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**CORRELATIONS BETWEEN HAND PREFERENCE AND CORTICAL
THICKNESS IN THE SECONDARY SOMATOSENSORY (SII) CORTEX OF
THE COMMON MARMOSSET, *CALLITHRIX JACCHUS***

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Abstract

Cortical asymmetries are well established in humans for language and motor regions and correlate with handedness. Here we investigate structural differences in the hemispheres of left- and right-handed common marmosets using surface photography and histology. The hand preferences of 11 marmosets were assessed over their adult life span using a simple reaching task. A significant correlation was found between the length of the right lateral sulcus/brain weight and the % right-hand preference ($r=0.86$, $p=0.001$). Cortical thickness on the superior bank of the right lateral sulcus posteriorly was also positively correlated with % right-hand preference ($r=0.69$, $p=0.025$). Comparison of this site with previously published functional maps of the marmoset cortex show this area corresponds to SII, a region involved in tactile processing and somatosensory discriminations. It is suggested that the correlation between SII thickness and right-hand preference would be consistent with the fact that right-handed marmosets are more proactive than left-handers in exploring novel objects by touch. Enlargement of a cortical area involved tactile discriminations could be a precursor to the evolution of right-handedness as a population bias.

Keywords: lateral sulcus, sylvian fissure, tactile discrimination, laterality

Introduction

Lateralized brain function is widespread amongst vertebrate species (Rogers and Andrew, 2002; Vallortigara and Rogers, 2005) and in some, but not all, species it is expressed as a hand or limb preference in the population. Toads prefer to wipe the face using the right hand (Bisazza et al, 1996) and several species of parrots show a strong population bias to hold food in the left foot (Harris, 1989; Rogers, 1980; Rogers, 2007). Hand preferences in non-human primates have been much debated, and some researchers have vehemently defended their claim that they do not exist (e.g. Crow, 2004), but there is now convincing evidence that chimpanzees prefer to use the right hand to hold tools (Hopkins et al., 2004) and that the prosimians reach out to grasp food using the left hand (Ward et al., 1993). Based on this evidence, McNeilage et al. (1987) proposed that primates use the right hand and limb to support their body, because the right side is stronger, and that an evolutionary shift away from left hand preferences for holding food to right preferences for manipulating food and objects occurred along with increasing bipedal posture. Accordingly, there should be intermediate species that show no population bias to use one hand or the other but whether these might be comprised of equal numbers of left- and right- handed individuals or of the majority showing no hand preference has not been considered.

The common marmoset, *Callithrix jacchus*, is an interesting species to study since approximately half of common marmosets prefer the left hand to pick up food and take it to the mouth to eat and the other half prefer the right hand (Hook and Rogers, 2000; de Sousa et al., 2001). Furthermore, the hand preference of each marmoset remains stable over its adult lifespan (Hook and Rogers, 2000).

Interestingly, different temperaments are expressed by left- and right-handed marmosets (Cameron and Rogers, 1999). Right-handed marmosets are more proactive than left-handed marmosets in terms of exploring new environments and novel objects (Cameron and Rogers, 1999). Thus hand preferences may be associated with the preferred use of a dominant hemisphere to control a range of functions. If so, we might expect to find structural differences between left- and right-handed marmosets in cerebral regions both within and outside the motor cortex.

For the motor cortex, Hopkins and Cantalupo (2004) reported a correlation between hand preference, determined in a task requiring co-ordinated use of both hands, and structural asymmetry of the precentral gyrus in chimpanzees. Dadda et al. (2006) showed that the asymmetry of the precentral gyrus in chimpanzees was restricted to the hand area of the motor cortex, a region known as the knob. Other than apes, asymmetry in the precentral gyrus has also been shown to correlate with hand preferences for bimanual tasks in capuchin monkeys (Phillips and Sherwood, 2005) and the hand representation in the motor cortex in squirrel monkeys is generally larger in the dominant hemisphere (i.e. opposite the preferred hand) than the non-dominant side (Nudo et al, 1992).

