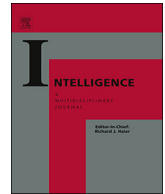




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More intelligent chimpanzees (*Pan troglodytes*) have larger brains and increased cortical thickness

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ABSTRACT

Though sometimes controversial, there is growing consensus that human general intelligence is associated with variation in a number of aspects of cortical organization including brain volume, white and gray matter volume, connectivity, and cortical thickness. Recent studies in great apes have shown, like humans, they exhibit both general and domain specific forms of intelligence when tested on a wide range of cognitive tests; however, whether individual variation in intelligence is associated with measures of cortical organization remains untested. Here we show that general intelligence in chimpanzees is associated with total brain volume, total gray matter volume, mean cortical thickness and regional variation in both gray matter volume and cortical thickness. These results suggest that increased gray matter volume and cortical thickness may produce enhanced computational cognitive processes and may have been selected for during primate brain evolution.

1. Introduction

The neurobiological basis of human intelligence has a long, and sometimes controversial, history in the social and biological sciences (Herrnstein & Murray, 1994; Rushton & Jensen, 2005). At the core of these debates has been determining the extent to which cultural, social, neurological and genetic mechanisms contribute to individual variation in domain general (or “g”) and domain specific forms of intelligence (Chabris et al., 2012; Davies et al., 2011; Posthuma et al., 2005). Deary (2001) defines intelligence as the ability to reason, think abstractly, comprehend complex ideas, problem solve and to learn through experience and by observing others. Domain specific intelligence refers to the parcellation of overall cognitive abilities into different aptitudes, such as verbal, spatial, mathematical skills with individuals having strengths or weaknesses in each of these different modes (Jensen, 2002). In contrast, domain general intelligence (or “g”) refers to a mental or problem solving ability that accounts for individual variation in performance across multiple cognitive tasks. Thus, though different dimensions of cognition or intelligence can be psychometrically revealed using factor or principle component analyses on multiple tasks, such as standardized IQ tests, the evidence suggest that an underlying “g” factor can account for significant proportion of between task variability.

Advances in neuroimaging over the past 30 years have increasingly

shown that individual differences in general and domain specific intelligence can be explained, in part, by variation in cortical organization including anatomical and functional connectivity. For instance, meta-analyses have revealed small but significant ($r = \sim 0.20$) phenotypic associations between intelligence and overall brain size (even after adjusted for body size) (McDaniel, 2005; Pietschnig, Penke, Wicherts, Zeiler, & Voracek, 2015; Witelson, Beresh, & Kigar, 2006) as well as region specific associations in gray and white matter volume, cortical thickness, surface area and gyrification (Basten, Hilger, & Fiebach, 2015; Menary et al., 2013a, 2013b; Ritchie et al., 2015; Schnack et al., 2015a, 2015b). These collective findings clearly show that individual differences in both “g” and domain specific intelligence can be attributed, in part, to neurobiological factors.

The intelligence of nonhuman animals has also been of long-standing interest in the behavioral and biological sciences dating back to the early writing of Romanes and others (Roitblat, Bever, & Terrace, 1984; Rumbaugh & Washburn, 2003; M. Tomasello & Call, 1997). However, in contrast to research with humans, the study of individual differences in nonhuman animal intelligence, including in primates, has historically been framed within the context of behavioristic or operant views of learned behavior rather than reflecting inherent, latent problem solving abilities, such as “g” (Rumbaugh & Washburn, 2003). That is, within species variation in learned behaviors were attributed to random, non-genetic factors, notably reinforcement history or

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experiential factors rather than potential neurobiological or genetic mechanisms (Lyn, Russell, & Hopkins, 2010; Russell, Lyn, Schaeffer, & Hopkins, 2011). More recent selective breeding, behavioral-genetic and genetic knock-in and knock-out studies in distantly related species such as fish and mice have increasingly identified the role of specific genes on different aspects of learned behaviors (e.g., Kolata, Light, & Matzel, 2008; Lu et al., 2010), thereby challenging entirely behavioristic interpretations of individual variation in learning. However, a comprehensive analysis of the neural correlates of individual differences in general intelligence “g” has yet to be undertaken in nonhuman animals, particularly in closely related primate species (Lamp et al., 2010).

