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Cerebral Petalias and Their Relationship to Handedness in Capuchin Monkeys (*Cebus apella*)

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Abstract

Cerebral asymmetries are thought to be associated with increased hemispheric specialization of function. We investigated cerebral petalias, the protrusion of one cerebral hemisphere relative to the other, and their relationship to lateralized behavior in capuchin monkeys (*Cebus apella*). Magnetic resonance images of the brain and behavioral data on a coordinated bimanual task were obtained from 13 capuchins. While a significant population-level left-frontal petalia was found, this was not related to handedness. The role of the morphologically asymmetric frontal cortex in capuchins is unclear, but may reflect developmental gradients or directional selection for various behavioral functions, such as extractive foraging or social group complexity.

Keywords

Handedness; lateralized behavior; petalias; *Cebus*

1. Introduction

Neuroanatomical asymmetries of the human brain are thought to underlie a range of lateralized behavior, including language, gesture, and skilled motor actions (see Toga & Thompson, 2003, for a review). In humans, one particularly prominent population-level neuroanatomical asymmetry is that of a right-frontal, left-occipital petalia (Holloway & De La Coste-Lareymondie, 1982; Lancaster, Kochunov, Thompson, Toga, & Fox, 2003; LeMay, 1976; Watkins et al., 2001). Petalias are the greater protrusion of one cerebral hemisphere relative to the other as expressed at the frontal and occipital poles of the skull or brain. Whether nonhuman primates display cerebral petalias has been investigated using endocasts (as the petalias leave impressions on the inner table of bone of the skull), cadaver specimens, and more recently, magnetic resonance images. However, the use of these different methodologies has produced conflicting results. LeMay (1976), using data from endocasts, reported that Old and New World monkeys had only a left-occipital protrusion. Falk et al. (1991), also using endocasts, reported only a right-frontal petalia in rhesus monkeys. Cheverud et al. (1990) reported a positive correlation between the size of the left-occipital petalia and right-frontal petalia using a larger sample of rhesus endocasts. In contrast, Holloway and De La Coste-Lareymondie (1982) reported that the combination of left-occipital and right-frontal petalias

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was rarely present in great ape endocasts, although left-occipital petalias were fairly frequent in gorillas. Moreover, they noted that among hominin fossil endocasts, the characteristic modern human-like petalia torque pattern does not reliably occur until the emergence of *Homo erectus*. Others have suggested that the petalia torque is unique to *Homo sapiens* and is related to a genetic mutation that was critical to the evolution of novel cognitive capacities in our lineage (Crow, 2004). In contrast to these studies, Hopkins and colleagues (Hopkins & Marino, 2000; Pilcher, Hammock, & Hopkins, 2001) used magnetic resonance imaging of great ape, Old World and New World monkey brains and found that great apes followed the human pattern, showing a right-frontal and left-occipital petalia asymmetry. However, Old World and New World monkeys did not display any significant cerebral asymmetries. Thus, whether nonhuman primates show cerebral petalias remains unclear.

The relationship between petalias and handedness in humans also remains unresolved. While there is some evidence that a wider right frontal lobe combined with a wider left occipital lobe is more common in right-handed individuals than non-right-handed individuals (Kertesz, Black, Polk, & Howell, 1986; LeMay & Kido, 1978), several recent voxel-based morphometry analyses of structural asymmetries have failed to find an association between petalias and hand preference (Good et al., 2001; Herve et al., 2006; Watkins et al., 2001).

Interestingly, no study has investigated both cerebral petalias and handedness in nonhuman primates. Here we investigate whether capuchins display cerebral petalias and if these are related to handedness. Capuchins are noted for their high degree of skilled motor and extractive foraging habits. Additionally, capuchins express strong and consistent hand preferences during tasks that require complex bimanual coordination (*e.g.*, Frigaszy & Mitchell, 1990; Spinozzi, Castorina, & Truppa, 1998; Westergaard & Suomi, 1993, 1996). Therefore, we hypothesized that petalias would be present and their pattern would be associated with handedness.

2. Method

2.1 Subjects

In vivo magnetic resonance images and behavioral data were collected from 13 capuchin monkeys (*Cebus apella*; male $n = 7$, female $n = 6$). Subjects were socially housed at Hiram College (Hiram, Ohio), Northeastern Ohio Universities College of Medicine (Rootstown, Ohio), or the College of Wooster (Wooster, Ohio). Ages ranged from 1 – 21 years ($M = 10.23$, $SD = 6.61$).

2.2 Behavioral Measures

Hand preference was determined for each subject through a coordinated bimanual task known as the tube task (Hopkins, 1995). This task was chosen because it elicits a high degree of hand preference in nonhuman primates (Vauclair, Meguerditchian, & Hopkins, 2005). Although different conclusions have been reached with respect to whether this task does (Spinozzi et al., 1998) or does not (Westergaard & Suomi, 1996) elicit population-level hand preferences in capuchins, it is clear that individuals show display strong handedness on this task.

