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## **Refining the Ecological brain: strong relation between the ventromedial prefrontal cortex and feeding ecology in five primate species**

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## Abstract

To survive in complex and seasonal environments, primates are thought to rely upon cognitive capacities such as decision-making and episodic memory, which enable them to plan their daily foraging path. According to the Ecological Brain hypothesis, feeding ecology has driven the expansion of the brain to support the corresponding development of cognitive skills. Recent works in cognitive neurosciences indicate that cognitive operations such as decision-making or subjective evaluation (which are contextual and dependent upon episodic memory), relied critically upon a small part of the frontal lobe, often referred to as the ventromedial prefrontal cortex (VMPFC). Several authors suggested that this area might be important for foraging, but this has never been tested. In the present study, we quantified the relation between the size of the VMPFC (along with other cerebral measures: the whole brain, the gyrus rectus and the somatosensory cortex) and key socio-ecological variables in five primate species (*Macaca mulatta*, *Macaca fuscata*, *Gorilla gorilla*, *Pan troglodytes* and *Homo sapiens*). We hypothesized that the size of the VMPFC would be greater in primates with a large dietary spectrum and complex foraging strategies. We also hypothesized that the impact of feeding ecology would be stronger on this specific region than on other regions (somatosensory cortex) or on more global cerebral measures (e.g. whole brain). In line with these hypotheses, we found that all cerebral measures were more strongly related to feeding ecology than group size, a proxy for social complexity. As expected, the VMPFC volume is more precisely related to feeding ecology than the whole brain, and appears to be critically related to dietary quality. Thus, combining a comparative approach with predictions coming both from behavioral ecology and cognitive neurosciences, our study provides convincing evidence that feeding ecology played a key role in the development of specific cognitive skills, which rely upon the expansion of a specific cortical area.

**Keywords:** decision-making; ventromedial prefrontal cortex; diet diversity; foraging strategies; primates

## 1. INTRODUCTION

Optimization of the ratio between resources-associated costs and benefits is a key selective pressure underlying natural selection in animals (Altmann, 2006; MacArthur & Pianka, 1966). Among primates, foraging behaviors have been described by some authors as a combination of more or less random exploration and reactions to environmental stimuli encountered along the way, such as visual or olfactory cues (Berridge, 2004; Kolling et al., 2012). However, most primates live in complex and patchy environments where preferred resources are not distributed uniformly in space and time, and/or may not be easily accessible through direct sensory cues (embedded foods). Because of the spatial distribution and seasonality of food in the environment, and given the high energy requirements of primates, other studies have pointed out that primates could not rely upon mere luck to find their energetic resources. Indeed, their trajectories suggest that they use mental representation of how food resources are distributed in space and time to plan their daily foraging path (Janmaat et al., 2006a, 2006b, 2016; Noser & Byrne, 2007). Thus, their foraging strategies rather imply mental representations of what, where and when a specific resource would be available as well as the course of action necessary to obtain it (Trapanese et al., 2018, van Schaik, 2016). Foraging behaviors in primates therefore seem to imply complex cognitive abilities such as value-based decision-making, episodic memory (which refers to the recollection of specific events that happened at a specific location and at a particular time) and planning (i.e. imagining future events and preparing actions accordingly). Based on this view, it has been suggested that these foraging-associated capacities were favored during the course of primate cognitive evolution (Cunningham & Janson, 2007; Hayden et al., 2011; Rosati, 2017; Zuberbühler & Janmaat, 2010).

This idea resonates with what is often referred to as the Ecological Brain hypothesis, according to which environmental parameters associated with foraging strategies and food resources have favored the evolution of cognitive complexity and brain size among primates (Milton, 1981, 1988). A recent study by De Casien et al. (2017) has actually provided a strong support for this hypothesis. The Ecological Brain hypothesis is sometimes perceived as conflicting with the Social Brain hypothesis, according to which cognitive abilities and the associated brain size were driven by an increase in social complexity (Dunbar, 1998). But strictly, these theories are not mutually exclusive, and they both rely upon the same idea that global cognitive abilities are associated with a global neuroanatomical measure (the whole brain size, the neocortex size or the encephalization quotient). Indeed, both sociality and ecology could have contributed to the modulation of cognition and brain size across species (De Casien et al., 2017; Dunbar, 1992; Foley & Lee, 1991; Sol et al., 2008; van Schaik et al., 2012). However, the idea that global brain size represents a good proxy for global cognitive skills lacks experimental support and is not confirmed when tested within a broad

comparative context (e.g. birds vs. primates, Güntürkün & Bugnyar, 2016). More critically, social interactions (e.g. number of individuals an animal can remember, number of third-party relationships, dominance ranks) and ecological knowledge (e.g. recognition of food types, food selection, knowledge of food processing and harvesting schedules, estimation of amounts) rely upon distinct brain systems, even though decision-making in both social and food dimensions could involve overlapping brain regions (Eichenbaum & Cohen, 2014; Lin et al., 2015; Peters & Büchel, 2010; Ruff & Fehr, 2014; Stanley & Adolphs, 2013). Thus, a major challenge for understanding primate cognition would rather be the identification of specific cognitive abilities, associated with their underlying neurobiological substrate, which both underlie adaptation to specific ecological or social challenges. In that frame, since the relative size of distinct brain regions varies across species (Barton & Harvey, 2000; Passingham & Wise, 2012), size differences of specific cortical areas could better capture the adaptations of cognitive capacities that occurred in response to particular ecological conditions. As such, a few studies focused on specific brain regions, such as the hippocampus or the olfactory cortex and their volumetric variations as a function of ecological variables across primates (Barks et al., 2015; Barton & Harvey, 2000).