There is also considerable evidence showing, in apes, structural asymmetries of the inferior frontal gyrus and planum temporale region, cortical areas homologous to Broca's area (Brodmann's area 44) and Wernicke's area (posterior area 22) of the human cortex (i.e. to the cortical regions for speech and language, Hopkins et al., 1998; Hopkins and Pilcher, 2001; Cantalupo and Hopkins, 2001). Recently, Hopkins

et al. (2007) found that asymmetries the fronto-orbital sulcus and planum temporale correlated with hand preference for tool using by chimpanzees. Such a relationship has important bearing on the question of evolution of cerebral asymmetry, language and hand preference, and is evidence against the claim made by some (e.g. Crow, 2004, 2005) that all of these are related and unique features of the human brain. In addition to these localised asymmetries in the motor cortex and language areas, corpus callosal size in several regions has been shown to be smaller in left-handed than right-handed chimpanzees (Dunham and Hopkins, 2006), suggesting that asymmetries maybe more widespread.

In summary, most studies on handedness in non-human primates to date have focused on chimpanzees and have investigated motor regions or cortical areas that may be pre-adaptations to language ability. Hence, we decided to compare left- and right-handed marmosets to investigate whether structural differences in the hemispheres were present and whether any such differences might be correlated with hand preference. If such an association were found, we reasoned, it might shed light on the evolutionary shift from left- to right-hand preference in primates. Our initial finding of a correlation between the length of the right lateral sulcus and hand preference, led to an investigation of cortical thickness in the surrounding somatosensory and motor areas.

Methods

Sample

The common marmosets (*Callithrix jacchus*) were raised and housed at the University of New England. They were housed as 2 to 4 individuals per cage and allowed free

movement between home cages (2.3m x 1m x 2m in height), indoor exercise rooms (22.6 m²) and outdoor cages (7.2 m²) via runways for details see Pines et al., 2007).

The home cages were maintained at 25 °C and relative humidity 54 % and with a 12:12 h light-dark cycle. All cages were furnished with play material, including branches, cane hoops, calico strips, tubes, tyres, and trays of straw. The marmosets were fed once daily on a variety of foods, including fruits, vegetables, egg, yoghurt, nuts and specially prepared health cake with vitamin and calcium supplement (see Kaplan and Rogers, 1999, for details).

The marmosets were never subjected to invasive procedures. They were euthanased only if they were suffering from kidney failure in the final stages of old age or, in three cases, following a serious accidental injury (Table 1). One marmoset died suddenly of an unknown cause.

Fourteen animals that died between 2000-2006 were considered for inclusion in this study. The brains were removed and immersion fixed in 10% formalin immediately after euthanasia, or within 2 hours following death in the case of the marmoset that died of an unknown cause. Gross examination of the brain led to the exclusion of 3 animals; one had obvious right-left asymmetry of the cerebral hemispheres, one had a small raised lesion on the surface of the parietal lobe, and one showed extreme malformation of the right temporal lobe. The remaining 11 brains from marmosets (4M:7F) aged 4-14 years have been included in the study (Table 1). One animal was excluded from the histological analysis due to poor tissue fixation.

Hand preferences

The hand preferences of all of the marmosets were determined at intervals of 10-12 months throughout their lifespan. The preferences were determined during normal feeding in the home-cage, using the method described in (Hook-Costigan and Rogers, 1995; Hook and Rogers, 2000). Hand use was scored when the subject used one hand to hold a piece of food and take it to the mouth. No more than 15 scores were recorded per day, and bouts of repeated use of the same hand were avoided by not allocating separate scores when the same piece of food was taken repeatedly to the mouth without the subject changing hands or the food being dropped and picked up. At each age a minimum of 100 unimanual holding scores were collected for each subject over a minimum of 8 days. From these scores the % right-hand use was determined as a mean across the life span. The standard error of the mean for each animal across all ages was also calculated to show the variation across age.

