

Differences between chimpanzees and bonobos in neural systems supporting social cognition

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Our two closest living primate relatives, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), exhibit significant behavioral differences despite belonging to the same genus and sharing a very recent common ancestor. Differences have been reported in multiple aspects of social behavior, including aggression, sex, play and cooperation. However, the neurobiological basis of these differences has only been minimally investigated and remains uncertain. Here, we present the first ever comparison of chimpanzee and bonobo brains using diffusion tensor imaging, supplemented with a voxel-wise analysis of T1-weighted images to specifically compare neural circuitry implicated in social cognition. We find that bonobos have more gray matter in brain regions involved in perceiving distress in both oneself and others, including the right dorsal amygdala and right anterior insula. Bonobos also have a larger pathway linking the amygdala with the ventral anterior cingulate cortex, a pathway implicated in both top-down control of aggressive impulses as well as bottom-up biases against harming others. We suggest that this neural system not only supports increased empathic sensitivity in bonobos, but also behaviors like sex and play that serve to dissipate tension, thereby limiting distress and anxiety to levels conducive with prosocial behavior.

Keywords: chimpanzee; bonobo; brain; social cognition

INTRODUCTION

Chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) are our closest living primate relatives, having diverged from a common ancestor with humans ~6 million years ago (Goodman *et al.*, 1990), and from each other just 1–2 million years ago (Becquet *et al.*, 2007; Hey, 2010). Despite their close phylogenetic relationship, chimpanzees and bonobos exhibit noteworthy differences in temperament and behavior, with bonobos exhibiting less severe aggression (Goodall, 1986; Kano, 1992; Wrangham and Peterson, 1996; Wrangham, 1999; Parish and de Waal, 2000), more adult play (Palagi, 2006), greater variety and frequency of sexual behaviors (de Waal, 1987, 1995; Parish, 1996), greater stress reactivity (Wobber *et al.*, 2010b), greater social tolerance (Hare *et al.*, 2007; Hare and Kwetuenda, 2010) and behaviors that may be indicative of greater empathy (de Waal, 1997) compared with chimpanzees.

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The neurobiological bases of these species differences in behavior have been only minimally investigated, largely due to the very limited availability of bonobo brains. A comparative *in vivo* MRI study found no significant differences in brain size between the two species ($n=4$ bonobos and $n=6$ chimpanzees) after controlling for body size (Rilling and Insel, 1999). A later study based on a sub-set of these MRI scans showed that the dorsal sector of the frontal lobe, as contrasted with the orbital and mesial sectors, occupies a larger proportion of the frontal lobe in chimpanzees than in bonobos (Schenker *et al.*, 2005). Another study used the same MRI scans from living bonobos, supplemented with additional post-mortem scans, to compare the volume of seven brain regions in chimpanzees and bonobos. Chimpanzees were found to have a larger cerebellum than bonobos after adjusting for brain size, and bonobos had greater leftward asymmetries in the striatum and motor hand area compared with chimpanzees (Hopkins *et al.*, 2009). Finally, a histological study compared the volume of the amygdaloid complex, including the basolateral division specifically, in a sample of great apes that included three chimpanzees and two bonobos. Although the sample size was too small to conclusively demonstrate significant species differences, there was a suggestion that bonobos had a larger lateral nucleus after correcting for brain size (Barger *et al.*, 2007).

Here, for the first time, we examine interspecies differences using two approaches that have the potential to reveal detailed brain-wide differences both in gray matter regions, and in the white matter circuitry that connects these regions. First, we use voxel-based morphometry (VBM) to show differences between local gray matter architecture in the two species. Second, we use MR diffusion imaging and tractography to show differences in white matter pathways. By focusing on brain regions that show inter-species differences both in local gray matter architecture and in associated white matter pathways, we are able to highlight evolutionary changes in neural circuitry at the network level.

In light of the above-specified differences in social behavior, we hypothesized that bonobos would have increased gray matter as well as increased white matter connectivity in brain regions implicated in empathy, emotion regulation, sexual behavior and anxiety. These regions include the anterior insula, amygdala, hypothalamus, and orbitofrontal cortex.

METHODS

Subjects

This study included neuroimaging data from a total of six bonobos and seven chimpanzees. *In vivo*, T1-weighted scans were obtained from three bonobos and four chimpanzees. In addition, diffusion-weighted scans were acquired from an independent sample of three bonobo and three chimpanzee cadaver brains. No animals were sacrificed for the purposes of this study, and all procedures were approved by the Emory University Animal Care and Use Committee. All cadaver brains were immersion fixed in formalin. Post-mortem intervals are listed for those specimens that they are known for in Supplementary Table S1. Demographic characteristics for both samples are provided in Table 1. All animals were at least 8 years of age, and adult brain weight is achieved by 7 years in chimpanzees (Herndon *et al.*, 1999).

Image acquisition

In vivo scans.