Here, we propose an innovative and holistic approach to assess how socio-ecological parameters can explain variations of brain measurements among five primate species (*Macaca mulatta*, *Macaca fuscata*, *Gorilla gorilla*, *Pan troglodytes* and *Homo sapiens*), when taking into account the phylogeny. We measured the whole brain volume to facilitate comparison with existing comparative studies, since most of them only used this measure. Additionally, we measured the primary somatosensory cortex (S1 cortex) as a control region, since it is located outside of the frontal lobe and is not supposed to be involved in any kind of executive function. We considered two regions of interest, referred to as the gyrus rectus and the ventromedial prefrontal cortex (VMPFC). The gyrus rectus is an easily identifiable brain region located on the ventromedial part of the prefrontal cortex, and it has largely been associated with value-encoding and decision-making behaviors among human and non-human primates (Bechara et al., 1998; Jocham et al., 2014; Noonan et al., 2017; Rushworth et al., 2012). In addition, based on recent functional imaging and electrophysiological studies in humans and monkeys, we considered a more specific region, the VMPFC, located on the ventral part of the gyrus rectus. Indeed, this region is reliably associated with valuation of items and outcomes based on contextual information and memory, and with subsequent decision-making behaviors (Barron et al., 2013; Bouret & Richmond, 2010; Clark et al., 2013; Lebreton et al., 2009, 2013; Papageorgiou et al., 2017; Peters & Büchel, 2010; Rushworth & Behrens, 2008; Rushworth et al., 2011; San-Galli et al., 2016; Strait et al., 2014). We thus hypothesized that the VMPFC should be a better proxy than the whole brain volume to explore the relationship between specific cognitive capacities and ecology. We also made the hypothesis that

the brain, the gyrus rectus and the VMPFC volumes would be larger among species with complex diets and dietary strategies than among species with simpler ones. More precisely, we hypothesized that the volume variation of the VMPFC would be more strongly related to foraging than other brain regions.

## 2. MATERIAL & METHODS

### 2.1. Sample

A total of 29 brain magnetic resonance (MRI) 3D reconstructions of five primate species were used in this study: *Macaca mulatta* (n=6), *Macaca fuscata* (n=6), *Gorilla gorilla* (n=5), *Pan troglodytes* (n=7) and *Homo sapiens* (n=5). Due to important damages, measurements of the brain and the ratio VMPFC/brain were missing for one gorilla, as it was the case for the volume of the somatosensory cortex of one rhesus macaque.

Japanese macaques and rhesus macaques were captive animals housed and scanned, respectively, at National Institutes for Quantum and Radiological Science and Technology (Chiba, Japan) and at Brain and Spine Institute (Paris, France). *Pan troglodytes* and *Gorilla gorilla* brains came from the Muséum national d'Histoire naturelle (Paris, France). They had been collected between 1920 and 1970 and subsequently preserved in formalin solution. We selected a sample of seven chimpanzee brains and five gorilla brains, based on the integrity of the regions of interest, located in the ventral part of the gyrus rectus (see below for details). The great apes brains were scanned at the University of Leuven (KUL). Brains for which the gyrus rectus was bilaterally damaged or distorted were excluded from the analysis. *Post-mortem* or *in-vivo* brain images of five modern humans were obtained from the open website [http://human.brain-map.org/mri\\_viewers/data](http://human.brain-map.org/mri_viewers/data) and from the open-access LPBA40 MRI dataset (Shattuck et al., 2008).

All specimens were sexually mature at the time of scanning. Although some non-human primates were captive specimens, we will ignore the potential effects of captivity on the brain measurements, assuming that they are negligible compared to the inter-species differences (according to Isler et al., 2008: endocranial volumes do not differ between captive and wild animals). We also tried to maintain a balanced sex ratio for each of the 5 species (M:F ratios: *Macaca mulatta* 3:3; *Macaca fuscata* 2:4; *Gorilla gorilla* 2:3; *Pan troglodytes* 3:4; *Homo sapiens* 2:2 and one subject of unknown sex).

### 2.2. Processing of brain MRI and measurements

Avizo v9.0 software was used for visualization, segmentation and quantification of brain tissues. We measured 3 regions of interest: the whole brain (without cerebellum), the gyrus rectus and the ventromedial prefrontal cortex (VMPFC). Additionally, we measured the volume of the primary somatosensory cortex (S1 cortex) as a control region. We anatomically defined these regions of interest and the corresponding landmarks on the basis of cytoarchitectonic maps (Carmichael & Price, 1994; Mackey & Petrides, 2010; Öngür et al., 2003), and on brain atlases of rhesus macaques and humans (Dubach & Bowden, 2009; Paxinos et al., 2008; Rohlfing et al., 2012; Sunkin et al., 2013).

Whole brain segmentation was firstly performed using the semi-automated tool which allows to select a single material or structure according to a specific gray level threshold. Manual corrections were made whenever necessary, for instance when the brain and the adjacent tissue had a similar gray level. As the cerebellum was missing for two gorilla brains, the cerebellum was systematically excluded of the whole brain measure in all specimens.

We also measured the volume of gray matter in the gyrus rectus. Indeed, the gyrus rectus is an easily identified brain region that includes the area of interest (the ventromedial prefrontal cortex). It thus provides an intermediate level of anatomical precision (here, the ventral prefrontal cortex) between the area of interest (VMPFC, identified on the basis of its functional role) and the whole brain. The gyrus rectus is more functionally heterogeneous than the VMPFC because it contains subcallosal areas, which are more related to autonomic responses (Freedman et al., 2000; Joyce & Barbas, 2018; Neubert et al., 2015), as well as a part of the frontal pole associated with higher cognitive abilities such as complex planning of future actions or managing competing goals (Mansouri et al., 2017; Semendeferi et al., 2001). Reliable inter-species boundaries of the gyrus rectus were defined according to the same brain atlases used for the delimitation of the VMPFC (**Fig. 1**). The anterior border of rostral and medial orbital gyri represents the anterior limit. Caudal limit is set at the most anterior part of the head of the caudate nucleus. Lateral and medial boundaries include the fundi of the rostral and medial orbital sulci.

