter. Please **DO NOT INCLUDE** people whom you contacted for professional reasons (e.g. your doctor, lawyer, hairdresser, priest, employer or supervisor, plumber or DIY consultant etc.) **UNLESS** you considered that interaction to have been of a mainly **SOCIAL** nature at the time. Please also indicate Males [M] and Females [F] after all initials. You can look at a list of names in your phone/address book if this helps.'

MRI data were acquired using a Siemens Trio 3.0 Tesla, whole body MRI system, with an eight channel head coil. High resolution (1 mm isotropic) anatomical whole brain images were obtained using a T1 weighted 3D-gradient-echo pulse sequence, with the following parameters (T1 190, TR 7.92, TE 2.48, FOV 224×256, matrix 256×256×256 pixels, flip angle 16°) acquired in sagittal plane. After MR acquisition, datasets were imported into BrainVoyager for re-alignment. Pre-processing required reformatting the image, and orienting it to a standardized sagittal plane orthogonal to the bicommissural plane.

A voxel-based morphometry protocol was performed on the anatomical scans using SPM2 (available at <http://www.fil.ion.ucl.ac.uk/spm/>).

First, a customized whole-brain T1-weighted template image and prior probability maps for gray matter, white matter, and cerebrospinal fluid were created from the anatomical scans of our 45 participants. These customized images were used as priors during subsequent image segmentation. The original T1 scans were then normalized and segmented using the optimized VBM approach developed by Good et al. (2001, 2002). Finally, the optimized parameters from the latter

normalization step were applied to the original anatomical scans which were segmented to obtain gray matter, white matter, and cerebrospinal fluid images in MNI space. These segments were modulated, smoothed with an 8 mm Gaussian kernel, and used for the statistical analysis.

We constructed two separate design matrices. The first tested for correlations between gray matter volume and intentionality performance using intentionality fail point as the regressor of interest. Memory fail point, age, and sex were included as covariates of no interest. The second tested for correlations between gray matter volume and social network size using network size as the main regressor, with age and sex again included as covariates of no interest. The neural correlates for each regressor of interest were examined using a simple *t*-test, with positive and negative relationships examined independently. Because the widespread use of overly stringent corrections for multiple comparisons in neuroimaging has recently been criticized as a known source of Type II errors (false negatives) (Lieberman and Cunningham 2009) we used the more liberal threshold of $p = 0.001$ uncorrected, with an extent threshold of $k > 5$ voxels within our a priori regions of interest (the mPFC, TPJ, STS, and FP). For added statistical rigor, small volume corrections at $p = 0.05$ were performed on uncorrected findings using 8 mm radius spheres centered on coordinates taken from Spreng et al. (2009).

In order to isolate areas where gray matter volume correlated with both intentionality and social network size, we then performed a conjunction analysis using the masking function of SPM2. First, a one-sample *t*-test was computed for one of the contrasts of interest (i.e. the contrast for areas varying parametrically with intentionality fail point) and the suprathreshold voxels from this analysis were used to form a mask. A second one-sample *t*-test was then computed for the other contrast of interest (i.e. the contrast for areas varying parametrically with social network size) and the mask from the first analysis was applied such that the resulting conjunction revealed regions of conjoint significance. The individual one-sample *t*-tests were thresholded at $p < 0.01$, such that the conjoint probability of the conjunction analysis, estimated using Fisher's method (Fisher, 1950; Lazar et al., 2002) was $p < 0.001$. As above, statistical results in the mPFC, TPJ, STS, and FP were considered significant at $p = 0.001$ uncorrected, with an extent threshold of $k > 5$ voxels.

Results

The mean number of social contacts reported was $36.7 \pm \text{SEM } 2.7$. As found by Stiller and Dunbar (2007), there was a significant Pearson correlation ($r = 0.254$, $N = 45$, $p < 0.05$) between social network size and intentionality fail point. In order to control for the potential contribution of memory abilities, we also ran this analysis as a partial correlation with memory fail point partialled out. This showed that the relationship between network size and intentionality remained significant and was, if anything, slightly stronger ($r_p = 0.330$, $N = 42$, $p = 0.024$ 2-tailed) when memory was partialled out.

To identify brain areas where cortical volume correlates with individuals' social cognitive competences, we conducted a whole brain voxel-based-morphometry (VBM) analysis by regressing gray matter volume against subjects' individual fail-points, as calculated using data from all 50 Theory of Mind questions. To control for the contribution of memory to these results, our model included a measure of memory performance calculated in a parallel manner using the 50 memory questions.