As described previously (Rilling and Insel, 1999; Rilling and Seligman, 2002), prior to scanning, animals were anesthetized with Ketamine (10 mg/kg) and then weighed. For ketamine injections, animals were placed in a squeeze cage. Animals were encouraged to voluntarily present a hip for i.m. injection, but in some cases it was necessary to use the squeeze mechanism to restrain the animals for injection. Subjects were scanned in a supine position using the human head coil. Throughout the scan, animals received a continuous IV infusion of propofol (10–20 mg/kg/h) for anesthesia. T1-weighted images of the entire brain were acquired with a 1.5 T Phillips NT scanner (Philips Medical Systems, The Netherlands) using a gradient-echo protocol with the following parameters: slice thickness = 1.2 mm, slice interval = 0.6 mm, repetition time (TR) = 19.0 ms,

echo time (TE) = 8.5 ms, number of signals averaged = 8, matrix = 256 × 256, field of view (FOV) = 180 mm. In one chimpanzee, the field of view was increased to 200 mm to accommodate the entire brain, and slice thickness and interval were adjusted to 1.4 and 0.7 mm, respectively.

Post-mortem scans.

Brains were removed from the formalin solution that they were stored in, rinsed with phosphate buffer, patted dry with paper towels and then sealed in a thin-walled plastic bag for scanning. Diffusion-weighted scans were acquired on a 4.7 T Bruker scanner with a spin-echo sequence at 1.5 mm isotropic resolution with a b value of 4500 s mm⁻² and 60 diffusion directions (Figure 1). We acquired two sets of diffusion-weighted data for subsequent averaging as well as five volumes with no diffusion weighting. Scan duration was 24 h.

Image analysis

In vivo scans.

Brain volumes were estimated from the brain masks generated with the brain extraction tool in FSL (Smith, 2002). A

Table 1 Sample demographics

Species	Specimen type	Name	Sex	Age (years)	Brain volume (mm ³)	Body weight (g)
Bonobo	<i>In vivo</i>	Jill	F	11.5	374 338	36 700.00
Bonobo	<i>In vivo</i>	Brian	M	8	342 148	35 000.00
Bonobo	<i>In vivo</i>	Lorel	M	28	356 332	41 500.00
Chimpanzee	<i>In vivo</i>	Laz	M	20	415 924	59 500.00
Chimpanzee	<i>In vivo</i>	Kengee	F	8	390 058	43 000.00
Chimpanzee	<i>In vivo</i>	Merv	M	21	428 801	62 500.00
Chimpanzee	<i>In vivo</i>	Mary	F	36	357 827	44 000.00
Bonobo	Cadaver	Mambo	M	15	407 862	
Bonobo	Cadaver	Psuke	M	27	352 108	
Bonobo	Cadaver	Tamuli	F	13	318 844	
Chimpanzee	Cadaver	Polyanna	F	14	397 504	
Chimpanzee	Cadaver	Jenda	F	48	354 375	
Chimpanzee	Cadaver	Artifee	F	28	346 373	

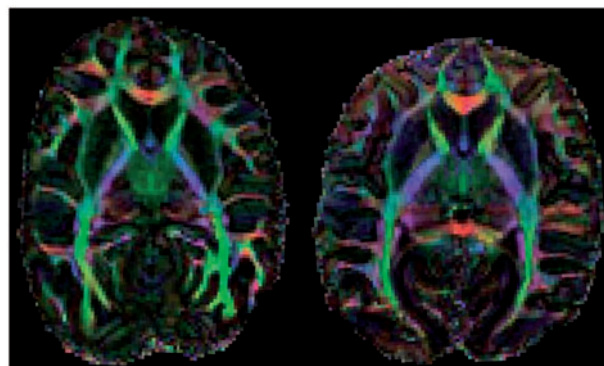


Fig. 1 Horizontal section through FA color map in one chimpanzee (left) and one bonobo (right).

VBM style analysis (Ashburner and Friston, 2000; Good *et al.*, 2001) was used to compare local gray matter volume estimates between chimpanzees and bonobos. This technique enables comparisons to be made across the entire brain, at every voxel (i.e. smallest volume element) of an image. Importantly, the technique controls for differences in brain size between the two comparison groups, thereby identifying differences in local gray matter volume estimates relative to whole brain size. T1 images were analyzed with FSL-VBM (Smith *et al.*, 2004). The first step was to create a combined chimpanzee and bonobo gray matter template. So as not to bias the template toward one species, an equal number of chimpanzees and bonobos were included. Therefore, we began by brain extracting images from three of the four chimpanzees and from all three bonobos using BET (Smith, 2002). Next, tissue-type segmentation was carried out using FAST4 (Zhang *et al.*, 2001). The resulting gray matter partial volume images were then aligned to geometric mid-space using the affine registration tool FLIRT (Jenkinson and Smith, 2001; Jenkinson *et al.*, 2002). The weighted average of all aligned images then served as the target to which all original images were non-linearly aligned using FNIRT (Andersson *et al.*, 2007a,b), which uses a b-spline representation of the registration warp field (Rueckert *et al.*, 1999). The resulting weighted average constituted the template for the following analysis.