[Insert Figure 1]

Based on the functional anatomy literature in humans and macaques, we defined the VMPFC as a region of interest critically involved in value-based decision-making and episodic memory (see introduction for complete references). In short, this region corresponds to the ventral part of the gyrus rectus and strongly overlaps with Brodmann area 14r, but we make no claim about the relation between our definition of the VMPFC and specific regions identified based on



cytoarchitectonic or connectivity maps. Indeed, we defined the VMPFC using two criteria: the region should closely match the results of functional studies and should be reliably identifiable using macroscopic anatomical landmarks. The anterior limit of the VMPFC was defined as the most anterior part of the cingular/paracingular cortex. The posterior limit was the genu of the corpus callosum. Superior/medial border was defined as the rostral sulcus, just before the folding of the cortex – *i.e.* the fundus of the rostral sulcus was not included in the region of interest (**Fig. 1**). In humans, we chose the superior rostral sulcus as the medial marker because it is present in all individuals whereas, as noted by Mackey and Petrides (2010), the inferior rostral sulcus only appears in 70% of their samples. Lateral border was defined as the medial orbital sulcus. As for the medial border, the fundus of the medial orbital sulcus was not included in the VMPFC. The application of these generic boundaries to segment the gyrus rectus and the VMPFC of individual specimens is shown on **Fig. 2**.

[Insert Figure 2]

In order to confirm the specificity of the structure-function relation between the VMPFC and socio-ecological variables, we examined another cortical region, the somatosensory cortex (S1 cortex) as a control region. The S1 cortex is located in the parietal lobe and it receives sensory inputs from several modalities (touch, proprioception, nociception and temperature; Kaas, 2004). It is a priori not involved in executive functions. We thus hypothesized that this control region would not be associated with the planning of foraging strategies and thus it should not be related to the same socio-ecological variables as the VMPFC. We used reliable inter-species boundaries to delimitate the S1 cortex among our primate sample (**Fig. 3**). Both in human and non-human primates, S1 is located on the postcentral gyrus which is immediately caudal to the central sulcus. Similarly to the gyrus rectus and the VMPFC, we thus measured the volume of gray matter of the post-central gyrus. The anterior limit of the S1 cortex corresponds to the central sulcus, and the inferior one to the inferior limit of the central sulcus. The fundus of the central sulcus is included in the S1 cortex. In humans and great apes, the posterior limit of S1 is the post-central sulcus. However in macaques, it is slightly observable on the dorsolateral surface between intraparietal and central sulci – in the continuity of the ascending branch of the intraparietal sulcus (Seelke et al., 2011). We thus set the posterior border of the S1 cortex in macaques immediately rostral to the superior parietal lobule, at the end of the cortical convexity formed by the slightly observable post-central sulcus. The fundus of the post-central sulcus is included in the S1 cortex.

229 **2.3. Ecological and phylogenetic data**

230 Among primates and mammals generally, brain size and life history have undergone correlated  
231 evolution (e.g. Barton, 1999; Isler & van Schaik, 2009; Ross, 2003; Schuppli et al., 2016b). It has  
232 also been shown that energetics, and especially basal metabolic rate (BMR), is positively correlated  
233 with brain size in primates, after controlling for the influence of body mass and for the potential  
234 effects of phylogenetic relatedness. We therefore compiled sixteen ecological and life-history  
235 parameters from published literature sources (**Table S1**). We included data related to body  
236 condition (body mass, crown-rump length, Quetelet index), energetics (basal metabolic rate, daily  
237 energy expenditure), diet (diet category, dietary quality), reproduction and life history traits (mating  
238 system, seasonal mating, gestation length, interbirth interval, birth mass, weaning age). We also  
239 included home range, daily traveled distance and group size. Because there is no strict consensus on  
240 the group size value within *H. sapiens*, we considered in our analyses the mean group size of two  
241 reliable measurements in this species (Hill & Dunbar, 2003: mean social network in contemporary  
242 societies, i.e. 124.9 individuals; Marlowe, 2005: mean group size of 48.2 individuals in foragers).  
243 Regarding energetic parameters, basal metabolic rate is measured at rest and thus is the lowest rate  
244 of energy expenditure (Pontzer, 2015). The daily energy expenditure refers to the energy expended  
245 by day and reflects body mass and activity level, as well as other species-specific parameters such  
246 as growth, reproduction and thermoregulation. Mating systems are species-specific patterns of  
247 coupling associations between males and females (Wolfe, 2015). Dietary quality index has been  
248 proposed to characterize the richness of the dietary spectrum, both in terms of diversity and  
249 energetics (Sailer et al., 1985). Low dietary quality values (about 100) characterize folivorous  
250 primates, whereas higher values represent a more diversified diet including fruits and/or animals.  
251 We used this variable because it is more precise than diet categories, which only refers to as  
252 folivory, frugivory/folivory, frugivory and omnivory.

253 All Japanese macaques in our sample were *M. f. fuscata* which is the mainland subspecies of *M.*  
254 *fuscata*. Concerning gorillas, we only included data coming from western lowland gorillas. We  
255 combined average data for subspecies of common chimpanzees. Concerning the modern human  
256 dataset, we chose in priority hunter-gatherer samples as references because we made the assumption  
257 that their ecological parameters (e.g. body composition and energetics, day range) represented more  
258 accurately the human species' ecology than samples from industrialized countries.

259 Regarding the phylogeny data, we used the topologies and branch lengths from the consensus tree  
260 provided by the 10kTrees website (Arnold et al., 2010; <https://10ktrees.nunn->

[lab.org/Primates/dataset.html](http://lab.org/Primates/dataset.html); version 3). This version provides a Bayesian inference of primate phylogeny which is based on collected data for eleven mitochondrial and six autosomal genes available in GenBank across 301 primate species. We computed the consensus tree on the basis of the species present in our sample to measure the respective phylogenetic distances between non-human primates and *Homo sapiens*.

## 2.4. Statistical analyses

Our statistical approach was designed to test how each of the five brain measures (hemispheric brain, gyrus rectus, VMPFC, ratio VMPFC/brain and the S1 cortex) were related to ecological or life-history parameters in addition to phylogeny. We constructed a generalized linear model for each response variable (cerebral measure) using the glm function in R version 3.5. Each response variable was averaged from left and right sides of the brain (N=22). However, in some cases (N=7), because some great apes brains were not perfectly preserved on both sides, we only kept the left or the right side measurement. As Student's t-tests did not reveal significant differences between males and females for any of the cerebral measures (all  $p > 0.5$ ), we pooled sexes in our analyses.