Brain preparation

Following fixation in 10% buffered formalin, the cerebrum and dura were removed and the brain was photographed in the superior, inferior, right and left lateral views using a Nikon digital camera. Brains were then cryoprotected in a solution of 30% sucrose until the brain had sunk. The frontal cortex was removed anterior to the temporal poles and the mid region of the brain was frozen and sectioned in the coronal plane at a thickness of 50 μ m. Every 10th section was collected in phosphate buffer and mounted on 2% gelatinised slides for cresyl violet staining.

Brain surface measurements

Surface measurements were made from photographs, prior to cryoprotecting. Measurements of the anterior posterior (AP) length of the brain and left and right lateral sulcus length were made using the digital images and 'Image J' image analysis

software (Rasband, 1997). The sulcal length was defined as the distance from the most anterior visible point on the sulcus to the posterior most point of the sulcus, from the lateral view (dotted line on Figure 1b).

Cortical thickness

For each brain, a coronal section 4 mm anterior to the external auditory meatus (Atlas reference A4, Stephan, 1980) was used as the reference section (section 0) for all cortical measurements. This level corresponds closely to the posterior end of the lateral sulcus. Cortical thickness was measured on the left and right side at the following anteroposterior levels, shown in Figure 1a: -3mm, -1mm -0.5mm, 0mm, 0.5mm, 1mm, 2 mm, 4mm relative to the reference section. In all these coronal sections, the cortical thickness was measured perpendicular to the cortical surface at 4mm from the superior midline. These measurements were chosen to correspond to parietal cortex (-3mm), SI area 2 (-1mm), SI area 1 (-0.5mm), S1 area 3b (0– 1mm), S1 area 3a (2mm) and motor cortex area 4 (4mm), as described by Krubitzer and Kaas, (1990), Huffman and Krubitzer, (2001) and Qi et al., (2002) and represented diagrammatically in Figure 1b. In the case of 3b and motor cortex, the areas could also be identified cytoarchitecturally.

For regions surrounding the lateral sulcus, cortical measurements were taken in all sections from -0.5 to 2mm (Figure 2). As there are few distinguishing features in the cortex, a line 2mm from the sulcal lip and perpendicular to the surface (i.e. within PV or SII) was chosen for the cortical measurements (a) and (e). These lines were then used as landmarks for measurements (b) and (d) which extended diagonally from the white matter border of (a) and (e) to the upper and lower lip of the lateral sulcus respectively. Line (c), chosen to lie within area VS, was taken from the deepest part of

the sulcus to the cortical white matter boundary. For sites a and b these were determined to lie behind SII (-0.5mm), in SII (0, 0.5, 1mm) and in the parietal ventral somatosensory area (PV) (2mm), by comparison with the functional map of Krubitzer and Kaas, 1990; Huffman and Krubitzer, 2001; Qi et al., 2002. Site c is probably the ventral somatosensory area (VS) noted by Qi et al., (2002). Sites d and e lie on the superior temporal lobe in auditory cortex according to the functional maps of Aitkin et al, (1986). Lateral sulcus sites were not measured for levels -3 and -1mm as these were too far behind the sulcus for the sulcus to be identified. Sites c, d and e were not included in the most anterior sections (4mm) due to changes in the cortical folding preventing measurement.

Corpus callosum

For each brain, measurements were also taken at the midline of the corpus callosum in six sections (-2 to 2mm). The mean thickness of the corpus callosum in these six coronal sections was used for correlation with hand preference.

Statistics

Simple linear regression was used to identify correlations between hand preference and lateral sulcal length, and cortical thickness measurements. Paired t-tests were used to compare left-right differences and ANCOVA was used to establish the effect of sex and age on these correlations.

Results

Hand preferences

As hand preference remains stable after 5-8 months of age (Hook and Rogers, 2000) an overall mean % right-hand preference was determined for each marmoset as a mean of scores ($R/L+R$, where L and R is the number of left and right hand scores respectively) obtained from an age of one year until death. The % right-hand preference is shown in Table 1 along with the standard error of the mean demonstrating the small within subject variability over age. The large range in individual right-hand preference (11.3% - 92.3%) clearly shows across subject variability and allows correlations to be investigated. These overall means were very close to the measure of hand preference obtained nearest to the time of death ($r=0.958$, $p=0.000$, 2-tailed).