All of the native gray matter images ($n=3$ bonobos and $n=4$ chimpanzees) were then non-linearly registered to this template. The registered partial volume images were then modulated (to allow the measurement of local expansion or contraction) by dividing by the Jacobian of the warp field. The modulated, segmented images were then smoothed with an isotropic Gaussian kernel with a sigma of 2 mm. Finally, local gray matter volume estimates were compared between chimpanzees and bonobos using a voxel-wise two sample t -test. The resulting t -statistic image was thresholded at $t=4.0$ which is equivalent to a two-tailed P -value of 0.01 with five degrees of freedom. Multiple comparison correction was not implemented due to limited statistical power associated with the small sample size and the accompanying risk of type 2 errors. However, as discussed above, by focusing on regions that show differences both in gray matter volume and, independently, in related white matter anatomy, we are able to further limit the chances of type I errors.

Post-mortem scans

Diffusion-weighted images were analyzed using the diffusion toolbox in the FSL software package (Smith *et al.*, 2004). Each diffusion-weighted volume was affine-registered to a B0 volume to correct for eddy-current effects before averaging the two acquisitions, and DTIFIT was used to calculate the diffusion tensor at each voxel, from which a fractional anisotropy (FA) image was calculated. A bias-free FA template was created using affine followed by nonlinear

registration as described above. Individual FA images ($n=3$ bonobos and $n=3$ chimpanzees) were then non-linearly registered to the template (Andersson *et al.*, 2007a,b). Two methods were then used to compare FA between species. To compare the peak anisotropy along white matter tracts, we used tract-based spatial statistics [TBSS, (Smith *et al.*, 2006)]. To compare the volume of local white matter pathways, we compared the Jacobians of the non-linear warp fields derived from the FA images. These Jacobians reflect the extent to which each template voxel must be either expanded or compressed to match the individual image. Both Jacobian values and FA values were compared between chimpanzees and bonobos using a two sample t -test. In parallel with the VBM analysis, the resulting t -statistic image was thresholded at $t=4.0$. Like the VBM analysis described above, comparisons are made across the entire brain, at each brain voxel.

Tractography.

Tractography methods can reconstruct white matter fiber tracts based on magnitude and direction of anisotropic water diffusion in each voxel of a diffusion-weighted image. The probabilistic tractography algorithm in FSL, with adaptation to a multi-fibre model, was used for pathway reconstruction (Behrens *et al.*, 2007). The Jacobian comparison of FA images described above yielded a difference in the bilateral ventral posterior frontal lobe. This region of interest (ROI) was warped from template space into individual subject space and then used as a seed mask for tractography. The ROI extended into gray matter. Therefore, an exclusion mask was placed in the gray matter ventral to the ROI extending back to the amygdala in order to restrict the pathway to white matter. For each subject, the total number of streamlines sent from their mask (i.e. 5000 times the number of voxels in the mask) was calculated. The average of these six values was multiplied by 0.001 and this threshold was applied to the pathway identified in all six subjects. The resulting pathway volumes were compared between chimpanzees and bonobos using a two sample t -test. To visualize group results, pathways were also thresholded more liberally at 0.0005 times the total sample number and warped back into template space. Individual pathways were then binarized and summed to create an overlap image that was then thresholded to show only those voxels where at least three of the six subjects showed evidence of a potential connection.

Finally, affine registration was used to warp tractography results into T1 space so that pathway terminations could be compared with regions where local gray matter volume estimates differed between species.

RESULTS

Overall brain size

Brain volumes obtained from the T1 scans indicated that the average chimpanzee brain volume (398 cc, $n=4$) was slightly

but significantly larger than the average bonobo brain volume (358 cc, $n=3$; $P<0.05$) (Table 1). These volume estimates are somewhat larger than other published values (Stephan *et al.*, 1981; Herndon *et al.*, 1999; Rilling and Insel, 1999), in part because they include some meninges and space between sulci at the brain periphery.

VBM results

VBM results show that after controlling for differences in overall brain size, bonobos had significantly higher local gray matter volume estimates than chimpanzees in limbic and paralimbic areas, and in portions of frontal and parietal cortex. On the other hand, chimpanzees had higher local gray matter volume estimates than bonobos in portions of parietal and occipital cortex (Table 2). More specifically, bonobos had higher local gray matter volume estimates in several areas of particular relevance to social cognition, and these were among the largest differences overall. These areas included the right anterior insula, right dorsal amygdala, right hypothalamus and right dorsomedial prefrontal cortex (Figure 2 and Supplementary Figure S1).

FA analysis

FA images were analyzed using two complementary techniques—TBSS analysis of FA, and FA-based warp field comparisons. It is important to note that these two techniques measure different aspects of white matter tracts. TBSS was developed specifically to measure changes in local diffusion anisotropy in a way that was robust to changes in local geometries such as tract thicknesses. By comparison, Jacobian comparisons explicitly measure the local volumetric change in tract geometry.

FA TBSS analysis

TBSS identified several regions where chimpanzees had higher FA values than bonobos (Table 3, Supplementary Figure S2). These were concentrated along visual system pathways, including the right optic tract, splenium of the corpus callosum and left parieto-occipital white matter. Chimpanzees also had higher FA in the left cerebellar white matter. There were no regions where bonobos had significantly higher FA than chimpanzees.