Before running our models, we first checked for correlations between the predictor variables in order to avoid redundancies due to multi-collinearity. Birthmass and gestation length were correlated with phylogeny (all  $r > 0.9$ , all  $p < 0.05$ ). As it was necessary to take into account phylogeny effects in statistical analyses for all of our brain measures, we did not include these two predictor variables linked to phylogeny. Body mass, basal metabolic rate (BMR) and daily energy expenditure (DEE) were also highly correlated ( $r > 0.9$ ) and we chose to only include body mass in our analyses because it is a raw measurement, contrary to BMR or DEE which were calculated with standard equations (see **Table S1**). Interbirth intervals and weaning age were highly correlated, so we only included weaning age in our analyses because it is directly related to the acquisition of adult-like diet repertoire and foraging skills (e.g. Schuppli et al., 2016a). Along the same lines, due to a high correlation between daily traveled distance and home range area, we only used daily traveled distance for modeling the brain measurements. The six following variables were therefore tested in our analyses: phylogeny, body mass, daily traveled distance, dietary quality, group size and weaning age. None of these variables were correlated to phylogeny, as previously shown by Kamilar and Cooper (2013) (low phylogenetic signal for daily traveled distance, dietary quality, weaning age and group size).

All five response variables' distributions revealed good fit with the lognormal distribution, so each variable was log-transformed prior to model fitting. We verified model assumptions with the

inspection of histogram of residuals and plots of residuals and fitted values. Each fitted model was compared with a null model, in which all predictors variables were removed, using a likelihood ratio test (package « lme4 »). Any full model that did not significantly outperform its respective null model was discarded and we did not report further on its parameter estimates. For each response, we tested several models corresponding to specific combinations of socio-ecological variables and phylogeny, and the best fitted model was chosen according to Bayesian Information Criterion (BIC) and Variance Inflation Factors (VIF). We employed the anova function to assess the percentage of variance explained by each predictor in the best fitted model for each of the five cerebral measurements. The detailed statistics for comparisons of the different models including different variables are presented in the supplementary material.

### 3. RESULTS

#### 3.1. Measurements of the brain, the gyrus rectus, the VMPFC and the somatosensory cortex

We present in **Table 1** the average volumes of the brain, the gyrus rectus, the VMPFC and the somatosensory cortex (S1) for each primate species in our sample, as well as the relative volume of the VMPFC compared to the brain hemisphere. The two macaque species had similar gyrus rectus and brain volumes, but Japanese macaques exhibited a larger VMPFC than rhesus macaques (Mann-Whitney test:  $U = 2.0$ ,  $p = 0.009$ ). The mean relative volume of the VMPFC of gorillas was intermediate between the values for rhesus macaques and Japanese macaques. The volume of all areas of interest was greater in modern humans than in all non-human primates.

**Table 1. Mean volumes of neuroanatomical structures: the brain hemisphere, the gyrus rectus, the VMPFC, the ratio VMPFC/brain hemisphere and the primary somatosensory cortex (S1) among our primate sample.** All measurements are expressed in mm<sup>3</sup> and represent the average of one hemisphere only. For the sake of consistency, the cerebellum was systematically excluded from all the measurements.

Species	Brain hemisphere	Gyrus rectus	VMPFC	VMPFC / Brain hemisphere	S1
<i>Macaca mulatta</i>	44643.6	320.9	89.9	0.0020	554.7
<i>Macaca fuscata</i>	45030.5	320.7	115.1	0.0026	562.7
<i>Gorilla gorilla</i>	122768.5	808.3	277.4	0.0023	2370.5
<i>Pan troglodytes</i>	98614.7	594.2	254.8	0.0026	1769.0
<i>Homo sapiens</i>	753584.2	4578.8	2296.1	0.0030	9949.1

### 3.2. Absolute volume of the brain

Comparison between the fitted and null models showed that the absolute volume of the brain (one hemisphere without cerebellum) was related to the following tested variables: phylogeny, daily range and group size (LRT,  $\chi^2 = 118.07$ ,  $\Delta df = 3$ ,  $P < 2.2e-16$ ; **Table 2**; **Fig. S1, S2, S3** and **S4**). The phylogeny accounted for 66% of the total variance, the daily traveled distance explained 30 % and group size only 3 %. Phylogeny was negatively linked to absolute brain volume, with higher brain volumes for species closest to humans. The daily traveled distance was positively associated with brain volume, with brain volume increasing with the daily distance traveled. We also reported a significant negative effect of group size on brain volume variation, with smaller brain volumes for high group sizes.

**Table 2.** Results of the best fitted generalized linear model examining the relationship between the absolute volume of the brain without cerebellum (n = 28), phylogeny, daily traveled distance and group size.

Factors	Estimate + SE	t - value	Pr(>   t  )
Phylogeny	- 1.757 ± 0.15	- 11.402	3.57e-11
Daily traveled distance	0.245 ± 0.01	21.097	5.31e-17
Group size	- 0.012 ± 2.00e-3	- 7.031	2.87e-7

### 3.3. Absolute volume of the gyrus rectus

Representative examples of the gyrus rectus for each species are shown on **Fig. 2**. Based on model comparison, the volume of the gyrus rectus was best explained by phylogeny, daily traveled distance and group size as predictor variables (LRT,  $\chi^2 = 105.76$ ,  $\Delta df = 3$ ,  $P < 2.2e-16$ ; **Table 3**; **Fig. S5, S6, S7** and **S8**). As for the brain volume, phylogeny accounted for more than half of the variance observed (58%), whereas socio-ecological parameters explained 40 % (respectively 35 % for daily traveled distance and 5 % for group size). Similarly to what we found for the brain volume, the daily traveled distance was positively related to the volume of the gyrus rectus, whereas phylogeny and group size were negatively linked to the volume of the gyrus.

**Table 3.** Results of the best fitted generalized linear model examining the relationship between the absolute volume of the gyrus rectus (n = 29), phylogeny, daily traveled distance and group size.