Subjects were individually presented with a piece of poly-vinyl-chloride tube 6 cm in length and 1.5 cm in diameter with peanut butter smeared inside. To remove the food, subjects had to hold the tube in one hand and use the other hand to retrieve the peanut butter. The hand used to retrieve the food was recorded as left or right. Capuchins received four sessions with the task. Subjects performed a mean of 102 responses ($SE \pm 19.04$) and showed high consistency in hand use across the four trials.

Handedness index (HI) scores were determined for each subject by using the hand preference formula $(\#R - \#L)/(\#R + \#L)$. The mean handedness index (MHI) was calculated by taking the

average HI of all trials for each individual. Z-scores were calculated for *MHI* to determine if individuals displayed significant hand preferences and to classify subjects as right-handed, left-handed, or ambidextrous. Subjects with z-scores greater than 1.95 or less than -1.95 were classified as unambiguously right- or left-handed. Subjects with z-scores between 1.95 and -1.95 were classified as having no hand preference.

2.3 MRI Procedure and Image Quantification Method

Capuchins were transported to the Brain Imaging Research Center in Pittsburgh, Pennsylvania for the MR procedure. Once at the facility, subjects were initially immobilized by ketamine injection (25 mg/kg) and acetylpromazine (1 mg/kg), and subsequently anaesthetized with propofol (160–330 micrograms/kg/minute). Subjects were placed into the scanner chamber and their heads were fitted inside a 16 cm head coil. A vitamin E capsule was taped above the left ear as a marker. Subjects remained anaesthetized throughout the MR procedure and respiration rate, heart rate, and oxygen consumption were continually monitored. T1-weighted images were acquired on a 3.0 T scanner (Siemens Allegra). Images were collected in sagittal plane using a gradient echo protocol (pulse repetition = 1500 ms, echo time = 3.04 ms, and a 256×256 matrix). Subjects were allowed to completely recover from the effects of the anaesthesia before return transport.

Images were reformatted into the ANALYZE 3D volume file format to facilitate re-slicing into orthogonal planes. Morphometric measurements were performed using ImageJ software version 1.26t (<http://rsb.info.nih.gov/ij/>) and followed the methodology of Hopkins & Marino (2000), wherein four measures of cerebral width are delineated: anterior-frontal, posterior-frontal, parietal, and occipital. For each region, measurements were taken from the midline to the lateral surface of the brain. These regions can be seen in Figure 1. An asymmetry quotient was calculated ($AQ = R - L / [(R + L) \times 0.5]$) for each region. Positive asymmetry quotients represent a right-side bias, whereas negative asymmetry quotients represent a left-side bias.

3. Results

Individual *MHI* values for the tube task, classification into dextral group, and asymmetry quotients for all regional petalias are displayed in Table 1. Figure 1 displays the mean ($\pm SE$) AQ score for each region. Data did not violate assumptions of normality; therefore parametric statistics were used. No sex differences were found in handedness or in cerebral width asymmetry for any of the regions; therefore subsequent analyses thus pooled male and female data.

As some have reported that hand preference in capuchins varies with age (Westergaard & Suomi, 1993), we examined the possible role of age in hand preference and petalia asymmetries. Of the four juveniles in our sample (Alou, DiMaggio, Shoeless and Sosa; see Table 1), three expressed a significant hand preference on the tube task. Age did not correlate with the directional *MHI*, $r = .26, p > .05$, but a positive correlation was found between age and absolute strength of handedness ($ABS - MHI$), $r = .63, p < .05$. Age did not correlate with cerebral petalia AQs (anterior-frontal, $r = -.14, p > .05$; posterior-frontal, $r = .07, p > .05$; parietal, $r = .54, p > .05$; occipital, $r = -.08, p > .05$).

To determine whether population-level asymmetry was seen for any of the cerebral width asymmetries, one-sample *t*-tests were conducted (tested against a population mean of 0). Population-level asymmetries were found for the anterior frontal ($t(12) = -2.65, p < .05$) and posterior frontal ($t(12) = -2.28, p < .05$) regions, with both showing a significant leftward bias. A one-way within-subjects ANOVA (with brain region as the within-subjects variable) indicated a significant difference in cerebral width among regions ($F(3, 36) = 3.92, p < .05$). Post hoc LSD tests revealed that the anterior-frontal asymmetry was significantly larger than

the parietal and occipital regions, and that the posterior-frontal asymmetry was significantly larger than the parietal region.

We then analyzed the data to determine if individuals displaying significant hand preferences showed more pronounced petalias. No significant effect of handedness was found on asymmetry for any of the cerebral regions (anterior-frontal, $F(2, 12) = .38, p > .05$; posterior-frontal, $F(2, 12) = .86, p > .05$; parietal, $F(2, 12) = .31, p > .05$; occipital, $F(2, 12) = .39, p > .05$). To further investigate a potential relationship between handedness and petalias, Pearson correlation coefficients were calculated relating AQ of each cerebral petalia to the MHI on the tube task. Handedness did not correlate with asymmetry of any of the cerebral regions (anterior-frontal, $r = .18, p > .05$; posterior-frontal, $r = .04, p > .05$; parietal, $r = -.10, p > .05$; occipital, $r = -.25, p > .05$).

