NeuroImage 61 (2012) 533–541

Contents lists available at SciVerse ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Cortical sulci asymmetries in chimpanzees and macaques: A new look at an old idea

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ARTICLE INFO

Article history:
Accepted 28 March 2012
Available online 5 April 2012

Keywords:
Chimpanzee
Brain asymmetry
Sulci morphology

ABSTRACT

Functional and neuroanatomical asymmetries are an important characteristic of the human brain. The evolution of such specializations in the human cortex has provoked great interest in primate brain evolution. Most research on cortical sulci has revolved around linear measurements, which represent only one dimension of sulci organization. Here, we used a software program (BrainVISA) to quantify asymmetries in cortical depth and surface area from magnetic resonance images in a sample of 127 chimpanzees and 49 macaques. Population brain asymmetries were determined from 11 sulci in chimpanzees and seven sulci in macaques. Sulci were taken from the frontal, temporal, parietal, and occipital lobes. Population-level asymmetries were evident in chimpanzees for several sulci, including the fronto-orbital, superior precentral, and sylvian fissure sulci. The macaque population did not reveal significant population-level asymmetries, except for surface area of the superior temporal sulcus. The overall results are discussed within the context of the evolution of higher order cognition and motor functions.

Introduction

Functional and neuroanatomical asymmetries are a prominent feature of the human brain, most notably in regions associated with perception and production of language and speech (Corballis, 2002; Davidson, 1995). For instance, clinical and functional imaging studies in humans have well established that the left inferior frontal gyrus (IFG) and posterior temporal lobe (PT) are involved in language production and comprehension skills, respectively (Beaton, 1997; Foundas et al., 1998; Keller et al., 2009a). There is also evidence of leftward anatomical asymmetries in the posterior temporal lobe (Shapleske et al., 1999) and, to a lesser degree, the IFG, particularly among right-handed individuals, which many believe underlies the functional asymmetries for language found in these brain regions (Keller et al., 2007, 2009a).

Given the importance of the IFG and PT in language functions, the question of whether population-level asymmetries occur in nonhuman animals, notably chimpanzees, is of considerable scientific interest to the study of human evolution (Binder et al., 1997; Bruner and Holloway, 2010; Keller et al., 2009a). Many scientists have argued that because language is unique to humans and strongly left hemisphere dominant, population-level asymmetries are an adaptation of the human brain that occurred after the split of the common ancestor with genus *Pan* (Crow, 2004, 2009; Williams et al., 2006). They argue that genetic differences between apes and humans were necessary for the development of language and the associated brain asymmetries found in human but not nonhuman primate brains (Williams et al., 2006). This proposed evolutionary model of behavioral and brain asymmetry (Annett, 1985, 2002; Crow, 2004, 2009; Williams et al., 2006) is considered saltational; that is, these theoretical perspectives suggest that a qualitative shift and unique change of the human central nervous system occurred after the split between humans and chimpanzees. Thus, there should be no continuity in homologous asymmetries between these species.

In contrast to the saltational views, others have suggested that the evolution of behavioral and brain asymmetries occurred along a continuum with homologies evident for more primitive or conserved brain systems and specializations unique to humans in more recently evolved and expanded regions (Balzeau and Gilissen, 2010; Hopkins and Cantalupo, 2008). Specifically, recent *in vivo* imaging and analysis of post-mortem brains suggest that chimpanzees, and possibly other nonhuman primate species show population-level leftward asymmetries in the PT (Gannon et al., 1998, 2008; Gilissen, 1992, 2001; Hopkins and Nir, 2010; Spocter et al., 2010), but less consistently for the IFG (Cantalupo and Hopkins, 2001; Hopkins et al., 2008; Keller et al., 2009b;

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doi:10.1016/j.neuroimage.2012.03.082

Schenker et al., 2010; Uylings et al., 2006). For example, measurement of the PT from MRI images reveals significant population-level leftward asymmetries in chimpanzees (Hopkins and Nir, 2010), but not in Old World monkeys (Lyn et al., 2011). Cytoarchitectonic studies have also shown that the volume of BA22, a constituent part of the PT, is larger in the left compared to right hemisphere in chimpanzees (Spocter et al., 2010) and rhesus monkeys (Gannon et al., 2008).

In the present study, we examined whether population-level asymmetries exist in sulci surface area and mean depth for 11 sulci of the chimpanzee and seven sulci from the macaque brain. For both species, we selected sulci from the frontal, temporal, parietal and occipital lobes (see Methods). Our main objective was to test the saltational hypothesis. According to this hypothesis, if population-level brain asymmetries emerged uniquely in humans as a consequence of either language and speech evolution, or other functional asymmetries, such as handedness as suggested by others (Corballis, 2003; Crow, 2004; Marchant and McGrew, 1991; Warren, 1980), then chimpanzees should fail to show significant population-level asymmetries in either surface area or mean depth for any of the sulci. Based on previous evidence of population-level asymmetries in the PT and, to a lesser extent, the IFG, we did not expect that the saltational hypothesis would be supported. Rather, we hypothesized that significant population-level asymmetries would be found in chimpanzees, particularly for sulci that serve as landmarks in defining the PT and IFG, including the sylvian fissure, precentral inferior, inferior frontal and fronto-orbital sulci. Our predictions for macaques were less confident because the existing literature on asymmetries in this genus has produced inconsistent results. Notwithstanding, if population-level asymmetries evolved prior to the split between apes and Old World monkeys, then it would be predicted that macaques monkeys would show population-level asymmetries for one or more sulci.