Factors	Estimate ± SE	t - value	Pr(>   t  )
Phylogeny	- 1.305 ± 0.19	- 7.064	2.10e-7
Daily traveled distance	0.256 ± 0.01	17.881	9.33e-16
Group size	- 0.013 ± 2.0e-3	- 6.684	5.28e-7

### 3.4. Absolute volume of the VMPFC

Representative examples of the VMPFC for each species are shown on **Fig. 2**. The model with phylogeny, dietary quality, weaning age and group size as predictor variables better explained the variation of the VMPFC in our sample (LRT,  $\chi^2 = 118.65$ ,  $\Delta df = 4$ ,  $P < 2.2e-16$ ; **Table 4**; **Fig S9, S10, S11, S12** and **S13**). Phylogeny accounted for 64 % of the variance observed, whereas dietary quality and weaning age explained respectively 20% and 12% of variance. Group size only accounted for a very little portion of the variance (3%). In the one hand, we still found a negative relationship between phylogeny and the volume of the VMPFC, as well as a negative effect of group size. On the other hand, we found that the dietary quality was positively associated with VMPFC: the VMPFC is bigger when the dietary quality is higher. Moreover, there was a negative relation between weaning age and the VMPFC, with a bigger VMPFC with earlier weaning ages.

**Table 4.** Results of the best fitted generalized linear model examining the relationship between absolute volume of the VMPFC (n = 29), phylogeny, dietary quality, weaning age and group size.

Factors	Estimate ± SE	t - value	Pr(>   t  )
Phylogeny	- 8.023 ± 0.31	- 25.600	6.19e-19
Dietary quality	0.012 ± 1.0e-3	9.338	1.84e-9
Weaning age	- 0.568 ± 0.04	- 12.958	2.51e-12
Group size	- 0.017 ± 3.0e-3	- 6.359	1.42e-6

### 3.5. Proportion of the VMPFC relative to brain volume

The best fitted model suggests that the ratio VMPFC/brain in our primate sample was better explained by the phylogeny and dietary quality (LRT,  $\chi^2 = 32.41$ ,  $\Delta df = 2$ ,  $P = 9.2e-8$ ; **Table 5**; **Fig. S14**, **S15** and **S16**). Dietary quality explained 41 % of the variance observed, whereas phylogeny explained about 28 %. As it was the case for the absolute measure of the VMPFC, the relative volume of the VMPFC was positively modulated by the dietary quality index, and negatively associated with phylogeny.

**Table 5.** Results of the best fitted generalized linear model examining the relationship between the volume of the VMPFC relative to the whole brain (n = 28), phylogeny and dietary quality.

Factors	Estimate + SE	t - value	Pr(>   t  )
Phylogeny	- 0.320 ± 0.08	- 3.869	6.94e-4
Dietary quality	2.088e-3 ± 3.70e-4	5.695	6.25e-6

### 3.6. Absolute volume of the somatosensory (S1) cortex

Variation of the absolute volume of the S1 cortex was better explained by the phylogeny, the daily



traveled distance and the group size (LRT,  $\chi^2 = 111.55$ ,  $\Delta df = 3$ ,  $P < 2.2e-16$ ; **Table 6**; **Fig. S17**, **S18**, **S19** and **S20**). The phylogeny explained 79% of the variance observed for the volume of the S1 cortex, whereas socio-ecological parameters explained 19% of the variance observed, with daily traveled distance accounting for 15% and group size for 4%. Similarly to what we found for the whole brain volume, phylogeny and group size had a negative impact on the volume of the S1 cortex, whereas the impact of daily traveled distance was positive. Contrary to the VMPFC, the best model to account for the volume of S1 does not include either dietary quality or weaning age.

**Table 6.** Results of the best fitted generalized linear model examining the relationship between absolute volume of the S1 cortex (n = 28), phylogeny, daily traveled distance and group size.

Factors	Estimate + SE	t - value	Pr(>   t  )
Phylogeny	- 2.892 ± 0.18	- 16.311	1.73e-14
Daily traveled distance	0.206 ± 0.01	15.314	6.91e-14
Group size	- 0.013 ± 2.00e-3	- 7.397	1.23e-7

#### 4. DISCUSSION

This study provides specific models describing the influence of phylogeny and key socio-ecological variables on several brain regions. One of the aims of our study was to go beyond the use of the overall brain volume as a proxy to infer a global cognitive capacity (e.g. Benson-Amram et al., 2016; Lefebvre et al., 2004;), which is crude and can lead to misinterpretations (e.g. Healy & Rowe, 2007; Logan et al., 2018). In line with our hypothesis, socio-ecological factors (diet quality and weaning age) implying a strong pressure from the environment to exhibit flexibility in foraging strategies had a specific influence on the VMPFC, a region associated with both episodic memory and decision-making. The influence of these factors was not detectable when using less specific regions (the whole gyrus rectus or the whole brain) or when using a control region not involved in executive functions (the primary somatosensory cortex, S1). The similarity across the socio-ecological factors influencing the size of these later regions is probably related to a global relationship between brain size and cognition/behavioral control (e.g. Deaner et al., 2007; Isler & van Schaik, 2014; Reader & Laland, 2002).

Regarding the overall brain volume, the best model describing this global measure included not only phylogeny but also daily range and group size (although its influence was negative). The strong influence of phylogeny on brain size is probably related to the constraints of evolutionary history; closely related species tend to display similarities in morphological traits because they inherited them from a common ancestor. Phylogeny also influenced the size of specific brain regions (gyrus rectus, VMPFC, primary somatosensory cortex), in line with the idea that the strong constraint of evolutionary history does not only apply to the brain as the whole, but also to specific cerebral regions.

