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Initiation of Joint Attention is Associated with Morphometric Variation in the Anterior Cingulate Cortex of Chimpanzees (*Pan troglodytes*)

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Abstract

In developing human children, joint attention is an important preverbal skill fundamental to the development of language. Poor joint attention skills have been described as a behavioral risk factor for some neurodevelopmental disorders, such as autism spectrum disorder. It has been hypothesized that the anterior cingulate cortex (ACC) plays an important role in the development of joint attention in human children. Here, we tested whether the morphometry and lateralization of the ACC differed between chimpanzees that were classified as either consistently or inconsistently engaging in joint attention with a human experimenter. Results showed that chimpanzees that performed poorly on the joint attention task had larger grey matter volumes in the ACC compared to apes that performed well on the task. In addition, both population-level asymmetries and sex differences in the volume of GM were found within the ACC. Specifically, females had relatively larger GM volumes in two of the three subregions of the ACC compared to males, and significant leftward asymmetries were found for two of the subregions whereas a rightward biases was observed in the third. Based on these findings, we suggest that the ACC plays an important role in mediating joint attention, not just in humans, but also chimpanzees. We further suggest that the differences found between groups may reflect inherent differences in the amount of white matter within the ACC, thereby suggesting reduced connectivity between the ACC and other cortical regions in chimpanzees with poor joint attention skills.

Introduction

At a critically young age, human children learn not only the meanings of sounds and sound patterns, but they learn how to participate in communicative interactions. This includes synchronizing their behavior with communicative partners, and directing communicative acts towards social partners as well as responding to the communicative behaviors of others. Early on, children rely mostly on nonverbal behavior (e.g. facial expressions, visual gaze, gestures, etc.) to communicate their needs and desires. By 12–15 months of age, typically developing children are aware that gaze direction and pointing refer to an external referent, and subsequently shift their attention to that referent (so-called responding to joint attention behavior) [e.g., Carpenter et al. 1998]. Developmentally speaking, responding to joint attention precedes production of these communicative behaviors. In other words, typically developing children respond appropriately to visual gaze and communicative gestures produced by social partners before they themselves initiate joint attention. In fact, individual differences in joint attention behaviors at as early as 12-months predict later linguistic competency in human infants [Mundy et al. 2007]. Given their universality in human

cultures, many have suggested that comprehension of and initiation of joint attention behaviors form the foundation for the subsequent development of language and speech [Abell et al. 1999; Amaral et al. 2008; Barnea-Goraly et al. 2004; Bauman and Kemper 2005; Belmonte et al. 2004; Bigler et al. 2007; Bloss and Courchesne 2007; Brambilla et al. 2003]. For example, a number of studies have shown that age of onset of joint attention behaviors predicts the rate of language development in typically developing children [Bates et al. 1975; Bates et al. 1987; Carpenter et al. 1998; Mundy et al. 2007; Nichols et al. 2005; Whalen et al. 2006].

The importance of joint attention (JA) for typical socio-communicative development has clearly been demonstrated in studies of children with Autism Spectrum Disorder (ASD). Previous researchers have noted significant overlap between social and communication impairment, particularly for children with autism functioning at the pre-linguistic level [Landa et al. 2007]. Several behavioral studies have shown that young children with ASD or at risk for ASD show impaired abilities in both the initiation of joint attention and in the receptive responding to joint attention cues such as gaze and pointing [Dawson et al. 2002; Ibanez et al. 2012; Presmanes et al. 2007]. Although the underlying neural mechanisms underlying ASD are not clear and likely involve multiple brain systems in relation to the endophenotype of interest [Amaral et al. 2008; Cody et al. 2002; DiCicco-Bloom et al. 2006; Girgis et al. 2007; Hadjikhani et al. 2006; Hazlett et al. 2006; Herbert et al. 2005; Lotspeich et al. 2004; Minshew and Williams 2007; Mosconi et al. 2006], the potential consequences of such abnormal social and communicative behavior on the developing brain are significant.