Brains

The brains from 11 marmosets were included in this study (Table 1). The mean brain weight was 8.3 ± 0.46 g (mean $\pm$ SD). Brain weights ranged from 8-9g for the 10 adult (6-14yrs) animals while the brain from the youngest animal (4yrs) weighed slightly less (7.2g). The AP length ranged from 3.2cm to 3.5cm (mean 3.3 ± 0.81 cm). There were no statistical differences in brain weight or AP length due to sex or age.

Lateral Sulcus length

There was a strong and significant positive correlation between the right lateral sulcus length/brain weight and the % right-hand preference (linear regression analysis, $N=11$, $r=0.859$, $p=0.001$; Figure 3a). ANCOVA analysis of these scores using sex as a fixed factor and % right-hand preference as a co-variate revealed a significant effect of hand preference ($F(1,8)=19.339$, $p=0.002$) but no significant effect of sex ($F(1,8)=0.595$, $p=0.463$).

No association was found between the left lateral sulcus length/brain weight and the % right-hand preference (linear regression, $N=10$, $r=0.007$, $p=0.984$; Figure 3b). An ANCOVA analysis of these data for left SF over brain weight (as above) revealed no effect of sex ($F(1,7)=2.073$, $p=0.193$) and no effect of hand preference ($F(1,7)=0.226$, $p=0.648$).

Age did not correlate significantly with the scores for right lateral sulcus /brain weight ($r=-0.372$, $p=0.260$) or for left lateral sulcus/brain weight ($r=-0.266$, $p=0.580$).

Cortical thickness

All measurements were made by one person (PW) blind as to hand preference. A series of measurements were repeated by a second scorer (CG) and by PW at a later time point to test for inter-rater and intra-rater reliability. The test-retest correlations for cortical thickness between raters was $r = 0.91$, $df\ 17$, $p < 0.001$ and for the repeat rater $r = 0.80$, $df\ 16$, $p < 0.001$, indicating good reliability. One case (#3) was excluded from the histological analysis due to poor tissue fixation. The cortical thickness for different anterior-posterior levels and cortical locations are shown in Figure 4. There were no significant differences between left and right cortices using paired t-tests.

Cortical thickness of the lateral sulcus at sites (a) and (b) in the right hemisphere at levels 0-1mm was correlated positively with % right-hand preference (a, $n = 10$, $r = 0.692$, $p = 0.025$; b, $r = 0.663$, $p = 0.035$ (Figure 5a,b). There was also a positive correlation between cortical thickness and % right-hand preference at level 0-1mm in

region a ($n = 10$, $r = 0.629$, $p = 0.052$), but not region b ($r = 0.46$, $P = 0.18$) in the left hemisphere (Figure 5c, d). There were no significant correlations with hand preference for cortical regions c, d and e at any level. In addition, there was no correlation between cortical thickness and % right-hand preference at the lateral sulcus at AP levels -0.5mm or 2mm, nor at 4 mm from the midline at any level from -3mm to 4mm. The strength of hand preference, calculated as the divergence from 50% right handed, showed no associations with cortical thickness.

Corpus callosum

There was no correlation between hand preference and the mean thickness of the body of the corpus callosum (-2 to 2mm) ($r = 0.03$, $p = 0.94$).

Discussion

The main findings of this study were significant positive correlations between the percent of right-hand preference and (1) the length of the lateral sulcus in the right hemisphere, adjusted for brain weight, and (2) the thickness of the right cortex on the superior lip of the lateral sulcus, at its posterior end. The right lateral sulcus is longer, and the superior lip thicker posteriorly, with increasing percent right hand use.

No such relationship was found for the length of the lateral sulcus in the left hemisphere. There was a positive correlation between cortical thickness and percentage right-hand preference for area (a) only in the left hemisphere but the p-value for this was 0.052. Sex or age had no influence on these data.

