The Default Mode Network in Chimpanzees (Pan troglodytes) is Similar to That of Humans

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The human default mode network (DMN), comprising medial prefrontal cortex, precuneus, posterior cingulate cortex, lateral parietal cortex, and medial temporal cortex, is highly metabolically active at rest but deactivates during most focused cognitive tasks. The DMN and social cognitive networks overlap significantly in humans. We previously demonstrated that chimpanzees (Pan troglodytes) show highest resting metabolic brain activity in the cortical midline areas of the human DMN. Human DMN is defined by task-induced deactivations, not absolute resting metabolic levels; ergo, resting activity is insufficient to define a DMN in chimpanzees. Here, we assessed the chimpanzee DMN’s deactivations relative to rest during cognitive tasks and the effect of social content on these areas’ activity. Chimpanzees performed a match-to-sample task with conspecific behavioral stimuli of varying sociality. Using [¹⁸F]-FDG PET, brain activity during these tasks was compared with activity during a nonsocial task and at rest. Cortical midline areas in chimpanzees deactivated in these tasks relative to rest, suggesting a chimpanzee DMN anatomically and functionally similar to humans. Furthermore, when chimpanzees make social discriminations, these same areas (particularly precuneus) are highly active relative to nonsocial tasks, suggesting that, as in humans, the chimpanzee DMN may play a role in social cognition.

Keywords: comparative cognition, functional neuroimaging, social cognition

Introduction

In the past decade, many functional neuroimaging studies have identified a network in humans, known as the default mode network (DMN), which exhibits a high degree of metabolic activity at rest but becomes less active during focused cognitive tasks (Gusnard and Raichle 2001). Significant overlaps between this DMN and neural activity associated with social cognitive processes, particularly those related to the self, have been described (Buckner et al. 2008; Schilbach et al. 2008; Mars et al. 2012). Such studies collectively suggest that the human brain’s default mode may involve reflection on the self and on social relationships and interactions—that social information and its related mental processes hold a privileged position in human cognition as a whole. Common chimpanzees (Pan troglodytes)—our closest living primate relatives, along with bonobos—have a highly complex social structure (de Waal 1982; Goodall 1986) and demonstrate sophisticated cognitive abilities both in captivity and in the wild. In an environment where social skill can be just as advantageous as physical strength, it is likely that a default mode of brain activity centered on social cognition may have been selected for in chimpanzees as appears to be the case in humans. Following a previous study demonstrating DMN-like resting brain activity in chimpanzees (Rilling et al. 2007), this study explores the relationship between chimpanzee social cognition and default mode function.

Initial publications describing the DMN (Gusnard and Raichle 2001; Gusnard et al. 2001; Raichle et al. 2001) ascribed function to several brain areas within the network. Among these, the posterior cingulate cortex (PCC) and precuneus are suggested to process emotion or, more recently, to contribute to episodic memory retrieval (Cavanna and Trimble 2006; Buckner and Carroll 2007; Buckner et al. 2008; Spreng et al. 2009). Also in the posterior part of the network, lateral parietal cortex and lateral posterior temporal cortex attend to salient and novel or unexpected external stimuli (Jenkins et al. 1994; Constantinidis and Steinmetz 2001; Gusnard and Raichle 2001), particularly biological motion (Grézes et al. 2001; Grossman and Blake 2001; Gusnard and Raichle 2001). The anterior portion of the DMN includes ventromedial prefrontal cortex (VMPFC), associated with integration of cognitive and emotional information and online monitoring of sensory inputs, and dorsomedial prefrontal cortex (DMPFC), associated with representing states of the self and of others (i.e. processes related to theory of mind) (Buckner and Carroll 2007; Spreng et al. 2009). More recently, medial temporal cortex and the hippocampus have been included in the DMN (Greicius et al. 2004; Vincent et al. 2006; Buckner et al. 2008), suggesting a strong memory component to DMN activity and function.