Comparative Studies of Joint Attention

The initiation and use of communicative gestures in conjunction with gaze alternation between a social agent and referent in chimpanzees has been described as identical to early performative communicative acts in human children (Bates et al., 1975). Studies from a number of different laboratories have demonstrated that chimpanzees and other great apes point referentially, communicate intentionally, and initiate joint attention during intra- and interspecies communication [Cartmill and Byrne 2007; Leavens et al. 2008; Leavens and Racine 2009; Leavens et al. 2009; Liebal et al. 2004; Liebal et al. 2005; Pika 2008; Pika et al. 2003; Pika et al. 2005]. Specifically, apes have been shown to gesture to request food items while simultaneously alternating their gaze between the referent and social agent [Leavens and Hopkins 1998; Leavens and Hopkins 1999; Leavens et al. 1996]. This ability is remarkably similar to the progression in the initiation of joint attention described in developing human children [Abbot-Smith et al. 2004; Bates et al. 1975; Bates et al. 1987; Lock 2001], at least as it relates to what some have described as imperative pointing or initiating behavioral requests. Additional studies have shown great apes (chimpanzees, bonobos, gorillas, orangutans) can alternate the type of communicative signal they use depending on the attentional state of a human experimenter(s) [Cartmill and Byrne 2007; Leavens et al. 2004b]. For instance, when a human experimenter is looking away from the subject, some apes will use non-visual signals to capture the humans' attention such as attention-getting sounds, hand clapping, tapping on the wall or cage mesh, spitting and throwing. In comparison, if the human experimenter is looking toward them, they tend to use visual communication signals such as manual gestures, lip pouting or offering food or objects from their cage to exchange. These findings clearly suggest that the apes understand the function of their communication and have some flexibility in their use of different signals as a means of attaining the attention of an otherwise inattentive audience. Moreover, it suggests that the apes understand that they need the attention of an inattentive social agent before they can successfully initiate a requesting communicative act.

Among great apes, however, there are considerable individual differences in the concomitant use of manual gestures and gaze alternation with some adult apes performing better or worse than others. For example, in several studies in captive chimpanzees from our laboratory, Leavens and colleagues [1998; 2004a] have shown that up to about 20% of the subjects tested failed to direct the attention of a human experimenter to an out of reach food item. Poss et al. [2006], using the same experimental paradigm, reported similar individual differences in a sample of 10 orangutans and 7 gorillas.

One question that emerges from these collective studies is whether neural processes or substrates might explain individual differences in JA skills in human infants and potentially great apes. Mundy and Newell [2007] and others [Benga 2005] have suggested that a core region involved in JA in humans is the anterior cingulate cortex (ACC). The ACC is often described as an interface region between limbic and cortical structures because of its variable layering pattern [Allman et al. 2001]. In humans, the anterior cingulate cortex (ACC) is widely known to be an important if not essential region involved with processing cognitive, emotional, motor, and sensory input [Bush et al. 2000; Devinsky et al. 1995]. Studies in monkeys have shown that stimulation or lesions of the ACC can result in changes in heart rate, blood pressure as well as vocalization and facial expressions [Hadland et al. 2003; Paus 2001; Smith 1945]. Accordingly, Mundy and Newell [2007] suggest that the ACC controls “volitional, goal-directed attention allocation that is constrained by and corrected by reward-related self-appraisal of behavior” (pp.3). The role of the ACC in attention-related processes that serve to regulate cognitive and emotional processing in adults has been further supported by functional brain imaging studies in humans [Bush et al. 2000; Paus 2001; Paus et al. 1998].

In the current study, we tested whether individual differences in joint attention behaviors were associated with variation in the volume and lateralization of grey matter in the ACC in captive chimpanzees. As noted above, previous studies have reported considerable individual differences in joint attention behaviors in chimpanzees [Leavens et al. 2008; Leavens et al. 2009] and the neural origin of these differences are poorly understood in apes. Based on the theory outlined by Mundy and Newell [2007], we hypothesized that chimpanzees who consistently engage in joint attention would show differences in either the volume or lateralization of grey matter in the ACC compared to individuals who are less consistent.

Methods

Subjects

All subjects were captive born chimpanzees from the Yerkes National Primate Research Center (YNPRC). The sample consisted of 70 captive chimpanzees including 22 males and 48 females. Within this cohort, the subjects ranged in age from 6 to 51 years (Mean = 21.52, s.d. = 11.59). All of the research in this study was conducted according to the American Psychological Association guidelines for the ethical treatment of animals and were approved by the Institutional Animal care and Use Committee of Emory University. The YNPRC is fully accredited by the American Association for Accreditation of Laboratory Animal Care. This manuscript adheres to the American Society of Primatologists principles for the ethical treatment of primates.

MRI Image Collection and Procedure

Scans were obtained at the time the chimpanzees were being surveyed for their annual physical examinations. For all scans, subjects were first immobilized by ketamine (10 mg/kg) or telazol (3–5mg/kg) and subsequently anaesthetized with propofol (40–60 mg/(kg/h))

following standard procedures at the YNPRC. Subjects were then transported to the MRI facility. The subjects remained anaesthetized 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 h). Subjects were placed in the scanner chamber in a supine position with their head fitted inside the human-head coil. Scan duration ranged between 40 and 60 min as a function of brain size.