Our parametric regression analysis revealed that performance on high-level intentionality questions predicts gray matter volume in the left TPJ as well as in the posterior FP bilaterally (see Table 1A for a full list of areas and Figs. 1 A and B for illustrations). The observation that individuals who can perform more complex intentionality calculations have more gray matter in these brain regions, which are known to activate during ToM tasks, suggests that gray matter

Table 1

Areas within the regions of interest in mPFC, TPJ, STS, and FP in which statistical findings survived thresholding at $p = 0.001$ uncorrected with an extent threshold of $k > 5$ voxels (A) when gray matter volume was correlated with intentionality competence and (B) when gray matter was correlated with social network size, (C) when gray matter was correlated with both intentionality and social network size (conjunction analysis). The number of surviving voxels, peak Z value, uncorrected probability level, and peak coordinates are shown for each region. Results surviving small volume correction at $p = 0.05$ are indicated with an asterisk.

# Voxels	Maximum Z value	Uncorrected Probability	x,y,z	Brain region
<i>A) Intentionality</i>				
241	3.7	<0.001	43 46 6	Frontal pole
126	3.5	<0.001	−50 −1 −11	Superior temporal gyrus
24	3.1	0.001	−49 −63 1	Middle temporal gyrus
6	3.1	0.001	−48 −48 25	Supramarginal gyrus (TPJ)*
16	3.1	0.001	−43 42 12	Middle frontal gyrus
8	3.0	0.001	−52 −28 7	Frontal pole
<i>B) Social network</i>				
11	3.3	0.001	10 51 25	Ventromedial frontal gyrus*
<i>C) Conjunction of intentionality and social network size</i>				
103	–	0.001	8 50 −23	Medial orbitofrontal gyrus
14	–	0.001	8 44 −7	Ventromedial frontal gyrus

volume may relate directly to processing power in this task. As a test of our a priori hypothesis that there would be an overlap between the areas in which gray matter volume correlated with intentionality ability and with social network size, we next performed a formal conjunction analysis (see Materials and methods) which searched specifically for regions where gray matter volume correlated with *both* intentionality competence and social network size. This revealed a conjoint relationship of that description in two regions of the VMPFC: one in the medial orbitofrontal cortex and a more circumscribed area in the ventral medial frontal gyrus (Fig. 1C Table 1C). Notably, the inverse contrasts, which tested for areas showing a negative correlation between gray matter volume and intentionality fail point, and between gray matter volume and social network size, revealed no significant findings at $p = 0.001$ uncorrected.

The observation that both subjects with the ability to process higher orders of intentionality and subjects having larger than average social groups, have greater gray matter volume in VMPFC substantiates the suggestion that these aspects of social cognition are closely related.

The social brain hypothesis holds that the primate brain has evolved to support the demands of increasingly large numbers of dynamically complex relationships in bonded social groups (Dunbar, 1998; Shultz and Dunbar, 2007). A simple interpretation of this hypothesis would predict that computational power in the same brain regions correlates both with intentionality processing ability and with social network size. Our current findings support this both behaviorally (by showing a significant positive relationship between intentionality fail level and network size) and neuroanatomically (by showing that gray matter volume in two areas of VMPFC predicts both measures: Fig. 1C and Table 1C).

Discussion

Our data support a previous finding that there is a significant correlation between the size of an individual's social network and their level of social cognitive competence (indexed as their ability to correctly understand others' belief states). We extend this by showing that these measures predict the gray matter volume of brain regions used in mentalizing and emotional processing. The quantitative relationship that we demonstrate between the levels of intentionality at which an individual can habitually work (an index of social cognitive competence) and the volume of neural material in the brain regions known to underpin Theory of Mind suggests that gray matter volume