There is now some evidence that great apes, including chimpanzees, bonobos and orangutans show a general intelligence “g”, though there is by no means uniform agreement. Indeed, some have suggested that certain species have evolved domain specific specializations in response to different ecological or social factors (Amici, Aureli, & Call, 2010; Amici, Barney, Johnson, Call, & Aureli, 2012; Burkhardt, Schiubiger, & van Schaik, 2016; Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007; Herrmann, Hare, Call, & Tomasello, 2010; Herrmann, Hernandez-Lloreda, Call, Hare, & Tomasello, 2010; Hopkins, Russell, & Schaeffer, 2014; Schmitt, Pankau, & Fischer, 2011). Thus, there remains some debate over the existence of “g” in nonhuman primates but, for the purposes of this study, pragmatically estimates of “g” can be statistically derived based on the cognitive measures used with any species. Within the larger theoretical framework of research on comparative intelligence, this is important for at least two reasons. First, it is difficult, if not impossible, to interpret these findings in terms of social or cultural factors that co-vary with genetic factors in humans (i.e., assortative mating). This is not to suggest that experiential, social or even cultural factors cannot influence intelligence in nonhuman primates as there is ample evidence for their occurrence in captive and wild populations (Buttelmann, Carpenter, Call, & Tomasello, 2007; Call & Tomasello, 1996; Carpenter, Tomasello, & Savage-Rumbaugh, 1995; Horner, Whiten, Flynn, & de Waal, 2006; Lyn et al., 2010; Mesoudi, Whiten, & Dunbar, 2006; Russell et al., 2011; Stoinski & Whiten, 2003; Stoinski, Wrate, Ure, & Whiten, 2001; Tagliabue, Reamer, Schapiro, & Hopkins, 2012; Michael Tomasello, Savage-Rumbaugh, & Kruger, 1993; Van Schaik et al., 2003; Whiten et al., 1999; Whiten, Horner, & de Waal, 2005; Whiten et al., 2007; Whiten & van Schaik, 2007). Nonetheless, evidence of active teaching by chimpanzees is weak (Musgrave, Morgan, Lonsdorf, Mundry, & Sanz, 2016) and, to the extent that we know that formal educational systems can influence intelligence in humans (Brinch & Galloway, 2012), we can certainly rule out the possibility that these sources of influence are absent in nonhuman primates. Second, Hopkins et al. (2014) recently showed that chimpanzee intelligence “g” was significantly heritable, and this was found in apes that had been reared by their conspecific mother or in a human nursery setting for the first 3 years of life. Thus social learning does not seem to be the most parsimonious explanation for the heritability, thereby further reinforcing the view that biological factors may underlie individual differences in intelligence, not just in humans, but also in other primate species.

As a means of testing whether and what associations are found between general intelligence and cortical organization, we investigated the neural correlates of individual differences in chimpanzee intelligence. Specifically, measures of cognitive performance and a general measure of “g” intelligence has been previously reported in chimpanzees by Hopkins et al. (2014). Here, *in vivo* MRI scans were obtained in 74 of these chimpanzees and, of specific interest in this study, was determining whether variation in overall chimpanzee intelligence was associated with (1) overall brain size, gray or white matter volume and (2) measurements of cortical thickness at each vertex of the cortical surface and for specified regions of interest as has been done in previous studies with humans (Luders et al., 2008; Menary et al., 2013a, 2013b; Narr et al., 2007; Schnack et al., 2015a, 2015b).

2. Methods

2.1. Subjects

Behavioral and neuroimaging data were available in 74 adult chimpanzees (*Mean Age* = 24.78 years, *SD* = 11.31) including 23 males and 51 females housed at the Yerkes National Primate Research Center (YNPRC). All procedures were carried out in accordance with protocols approved by YNPRC and the Emory University Institutional Animal Care and Use Committee.