Besides phylogeny, brain size was also significantly related to ecology: bigger brains are associated with longer distances traveled by day. This is in accordance with previous studies showing associations between brain size and home range size (which is correlated with distances traveled by day) (Gilissen, 2005; Powell et al., 2017). Our results are also somehow consistent with those recently published by De Casien et al. (2017) who showed that, among primates, brain size was related to dietary factors more than to social parameters; frugivorous primates having bigger brains than folivorous ones. Although we found a better relationship between brain size and daily traveled distance than diet quality, the two studies converge in showing that brain size seems to be better predicted by feeding ecology than by group size. Moreover, when entered as a covariate, group size — which has been used as a proxy for social complexity in primates (Dunbar, 1998) — has a negative influence on brain size and its influence is one order of magnitude less (3% of the total variance) than that of phylogeny (66%) and ecology (30%). This might look at odds with the Social Brain hypothesis (Dunbar, 1998). This hypothesis suggests that social challenges favored the evolution of larger brains, and especially larger neocortex size, with species living in larger groups having bigger brains to deal with the associated complex social interactions (Barrett et al., 2003; Dunbar & Shultz, 2007; van Schaik & Burkart, 2011). Cognitive adaptations are expected to improve the effectiveness with which a species deals with social challenges (coalition formation, social learning of skills...), and social factors have been suggested as selective forces to favor increases in cognitive abilities (Street et al., 2017). Nevertheless, disentangling the respective role of social factors and ecological factors involved in the increase of cognitive abilities remains tricky, especially because some social factors, such as group size, are not independent from ecological factors. Indeed, group size in primates is often limited by feeding competition, for example as group size increases, there is an inevitable increase in scramble competition and consequently individual daily traveled distance increases (van Schaik, 2016). Moreover, it appears that in more stable and productive environment, groups of a given species tend to be larger (e.g. Chapman & Chapman, 2000; Emery Thompson, 2017). Consequently, the weak negative influence of group size (when associated with other covariates such as phylogeny and daily traveled distance) that we reported is

difficult to interpret, especially because when considered individually, group size positively affects all brain measures. Thus, given these limitations and our limited sample (5 species), the putative effects of group size must be treated cautiously, and testing the Social Brain hypothesis would require clarifying the prediction regarding the influence of sociality on specific vs. generic cognitive skills, as well as the corresponding brain regions. Lastly, it should be kept in mind that group size could be a very crude (or even inaccurate) measure of social complexity, and more work is necessary to find a better proxy of the quality of social interactions (e.g. social network size). For example, larger group size may not always be associated with a corresponding increase of differentiated relationships at the individual level (Bergman & Beehner, 2015; De Casien et al., 2017; Dunbar & Schultz, 2007). Thus, this measure (even if largely used in primate studies) could inaccurately capture what the Social Brain hypothesis actually entails and refining this hypothesis would also benefit from a clarification of the specific social and cognitive processes at play. Nevertheless, whatever the relation between group size and social skills and whatever the limitations of our study, feeding ecology remains a better predictor of brain volume compared to group size in our sample. Thus, even if the ecological and social hypotheses are not mutually exclusive (Rosati, 2017), our work reinforces the idea that ecological parameters, and particularly those related to foraging, could have played a stronger role than sociality in the evolution of overall brain volume (home range size: Clutton-Brock & Harvey, 1980; Powell et al., 2017; ephemeral food resources: Milton, 1981, 1988; extractive foraging: in van Schaik, 2016).

Given the limitations of whole brain measures, we designed this study to capture the relation between specific cognitive operations and key socio-ecological factors by measuring the volume of a specific brain region, the VMPFC, which is associated with decision-making and valuation based on episodic memory (e.g. Barron et al., 2013; Rushworth et al., 2012; San-Galli et al., 2016). Indeed, these processes are thought to be crucial for behavioral flexibility and acquisition of food resources or “foraging cognition” among primates (Cunningham & Janson, 2007; Noser & Byrne, 2007; Rosati, 2017; Zuberbühler & Janmaat, 2010). To our knowledge, our study is the first to focus on this specific brain region at the interspecific level, and we demonstrate that this approach provides a significant insight into the relationship between cognition, neuroanatomy and ecology. In fact, the best model to capture the difference in size of the VMPFC across species included not only phylogeny and group size (as it was the case for the whole brain and other control regions’ size), but also diet quality and weaning age. This clearly suggests that coping with these socio-ecological factors would involve the cognitive operations in which the VMPFC plays a critical role. Primate species with a more diversified diet, including fruits and/or animal items, should require a solid capacity of selecting which course of action to take based on expected costs and benefits, compared to species which have an easier access to resources such as leaves and stems. Thus, the cognitive

operations involving the VMPFC (selecting actions based on memorized information and according to a specific context) may have been favored among primates that forage in complex and variable environments for ephemeral or seasonal food resources such as fruits. The negative influence of weaning age on the VMPFC that we reported could be interpreted along the same lines: all other things being equal, being weaned earlier could mean that animals must start earlier to make appropriate foraging decisions, in part by selecting the right food and the right way to obtain it. In other words, the VMPFC might provide the cognitive tools to survive both when animals need to obtain diverse food resources from a rich environment and when they must learn to forage on their own earlier in their life. Even if similar arguments had been already advanced based on experiments in individual species (rhesus macaques: San-Galli et al., 2016 or humans: Rushworth & Behrens, 2008), the present work is the first direct demonstration of a relationship between a specific brain region and a set of specific ecological variables across several primate species.

We also measured the cortical volume of the gyrus rectus, an easily identifiable part of the ventral prefrontal cortex related to decision-making and planning (Bechara et al., 2000). Interestingly, the gyrus rectus showed the same relationship with ecology than the whole brain; they were larger among species traveling longer daily distances, and smaller among species with large group size. As for the whole brain, this latter parameter only explained a small part of the total variance observed in our sample (5% for the gyrus rectus). In other words, looking at this region of the prefrontal cortex provides no additional insight into the relation between brain and ecology. This might be due to the fact that the prefrontal cortex is the major source of variability among primate brains (Passingham & Smaers, 2014; Preuss & Goldman-Rakic, 1991; Smaers et al., 2017). In that context, the size of the gyrus rectus would simply represent the global expansion of the prefrontal cortex across species, and the corresponding increase in executive capacities. Following that hypothesis, ecological variables would simply put a global pressure on all executive functions, rather than on other functions such as sensory or motor processing. This is however probably not the case, because the same variables also explained the relative expansion of the primary somatosensory cortex S1. In the one hand, this is surprising, because it is hard to relate primary somatosensory processing and variables such as daily traveled distance and group size. On the other hand, it indicates that the neuroanatomical correlates of these variables is highly non-specific; rather than driving the increase in a set of specific structures, it seems to boost a global cortical expansion.