Several lines of evidence suggest significant overlap between DMN activity and social cognitive function in humans. Studies of theory of mind in particular consistently demonstrate activation in DMN areas, particularly MPFC, temporal-parietal junction, and PCC/precuneus (Rilling et al. 2004; Amodio and Frith 2006; Spreng et al. 2009; Mars et al. 2012). Mitchell et al. (2006) present evidence showing that ventral MPFC is specific to thinking about oneself and similar others whereas dorsal MPFC is more responsive to thinking about dissimilar others. The consistent convergence of these areas’ activity at rest has been replicated in many imaging studies (Buckner et al. 2008). Further support for overlap of DMN and social cognitive function comes from studies noting abnormal default network function in disorders involving social cognitive deficits, particularly autism (Cherkassky et al. 2006; Kennedy et al. 2006) and schizophrenia (Bluhm et al. 2007; Zhou et al. 2007).

Previously, we described patterns of regional metabolic brain activity at rest in 5 chimpanzees (Rilling et al. 2007). In this study, a whole-brain analysis revealed that the areas of the chimpanzee brain that are most active at rest overlap significantly with those identified as part of the DMN in humans, particularly along the cortical midline (MPFC, PCC, and precuneus). (Similar resting activity in DMN areas has also been described in macaques (Vincent et al. 2007; Hayden et al. 2009; Kojima et al. 2009)).
However, this finding is not sufficient to demonstrate that chimpanzees have a DMN similar to that of humans. The human DMN has primarily been defined as the areas that "deactivate" to tasks requiring focused attention compared with rest. In the present study, we first explored activation and deactivation of the chimpanzee DMN using 2 working memory tasks, 1 with social content and 1 without (Experiment 1 below). As in humans, we find that the areas that are active at rest in the chimpanzee brain also deactivate during tasks that rely on working memory.

In a second experiment (Experiment 2 below), we further explored the overlap of chimpanzee DMN and social cognitive brain activity using new stimuli and varying the intensity of the social content. We demonstrate that tasks in which subjects are asked to make social discriminations produce higher levels of activity in cortical midline structures—particularly the precuneus—than do tasks involving nonsocial discriminations. The similar anatomical extent of activation in social and resting conditions suggests that portions of the DMN in chimpanzees may overlap with regions involved in social cognition, and that processing social information may be a special cognitive category in chimpanzees that involves specific brain networks, as it does in humans. It follows that the DMN may have evolved in parallel with neural networks specific to social cognition, and that the cognitive pressures of complex social interactions may have been a driving force in brain evolution throughout the hominid lineage.

**Materials and Methods**

**Subjects**

Four adult chimpanzees (1 female, 3 males, ages 14–21 years) at the Yerkes National Primate Research Center (NPRC) were tested in this study. Each chimpanzee had been extensively trained to perform a match-to-sample (MTS) paradigm and was familiar with the general structure of this method of testing (Parr et al. 2000; Parr 2011).

Subjects were pair-housed in adjacent enclosures that have indoor and outdoor access. All subjects were raised in peer groups by humans at Yerkes, and were later moved to social groups containing at least 2 individuals in an area that contained many other chimpanzees with whom they had visual, auditory, and limited physical contact through mesh. These rearing and living conditions provide the opportunity for appropriate social contact during development.

**Testing Procedures**

Subjects performed MTS tasks using a computerized-joystick testing paradigm in their home cage. In the MTS paradigm, the subject first sees a single stimulus (the sample), either a still image or—in the case of the present study—a brief video. This sample is then removed and replaced with 2 stimuli, one of which (the match) matches the sample on some dimension that the subject must identify. In addition to its extensive use in nonhuman primate cognitive testing, the MTS paradigm has been used in many studies of human cognition, including to probe emotional processing using both social and nonsocial stimuli (e.g., pictures of faces and of scenes) (Hariri, Mattay, et al. 2002, Hariri, Tessitore, et al. 2002). To our knowledge, the specific task used in the present study, MTS using videos with social content, has not been used in human functional neuroimaging studies. Although explicitly comparable data from human subjects would be ideal, we note that a wide range of tasks has been shown to deactivate the DMN in humans and that it is therefore reasonable to assume that this task is a valid test of the DMN in chimpanzees.