2.2. MRI scanning procedure

Detailed methods of the scanning parameters and post-image analyses have been described elsewhere (Hopkins, Li, Crow, & Roberts, 2017; Keller, Roberts, & Hopkins, 2009). Briefly, T1-weighted magnetization-prepared rapid-acquisition gradient echo (MPRAGE) MR images were obtained using a Siemens 3T Trio MR system (*TR* = 2300 ms, *TE* = 4.4 ms, *TI* = 1100 ms, *Flip angle* = 8°, *FOV* = 200 mm × 200 mm). Chimpanzee images were acquired at Yerkes National Primate Research Center (YNPRC) in Atlanta, Georgia. The data matrix size was 320 × 320 with slice thickness set to 0.6 mm. Subjects were first immobilized by ketamine injection (10 mg/kg) and subsequently anesthetized with propofol (40–60 mg/kg/h) following standard procedures at the YNPRC. Subjects were then transported to the MRI facility and remained anesthetized for the duration of the scans as well as the time needed to transport them between their home cage and the imaging facility (total time, ~1.5 to 2 h). Subjects were placed in the scanner in a supine position with their head fitted inside the human-head coil.

2.3. Image analysis

The quantification of cortical thickness and gyrification was performed using FSL (<http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/>) and FreeSurfer (<https://surfer.nmr.mgh.harvard.edu/>) software. In particular, within FSL, each brain scan was skull-stripped, bias field corrected, and normalised to the standard MNI152 template brain using a 7 degrees of freedom transformation (i.e. 3 translations, 3 rotations and 1 uniform scaling) which preserved the morphological shape of individual brains. Next each brain was segmented using the conventional FreeSurfer process stream (<https://surfer.nmr.mgh.harvard.edu/>). The surface-based module in FreeSurfer enables high quality pial surface reconstruction from the brain volume data by following the signal intensity gradient between gray matter and CSF with subvoxel accuracy (Dale, Fischl, & Sereno, 1999) on the 3D T1 weighted images. At each surface location, curvature-based descriptors (e.g., the spatial relationship of a vertex to neighbouring vertices) were computed and served as natural anatomical landmarks via which the inter-subject correspondence was found between an individual brain and a reference template through a non-rigid matching process. As such, the vertex-wise correspondence was determined so as to put all brains in a common coordinate system and this allowed convenient vertex-by-vertex comparison in corresponding folds and regions (Fischl, Sereno, Tootell, & Dale, 1999). In this study, the primary focus for the surface based analysis was cortical thickness (CT). CT at each surface location (or vertex) is defined as the average of the closest distance in either direction between the white and the pial surfaces (Fischl & Dale, 2000). In order to increase the signal-to-noise ratio of the vertex-based comparison, a Gaussian smoothing with full-width half-maximum of 15 mm was applied to the computed values of CT. The measures of total brain volume, gray, white matter volume, surface area and mean cortical thickness for each subject was also provided by FreeSurfer.

By using an atlas-based labelling technique in FreeSurfer, individual brains can be parcellated into 68 gyral based regions (two hemispheres X 34 maps/regions) and average values of CT can be computed for all

regions in every brain. As we have done previously, the chimpanzee brains were warped into human space and the Desikan-Killiany labels were applied to the 34 homologous regions in each hemisphere (Hopkins et al., 2017). Thus, region specific measures of CT and SA were obtained for the 34 regions within the Desikan-Killiany atlas as applied to the chimpanzee brain.

2.4. Chimpanzee Intelligence (g)

To assess general intelligence (“g”), the chimpanzees were tested on a slightly modified version of the Primate Cognition Test Battery (PCTB), a 12-item measure of physical and social cognition developed for use in apes and human children that has been described in detail elsewhere (Hopkins, Russell, & Schaeffer, 2014; Lacreuse, Russell, Hopkins, & Herndon, 2014; Russell et al., 2011). Broadly, the PCTB is divided into two domains, physical and social cognition (Herrmann, Hernandez-Lloreda, et al., 2010). Within the social cognition domain, there are two constructs measured including theory of mind and communication. In contrast, within the physical cognition domain, there are three measured constructs including understanding of causality, spatial cognition and quantity discrimination. Each chimpanzee was tested twice on the 12 tasks separated by at least 7 days and the order of the tests was counterbalanced across subjects and test sessions. Based on the mean performance on each of the 12 items, the data were subjected to a Principal Axis Factor analysis with no rotation to derive a single measure of “g” for each chimpanzee (see Woodley, Fernandes, & Hopkins, 2015). The “g” measure was then then regressed on the volumetric and cortical thickness values after adjusting for co-variation with age and sex.