Finally, measuring the ratio VMPFC/brain further established the specificity of the relationship between VMPFC and ecological variables. First, in contrast with other measures (such as whole brain, gyrus rectus and VMPFC sizes), the relative size of the VMPFC showed no significant influence of group size, in line with the idea that the effect of group size remains relatively limited

and neuroanatomically unspecific. Secondly, the relative volume of the VMPFC showed a stronger influence of dietary quality than the absolute VMPFC volume (explaining 41% vs. 20% of the variance), in line with the idea that the relationship between VMPFC and this ecological variable is stronger than for the rest of the brain.

Altogether, it seems reasonable to conclude that the specific cognitive operations associated with the VMPFC are strongly related to an increase in dietary quality and potentially to the complexity of associated foraging strategies. Our results are in line with several studies that emphasize the key influence of feeding ecology on evolution of primate cognition (De Casien et al., 2017; Powell et al., 2017; Rosati, 2017; Schuppli et al., 2016b; Zuberbühler & Janmaat, 2010). Even if the primate species tested in our study spanned a large range of brain sizes found in living primates (suggesting that the results may reflect a general pattern for Old World primates, at least), our conclusions must be taken with caution given our small sample size, and our analysis should be extended to more primate species. In addition, our study confirms that the relationship between feeding ecology and cognition is strong enough to be detected by using such a crude proxy for cognitive skills as brain size (cf. the positive effect of daily traveled distance not only on the whole brain but also on the gyrus rectus and on the somatosensory cortex). The exact cognitive operations and the neuroanatomical substrates underlying this relation, however, still needs to be established. Our work provides a significant step in that direction, by demonstrating that the relationship between ecology, neurobiology and cognition can be better captured with a more specific brain measure, and presumably a more specific cognitive operation. The strong modulation of VMPFC size by the diet quality paves the way for a more specific exploration of the neurobiological and cognitive operations underlying foraging. Conversely, this works also provides a critical insight into the ecological function of distinct brain systems, complementing the studies conducted in laboratory settings (Kolling et al., 2012; San-Galli et al., 2016). More generally, the capacity to guide behavior in complex and variable environment in order to fulfill energetic requirements may have had a major impact on primate evolution. Together with previous studies (Foley & Lee, 1991; Reader & Laland, 2002; Zink & Lieberman, 2016), we suggest that foraging strategies, together with extractive abilities (e.g. tool use), manipulative complexity and food processing techniques played a primary role in the evolution of cognition in hominids (i.e. *Pongo*, *Pan*, *Gorilla* and *Homo* including their immediate ancestors). Efficient foraging and associated behavioral and technical innovations (van Schaik, 2016) may have been particularly favored among hominin species (i.e. modern humans, their direct ancestors, and their extinct relatives) who complexified foraging strategies and increased their dietary ranges to face a critically changing environment.

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885 **FIGURE CAPTIONS**

886

887 **Figure 1.** Reliable inter-species boundaries of the gyrus rectus and the ventromedial prefrontal  
888 cortex in primates. Left: coronal view; right: sagittal view. Yellow: Gyrus rectus; red: VMPFC.  
889 Abbreviations: *cc*: corpus callosum; *cis*: cingulate sulcus; *rs*: rostral sulcus; *mos*: medial orbital  
890 sulcus; A: Anterior; P: Posterior; D: Dorsal; V: Ventral.

891 [Figure size: 1.5 column]

892

893 **Figure 2.** Delimitation of the gyrus rectus and the ventromedial prefrontal cortex on brain MRI of  
894 non-human primate species and humans. From top to bottom: *Macaca mulatta* (*in-vivo*), *Macaca*  
895 *fuscata* (*in-vivo*), *Gorilla gorilla* (*post-mortem*), *Pan troglodytes* (*post-mortem*) and *Homo sapiens*  
896 (*post-mortem*). Left: coronal views; right: sagittal views. Yellow: Gyrus rectus; red: VMPFC. Scale  
897 bar = 1 cm.

898 [Figure size: 1.5 column]

899

900 **Figure 3.** Reliable inter-species boundaries of the somatosensory cortex (*blue*) in primates. Left:  
901 lateral view; middle: axial view; right: sagittal view. Abbreviations: *cis*: cingulate sulcus; *cs*:  
902 central sulcus; *pcs*: precentral sulcus; *pocs*: postcentral sulcus; A: Anterior; P: Posterior; M:  
903 Medial; L: Lateral; D: Dorsal; V: Ventral.

904 [Figure size: 2 column]