The chimpanzees were scanned using a 3.0 T scanner (Siemens Trio, Siemens Medical Solutions USA, Inc., Malvern, Pennsylvania, USA) at the YNPRC. T1-weighted images were collected using a three-dimensional gradient echo sequence (pulse repetition= 2300 ms, echo time=4.4 ms, number of signals averaged=3, matrix size =320 × 320, with .6 × .6 ×.6 resolution). After completing MRI procedures, the subjects were returned to the YNPRC and temporarily housed in a single cage for 6–12 h to allow the effects of the anesthesia to wear off, after which they were returned to their home cage. The archived MRI data were transferred to a PC running Analyze 8.1 software for post-image processing.

Initially, each T1-weighted MRI scan was skull stripped and the volume segmented into grey matter, white matter and CSF using FSL (Analysis Group, FMRIB, Oxford, UK) [Smith et al. 2004; Zhang et al. 2001]. Next, each individual MRI scan was linearly registered to a previously constructed symmetrical template of the chimpanzee brain using procedures that have been described elsewhere [Li et al. 2009]. The matrix derived from the linear registration was saved and then applied to the segmented grey matter (GM) volume. Thus, each individual subjects GM volume was aligned to the same stereotaxic space as the template brain.

Region of Interest

Object maps or masks of the ACC were subsequently drawn on the template brain, primarily in the coronal plane but with significant use of multidimensional viewing planes. We opted to trace the ACC regions-of-interest on the template brain instead of each individual scan because we sought to establish how far each individual subjects' grey matter volume deviated from the average chimpanzee brain. Because all the individual MRI scans were used to develop the template brain, this allowed us to simplify our analyses without potential biases introduced by tracing each individual brain. The ACC was quantified in the sagittal and coronal plane following the procedure used by Bush et al. [Bush et al. 2000] in human subjects (see Figure 1). For each subject, the mid-sagittal slice was identified. Moving 1 mm laterally in both the left and right hemisphere, a box was drawn around the corpus callosum (CC). The box surrounding the CC was then split at the anterior-posterior midpoint in order to divide the CC into anterior and posterior regions (Point A in Figure 1). Next, a vertical line was drawn perpendicular to the genu of the CC through the medial plane (Point B in Figure 1). The ACC was divided into three regions (see labels 3, 4 and 5 in Figure 1) and traced in the coronal plane. Region 24p was the gyrus that superior to the CC and was bordered anterior by vertical line (Point B in Fig 1) and posterior by vertical line (Point A in Fig 1) (colored yellow, in Figure 1c). The superior border was the cingulate sulcus and the inferior border was the superior bank of CC (see Figure 1b). Region 24 was the portion of the cingulate that was anterior to vertical line (Point B in Figure 1) and was bordered anteriorly by the cingulate sulcus and posteriorly by the vertical line (colored blue in Figure 1c). The superior border was the cingulate sulcus and the inferior border was the superior tip of the orbital frontal sulcus (see Figure 1b). The lateral border was the white matter belonging to the medial prefrontal cortex and the medial border was the mid-sagittal sulcus. Lastly, region 25 was that portion of the ACC that was inferior to the rostrum and genu of the CC. The anterior border was vertical line Point B in Figure 1 and the inferior border was the cingulate sulcus. The anterior border of region 25 was the rostrum and genu of the CC

and the inferior border was the medial orbital sulcus (Figure 1b). The lateral border for area 25 was the internal capsule.

The area 24p, 24 and 25 object maps that were drawn on the template brain were then applied to the segmented grey matter images for each subject in order to compute the volume for each region and hemisphere. To control or adjust for potential overall differences in cortical grey matter, we also computed the entire grey matter volume for the left and right hemispheres. Grey matter belonging to the brain stem and cerebellum were excluded from these calculations. Subsequently, we computed the percentage of grey matter belonging area 24p, 24 and 25 for each hemisphere by dividing the regional GM volume by the total grey matter volume and multiplying by 100. Thus, the values reflected the amount of grey matter for area 24p, 24 and 25 as a percentage of total grey matter volume in each hemisphere.

