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

Margot Louail (1, 4), Emmanuel Gilissen (2, 3), Sandrine Prat (4)*, Cécile Garcia (5)*, Sébastien Bouret (1)*

*: These authors contributed equally to the supervision of this work and are co-last authors.

Corresponding author: Sébastien Bouret: sebastien.bouret@icm-institute.org

Affiliations

(1) Team Motivation Brain & Behavior, ICM - Institut du Cerveau et de la Moelle épinière, CNRS UMR 7225 - INSERM U1127 -UPMC UMR S 1127, Hôpital Pitié-Salpêtrière, 47 Boulevard de l'Hôpital, 75013 Paris, France.

(2) Department of African Zoology, Royal Museum for Central Africa, Tervuren, Belgium.

(3) Université Libre de Bruxelles, Laboratory of Histology and Neuropathology, Brussels, Belgium.

(4) UMR 7194 (HNHP), MNHN/CNRS/UPVD, Association Sorbonne Université, Musée de l'Homme, 17 Place du Trocadéro, 75116 Paris, France.

(5) UMR 7206 Eco-anthropologie et Ethnobiologie, CNRS - MNHN - Paris Diderot, Musée de l'Homme, 17 Place du Trocadéro, 75116 Paris, France.

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

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6
7 5 Bouret (1)*

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12 7 Corresponding author: Sébastien Bouret: sebastien.bouret@icm-institute.org
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15 8
16
17 9 **Affiliations**

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20 10 (1) Team Motivation Brain & Behavior, ICM - Institut du Cerveau et de la Moelle épinière, CNRS
21
22 11 UMR 7225 - INSERM U1127 -UPMC UMR S 1127, Hôpital Pitié-Salpêtrière, 47 Boulevard de
23
24 12 l'Hôpital, 75013 Paris, France.

25 13 (2) Department of African Zoology, Royal Museum for Central Africa, Tervuren, Belgium.
26

27 14 (3) Université Libre de Bruxelles, Laboratory of Histology and Neuropathology, Brussels, Belgium.
28

29 15 (4) UMR 7194 (HNHP), MNHN/CNRS/UPVD, Association Sorbonne Université, Musée de
30
31 16 l'Homme, 17 Place du Trocadéro, 75116 Paris, France.

32
33 17 (5) UMR 7206 Eco-anthropologie et Ethnobiologie, CNRS - MNHN - Paris Diderot, Musée de
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35 18 l'Homme, 17 Place du Trocadéro, 75116 Paris, France.

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33 **Abstract**

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3 35 To survive in complex and seasonal environments, primates are thought to rely upon cognitive
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5 36 capacities such as decision-making and episodic memory, which enable them to plan their daily
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7 37 foraging path. According to the Ecological Brain hypothesis, feeding ecology has driven the
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9 38 expansion of the brain to support the corresponding development of cognitive skills. Recent works
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11 39 in cognitive neurosciences indicate that cognitive operations such as decision-making or subjective
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13 40 evaluation (which are contextual and dependent upon episodic memory), relied critically upon a
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15 41 small part of the frontal lobe, often referred to as the ventromedial prefrontal cortex (VMPFC).
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17 42 Several authors suggested that this area might be important for foraging, but this has never
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19 43 been tested. In the present study, we quantified the relation between the size of the VMPFC (along
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21 44 with other cerebral measures: the whole brain, the gyrus rectus and the somatosensory cortex) and
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23 45 key socio-ecological variables in five primate species (*Macaca mulatta*, *Macaca fuscata*, *Gorilla*
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25 46 *gorilla*, *Pan troglodytes* and *Homo sapiens*). We hypothesized that the size of the VMPFC would be
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27 47 greater in primates with a large dietary spectrum and complex foraging strategies. We also
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29 48 hypothesized that the impact of feeding ecology would be stronger on this specific region than on
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31 49 other regions (somatosensory cortex) or on more global cerebral measures (e.g. whole brain). In line
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33 50 with these hypotheses, we found that all cerebral measures were more strongly related to feeding
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35 51 ecology than group size, a proxy for social complexity. As expected, the VMPFC volume is more
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37 52 precisely related to feeding ecology than the whole brain, and appears to be critically related to
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39 53 dietary quality. Thus, combining a comparative approach with predictions coming both from
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41 54 behavioral ecology and cognitive neurosciences, our study provides convincing evidence that
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43 55 feeding ecology played a key role in the development of specific cognitive skills, which rely upon
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45 56 the expansion of a specific cortical area.

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

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61 **1. INTRODUCTION**

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

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

95 comparative context (e.g. birds vs. primates, Güntürkün & Bugnyar, 2016). More critically, social
96 interactions (e.g. number of individuals an animal can remember, number of third-party
97 relationships, dominance ranks) and ecological knowledge (e.g. recognition of food types, food
98 selection, knowledge of food processing and harvesting schedules, estimation of amounts) rely
99 upon distinct brain systems, even though decision-making in both social and food dimensions could
100 involve overlapping brain regions (Eichenbaum & Cohen, 2014; Lin et al., 2015; Peters & Büchel,
101 2010; Ruff & Fehr, 2014; Stanley & Adolphs, 2013). Thus, a major challenge for understanding
102 primate cognition would rather be the identification of specific cognitive abilities, associated with
103 their underlying neurobiological substrate, which both underlie adaptation to specific ecological or
104 social challenges. In that frame, since the relative size of distinct brain regions varies across species
105 (Barton & Harvey, 2000; Passingham & Wise, 2012), size differences of specific cortical areas
106 could better capture the adaptations of cognitive capacities that occurred in response to particular
107 ecological conditions. As such, a few studies focused on specific brain regions, such as the
108 hippocampus or the olfactory cortex and their volumetric variations as a function of ecological
109 variables across primates (Barks et al., 2015; Barton & Harvey, 2000).