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Figure1  
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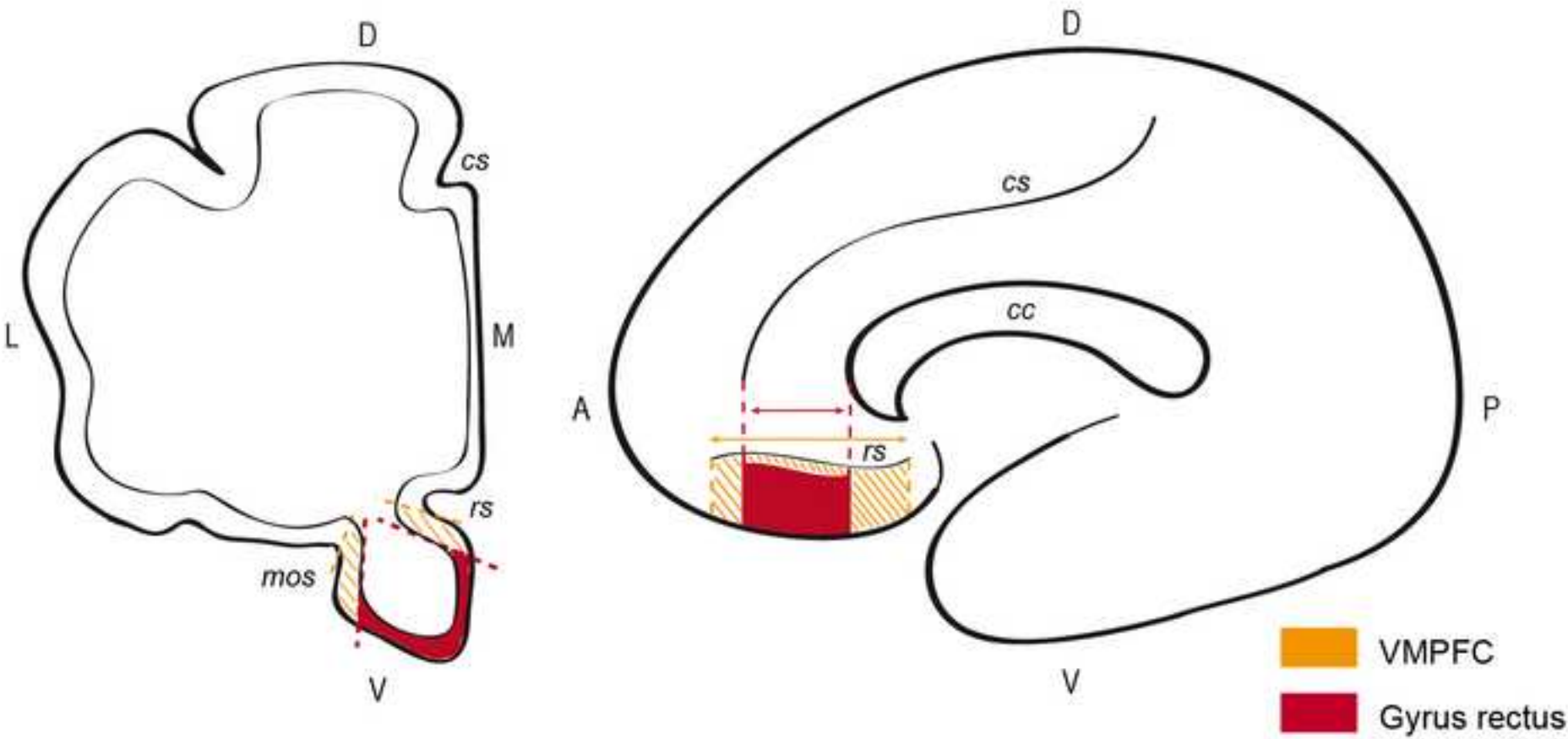




Figure2  
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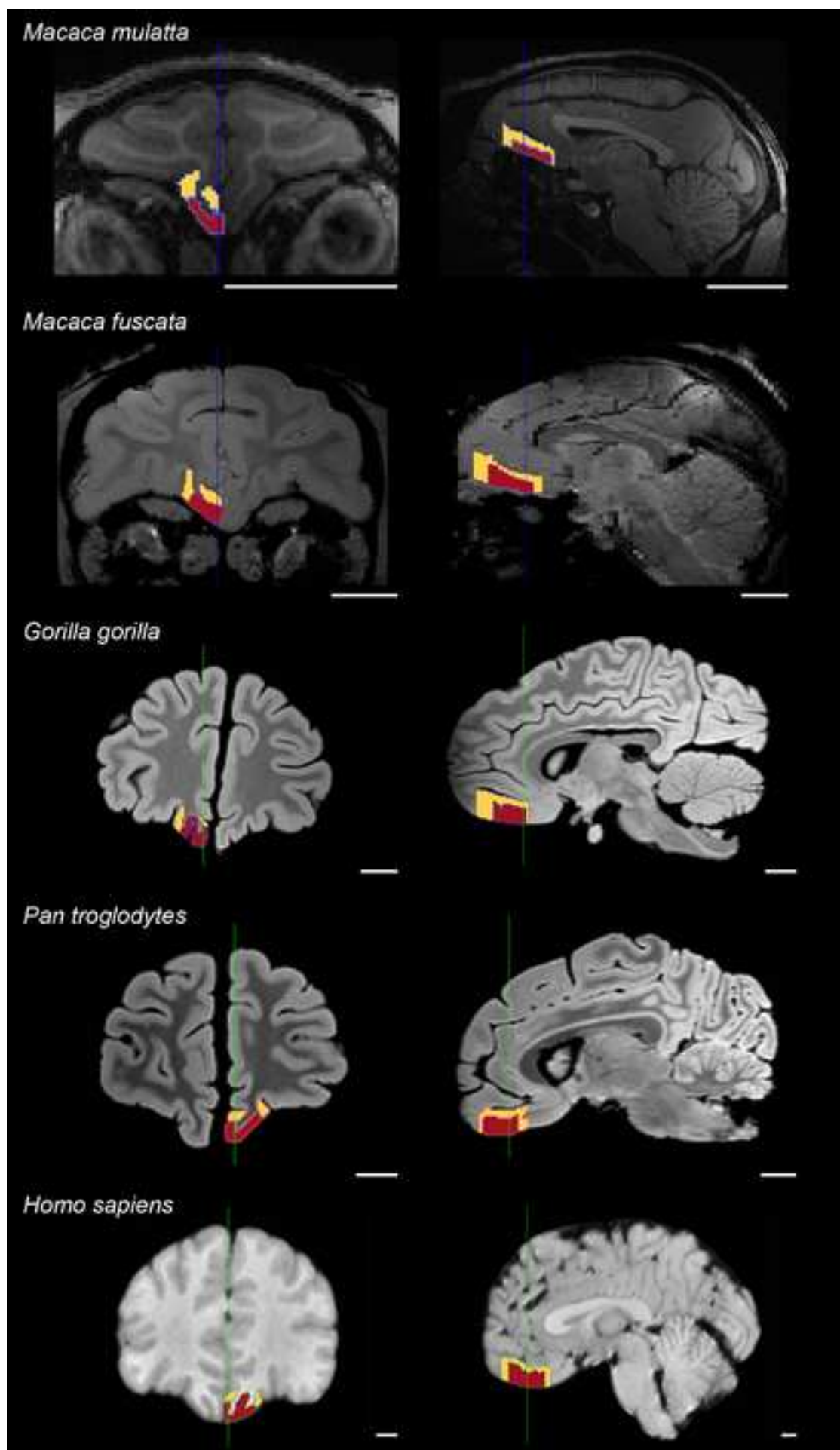


Figure3  
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