FA Jacobian comparison

Comparison of the warpfields that registered each subject's FA image to the FA template revealed several regions of relative expansion in bonobos compared with chimpanzees (Table 4, Supplementary Figure S3). It is important to note that the contrast that drives the Jacobian estimation comes from FA, which highlights white matter. Changes in the local Jacobian therefore reflect changes in local white matter volumes, even if they appear at the boundary between gray and white matter on the average template. Of particular relevance to social cognitive differences between the two species is expansion in bilateral ventral frontal lobe in bonobos

Table 2 Brain regions showing species differences in local gray matter volume estimates at a threshold of $t>4.0$ ($P<0.01$ uncorrected for multiple comparisons)

Brain region	No. of voxels
Bonobo > chimpanzee	
L dlpc (area 46)	86
R dmpfc	64
R dorsal premotor cortex	49
R ventral premotor cortex (45)	45
R anterior insula	943
Hypothalamus and adjacent basal forebrain	215
R dorsal amygdala	174
R insula	20
L temporal pole	28
L mid insula/claustum	19
R amygdalo-hippocampal region	49
L post-central sulcus/anterior intraparietal sulcus?	129
L anterior STG	181
L entorhinal cortex	25
R intraparietal sulcus	346
R pontine nuclei	117
R inferior posterior parietal cortex	25
L inferotemporal cortex (IT)	30
Bilateral cerebellum	59
L posterior cingulate sulcus	88
Anterior parieto-occipital sulcus	90
R calcarine sulcus	33
Left visual cortex	148
Left dorsal visual cortex	117
Chimpanzee > bonobo	
R frontoorbital sulcus (44/45)	10
R Dorsal insula	10
L frontal operculum	47
R anterior STG	57
R dorsal STS	45
R intraparietal sulcus/post-central sulcus	23
L tectum	18
Retrosplenial cortex	23
L temporo-parietal junction (TPJ)	54
R calcarine sulcus	92
L posterior intraparietal sulcus (IPS)	159
R extrastriate visual cortex	581
R fusiform gyrus	99
R calcarine sulcus (V1)	77
L calcarine sulcus (V1)	1410
R dorsomedial extrastriate	130
L lunate sulcus	137
R occipital pole	161
L occipital pole	91

Spatial extent of the regions is given in number of 0.8 mm isotropic voxels.

(Figure 3), as well as in the right anterior insula. On the other hand, compared with bonobos, chimpanzees showed pronounced relative enlargement of the white matter in the vicinity of the medial thalamus (Figure 3). Chimpanzees also showed expansion relative to bonobos in primary motor cortex, the ventral temporal lobe, portions of the parietal and occipital lobes and in cerebellar white matter (Supplementary Figure S3).

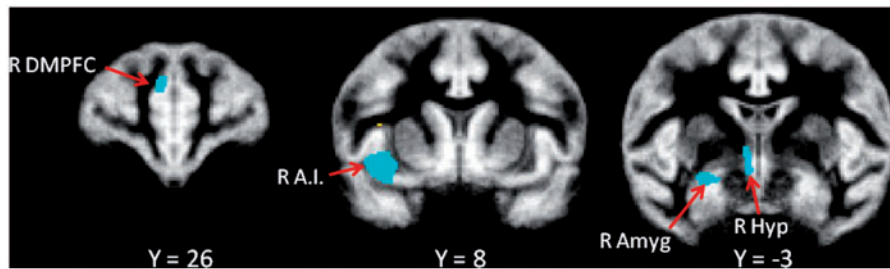


Fig. 2 Differences in local gray matter volume estimates between chimpanzees and bonobos based on analysis of T1-weighted images. The t -statistic image is thresholded at $t > 4.0$ and overlaid on the common species gray matter template. The figure shows three coronal sections through the gray matter template at different anterior–posterior levels. Regions in blue have higher local gray matter volume estimates in bonobos; regions in yellow have higher local gray matter volume estimates in chimpanzees. The Y -coordinate is relative to $Y = 0$ at the anterior commissure.

Table 3 Brain regions showing species differences in white matter fractional anisotropy (FA) as determined by tract-based spatial statistics (TBSS) at a threshold of $t > 4.0$ with at least 10 contiguous voxels

Brain region	No. of voxels
Bonobo > chimpanzee	
None	
Chimpanzee > bonobo	
R genu	10
R inferior frontal white matter	17
R genu	10
R optic tract	14
R cerebral peduncle	10
Splenium of corpus callosum	13
L lateral splenium	10
L inferior parietal white matter	14
L parietal/occipital white matter	37
R parietal/occipital white matter	13
L cerebellar white matter	50

Spatial extent of the regions is given in number of 1.0 mm isotropic voxels.

Tractography results

To determine whether the species difference in ventral posterior frontal lobe volume identified in the FA comparison was related to the VBM results, we used tractography to delineate the pathway passing through this ROI. The pathway was tracked in native diffusion space for each of the three individual chimpanzee brains and each of the three individual bonobo brains and then warped back into FA template space to visualize the group average trajectory. The resulting tract connected the ventral anterior cingulate cortex with the amygdala bilaterally (Figure 4 and Supplementary Figure S4). Pathway volumes calculated in native space revealed that all three bonobos had a larger pathway than all three chimpanzees in both the left [$t(4) = 5.06$, $P < 0.01$] and right [$t(4) = 2.82$, $P < 0.05$] hemisphere (Table 5). Warping the average pathway into T1 space revealed that it made contact with the region of expanded amygdala volume in bonobos (Supplementary Figure S5).