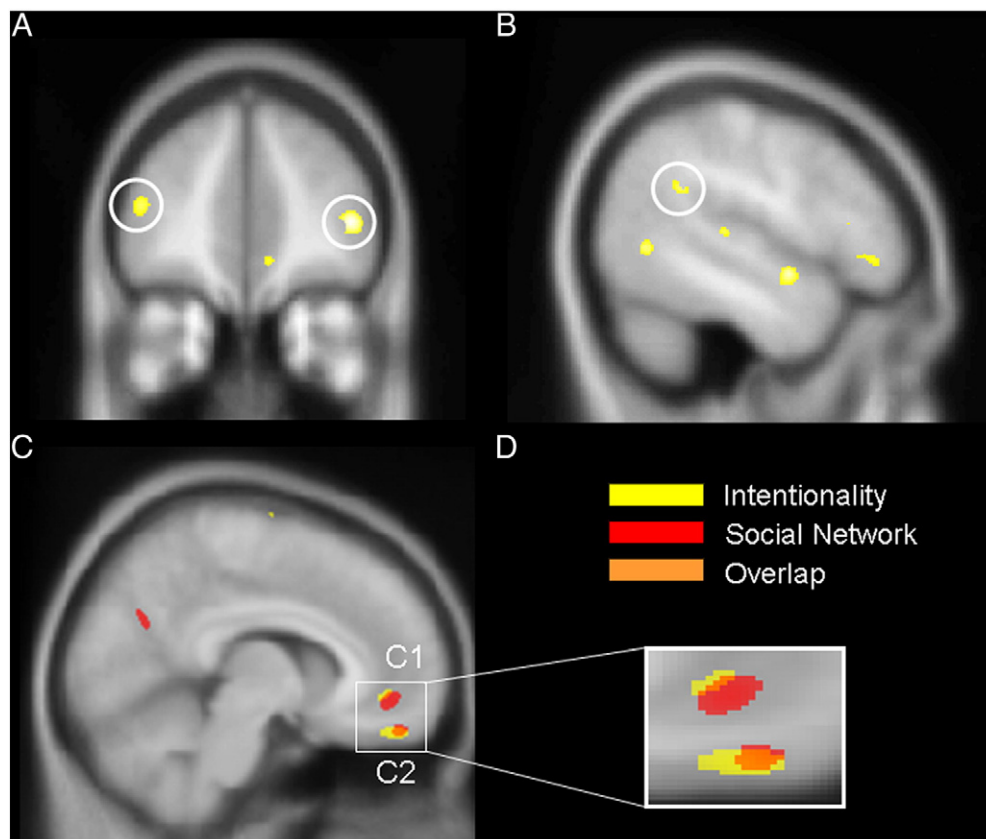


Fig. 1. There was a significant positive correlation between the volume of gray matter in the bilateral frontal pole (FP), an area commonly associated with Theory of Mind, and performance on high order intentionality tasks (A). A similar correlation was observed in the left temporo-parietal junction (TPJ) (B). These results are rendered on the MNI 152 brain at a visualization threshold of $p = 0.005$. In C a conjunction analysis reveals regions of shared positive correlation with both intentionality performance and social network size in the (ventral) medial frontal gyrus (C1) and in the medial orbitofrontal cortex (C2). Here, correlations with intentionality are depicted in yellow, and correlations with social network size are depicted in red, both at $p = 0.01$. Areas of overlap, depicted in orange, are significant at $p = 0.001$ (Fisher, 1950; Lazar et al., 2002) and suggest a common neural underpinning for these two socio-cognitive capabilities.

in the ToM network itself may serve as an index of processing power in these tasks. This is in line with a recent study which used the IMT task to show that ability on high order intentionality is predictive of gross volume in the orbital prefrontal cortex (Powell et al., 2010), as well as a clinical study (Herold et al., 2009) which demonstrated that performance on a faux pas test predicted gray matter deterioration in the frontal pole and orbitofrontal cortices of schizophrenic patients. Our data are more difficult to interpret when compared with findings from studies of autism, partly because these are somewhat inconsistent (Brieber et al., 2007; Girgis et al., 2007; Hardan et al., 2006; Ke et al., 2008), partly because some of them have used different anatomical measures, and also because the extent to which studies of such clinical cases can inform us about quantitative individual differences among normal adults has yet to be determined.

Of the Theory of Mind regions in which we observed enhanced gray matter volume in people who exhibited a higher fail point on our intentionality task (the IMT), the left TPJ is the most strongly linked to ToM, see Van Overwalle (2009) for a recent meta-analysis of over 200 neuroimaging studies of social cognition. Observation of greater gray matter volume in this region in high performers is in particularly good keeping with the literature because the IMT is a test of belief inference (see Supplementary information for sample questions). Although left TPJ is not quite so frequently active during ToM processing as right TPJ, which is widely acknowledged as playing a key role in belief inference (Saxe et al., 2004), it is nevertheless active during identification of goals and intentions in a wide range of tasks including cartoons (Gallagher et al., 2000), videos (German et al., 2004) and text-based stories (Perner et al., 2006; Saxe, 2006; Saxe

and Kanwisher, 2003; Saxe and Powell, 2006). Medial prefrontal cortex (mPFC) is also commonly activated during these tasks, but instead of belief inference, it appears to be involved in decoupling the perspectives of other people from one's own (Frith and Frith, 2001; Gallagher and Frith, 2003). This distinction between TPJ and mPFC is illustrated by observation of stronger responses in the former, but not the latter, during inferred beliefs compared to true beliefs (Sommer et al., 2007). Furthermore, patients with lesions to the prefrontal cortex are unimpaired on simple false belief tasks, but markedly impaired on more difficult ones (Stuss et al., 2001). Achieving a high fail point on the IMT requires inference about multiple layers of belief. For instance, a typical True/False question in the task reads 'Sam thought that Henry knew the Post Office was in Bold Street and hence that Henry must have intended to mislead Sam'. To answer correctly, participants have to infer the beliefs of several other individuals, while suppressing their own belief. We conjecture that the observed correlation between this task and mPFC gray matter volume may therefore relate to a superior ability to separate out these various layers.