4. Discussion

The results of this study showed that population-level left-frontal petalia asymmetry is present in capuchins. However, no relationship exists between handedness and petalias in any region.

Our finding of a left-frontal and no occipital petalia contrasts with the other published studies on petalias of New World monkeys (Hopkins & Marino, 2000; LeMay, 1976; Pilcher et al., 2001). LeMay reported a left-occipital and no frontal protrusion in her sample whereas Hopkins & Marino (2001) and Pilcher et al. (2001) reported no significant asymmetries in cerebral width or asymmetries for New World monkeys. We collected data from MR images instead of endocasts; this may account for the different conclusions in our study and that of LeMay and colleagues. In fact, LeMay et al. (1982) noted that measurement of asymmetries in New World monkey endocasts was particularly challenging because of their small brain size and difficulty in determining a midline to correspond to the interhemispheric fissure. The difference between our results and those of Hopkins and Marino likely reflect the relatively small sample size of capuchins employed in their study.

The functional significance of this petalia pattern in capuchins is unclear. We predicted that petalias would be associated with handedness on the tube task, as lateralized behavior on this task is correlated with another cerebral asymmetry in capuchins, namely the depth of the central sulcus in the region of hand representation of the primary motor cortex (Phillips & Sherwood, 2005). Additionally, a relationship between handedness and cerebral petalias has been reported in some human studies (Kertesz et al., 1986; LeMay & Kido, 1978). To our knowledge, there are no other within-species correlative studies of cerebral petalias and handedness in nonhuman primates. However, a relationship between petalias and handedness has not been detected in chimpanzees (Hopkins, pers. comm). Taken together with recent voxel-based morphometry studies of humans that have also failed to reveal a relationship between petalias and handedness (Good et al., 2001; Herve et al., 2006; Watkins et al., 2001), it would appear that this type of cerebral asymmetry is not a correlate of hand preference in primates. Instead, petalias may indicate general hemispheric specialization reflecting regionally-specific disproportionate growth of grey or white matter tissue volume on one side.

We speculate that the left-frontal petalia pattern observed in capuchins might reflect a lateralized expansion of a portion of the prefrontal cortex, indicating greater hemispheric division of function. Frontal petalias are also seen in humans and possibly great apes (Hopkins & Marino, 2000; LeMay, 1976; Pilcher et al., 2001; Watkins et al., 2001; Holloway & De La Coste-Lareymondie, 1982), although the petalias show the opposite pattern (*i.e.*, a right-frontal petalia). In humans this possibly reflects the prefrontal cortex's role in speech (Toga & Thompson, 2003). The role of the morphologically asymmetric frontal cortex in capuchins remains unclear, but may reflect developmental gradients of the cerebral hemispheres (Best,

1988) or directional selection for various behavioral functions, such as extractive foraging or social group complexity.

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Figure 1.
MRI image of the first axial slice above the third ventricle, where measurements of cerebral width were taken.

Figure 2. Mean ($\pm$ standard error) asymmetry quotients for each cerebral region. Positive values represent a right-side bias, whereas negative values represent a left-side bias.

Table 1
Mean handedness index (MHI), classification into dextral group (R=right-handed, L=left-handed, A=ambidextrous) and asymmetry quotients (AQ) for cerebral width regions for each subject. Positive asymmetry quotients represent a right-side bias, whereas negative asymmetry quotients represent a left-side bias.

Subject	Sex	Age	MHI	z-score	Dextral Group	Anterior Frontal Petalia AQ	Posterior Frontal Petalia AQ	Parietal Petalia AQ	Occipital Petalia AQ
Alou	M	2.5	0.81	7.40	R	-10.53	-12.66	-6.45	0.00
Carlos	M	5	-0.95	-8.61	L	-8.70	-19.78	-1.98	0.00
DC	F	21	0.96	5.39	R	-16.98	-13.89	-1.33	3.85
DiMaggio	M	1	0.39	10.44	R	3.51	0.00	-4.08	0.00
Georgia	F	6	-0.75	-9.41	L	0.00	-5.26	-2.30	3.51
Gizmo	F	16	0.60	4.31	R	-2.04	1.23	2.33	0.00
Jake	F	15	1.00	12.85	R	9.43	7.32	3.53	-1.64
LC	F	15	0.85	7.14	R	-2.22	-3.13	-1.45	-7.41
Miro	M	12	1.00	7.02	R	-11.76	-11.76	0.00	0.00
Noel	F	14	-0.82	-2.00	L	-3.51	2.53	2.41	0.00
Shoeless	M	1.5	-0.14	-0.68	A	-3.17	-4.55	-2.11	0.00
Sosa	M	3.5	-0.62	-8.64	L	-15.38	2.30	2.11	0.00
Vincent	M	18	-1.00	-14.59	L	-13.95	-6.90	0.00	0.00