DISCUSSION

VBM analyses of T1 scans revealed that bonobos have more gray matter than chimpanzees in the hypothalamus, the right dorsal amygdala and the right anterior insula. DTI analyses additionally showed that the pathway connecting the amygdala with the ventral anterior cingulate cortex is larger in bonobos than chimpanzees. These species differences in brain anatomy can be plausibly linked with known species differences in temperament and behavior.

Anxiety and stress reactivity

Bonobos exhibit a stronger stress hormone response to feeding competition (Wobber *et al.*, 2010b), and have been described as more nervous than chimpanzees (de Waal, 1997). The larger right amygdala, hypothalamus and right anterior insula of bonobos are a potential neural substrate for this difference in stress and anxiety. The amygdala difference is concentrated in its dorsal aspect, in the vicinity of the central nucleus (Amunts *et al.*, 2005; Barger *et al.*, 2007), a region strongly implicated in fear and anxiety that is known to activate the hypothalamic–pituitary–adrenal (HPA) axis and autonomic nervous system by way of connections with the hypothalamus (Davis, 1997; Ledoux, 1998). Interestingly, this nucleus is larger in human patients with generalized anxiety disorder compared with healthy controls (Etkin *et al.*, 2009). Human subjects who are prone to anxiety have increased activity in the anterior insula during emotion processing (Paulus and Stein, 2006). The anterior insula also tracks risk (Bossaerts, 2010) and predicts risk-averse choices (Kuhnen and Knutson, 2005), and bonobos are more risk-averse than chimpanzees (Heilbronner *et al.*, 2008).

Sexual behavior

Compared with chimpanzees, bonobos have higher rates of sexual interactions in captivity (de Waal, 1995) but not in the wild (Stanford, 1998; Hashimoto, 2002). In both contexts, bonobos exhibit a greater diversity of sexual behaviors, including all possible age–sex combinations (de Waal, 1987; Parish and de Waal, 2000). The hypothalamus and amygdala

Table 4 Brain regions in which the Jacobian warp field of the FA images differed between species at a threshold of $t > 4.0$ with at least 10 contiguous voxels

Brain region	No. of voxels
Bonobo > chimp	
L inferior frontal gyrus	118
Genu of corpus callosum	10
L head of caudate	32
R lateral inferior frontal cortex	81
R ventral posterior frontal white matter	828
L medial orbital gyrus and white matter	505
R mid-insula	236
R anterior STS	186
R superior frontal gyrus	21
L ventral anterior thalamus	231
Bilateral mid cingulate sulcus	975
R dorsal posterior insula	1441
R cerebral peduncle	532
L cerebral peduncle	1037
L putamen	35
R posterior intraparietal sulcus	94
R inferior lateral extrastriate cortex	2935
L anterior bank of lunete (V2)	158
R visual cortex	55
Chimpanzee > bonobo	
R ventral rim of cingulate sulcus	30
R motor cortex (precentral gyrus)	797
MD and adjacent midline thalamic nuclei	2657
R medial temporal white matter	29
R ventrolateral thalamus	69
R perirhinal cortex	455
R hippocampus	51
L fusiform gyrus	555
R intraparietal sulcus	22
R posterior STS	237
R optic radiation	301
L optic radiation	84
L optic radiation	124
L optic radiation	239
L posterior bank of parieto-occipital sulcus (extrastriate visual cortex)	162
R superior cerebellar peduncle	34
R lateral cerebellum	1165
R lateral cerebellum	50
L lateral cerebellum	843
L lateral cerebellum	84
L dorsal extrastriate cortex	31
L dorsal extrastriate cortex	162
R dorsal extrastriate cortex	18
R ventral occipital cortex	128
L ventral occipital cortex	52

Spatial extent of the regions is given in number of 0.8 mm isotropic voxels.

are key nodes of a network that controls sexual behavior in non-human animals (Newman, 1999; Breedlove *et al.*, 2007). Functional neuroimaging experiments have similarly implicated the hypothalamus and amygdala in the human response to visual sexual stimuli (Karama *et al.*, 2002; Hamann *et al.*, 2004). Given that bonobos use sex to reduce tension (de Waal, 1987; Parish, 1996; Hare *et al.*,

2007; Hohmann *et al.*, 2008), the enlarged bonobo amygdala could be eliciting fear and anxiety, while simultaneously motivating sexual behavior that helps dissipate it.

Play

Bonobos are thought to have retained certain juvenile characteristics into adulthood (Shea, 1983; Wrangham and Pilbeam, 2001; Lieberman *et al.*, 2007) (i.e. paedomorphism), including extraordinary playfulness (de Waal, 1997). In addition to sex, bonobos use play to diffuse social tension (Enomoto, 1990) and rates of play are higher among adult bonobos than adult chimpanzees (Palagi, 2006). After controlling for overall brain size and body size, both amygdala and hypothalamus size are correlated with frequency of social play across primate species (Lewis and Barton, 2006), so the larger amygdala and hypothalamus of bonobos could also relate to this difference in play frequency.