2.5. Data analysis

The “g” measure was regressed on the global volumetric, surface area and mean cortical thickness values after adjusting for co-variation with age and sex. For the vertex-based analyses, the cortical thickness was modeled as a straight line with the variation of the surface area and thickness to age as the slope or the correlation coefficient of the regression model at each vertex. The *t*-tests under the null hypothesis of no relationship between the thickness and “g” factor were performed with alpha set to $p < .05$, adjusting for subject sex and age but uncorrected for multiple comparisons. For the subsequent ROI based comparisons, cognitive performance was correlated with CT measures, averaged for the corresponding region across the two hemispheres. We also computed measures of surface area, gray and white matter volume, cortical thickness and total brain volume for each hemisphere. For the ROI analyses, we ran partial correlation analyses based on the raw thickness values as well as adjusting for the mean thickness for the entire brain while controlling for sex and age. The use of adjusted thickness values was done in order to determine whether any region-specific associations were significant after accounting for overall mean cortical thickness. For the adjusted partial correlation analyses, for each chimpanzee, their mean CT thickness value between the two hemispheres was subtracted from their average thickness for the entire brain value for each Desikan region. We also computed separate adjusted CT values for the left and right hemispheres following the same procedure.

3. Results

3.1. Descriptive data

To determine whether the subject variables age and sex were associated with the cognitive and overall brain measures, in the initial analysis, we performed a MANCOVA with sex as the between group factor and age as a covariate. The overall “g” score as well as the mean surface area, cortical thickness and gray matter, white matter and total brain volume were the dependent measures. We found an overall

Table 1

Descriptive data on brain global brain measure.

	Females	Males	Age
“G” Score	−0.009 (0.121)	−0.149 (0.184)	−0.082
Surface Area	3.596 (0.035)	3.827 (0.053)	−0.299 **
Cortical Thickness	1.379 (0.015)	1.449 (0.022)	−0.318 **
Gray Matter	4.738 (0.075)	5.273 (0.113)	−0.355 **
White Matter	6.742 (0.112)	7.066 (0.170)	0.328 **
Total Brain Volume	2.647 (0.035)	2.846 (0.053)	−0.037