In Experiment 1, 2 task conditions, "social" and "nonsocial," were compared with the resting state data collected previously (subjects resting in the home cage without an experimenter present, described by Rilling et al. (2007)). In the social condition, each subject viewed a 5-s video clip (the sample) depicting 2 or more unfamiliar conspecífics engaged in a social behavior—either playing or grooming, both familiar unambiguous social interactions (Supplementary Video 1)—and then chose between 2 still images: 1 depicting the same behavior (correct match), and 1 depicting a different behavior (incorrect choice) (Supplementary Fig. 1). Twelve videos of each stimulus type were presented in randomized order. Still images were not taken from the video clips the subjects viewed; therefore, they were not matched on simple visual features or the identity of the conspecifics but rather on the nature of the behavior depicted. Several of these videos were not novel to the subjects, but rather were drawn from a pool of video footage that had been used in previous studies in this laboratory. The nonsocial condition was the same MTS task using clip art images with no social content. These scans had been collected in a previous study (Parr et al. 2009).

In Experiment 2, subjects performed MTS tasks with novel video stimuli featuring conspecifics. First, the social condition in Experiment 1—2 or more conspecifics playing or grooming—was repeated with new stimuli to increase statistical power and assess replicability. (For these analyses, the "social" condition from Experiment 1 is referred to as "social #1," and its replication "social #2." Second, a "low social" condition showed novel videos (Supplementary Video 2) and still images (Supplementary Fig. 2) of single chimpanzees walking and climbing. We consider this "low social" rather than nonsocial on the assumption that any conspecific will elicit some degree of social cognitive response, regardless of the behavior. As in Experiment 1, 12 videos of each stimulus type were presented in randomized order and the still images that were used were not taken from these videos. Data from these task conditions were compared with those obtained in Experiment 1.

**Image Acquisition**

For each task-related PET scan, the subject's cage mate was removed from the home cage. Food was withheld, so that no glucose in the subject's bloodstream would compete with the radioactively labeled glucose in the tracer. A 15 mCi dose of $[18F]$-fluorodeoxyglucose (FDG) was administered to the subject orally, mixed with sugar-free Kool-Aid (also so as to avoid introducing glucose into the subject's bloodstream). After dosing, the subject was tested in the MTS task for 45–60 min (when the absorption of $[18F]$-FDG begins to asymptote (Parr et al. 2009)), completing on average 216 trials. During testing, as with training, correct answers were reinforced with small amounts of sugar-free Kool-Aid. As the majority of FDG uptake occurs in the first 15 min after dosing, it was necessary for the subject to begin working within a few minutes of receiving the dose and to continue working steadily during that critical uptake period. If the subject did not test well, or appeared stressed or distracted, the scan was canceled. Of 12 scheduled scans, 3 were canceled and rescheduled due to the subjects' failure to test and 1 due to computer malfunction.

At the end of the uptake period, Yerkes NPRC veterinary staff accessed the subject for sedation with 5 mg/kg Telazol. After sedation, the veterinary staff prepared the subject for the scan and placed a catheter in the cephalic vein for propofol anesthesia. The subject was then transported by van to the Emory PET Center, approximately a 5-min drive from Yerkes NPRC, for image acquisition using a Siemens High-Resolution Research Tomograph (HRRT) (CPS, Knoxville, TN), with an approximate spatial resolution of 2.2 mm FWHM. Upon arrival at the scanner, the subject was intubated by the veterinary staff and given propofol anesthesia (10–40 mg/kg/h) via catheter. The administration of propofol was maintained for the duration of the scanning procedure. The subject was then positioned in the scanner and 2 scans were collected: a transmission scan (duration of ~10 min) and an emission scan (~20 min). Transmission data were collected with a Cs-137 point source. An attenuation image was reconstructed, segmented into air, tissue (water), and bone, and the Cs-137 attenuation coefficients were replaced with the appropriate 511-keV attenuation coefficients. Attenuation correction factors were determined by foreprojecting these images to reconstruct the image. The reconstructed image was produced in the Vinci file format.