Empathy

Anecdotal observations have led to the suggestion that bonobos may be more empathic than chimpanzees (de Waal, 1997). Psychopathy, a disorder marked by lack of empathy, is associated with reduced size and function of the amygdala (Gordon *et al.*, 2004; Yang *et al.*, 2009), as well as reduced functional connectivity between the amygdala and ventromedial prefrontal cortex (VMPFC) (Marsh *et al.*, 2008). These results and others have led to the hypothesis that the pathway from the amygdala to the VMPFC is involved in perceiving distress in others and in learning to avoid behaviors that provoke such distress (Blair, 2008). Our results show that bonobos have more gray matter in the dorsal amygdala and a larger pathway linking the amygdala with VMPFC compared with chimpanzees. There is evidence that testosterone impairs the functioning of this pathway in humans (van Wingen *et al.*, 2010), and chimpanzee males have both higher baseline testosterone metabolite levels (Sannen *et al.*, 2004), as well as a more pronounced increase in testosterone in response to feeding competition (Wobber *et al.*, 2010b) compared with bonobo males. Thus, species differences in pathway size may be augmented by differences in testosterone-mediated functional suppression. There is also suggestive evidence, in the form of the ratio of the second to fourth finger length (2D:4D), that chimpanzees may have higher prenatal androgen levels than bonobos (or humans) (McIntyre *et al.*, 2009). Prenatal testosterone levels are inversely correlated with measures of empathy in human children (Chapman *et al.*, 2006). Thus, organizational effects of prenatal androgens could contribute to species differences in the size of the pathway linking the amygdala and VMPFC, as well as other empathy-related structures.

The anterior insula is also strongly implicated in empathy, presumably through a mechanism that involves simulation of visceral somatic states (Singer *et al.*, 2009), and disorders characterized by empathic deficits are associated with reduced size and function of the anterior insula (Bird

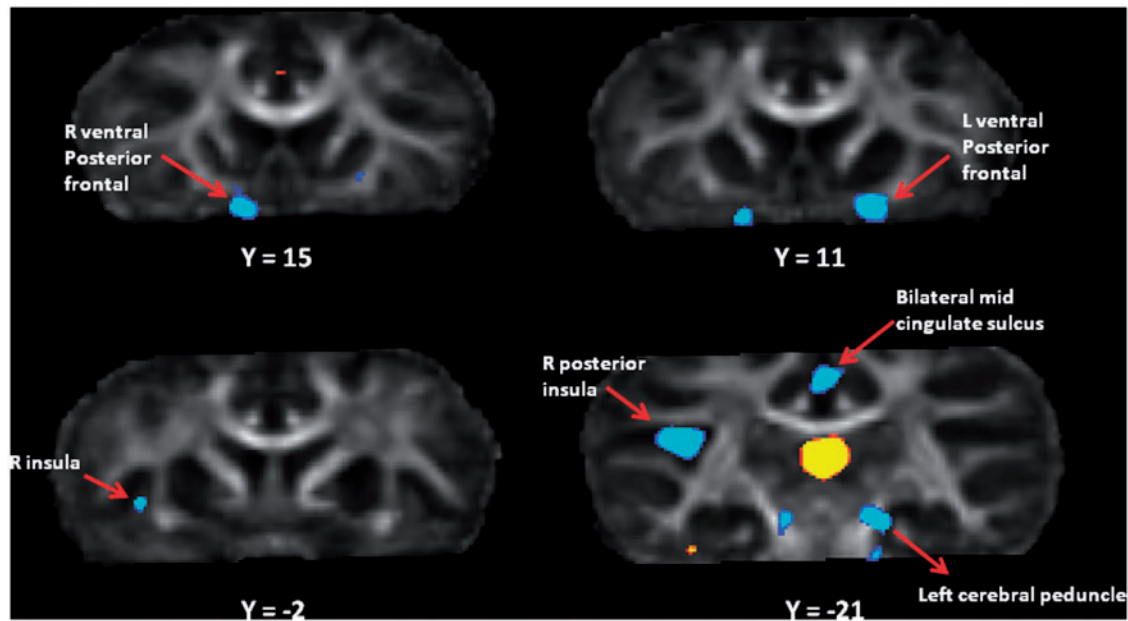


Fig. 3 Differences in Jacobian warp fields between chimpanzees and bonobos based on analysis of diffusion-weighted images. The t -statistic image is thresholded at $t > 4.0$ and overlaid on the common species FA template. The figure shows four coronal sections through the FA template at different anterior–posterior levels. Regions in blue are larger in bonobos (larger Jacobians from template to subject space) and regions in yellow are larger in chimpanzees. The Y -coordinate is relative to $Y = 0$ at the anterior commissure.