** $p < .01$. Values under age reflect partial correlation coefficients

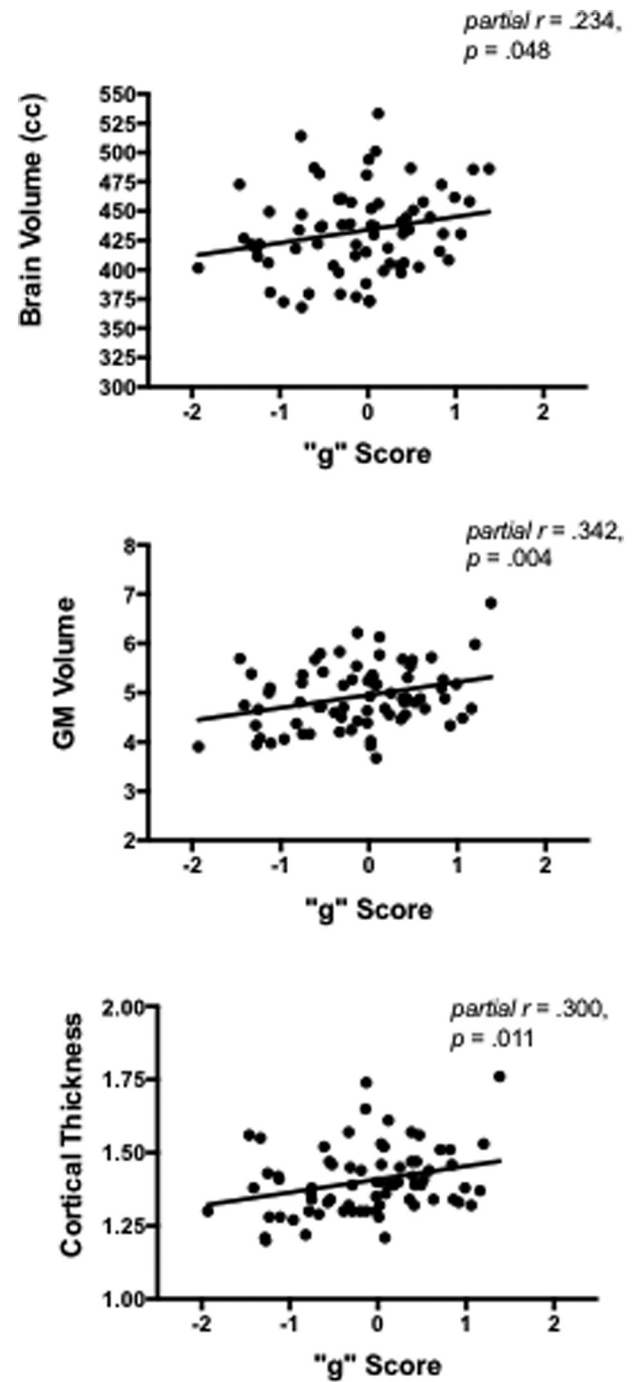


Fig. 1. Partial correlation coefficients between general intelligence “g” and a) total brain volume b) mean gray matter volume and c) average cortical thickness.

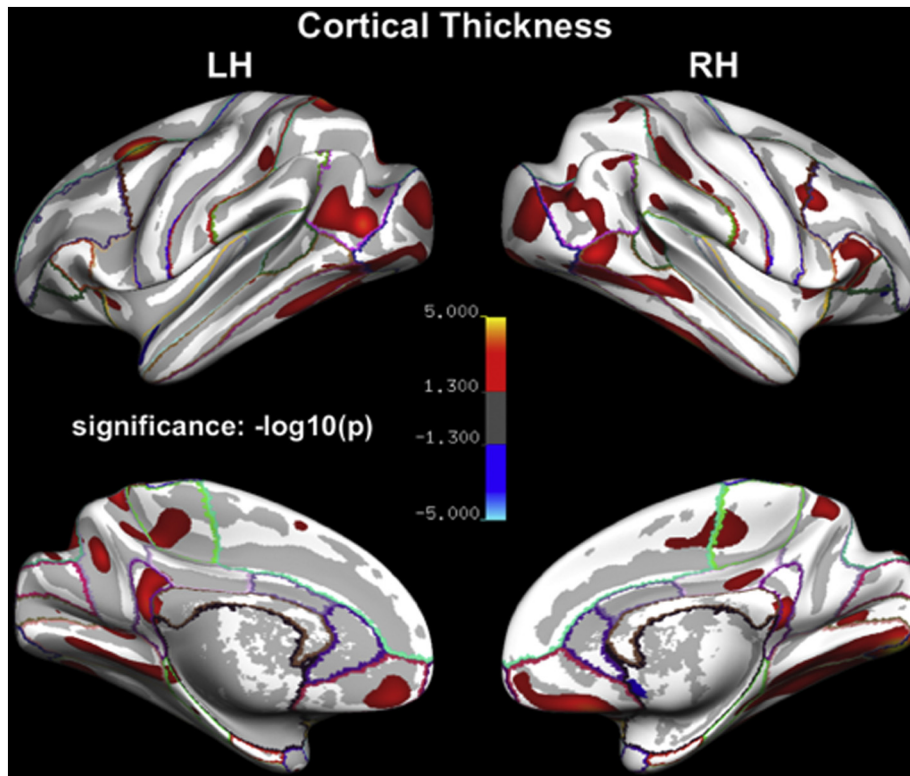


Fig. 2. 3D rendering of the lateral (upper panel) and medial (lower panel) brain regions within the left and right hemisphere associated with general intelligence “g” based on the vertex analysis.