In addition to findings in the TPJ and vMPFC, our data showed correlations between intentionality performance and gray matter volume in the frontal pole and STS, both areas that have been linked to calculation of what a person is likely to do or think (Gallagher and Frith, 2003). The frontal polar result is particularly interesting because it is in keeping with the findings of Herold et al. (2009) regarding gray matter deterioration and Theory of Mind impairment in schizophrenic patients. Prefrontal cortex is involved in planning for the future and in anticipating the future state of the world, including the state of the minds of others (Coltheart, 1989; Walter et al., 2004). The particular

region of frontal pole in which we observed this correlation is also associated with prospective memory (Burgess et al., 2001). Within Theory of Mind tasks, this region is believed to be involved in prediction of thoughts and feelings (Frith and Frith, 2006; Walter et al., 2004), and has been shown to activate during prospective intentionality calculations (den Ouden et al., 2005).

Turning to the STS, the specific portion of this structure in which we observed a correlation between gray matter volume and intentionality falls towards the rear of the anterior temporal lobe. Because the anterior temporal lobe is critical for semantic memory (Patterson et al., 2007) as well as for Theory of Mind, some authors have suggested that it may be important for predicting what a person is likely to do or think (Frith and Frith, 2006). This area has recently been observed to activate during a task in which mental state is judged using the eyes only (Castelli et al., 2010), and was also more active during the social emotion of embarrassment, in which one typically mentalizes about the thoughts and reactions of others, than during the less social emotion of guilt (Takahashi et al., 2004). Our current data add to these findings by showing that greater gray matter volume in this area is associated with a superior score on our mentalizing task.

Moving to the results of our conjunction analysis, the correlation which we observed between mPFC gray matter volume and both IMT performance and social network size suggests that the cognitive abilities underpinning these two behavioral phenomena draw upon common computational resources. This in turn suggests that there may be a deep biological basis for individual differences in both social skills and sociality. Appropriately, this shared resource falls in a region which is known to be important for mentalizing about the emotional states of others. The orbitofrontal cortex plays a well established role in emotional processing, for recent reviews, see Rempel-Clower (2007); Rolls (2008); Rudebeck et al. (2008); Szily and Keri (2008), and is also important for various forms of empathy (Farrow et al., 2001; Moll et al., 2002; Shamay-Tsoory et al., 2009). Furthermore, both medial orbitofrontal cortex and medial prefrontal gyrus have been shown to respond selectively to mentalizing about emotional states (Vollm et al., 2006; Walter et al., 2004), a capacity which might reasonably be expected to impact upon one's ability to maintain close friendships.

Taken together, these findings add weight to the social brain hypothesis which states that, in primates as a whole (i.e. including humans), the ability to handle social complexity (as reflected in social group size) is a function of neocortical volume and, in particular, of frontal neocortex volume (Dunbar, 2003; Dunbar, 2011). The current results present the strongest support for this hypothesis to date since, rather than looking at large scale cortical volume, we use the high spatial precision of Voxel Based Morphometry to show the precise cortical regions in which gray matter volume correlates with performance on a complex social task, while prior studies have examined gross anatomy of much larger brain regions, i.e. the entire dorsal and orbital prefrontal cortices (Powell et al. 2010). Furthermore, the current results show that these regions of increased volume overlap with the network of brain structures which are functionally associated with social network size. Importantly, these results also refine the claim of the social brain hypothesis (1) by demonstrating that this relationship is sufficiently fine-tuned to be evident at the within-species (i.e. between-individual) level and not just at the between-species level, and (2) by suggesting that the region most critical to this shared processing falls in the ventral portion of medial frontal cortex. While previous behavioral studies have shown that social cognition is especially taxing compared to conventional executive function cognition (Kinderman et al., 1998), the present findings provide the first neurophysiological evidence to support this claim. In this respect, we provide the first clear evidence as to why, in broader evolutionary terms, sociality has required significant investment in the neural matter, as implied by the social brain hypothesis.

From an evolutionary perspective, our demonstration that humans exhibit a quantitative relationship between gray matter volume in selected brain regions and social cognitive abilities suggests an underlying biological continuum which might reasonably be expected to reach back into the nonhuman primates, and perhaps to mammals more generally. Quite how this continuum might be instantiated in these species remains to be seen. We do not know enough about primate (or even mammalian) social cognition, let alone about the functional differences in neurophysiology between species, to do more than speculate at this stage (Dunbar, 2009). However, our findings should stimulate a search for correlations between these same regions and socio-cognitive skills in non-human primates in order to test this claim. Understanding how such relationships relate to cognition in general and the scale of our social world may go some way to allowing us to understand exactly why it is that humans differ from other species of animals (Dunbar, 2008; Dunbar, 2009).

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