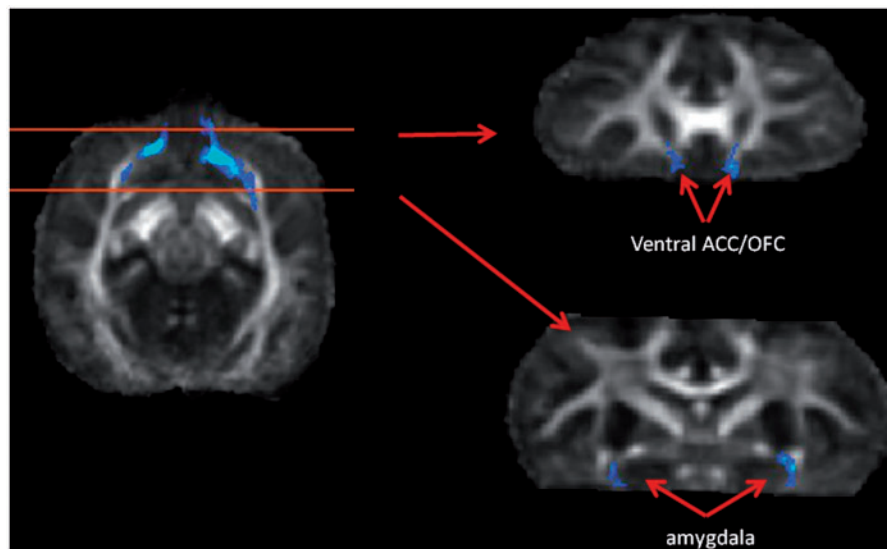


Fig. 4 Group tractography result from posterior ventral frontal ROI derived from the jacobian comparison shown in Figure 3. Tracts from all three bonobos and all three chimpanzees were registered to template space, binarized and summed. The resulting map shows voxels where at least three of six subjects had a possible connection.

et al., 2010) (Veit *et al.*, 2002; Birbaumer *et al.*, 2005; Sterzer *et al.*, 2007; Seeley, 2010). Bonobos have more gray matter in the anterior insula than chimpanzees, specifically within the ventral region that is consistently associated with social–emotional processing (Allman *et al.*, 2010; Kurth *et al.*, 2010) and that reliably coactivates with the amygdala (Mutschler *et al.*, 2009). Thus, the neurobiological characteristics that differentiate chimpanzees from bonobos bear a

striking similarity to those that differentiate patients with empathy deficits from normal controls.

Social tolerance

Bonobos exhibit highly tolerant food sharing in the wild (Kuroda, 1984; White, 1994; Fruth and Hohmann, 2002) [but see (Jaeggi *et al.*, 2010)], and bonobos showed greater

Table 5 Amygdala to ventral ACC pathway volumes in bonobos and chimpanzees

Species	Left volume (mm ³)	Right volume (mm ³)
Bonobo (Mambo)	1676.31	1135.27
Bonobo (Psuke)	2010.43	1577.59
Bonobo (Tamuli)	2025.62	1980.17
Chimpanzee (Artifree)	1104.92	1080.23
Chimpanzee (Jenda)	749.87	364.50
Chimpanzee (Polyanna)	429.08	358.82

tolerance of co-feeding than chimpanzees in direct experimental comparisons (Hare *et al.*, 2007; Hare and Kwetuenda, 2010; Wobber *et al.*, 2010a). Bonobos may therefore be better at inhibiting selfish behaviors than chimpanzees are (Hare *et al.*, 2007). This may be supported by their larger pathway linking ventral ACC with the amygdala, a pathway that has been implicated in emotion regulation in humans (Davidson *et al.*, 2000; Pezawas *et al.*, 2005). This same pathway might also be involved in controlling aggressive impulses, another behavior that differs between these two species.

Aggression

Chimpanzees exhibit more severe aggression than bonobos. Within social groups, chimpanzee aggression involves male aggression against females, male infanticide and intense male competition for dominance status. In contrast, male aggression against females is rare in bonobos (perhaps due to strong bonds among females), male infanticide has not yet been observed and reconciliation following conflict is more common and more often initiated by the aggressor than among chimpanzees (Goodall, 1986; de Waal, 1987; Parish, 1996; Wrangham and Peterson, 1996; Parish and de Waal, 2000). Chimpanzees are strongly xenophobic. Between group interactions are typically hostile and can involve lethal aggression (Wrangham, 1999). In bonobos, intergroup encounters can be hostile, but in contrast to chimpanzees, also affiliative (Idani, 1990; Kano, 1992). Wrangham and Pilbeam (2001) suggests that bonobos evolved due to selection against aggression and that they share a number of traits with domesticated versions of wild animals that also show reduced aggression. For example, both bonobos and dogs are less aggressive, as well as more juvenilized, than chimpanzees and wolves, respectively.

Evidence suggests that the pathway linking the ventral ACC and the amygdala normally functions to restrain aggression via both top-down suppression of aggressive impulses from the amygdala (Davidson *et al.*, 2000; Meyer-Lindenberg *et al.*, 2006), and through a bottom-up relay of perceived distress in others to VMPFC that inhibits anti-social behavior (Blair, 2008). Thus, underdevelopment of this pathway, as found in chimpanzees, might be expected to augment both impulsive aggression due to lack of

top-down control, as well as instrumental aggression due to lack of bottom-up biases against harming others. As mentioned above, this effect may be compounded by higher testosterone levels in male chimpanzees that inhibit functionality in this pathway, especially since testosterone is positively correlated with aggression in male chimpanzees (Muller and Wrangham, 2004).