An anatomical magnetic resonance image (MRI) was collected from each subject for co-registration with that individual's functional PET images for improved anatomical localization of functional activations, following methods previously described (Rilling et al. 2007; Parr et al. 2009).
Analysis of PET Images

Each image was coregistered to that individual's structural MR image, using SPM5 (http://www.fil.ion.ucl.ac.uk/spm) (Friston et al. 1995). All non-brain voxels were masked out of the PET image using a mask created from the subject's MRI. The subject's MRI was then spatially normalized to a template created from 11 (6 females, 5 males, age 14–22 years) chimpanzees' MR images; this spatial transformation was then applied to the masked PET image (Friston et al. 1995). This spatially normalized PET image was then masked a second time, using a mask created from all subjects' MR images that included only voxels representing brain tissue in all subjects. These procedures ensured that each PET image from each subject would be aligned to the same space, and would contain only brain voxels common to all subjects, so that later analyses would not entail comparison across subjects of brain to nonbrain voxels. Each spatially normalized and masked PET image was then divided by its mean intensity value, setting the mean of each scan to one. Therefore, comparisons of regional cerebral glucose metabolism could be made across subjects and across conditions, eliminating variation created by differential levels of FDG uptake, differing elapsed time between dosing and scanning, varying body mass, and so on. These intensity-normalized images were smoothed at 4 mm FWHM. This smoothing kernel was determined by doubling the resolution of the original images, a standard practice for functional neuroimaging data (Worsley et al. 1992).

Normalized and smoothed images were analyzed using a 2-way repeated-measure ANOVA with 12 degrees of freedom in SPM5. Two main effects, condition and subject, were assessed in the model. The conditions assessed in Experiment 1 were social, nonsocial, and rest. In Experiment 2, the conditions assessed were social #1, social #2, and low social, as well as the nonsocial condition from Experiment 1. In addition to individual comparisons, all 3 conditions involving conspecific stimuli (social #1, social #2, and low social) were combined (referred to as “all social”) in Experiment 2 to compare with the nonsocial condition. Because of the small sample size, no corrections for multiple comparisons were included. A priori hypotheses justified a liberal threshold of $P < 0.05$.

Results

Experiment 1

The first experiment assessed chimpanzees' brain activity during 2 working memory tasks, matching clip art images (nonsocial condition) and matching video scenes of conspecifics' social interactions (social condition #1), relative to activity at rest.

The activations during the task conditions relative to rest reflect the visuo-motor demands of the task (Supplementary Fig. 3). Very large activations appear in the cerebellum, which is frequently implicated (in both human and nonhuman primate studies) in visual tracking of motor behavior (Miall et al. 1987; Miall and Reckess 2002) and integration of visual and sensorimotor stimuli, likely resulting from the subjects’ matching of their motor control of the joystick with the visual stimulus of the cursor. (Activation was also seen in left primary motor cortex; most subjects used their right hand to control the joystick.) These results motivated a more constrained exploration in which the cerebellum and brain stem were masked to reveal more subtle changes in activation potentially related to cognitive or emotional processes. (All other results presented below are from these masked analyses.) When cerebellum and brain stem are masked out, activations during tasks relative to rest lie primarily in limbic regions including the amygdala and adjacent medial temporal cortex, in addition to left primary motor cortex (Supplementary Fig. 4).