significant effect of sex $F(6, 66) = 3.083, p < .01$ and age $F(6, 66) = 10.168, p < .001$. Subsequent univariate F-tests revealed no significant effect of age or sex on the “g” scores; however, for the overall brain measures, significant sex differences were found for surface area $F(1, 71) = 12.690, p < .001$, cortical thickness $F(1, 71) = 6.507, p < .013$, gray matter volume $F(1, 77) = 14.956, p < .001$ and total brain volume $F(1, 77) = 9.335, p < .003$. For all measures, males had higher values than females (see Table 1) and this was not surprising given that no adjustment was made for body weight. To further assess the role of age on each measure, we performed partial correlation coefficients between age and each outcome measure while statistically controlling for sex. Age was significantly negatively associated with gray matter volume, surface area, and cortical thickness and positively associated with white matter volume (see Table 1).

3.2. Chimpanzee intelligence and general measures of cortical organization

We next performed partial correlation coefficients between the “g” scores and the total brain volume, gray and white matter volume, surface area, and mean cortical thickness while statistically controlling for age and sex. Significant associations were found between “g” and total brain volume (*partial* $r = 0.380, p = .019$), mean gray matter volume (*partial* $r = 0.300, p = .012$) and cortical thickness (*partial* $r = 0.259, p = .030$) (see Figs. 1 a to 1c). Chimpanzees with higher “g” scores had greater total brain size, gray matter volume and cortical thickness.

3.3. Vertex and ROI based analyses

We next considered the relationship between “g” and regional variation in cortical thickness. For this initial analysis, as noted above, we performed a vertex-based analysis examining the change in CT with the “g” scores at each vertex location, when statistically controlling for sex and age (Fig. 2). Significant positive associations ($p < .05$) were

found for a number of cortical regions including the bank of the superior temporal sulcus, inferior parietal and temporal cortex, fusiform, medial orbital frontal cortex, pars triangularis, para-hippocampus, superior frontal and parietal cortex, middle temporal gyrus, lateral occipital, lingual, and the insula. The vertex-based analyses were largely confirmed when we correlated the “g” scores with the raw and adjusted cortical thickness measures of the 34 Desikan-Killiany regions (see Table 2). For both CT measures, significant positive associations were found between “g” and the regional CT values for the bank of the STS, fusiform, inferior and superior parietal, inferior and middle temporal, medial orbital frontal, lateral occipital, lingual, pars triangularis, posterior cingulate, precuneus, rostral anterior cingulate, and insula, respectively. In all instances, the associations between “g” and the average ROI cortical thickness measures were positive indicating that higher thickness scores were associated with higher “g” scores.

4. Discussion

Our results show that individual difference in general intelligence in chimpanzees is associated with (1) total brain size (2) total gray matter volume and (2) overall and region-specific variation in cortical thickness. While there have been numerous studies in nonhuman primates examining the role of different brain regions on cognitive functions, such as memory (Squire, Zola-Morgan, & Chen, 1988) or executive functions (Miller, 2000), we believe these are the first evidence showing a significant association between general intelligence and neuroanatomical organization in chimpanzees, and indeed, nonhuman primates.

The brain regions associated with “g” in the chimpanzees were distributed throughout the temporal, parietal and frontal lobes but some are particularly germane due to their theoretical implications in the development and evolution of higher order cognitive functions (Fjell et al., 2015). For instance, using a region-of-interest approach, it was recently found that individual differences in receptive joint attention in chimpanzees were associated with variation in gray matter in

Table 2
Partial correlation coefficients between “g” and cortical thickness for each desikan region.