A second hypothesis we tested was related to theories suggesting that brain asymmetries evolved in the context of decreasing ratios in the size of the corpus callosum (CC) relative to whole brain volume and neocortical surface area (Oliveras et al., 2001; Rilling and Insel, 1999a). Comparative studies of the size of the CC in mammals, as well as within primate species, have shown that as brain size increased during evolution, the CC did not keep pace (Oliveras et al., 2001; Rilling and Insel, 1999a). Thus, humans have a relatively small CC for a species of our brain size followed by great apes, and then the more distantly related Old and New World monkeys. The suggestion is that as primate brains got larger, each hemisphere became increasingly disconnected which resulted in increasingly intra- rather than interhemispheric connectivity (Aboitiz et al., 2003; Hopkins and Cantalupo, 2008; Ringo et al., 1994). This, in turn, resulted in increasingly functional and anatomical specializations within each hemisphere. Because chimpanzees have a smaller ratio in CC size to brain volume compared to macaque monkeys, this theory predicts that chimpanzees would show larger asymmetries than macaques. We tested this hypothesis by comparing the absolute degree of sulci asymmetry in macaque monkeys and chimpanzees in five sulci that were common to both genera.

Sulci were quantified using a software program called BrainVISA (BV). BV focuses on cortical folding patterns of the brain and uses sulcus-based morphometry (Mangin et al., 2004). This method differs from historical approaches, because it quantifies both the surface area and mean depth of the sulci rather than relying solely on the linear length of the outer contour of the sulcus, the primary measure employed in many previous studies of brain asymmetry in human and nonhuman primates measured from cadaver specimens (Gannon et al., 2008; Gilissen, 1992; Heilbronner and Holloway, 1988, 1989; Imai et al., 2011; LeMay, 1985; Witelson and Kigar, 1992; Yeni-Komshian and Benson, 1976), cranial endocasts (Cheverud et al., 1990; Falk et al., 1986, 1990), and MRI (Cantalupo et al., 2003; Hopkins et al., 2000; Ide et al., 1996; Liu and Phillips, 2009; Zilles et al., 1996). This is an important distinction because measures of length, by themselves, may not capture all size dimensions of the sulci. By contrast, BrainVISA captures all dimensions of variability in organization (i.e., length and depth) and therefore offers a new and potentially more thorough means of assessing asymmetries in cortical sulci.

Methods

Subjects

In vivo magnetic resonance images (MRI) were obtained from 127 captive chimpanzees (*Pan troglodytes*), including 76 females and 51 males, ranging in age from 6 to 53 years. The chimpanzees were housed at the Yerkes National Primate Research Center (YNPRC) and the University of Texas M. D. Anderson Cancer Center (UTMDACC).

Magnetic resonance images (MRI) were obtained from 28 bonnet monkeys (*Macaca radiata*) and 21 rhesus monkeys (*Macaca mulatta*) housed at the Wake Forest University Primate Center (WFUPC). Within the bonnet monkey sample, there were 11 females and 17 males, ranging in age from 8 months to 10 years of age ($M = 4.24$, $SD = 2.65$). The rhesus monkey sample was comprised of 16 males and 5 females ranging in age from 6 to 11 years of age ($M = 9.1$, $SD = 2.3$). This study was conducted in accordance with the Guidelines of the Committee on the Care and Use of Laboratory Animal Resources (NRC, 1996) and approved by each institution's animal care and use committee.

MRI image collection

Scanning procedures

All chimpanzee magnetic resonance image (MRI) scans followed standard procedures at the YNPRC and UTMDACC. Subjects were scanned during their scheduled physical examination surveys and anaesthetized with propofol (40–60 mg/(kg/h)). The chimpanzee was placed in a supine position in the scanner with its head in a human-head coil. The scanning process ranged between 35 and 50 minutes depending on brain size. Upon completion of the MRI, chimpanzees were temporarily singly housed for 2–6 hours to allow the anesthesia to wear off before being returned to their home group.

Monkeys were given initial ketamine anesthesia (15 mg/kg, i.m.) and atropine (0.07 mg/kg, i.m.), then transported to the mobile MRI scanner, intubated and maintained under isofluorane (1.25%) throughout the scan. The subjects 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 hour). Subjects were placed in the scanner chamber in a supine position with their head fitted inside the human-knee coil. Scan duration ranged between 24 and 28 minutes as a function of brain size. After completing MRI procedures, the subjects were temporarily housed in a single cage for 1–2 hours 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 BrainVISA software for post-image processing.

Imaging parameters

For the chimpanzees, 68 individuals were scanned using a 3.0 T scanner (Siemens Trio, Siemens Medical Solutions USA, Inc., Malvern, Pennsylvania, USA). 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 0.6 × 0.6 × 0.6 resolution). The remaining 59 chimpanzees as well as all the macaques were scanned using a 1.5 T G.E. echo-speed Horizon LX MR scanner (GE Medical Systems, Milwaukee, WI). T1-weighted images were collected in the transverse plane using a gradient echo protocol (pulse repetition = 19.0 ms, echo time = 8.5 ms, number of signals averaged 8, matrix size = 256 × 256, with 0.7 × 0.7 × 1.2 resolution). Examples of T1-images from both species are illustrated in Fig. 1.