When either task is subtracted from rest (i.e. rest-social, rest-nonsocial), cortical midline areas including precuneus, PCC, and anterior medial prefrontal cortex (MPFC) are active (Fig. 1A,B); this pattern of activation overlaps significantly with the areas that are most active at rest in chimpanzees, as we reported previously (Rilling et al. 2007). Other areas that are more active at rest than during these 2 tasks include lateral parietal cortex, dorsolateral prefrontal cortex (DLPFC), lateral temporal cortex, and lateral occipital cortex (Supplementary Fig. 5 and 6; Table 1 and 2).

When the social condition is compared with non-social (social–non-social), the dominant activation is in the precuneus (Fig. 1C). Additional activations appear in the left DLPFC and inferior frontal sulcus (IFS), and bilateral superior and inferior frontal gyri (Supplementary Fig. 7).

Experiment 2

A second experiment was motivated by the finding that activity in the cortical midline structures included in the DMN was higher during social cognition in chimpanzees than during nonsocial cognition. In this second experiment, we manipulated the degree of social complexity in the task conditions to further tease apart the nature of this activation. Experiment 1’s social condition was repeated to increase statistical power and assess replicability (social #2), and a low social condition presented videos of single conspecifics engaged in nonsocial behavior.
When each of the 3 social conditions is compared with the non-social condition individually (social #1–non-social, social #2–non-social, low social–non-social) (Fig. 1C–E), and when combined (all social–non-social) (Fig. 1F; Supplementary Fig. 8; Table 3), the dominant activation is consistently in the precuneus. (Additional activations appear in the left DLPFC and IFS, bilateral dorsal parietal cortex, and bilateral superior and inferior frontal gyri.) Furthermore, the level of activity within the precuneus scales with the degree of social complexity: the maximum t-statistic is higher in contrasts social #1–nonsocial and social #2–nonsocial, and lower in low social–nonsocial. To further explore this trend, a region of interest (ROI) was defined as a 3-mm radius sphere centered on the voxel with the highest activation in the rest–all tasks contrast (Fig. 2). In each of the 4 chimpanzees, activation within the ROI was highest at rest (as required by the contrast), followed by the 2 social conditions, then the low social condition, and finally the nonsocial condition (Fig. 3).

### Discussion

The human default network was originally described (Gusnard and Raichle 2001; Gusnard et al. 2001; Raichle et al. 2001) in terms of regions that deactivate during focused and attention-demanding tasks. While chimpanzee resting state activity shows considerable anatomical similarity to the human default network (Rilling et al. 2007), it was defined as the areas with the overall highest levels of activity at rest irrespective of other conditions. This study takes that result a step further, demonstrating deactivations relative to rest in those areas during...
A variety of tasks much as is seen in the human functional neuroimaging literature. The locations of these deactivations in chimpanzees are broadly similar to those described by Raichle et al. (2001): the areas more active at rest than during working-memory dependent tasks include medial and lateral parietal cortices and medial prefrontal cortex (although the present study shows much less frontal deactivation in chimpanzees than in humans, with the greatest similarities between the 2 species occurring in parietal brain areas). In this way, the present study further supports the presence of a default mode of brain function in chimpanzees, which is similar both anatomically and functionally to that of humans.

Activity in Precuneus and Posterior Cingulate

We found that medial parietal cortical areas, including the precuneus and PCC, were highly active at rest (when contrasted with any task) in chimpanzees, and that the precuneus remains highly active during social cognitive tasks (when contrasted with a nonsocial task). These areas are consistently identified with the DMN in humans (Gusnard and Raichle 2001), and also with both other- and self-related mental activity (particularly autobiographical episodic memory recall) (Buckner and Carroll 2007; Harrison et al. 2008). The precuneus is associated with several processes related to understanding the self, including episodic memory retrieval and the experience of one's own agency (Cavanna and Trimble 2006). The precuneus is strongly connected with other areas of the DMN, particularly medial PFC, and shows the highest level of metabolic activity within the DMN in humans (Cavanna and Trimble 2006). If this region has similar functions in humans and chimpanzees, then these results suggest that chimpanzees may engage in thinking related to their own past experiences or to experiences with other individuals (or both) both at rest and during a social cognitive task.