JA Behavioral Task

For the behavioral task, the focal subject was separated briefly from their social group, but remained in their home enclosure. An experimenter (E1) sat down on a small stool approximately one meter from the front of and on one far side of the subject's enclosure. A second experimenter (E2) then approached the enclosure from the opposite side as E1 and placed a small cache of preferred food (e.g. a bunch of grapes) on the ground approximately one meter from the front of the enclosure. E2 then left the area, and the trial started. The subject's behavior was recorded for 60 seconds. During this time, E1 maintained eye contact with the subject and behaved in a natural and attentive manner. At the end of 60 seconds, the trial was ended and E1 gave a small amount of the food to the focal subject (regardless of how and if they interacted with them). Each chimpanzee participated in three trials.

All trials were audio/video recorded for later behavioral scoring. For each previously recorded trial, we recorded if the chimpanzees successfully engaged in joint attention with the human experimenter. Success was defined as the chimpanzees pointing to either the food or the human while simultaneously alternating their gaze between the referent (the food) and the social agent (E1). The initiation of each behavior (i.e. manual pointing or gaze) had to occur within 5 seconds of the previous behavior. Data were collected from 73 chimpanzees (25 males, 48 females), of which MRi scans were available in seventy of these apes.

Results

Of the 73 chimpanzees tested on the JA task, 24 individuals (9 males and 15 females) never successfully initiated joint attention on any of the three trials and were therefore categorized as poor-initiators. Thirty-six subjects (11 males and 25 females) initiated joint attention on one or two of the three trials and they were classified as moderate-initiators. The remaining 13 subjects (5 males, 8 females) initiated joint attention on all three trials and were classified as good-initiators. We decided on three categories for two reasons 1) we selected the largest number of categories while maintaining adequate sample sizes in each, and 2) it seemed behaviorally most relevant to compare among those apes that a) never IJA, b) sometimes IJA, and c) always IJA. A Mann-Whitney *U* test indicated that there was no difference in JA behavior between females and males $U=590$, $z = .11$, $p=.91$.

For the statistical analysis, we compared the percentage of GM for areas 24p, 24, and 25 for each hemisphere as a function of sex and IJA performance. Region (24p, 24, 25) and hemisphere (left, right) were the repeated measures while sex (male, female) and IJA performance (poor, moderate, good) served as between group factors. Significant main effects for IJA grouping $F(2, 63)=3.760$, $p < .03$ and sex $F(1, 63) = 9.649$, $p < .003$ were found. Additionally, significant two-way interactions were found between sex and region $F(2, 126)=8.143$, $p < .001$ and between region and hemisphere $F(2, 126)=9.534$, $p < .001$.

The mean GM percentage for each JA group is shown in Figure 2. Post-hoc analysis indicated that chimpanzees who were classified as poor on the IJA task had significantly higher GM percentages than individuals classified as moderate or good on the IJA task. The mean percentage GM for area 24p, 24 and 25 in males and females are shown in Table 1. Post-hoc analysis showed that females had higher percentages of GM for area 24 and 24p compared to males. No significant sex differences were found for area 25. Finally, for the region by hemisphere interaction, paired samples *t*-tests were performed as a post-hoc test comparing the percentage of GM for the left and right hemisphere within each region. Significant leftward asymmetries were found for area 24 and 25 while significant rightward biases were found for area 24p (see Figure 3).

Discussion

The results of this study revealed three main findings. First, individual differences among chimpanzees in the engagement in joint attention with a human social partner were associated with variation in the volume of grey matter in the ACC. Second, females had relatively larger GM volumes in area 24p and 24 compared to males. Third, chimpanzees show population-level GM volume asymmetries within the ACC. Significant leftward asymmetries were found for areas 24 and 25 while rightward biases were found for area 24p.

With respect to joint attention, these data provide the first evidence linking individual differences in JA behaviors with the ACC in nonhuman primates and the results are consistent with the theory proposed by Mundy and Newell (2007). The findings are also consistent with studies in children and adults with ASD, populations that typically have poor JA skills and for which differences in the organization of the ACC have been reported [Mundy 2003; Mundy et al. 2007; Paus 2001]. We are not suggesting that the chimpanzees that perform poorly on the JA task described here may be characterized as having autism; rather, we are suggesting that chimpanzees that perform poorly on this JA task have a phenotype that parallels that observed in ASD with respect to the initiation of joint attention. We are further suggesting that potential mechanisms that underlie changes in cortical organization within the ACC that influence JA skills in humans may similarly be operating in chimpanzees.