The measure of hand preference that we have used in these calculations was determined for picking up food and taking it to the mouth to feed, referred to as simple reaching. As this measure is stable across the common marmoset's adult life (Hook and Rogers, 2000; also note small standard error score of hand preferences in Table 1), it represents a consistent functional difference between the hemispheres. Hook and Rogers (2007) tested marmosets of the same colony on four different reaching tasks in addition to simple reaching and found that each individual displayed the same hand preference across tasks, apart from some variation when the marmoset had to reach into a bowl through a hole in a transparent lid to obtain food. On this later task, half of the marmosets switched the hand used to reach for food. Although research on other primate species has noted that the strength and sometimes direction of hand preference may vary with the complexity of the task (Fagot et al., 1991; Hopkins and Cantalupo, 2004), common marmosets show remarkably stable hand preferences across tasks and age. All of the tasks used by Hook and Rogers (2008) required visuospatial reaching to various degrees (e.g. reaching for a piece of food hanging on a string, on which task hand preference was the same as simple reaching) and we note that SII has connections with visuomotor fields in frontal cortex and so might form part of a circuit involved in such reaching behaviour (Krubitzer and Kaas, 1990).

A large study on lateral sulcal asymmetries in apes, Old World and New World monkeys found a population difference in New World monkeys, lateral sulcus being longer on the left side (Hopkins et al 2000). The sample did not include marmosets, but would be consistent with a population effect found for marmosets and three other species by Heilbroner and Holloway (1998), measured with a tape directly from the

brain surface. However, the method of measuring was important; for *M mulata* measurements made from photographs of the cortical surface were not significantly different on the two sides despite measurements directly from the brain showing an asymmetry. The lower sensitivity with photographic measurements may explain the lack of any lateral sulcus asymmetry in the present sample, in which measurements were also taken from scanned images. Despite this, we found a strong correlation here between right sulcal length relative to brain weight and right-hand preference. Longer sulcal lengths on the left have generally been shown to relate to differences in the posterior temporal lobe, the left side having a larger planum temporale in the primates studied previously (reviewed Toga and Thompson, 2003). This area corresponds to Wernicke's area (Brodmann's area 22) in humans, associated with left hemisphere dominance for language.

The surprising finding here was that it was the superior lip of the sulcus, not the anticipated inferior lip of the posterior temporal lobe, which was thicker in right-handed animals. The association between cortical thickness and hand preference was significant for the right cortex. The area showing this association was relatively localised, extending from the posterior end of the sulcus approximately 1mm in the anteroposterior plane (sections at 0- 1mm), and approximately 2mm superiorly from the sulcal lip. This area corresponds closely to SII as depicted in electrophysiologically determined maps (eg Krubitzer and Kaas, 1990; Huffman and Krubitzer, 2001; Qi et al., 2002). For the left cortex there was a suggestion of a similar effect for area (a) and this deserves further investigation with more subjects. No association was found for the fundus of the sulcus, comprising the ventral somatosensory area, or for the inferior lip, likely to be auditory cortex (Aitkin et al,

1986; Qi et al, 2002). Similarly no association with hand preference was found for areas anterior to this region, in the parietal ventral somatosensory area, or posteriorly into what may be Brodmann's area 1. Finally there was no correlation found in the areas likely to be 3b, area 1/2, or motor cortex, indicating a highly localised association restricted to SII. Since the marmoset motor cortex has no identifiable knob area, corresponding to the hand, seen in chimpanzees and humans, cortical thickness was measured in the presumptive hand area, based on distance from the midline (Burman et al, 2008). We found no association between size of this region and hand preference. This may reflect the task used to assess handedness since, even in chimpanzees, no association has been found between the size of this presumptive motor region and hand preference in simple reaching tasks (Hopkins and Cantalupo, 2004).