Synthesis

Our results can be usefully interpreted within a recently proposed model of the neurobiology of human empathy and callousness (Blair, 2008; Shirtcliff *et al.*, 2009). Callous individuals are characterized by hypoarousal of the stress system in response to their own distress. Because we normally empathize with others by simulating their distress (Singer and Lamm, 2009), callous individuals are also deficient in representing the distress of others. For example, criminal psychopaths are autonomically insensitive to the suffering and distress of others (Blair *et al.*, 1997). These psychological deficits are paralleled by deficits in the structure and function of empathy-related areas including the amygdala and anterior insula, as well as the connections linking the amygdala to VMPFC. Further, deficits in empathy may contribute to increased aggression insofar as harming others will be less aversive to those with a reduced capacity to experience distress. In parallel, we suggest that the enlarged dorsal amygdala, anterior insula and amygdala to vACC pathway in bonobos allows them to more strongly represent distress of both self and others compared with chimpanzees. This translates into greater empathy, as well as reduced aggression. However, excessive distress and anxiety can interfere with helping behavior (Batson, 1998). In bonobos, this may be prevented in part by a stronger regulatory pathway from ventral ACC to amygdala and in part by increased rates of play, sexual behavior and reconciliation that serve to limit anxiety and distress to a level that supports prosocial behavior.

Other species differences

The above discussion is focused on species differences in the neural system involved in understanding others' emotions. However, humans have an additional neural system for understanding others that involves making cognitive inferences about others' thoughts. Both the medial prefrontal cortex and the temporo-parietal junction have been consistently implicated in this function (Gallagher and Frith, 2003; Saxe and Kanwisher, 2003). Thus, it is interesting that bonobos also have higher local gray matter volume estimates in the dorsomedial prefrontal cortex compared with chimpanzees. Although the question of whether chimpanzees possess a theory of mind is still debated (Byrne and Whiten, 1992; Tomasello *et al.*, 2003; Penn and Povinelli, 2007), our results suggest that further investigation of bonobo mentalizing capacities may be of interest. Indeed, a recent experimental study concluded that bonobos were more skilled than

chimpanzees at tasks related to theory of mind (Herrmann *et al.*, 2010).

Our FA analysis revealed a large area of the medial thalamus that is larger in chimpanzees than bonobos. This difference is concentrated in the region of the medial dorsal thalamic nucleus and could reflect differences in the white matter axons that penetrate the medial dorsal nucleus, or alternatively differences in the adjacent white matter pathway—the fornix. Chimpanzees also showed expansion relative to bonobos in several visual cortical regions, including portions of both the ventral and dorsal visual streams, and chimpanzees showed higher FA values along visual system white matter pathways, which might imply greater myelination or fiber density in these pathways (Pierpaoli and Basser, 1996; Beaulieu, 2002; Le Bihan, 2003). Although the functional significance of these differences is uncertain, we note that chimpanzees outperform bonobos on tasks requiring the use of tools (Herrmann *et al.*, 2010) and also more often use tools in the wild (Schaik *et al.*, 1999; Hohmann and Fruth, 2003). Neural specializations may have evolved to support this ability, and human tool use relies heavily on the dorsal and ventral visual streams (Frey, 2007). Finally, in both the FA and T1 analyses, chimpanzees showed evidence of expansion in the right superior temporal sulcus relative to bonobos. This region is involved in the perception of biological motion and also in understanding intentions behind actions (Perret *et al.*, 1985; Allison *et al.*, 2000), raising the possibility that chimpanzees may excel at this aspect of social cognition relative to bonobos.

Limitations

Access to bonobo brains is limited due to their endangered status, and our sample size is accordingly limited. We therefore cannot exclude the possibility that some of our group differences are type 1 errors due to chance sampling. This concern is mitigated to some extent by the overlapping results from the independent FA and T1 data sets, particularly with respect to consistent differences in the right anterior insula and amygdala in favor of bonobos, and consistent differences in visual cortical areas in favor of chimpanzees. Moreover, some of our results converge with earlier results, such as the finding that chimpanzees have a larger cerebellum than bonobos (Hopkins *et al.*, 2009) and bonobos have a larger lateral amygdala nucleus after controlling for brain size (Barger *et al.*, 2007). Our group differences could also be explained by a confounding variable. For example, rearing history can impact brain development and subsequent anatomy (Sanchez *et al.*, 1998). Although we do not have information on the rearing history of all of the animals included in this study, we do know that two of our bonobo subjects were mother-reared and two of our chimpanzee subjects were nursery-reared by humans (Schenker *et al.*, 2005). Although we cannot exclude this as a potential explanation for our results, the nursery-reared chimpanzees were not

raised in an impoverished social environment, but instead had frequent human contact along with the opportunity for daily play with other chimpanzees. Thus, we favor heritable species differences as the most likely factor driving these neurobiological differences. Finally, given evidence for developmental delay and paedomorphosis in bonobos, it would be informative to compare the two species at earlier developmental stages to determine how these differences in adult brain anatomy arise in ontogeny.

SUPPLEMENTARY DATA

Supplementary data are available at SCAN online.

Conflict of Interest

None declared.

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