It could be suggested that the effects reported here are not limited to the ACC but instead reflect more global differences in GM organization in these chimpanzees. To specifically verify that it was variability in the volume of GM in the ACC (and not, for example, cortical gray matter volume in general) that was associated with differences in JA behaviors, we conducted an additional analysis. For this test, we compared the total GM volume for each hemisphere (excluding cerebellar GM and brainstem as described above) as a function of IJA performance. Hemisphere (left, right) was the repeated measure while and IJA performance (poor, moderate, good) served as the between group factor. No significant main effects for IJA grouping $F(2, 67) = .990, p = .38$ was found. Therefore, the observed differences in JA behaviors are associated specifically with volumetric differences in GM in the ACC.

We also performed an additional analysis examining whether the effects reported here were driven specifically by variation in JA or was simply related to the subject's tendency to produce manual gestures (i.e. the production of a manual gesture along with the alternation of gaze between the food and social referent). For this analysis, we determined whether or not the chimpanzee subjects produced at least one gesture on each of their three trials. We then classified the chimpanzees as either a) not producing a manual gesture on any of the three trials, b) producing a gesture on one or two of the three trials or c) producing at least one manual gesture on all three trials. We then compared the percentage of GM for areas

24p, 24, and 25 for each hemisphere as a function of gesture category. Region (24p, 24, 25) and hemisphere (left, right) were the repeated measures while gesture grouping served as the between group factor. No significant main effect for gesture grouping was found $F(2, 66)=1.703$, $p = .19$. This suggests that JA was the behavior distinguishing individual variation in GM within the ACC.

At present, we can only speculate as to what the mechanisms or neural foundations may account for this result but we offer one suggestion. Recall that chimpanzees who perform poorly on the JA task have larger GM percentages within the ACC compared to moderately and good performing apes. Though we did not quantify white matter volumes in this study, it seems logical to assume that those chimpanzees who perform well on the JA task would have more white matter within the ACC. White matter reflects increased myelination of axons and connectivity of this region with other regions in the brain, suggesting that chimpanzees who perform poorly may have fewer cortical connections within some or all of the ACC. Several recent studies have suggested that among primates, humans and great apes but not more distantly related Old or New World monkeys, possess spindle cells or von Economo neurons within the ACC and the fronto-insular cortex [Allman et al. 2010; Allman et al. 2005; Nimchinsky et al. 1999]. Unlike pyramidal cells, spindle cells have long axons extending from the soma and some have suggested that they may serve the function of connecting distant cortical regions involved in higher order social cognition including empathy, theory of mind, self-recognition and joint attention [Allman et al. 2005]. Thus, we would speculate that the differences in the percentage of GM found within the ACC in chimpanzees with different JA abilities may reflect variation in the degree or quantity of spindle cells, the consequence of which is reduced connectivity among cortical regions involved in higher order social cognitive processes.

Significant population-level asymmetries were also found within different regions of the ACC. Recall that significant leftward asymmetries were found for Area 24 and 14 whereas rightward biases were found for Area 24p. As far as we know, these are the first evidence of population-level asymmetries in the anterior cingulate cortex of chimpanzees, and indeed, nonhuman primates. The evidence of population-level asymmetries in the ACC is consistent with a growing body of data on neuroanatomical asymmetries in nonhuman primates [Bogart et al. 2012; Hopkins et al. 2010; Lyn et al. 2011] and these collective findings continue to challenge the long held belief that behavioral and brain asymmetries are unique to humans, as suggested by some [Crow 2004; Crow 2009]. It should be noted that microstructural asymmetries have been reported within the ACC in great apes. Notably, significant rightward asymmetries have been found in the number of von Economo neurons and these observations are consistent with our evidence of lateralization within the ACC [Allman et al. 2010]. The exact relationship, if any, between the patterns of asymmetry found in GM volume and von Economo neurons in chimpanzees is not clear but perhaps warrants some further investigation.

The functional significance of the asymmetries reported here are as yet unknown. Anatomical and functional asymmetries have similarly been reported in humans, with leftward asymmetries being more consistently reported, particularly as it relates to the degree of cortical folding and sulcal variability in the dorsal portions of the ACC [Huster et al. 2007; Paus et al. 1996; Yucel et al. 2001]. We did not measure the degree of sulcal variability within the ACC in our sample, but our impression is that chimpanzees exhibit less variability than what has been described in the human ACC. Notwithstanding, we would point out that the methods employed in this study were designed to minimize sulcal variability by virtue of the fact that we drew the object maps for the regions of interest on a chimpanzee template brain. Templates, human or otherwise, tend to highlight *consistencies* in sulcal variability across subjects rather than inconsistency.