	Raw values			Adjusted values		
	CT	Left	Right	CT	Left	Right
Bank STS	0.311 **	0.271 *	0.320 **	0.324**	0.290*	0.337**
Caudal Anterior Cingulate	0.213	0.215	0.185	0.243*	0.247*	0.219
Caudal Middle Frontal	0.118	0.088	0.134	0.167	0.148	0.177
Cuneus	0.076	0.041	0.100	0.155	0.126	0.177
Entorhinal	-0.005	-0.072	0.055	0.056	-0.007	0.102
Fusiform	0.280 *	0.209	0.311 **	0.299*	0.255*	0.323**
Inferior Parietal	0.370 ***	0.332 **	0.367 **	0.371**	0.348**	0.369**
Inferior Temporal	0.445 ***	0.403 **	0.429 **	0.429***	0.411***	0.417***
Isthmus_Cingulate	0.111	0.109	0.095	0.170	0.170	0.160
Lateral Occipital	0.386 ***	0.323 **	0.412 **	0.366**	0.320**	0.398***
Lateral Orbital Frontal	0.179	0.111	0.227	0.227	0.174	0.266*
Lingual	0.312 **	0.292 **	0.279 *	0.318**	0.305**	0.313**
Medial Orbital Frontal	0.275 *	0.217	0.289 *	0.304**	0.261*	0.318**
Middle Temporal	0.268 *	0.195	0.317 **	0.289*	0.233	0.332**
Para_Hippocampal	0.200	0.207	0.169	0.231	0.238*	0.207
Para_Central	0.170	0.205	0.125	0.215	0.248*	0.175
Pars Opercularis	0.119	0.038	0.171	0.174	0.108	0.216
Pars Orbitalis	0.118	0.102	0.081	0.165	0.151	0.131
Pars Triangularis	0.262 *	0.214	0.247 *	0.286*	0.247*	0.277*
Peri_Calcarine	0.009	-0.036	0.057	0.119	0.075	0.168
Post Central	0.098	0.085	0.101	0.177	0.173	0.181
Post Cingulate	0.302 *	0.316 **	0.270 *	0.321**	0.334**	0.297*
Precentral	-0.074	-0.072	-0.071	0.016	0.012	0.026
Precuneus	0.253 *	0.227	0.251 *	0.283*	0.264*	0.284*
Rostral Anterior Cingulate	0.265 *	0.265*	0.235 *	0.290*	0.293*	0.259*
Rostral Middle Frontal	0.134	0.040	0.205	0.187	0.118	0.240*
Superior Frontal	0.180	0.162	0.191	0.219	0.208	0.227
Superior Parietal	0.284 *	0.261 *	0.283 *	0.282*	0.276*	0.280*
Superior Temporal	0.031	0.001	0.057	0.099	0.078	0.120
SupraMarginal	0.150	0.083	0.202	0.196	0.147	0.237*
Frontal Pole	0.008	-0.120	0.157	0.068	-0.058	0.198
Temporal Pole	0.084	0.146	-0.002	0.136	0.194	0.047
Traverse Temporal Gyrus	0.065	0.003	0.110	0.126	0.074	0.166
Insula	0.284 *	0.252 *	0.277 *	0.307**	0.278*	0.315**

*** $p < .001$, ** $p < .01$, * $p < .05$. All coefficients are adjusted for the subject variables sex and age

the posterior superior temporal gyrus, including portions of the STS (Hopkins et al., 2014). In the present study, we found that higher “g” scores were associated with larger cortical thickness at the bank of the STS, further implicating this region in cognitive functions. Similarly, higher “g” scores were associated with cortical thickness for the Pars triangularis and surface area for the Pars opercularis. Each of these regions within the inferior frontal gyrus makes up Broca’s area (Amunts & Zilles, 2006; Keller, Crow, Foundas, Amunts, & Roberts, 2009; Zilles & Amunts, 2010). Morphologically, the Pars triangularis cannot be quantified in chimpanzee brains because they lack the horizontal ramus that is needed to define the inferior border of this region (Amunts & Zilles, 2006; Keller, Crow, et al., 2009; Zilles & Amunts, 2010). Notwithstanding, Brodmann area 45 cells are found in the gyrus immediately anterior to the fronto-orbital sulcus, which approximates where the morphological region corresponding to the Pars triangularis exists in human brains (Schenker et al., 2010). Likewise, Brodmann area 44 cells are found within the Pars opercularis in both humans and chimpanzees and comparable sulci can be used to morphologically define this region in both species.