Iacoboni et al. (2004), using fMRI, demonstrated increased activity relative to rest in the precuneus (as well as DMPFC) when subjects viewed videos of actors engaged in dyadic social interactions, similar to the high social conditions in this study. This precuneus activity appeared in this condition relative to rest, and also relative to a condition in which videos were shown of actors behaving alone (similar to the low social condition in this study). The authors suggest that this medial parietal activity is a response to social relationships and interactions in particular, more so than simply to observing other individuals. The precuneus activation seen in the present study is similar to that described in humans by Iacoboni et al. (2004) in many ways, with one critical difference: this area is not more active during the social cognitive tasks than it is at rest. In chimpanzees, precuneus activity remains highest at rest relative to task conditions, regardless of those tasks' degree of social content. This discrepancy is likely attributable to the fact that the human study involved passive viewing of social stimuli, whereas our chimpanzee task involved active responding; as it is a goal-oriented task drawing on working memory, some deactivation of the DMN is expected. (Methodological differences between fMRI and PET may also contribute to differing results.) However, results from Experiment 2 indicate that, much as, in humans, this precuneus activation in particular does scale with the degree of social content in the task.

The overall greatest levels of precuneus activation are seen at rest (compared with any task) and during the social cognitive tasks (compared with the nonsocial tasks, but not compared with rest). This result suggests, first, that ongoing mental processes at rest may also be present during social cognition—that the resting state shares features with social cognition in chimpanzees. Second, based on human functional neuroimaging, this mental activity may be related to autobiographical memory recall and thoughts about the self and others. Several studies associate reflection on the self—one's own mental states, memories, and characteristics—with activity in midline parietal areas (Lou et al. 2004; Seger et al. 2004; Northoff et al. 2006; Uddin et al. 2007), collectively suggesting that these areas are a critical component of the neural instantiation of the mental representation of self. Retrieval of episodic memories about the self is particularly emphasized in much of this research (Northoff et al. 2006). Seger et al. (2004) additionally demonstrate that making judgments about the self and judgments about another person both activate the precuneus, albeit in different portions: the authors distinguish superior and posterior segments of the precuneus, related to judgments about the self and about others, respectively.

Activity in Limbic Areas

We found significant activation in midline limbic areas during task conditions relative to rest (Supplementary Fig. 4). This result differs from the pattern of task-related activity typically seen in human subjects (e.g., the task-positive network); we believe that the limbic activations primarily reflect the chimpanzees' level of emotional arousal on scan days. Unlike during resting state scans, when the chimpanzees are scanned for a task, there is by necessity an experimenter present during task conditions. This human interaction, coupled with any anxiety the chimpanzees may experience in connection with testing and scanning procedures, may result in high levels of emotional arousal reflected in limbic brain activity.

Conclusion

The results of the present study and of Vincent et al. (2007) and Kojima et al. (2009) suggest that the default mode is present in both chimpanzees and multiple macaque species. Kojima et al. (2009) further demonstrate that the DMN in macaques is not only highly active at rest, but also less active during tasks; that is, it deactivates in a functionally similar way to that of humans. The present study not only replicates that finding in a great ape species more closely related to humans, but also indicates a human-like overlap between DMN and social cognitive processes in the chimpanzee. It is as yet unknown how far that social emphasis in DMN might extend in the primate order. Primates as a whole are characterized by a high degree of sociality, increased encephalization relative to general mammalian trends, and well-developed cognitive capacities across multiple domains. Further studies of the interplay between resting brain function and other aspects of primates' mental life will help elucidate the foundation of human cognitive specializations.

Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org.
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