The sex differences found in the percentage of GM within area 24p and 24 were not anticipated and robust sex differences in neuroanatomy and organization have not been previously reported in chimpanzees, likely due to the relatively small numbers of subjects or because the studies were limited to a single sex. In humans, most studies have not adopted a similar approach to those employed in this study, so it is difficult to interpret our findings within a comparative framework. Allen and colleagues [2003] used a region-of-interest approach to quantify the ACC in humans and failed to find a sex difference in grey matter volumes after adjusting for overall grey matter volumes. We believe that interpretation of the functional relevance of the sex differences reported here warrants some caution due to the discrepancies in sample size between male and female chimpanzees in this analysis.

There are at least two potential limitations to this study. First, as mentioned above, we drew the object maps on a template and then applied the maps to grey matter volumes constructed from MR images of individual subject's brains that had been linearly registered to that template. Thus, rather than trace the ACC in each subject, we instead adopted an approach that has come to be commonly used in human ROI based studies. Some might argue that the linearly registered volumes may have unwittingly biased the results. This is a valid concern but, with a larger sample size, as employed in this study, this issue is probably less problematic because we have sampled a reasonable amount of variability in the structural variants used to define the ACC. Moreover, all the subjects that were registered to the template were used to create the template. So what is effectively being measured in this study is the extent to which any individual deviates from the normative or standard ACC structure, much like standardized *z*-scores work in many psychometric studies.

A second issue relates to the definition of initiation of joint attention as applied in this study. Recall that we defined successful JA as incidences in which the chimpanzees produced a manual communicative gesture while alternating their gaze between the social agent and the referent (i.e. the food). This definition is consistent with some early conceptions of JA but, more recently, some have distinguished between imperative, informative and declarative communicative acts and how they might relate to JA [Liszkowski et al. 2004; Tomasello 2008]. Imperative pointing or what is sometimes called initiating behavioral requests reflect an individuals' request for something from another social agent whereas declarative pointing is motivated by the individuals simple desire to share information with another individual without any explicit reason or expectation. Further to this point, some have suggested that declarative pointing reflects the initiation of joint attention whereas imperative pointing reflects the initiation of a behavioral request, which have been posited to have different underlying cognitive or motivational processes [see Leavens 2012 for review] Whether this is a meaningful distinction from the standpoint of cortical organization of the ACC is unclear and there is plenty of data showing considerable overlap in the cognitive foundations of each of these forms of initiating joint attention [Gernsbacher et al. 2008; Leavens and Racine 2009; Southgate et al. 2007].

In summary, individual differences in the initiation of joint attention is linked to variability in the volume of grey matter within the anterior cingulate cortex. These findings are consistent with the proposed role of the ACC in the development of joint attention in children as proposed by Mundy and Newell [2007]. Future research should focus on assessing the role of other brain regions on, not just the initiation of joint attention but also the responding to joint attention by chimpanzees. These findings will provide a framework for understanding the role of the ACC in the evolution and development of joint attention abilities in primates, including humans.

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Figure 1.

a) Mid-sagittal view of a chimpanzee brain with the landmarks delineating areas 24p, 24 and 25 b) coronal view of the tracing of the grey matter corresponding to area 24 when drawn on the template brain. The superior border was the cingulate sulcus and the inferior border was the superior tip of the orbital frontal sulcus. The lateral border was the white matter belonging to the medial prefrontal cortex and the medial border was the mid-sagittal sulcus c) coronal view of area 24p and area 25 regions of interest when drawn on the template brain. For area 24p, the superior border was the cingulate sulcus and the inferior border was the corpus callosum. For area 25, the inferior border was the superior tip of the orbital frontal sulcus and the superior border was the corpus callosum. The lateral border was the internal capsule and the medial border was the mid-sagittal sulcus.

Figure 2. Mean percentage grey matter ($\pm$ s.e.) for chimpanzees classified as poor-initiators, moderate-initiators and good-initiators.

Figure 3.
Mean AQ scores ($\pm$ s.e.) for each region for the ACC.

Table 1

Mean Percentage Grey Matter (+/- s.e.) for Areas 24p, 24 and 25 in Male and Female Chimpanzees

	Area 24p	Area 24	Area 25	Total
Females	1.556 (.051)	1.332 (.037)	.298 (.010)	1.063 (.030)
Males	1.276 (.070)	1.168 (.050)	.262 (.014)	.902 (.042)
Total	1.417 (.043)	1.250 (.031)	.280 (.008)	

Values represent percentage of total grey matter volume