The association between “g” and portions of the inferior parietal lobe are also of interest because of their implications in the function and use of tools (Gannon, Kheck, Braun, & Holloway, 2005; Lewis, 2006; Stout & Chaminade, 2012). For instance, Peeters et al. (2009) found that humans and rhesus monkey differ with respect to activation of the left inferior parietal cortex when viewing conspecific use tools. These authors concluded that the absence of activation of this region in rhesus monkeys when viewing tool use is consistent with their lack of naturally occurring use of tools in the wild. Gilissen and Hopkins (2013) found that the hand used for tool use was associated with left-right differences

in the area measures of the parietal operculum in chimpanzees. Much has been written regarding the cognitive and neural foundations of tool manufacture and use in primates (Lewis, 2006; Stout & Chaminade, 2012) and within the context of this study, the PCTB task included measures in tool use performance and understanding tool use functions. This may account for the association found between the “g” scores and parietal cortex. Finally, individual variation in “g” scores were associated with the insula, a region of the brain implicated in a variety of higher order socio-emotional and cognitive functions such as empathy (Brooks & Tracey, 2007; Craig, 2009; Lamm & Singer, 2010; Uddin & Menon, 2009). Interestingly, recent comparative studies have shown that humans and great apes, including chimpanzees, have a disproportionately large insula within primates (Bauernfeind et al., 2013).

In addition to the regions associated with increased “g”, it is also worth noting those regions that were not. Specifically, much has been written regarding comparative differences in the proportional size of regions within the frontal lobe and specifically prefrontal cortex and how this may relate the evolution of higher cognitive function (Schoenemann, Sheehan, & Glotzer, 2005; Sherwood, Holloway, Semendeferi, & Hof, 2005; Smaers, Gomez-Robles, Parks, & Sherwood, 2017). If the evolution of intelligence acted on individual differences and this was manifest in associations between “g” and variation in cortical organization, one might have predicted that regions within the prefrontal cortex, such as the dorsal lateral and medial regions, would have significantly correlated with the “g” scores. This was not the case for the findings reported here; however, this could be attributable to a variety of factors such as the sensitivity of these measures within the PCTB task to measure underlying problem solving abilities. Moreover, other dimensions of cortical organization within the prefrontal cortex

may be more strongly associated with “g” rather than cortical thickness.

Despite the novelty of the results reported here, there are at least two limitations. First, it is unclear what “g” actually measures as a construct within chimpanzees. A measure of general intelligence presumably reflects an inherent underlying cognitive or problem-solving ability; however, this has yet to be validated in chimpanzees and other great apes using the set of measures comprising the PCTB. Thus, “g”, as defined in this study, is a statistical measure of general cognitive performance on the PCTB tasks but it remains to be determined whether it has any construct validity when used as predictor of subsequent problem-solving abilities for novel, yet-to-be-learned tasks by chimpanzees. Second, for the results presented in Table 2, we warped the Deskin-Killiany maps from the human brain into the chimpanzee brain. Given the differences in brain size and sulci variability between humans and chimpanzees, it would be erroneous to assume that the regions from the human brain perfectly map onto the chimpanzee cortex. Nonetheless, it should be emphasized that this limitation does not apply to the vertex-based analyses, which were largely consistent with the ROI results. Clearly future studies should derive chimpanzee specific cortical parcellations so as to further study region specific variation in cortical thickness and surface area.

In summary, the findings reported here show that individual differences in general intelligence scores in chimpanzees are associated with overall brain size, gray matter volume, and region specific cortical thickness. These results reinforce the view that brains with larger surface areas and thicker cortex are potentially computationally more efficient in basic cognitive functions. Though the results reported do not directly address the mechanisms underlying these associations, previous studies have found that both (1) general intelligence scores and (2) variability in brain size and cortical folding are significantly heritable in chimpanzees. To what extent these phenotypes are mediated by common genetic mechanisms remains to be addressed in future studies, which have the potential to provide invaluable data on the biological and evolutionary basis of human intelligence and cortical organization.

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