Of importance to this study is the fact that there are very few anatomical landmarks in the marmoset cortex to positively identify cortical regions. Cortical regions can vary between animals and may not always be determined by sulcal features. We have relied on maps and diagrams published by others to aid in distinguishing between brain regions, but it must be noted that for some regions, especially area 1/2 of the somatosensory cortex, there has not been any extensive electrophysiological mapping undertaken. It would obviously be of interest to confirm our findings using functional mapping to identify the areas.

Results on somatosensory asymmetries and handedness in humans are conflicting. While there have been no reports, to our knowledge, on asymmetries in SII, SI has been reported to be larger on the left in some studies (Sörös et al, 1999; Jung et al,

2003) but not others (White et al., 1997; Zhu et al 2007). Perceptual thresholds have been shown to be lower on the left in right-handed subjects (Meador et al. 1998).

Sörös et al (1999) found the size of SI to be correlated in right-, but not left-, handed subjects, whereas Jung et al (2003) found no correlation with handedness.

Somatosensory asymmetries have not been reported in non-human primates.

For the marmosets studied here, what might explain an association between the thickness of SII and right-hand preference? Neurons in SII respond to cutaneous stimulation from the body surface with topographic organization. Cells are activated by light touch of the skin and movement of hairs, with relatively large receptive fields compared to the neurons of the primary somatosensory area 3b, for example (Krubitzer and Kaas, 1990). The receptive fields of SII neurones commonly involve several digits and the palm, rather than a single finger. While cells in SII typically have contralateral receptive fields, bilateral responses have been reported in macaque monkeys (Whitsel et al, 1969; Kaas, 2004). fMRI results indicate that in humans the SII/PV region also receives inputs from both hands and activation increases with bilateral stimulation (Disbrow et al, 2001). The SII area has been implicated in tactile attention and texture and roughness discrimination (Burton et al, 1999; Pruett et al, 2000; Kaas, 2004) and lesions of the SII/PV region in rhesus monkeys result in impaired ability to make tactile discriminations and identifications (Murray & Mishkin, 1984). SII is likely involved in both parallel and serial processing of tactile information. Thus SII receives direct sensory inputs from the thalamus. Parallel processing of information through both SI and SII has also been described (Zhang et al., 1996, 2001). In addition SII receives inputs from several cortical areas including 3a, 3b and area 1, and SII projections include PV, perirhinal cortex and frontal eye fields

(Friedman et al, 1986; Krubitzer and Kaas, 1990; Kaas, 2004). SII has therefore also been considered part of a hierarchical circuit for tactile processing which progresses from anterior parietal cortex (SI), through lateral parietal (SII and PV) to perirhinal cortex and then hippocampus and which is involved in discrimination, recognition and memory of objects (Kaas, 2004). A recent study by Burish et al (2008), in marmosets, has shown that stimulation of SII can occasionally lead to body movements, especially from the face, again indicating its complex circuitry.

A possible basis for a correlation between SII thickness and percent right-hand preference is consistent with the fact that right-handed marmosets are more proactive than left-handed marmosets in exploring new environments and novel objects (Cameron & Rogers, 1999; Rogers, 2007). Such exploration includes more touching of objects (Cameron and Rogers, 1999) and this would increase activity in areas like SII. Hence SII's morphological development might be secondary to the expressed behaviour of left-hemisphere dominant (and right-handed) animals or its development may lead right-handers to engage in more explorative behaviour.

Since SII has strong callosal connections to contralateral SII and PV, we hypothesised that the increased size of SII in right-hand preferring marmosets might also show as a correlation between callosal size and handedness. No such correlation was found and it is likely that the very localised cortical changes found here are insufficient to significantly modify callosal connections. However, it should be noted that our plane of section (coronal) was not optimal for measuring callosal areas, and this would be worth reassessing in the parasagittal plane.

To our knowledge this is the first study to report an association between cortical thickness in the somatosensory area and hand preference in a non-human primate. Enlargement of a cortical area involved in tactile discrimination could be a precursor to the evolution of right-handedness as a population bias. The increasing manipulation of objects with increasing right-handedness that took place during the evolution of primates, as highlighted by McNeilage et al. (1987), may have a parallel within a species; viz., increasing somatosensory processing with increasing right-hand preference.

It is puzzling why the effect would be more marked in the right cortex and it would be interesting to know whether a larger SII area is present from birth and leads to more manual exploration or whether such behaviour has caused the morphological development and plasticity in SII. It would also be worth testing whether right-handed animals have superior manipulative and tactile discriminative skills, as might be indicated by the enlarged SII areas.

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Figure legend

Figure 1: a) Superior view of a common marmoset brain showing the antero-posterior levels where cortical thickness was measured. The dotted line shows where the cortical measurements were made 4mm lateral on each side. b) Lateral view of a common marmoset brain showing the locations of motor area (M), primary somatosensory areas (3a, b, 1, 2), secondary somatosensory area (SII) and the parietal ventral area (PV) in cortex adjacent to the lateral sulcus (LS), as described by Krubitzer and Kaas, 1990, Huffman and Krubitzer, 2001 and Qi et al., 2002. Bar = 2mm

Figure 2: Diagrammatic representation of part of the parietal lobe in coronal section showing the location of the cortical areas a-e measured adjacent to the lateral sulcus (LS). The thicker dotted line shows where the cortical measurements were made 4mm lateral from the midline (M). Bar = 1mm

Figure 3: Linear regressions showing a) the correlation of right lateral sulcus length divided by brain weight with % right-hand preference, b) No correlation is seen for the left lateral sulcus length.

Figure 4: Graph showing the cortical thickness (mm) and SEM at different anterior-posterior levels and cortical locations for the left and right cortex for all marmosets regardless of hand preference. Cortical thickness at 4mm from the midline are shown for each of the anteroposterior levels from anterior 4mm to posterior -3mm at the left of the graph. Cortical thickness for each of the five locations around the lateral sulcus (a-e), are shown for each anteroposterior level on the right of the graph. The anterior

most sections did not have uniform cortex for measurements at c-e, and the posterior most measurements (-1mm & -3mm) are behind the lateral sulcus therefore a-e are not present. This graph shows the consistency of cortical thickness at 4 mm from the midline, the symmetry of left and right cortices and the pattern of cortical thickness around the lateral sulcus with diagonal measurements being consistently longer. The correlations found with hand preference are not apparent in this graph, as data from all animals have been averaged.

Figure 5: Linear regressions showing the correlations of cortical thickness with % right-hand preference in the right hemisphere for a) the upper surface of the lateral sulcus (cortical thickness at location a, 0-1mm) and b) the upper lip of the lateral sulcus (location b, 0-1mm). The correlations of cortical thickness with % right-hand preference in the left hemisphere are shown for c) the upper surface of the lateral sulcus (location a, 0-1mm) and d) the upper lip of the lateral sulcus (location b, 0-1mm).

Table 1

Case Number	Sex	Age (y)	Brain weight (g)	% Right hand use	Reason for euthanasia
1	F	4	7.2	81.5 (7.5)	Unknown
2	F	6	9.0	80.4 (1.3)	Accident
3*	M	7	8.1	92.3 (1.4)	Renal failure
4	F	8	8.2	23.8 (5.1)	Renal failure
5	M	8	8.4	11.3 (1.8)	Renal failure
6	M	10	8.2	71.4 (5.6)	Renal failure
7	F	10	8.3	38.6 (5.7)	Renal failure
8	M	11	8.3	92.2 (1.7)	Renal failure
9	F	12	8.9	12.9 (1.9)	Renal failure
10	F	13	8.1	77.8 (2.5)	Renal failure
11	F	14	8.3	50.1 (4.8)	Accident

General characteristics of the 11 marmosets included in this study. The numbers in brackets are the standard errors of the mean for % right-hand use calculated across age. Note that they are quite small and show that the hand preference of an individual is consistent across age. *This case was excluded from the histological analysis due to poor fixation of tissue.

Figure 2

Figure 1a

Figure 1b

Figure 3

a

b

Figure 4

Figure 5