110 Here, we propose an innovative and holistic approach to assess how socio-ecological parameters
111 can explain variations of brain measurements among five primate species (*Macaca mulatta*,
112 *Macaca fuscata*, *Gorilla gorilla*, *Pan troglodytes* and *Homo sapiens*), when taking into account the
113 phylogeny. We measured the whole brain volume to facilitate comparison with existing
114 comparative studies, since most of them only used this measure. Additionally, we measured the
115 primary somatosensory cortex (S1 cortex) as a control region, since it is located outside of the
116 frontal lobe and is not supposed to be involved in any kind of executive function. We considered
117 two regions of interest, referred to as the gyrus rectus and the ventromedial prefrontal cortex
118 (VMPFC). The gyrus rectus is an easily identifiable brain region located on the ventromedial part of
119 the prefrontal cortex, and it has largely been associated with value-encoding and decision-making
120 behaviors among human and non-human primates (Bechara et al., 1998; Jocham et al., 2014;
121 Noonan et al., 2017; Rushworth et al., 2012). In addition, based on recent functional imaging and
122 electrophysiological studies in humans and monkeys, we considered a more specific region, the
123 VMPFC, located on the ventral part of the gyrus rectus. Indeed, this region is reliably associated
124 with valuation of items and outcomes based on contextual information and memory, and with
125 subsequent decision-making behaviors (Barron et al., 2013; Bouret & Richmond, 2010; Clark et al.,
126 2013; Lebreton et al., 2009, 2013; Papageorgiou et al., 2017; Peters & Büchel, 2010; Rushworth &
127 Behrens, 2008; Rushworth et al., 2011; San-Galli et al., 2016; Strait et al., 2014). We thus
128 hypothesized that the VMPFC should be a better proxy than the whole brain volume to explore the
129 relationship between specific cognitive capacities and ecology. We also made the hypothesis that

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

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135 **2. MATERIAL & METHODS**

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136 **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 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).

160 **2.2. Processing of brain MRI and measurements**

162 Avizo v9.0 software was used for visualization, segmentation and quantification of brain tissues.
163 We measured 3 regions of interest: the whole brain (without cerebellum), the gyrus rectus and the
164 ventromedial prefrontal cortex (VMPFC). Additionally, we measured the volume of the primary
165 somatosensory cortex (S1 cortex) as a control region. We anatomically defined these regions of
166 interest and the corresponding landmarks on the basis of cytoarchitectonic maps (Carmichael &
167 Price, 1994; Mackey & Petrides, 2010; Öngür et al., 2003), and on brain atlases of rhesus macaques
168 and humans (Dubach & Bowden, 2009; Paxinos et al., 2008; Rohlfing et al., 2012; Sunkin et al.,
169 2013).

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

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

189 [Insert Figure 1]

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

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

207
208 [Insert Figure 2]

209 In order to confirm the specificity of the structure-function relation between the VMPFC and socio-
210 ecological variables, we examined another cortical region, the somatosensory cortex (S1 cortex) as
211 a control region. The S1 cortex is located in the parietal lobe and it receives sensory inputs from
212 several modalities (touch, proprioception, nociception and temperature; Kaas, 2004). It is a priori
213 not involved in executive functions. We thus hypothesized that this control region would not be
214 associated with the planning of foraging strategies and thus it should not be related to the same
215 socio-ecological variables as the VMPFC. We used reliable inter-species boundaries to delimitate
216 the S1 cortex among our primate sample (**Fig. 3**). Both in human and non-human primates, S1 is
217 located on the postcentral gyrus which is immediately caudal to the central sulcus. Similarly to the
218 gyrus rectus and the VMPFC, we thus measured the volume of gray matter of the post-central
219 gyrus. The anterior limit of the S1 cortex corresponds to the central sulcus, and the inferior one to
220 the inferior limit of the central sulcus. The fundus of the central sulcus is included in the S1 cortex.
221 In humans and great apes, the posterior limit of S1 is the post-central sulcus. However in macaques,
222 it is slightly observable on the dorsolateral surface between intraparietal and central sulci – in the
223 continuity of the ascending branch of the intraparietal sulcus (Seelke et al., 2011). We thus set the
224 posterior border of the S1 cortex in macaques immediately rostral to the superior parietal lobule, at
225 the end of the cortical convexity formed by the slightly observable post-central sulcus. The fundus
226 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->

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

266

267 **2.4. Statistical analyses**

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

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

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

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

304 **3. RESULTS**

306 **3.1. Measurements of the brain, the gyrus rectus, the VMPFC and the somatosensory cortex**

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

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315 **Table 1. Mean volumes of neuroanatomical structures: the brain hemisphere, the gyrus**
 316 **rectus, the VMPFC, the ratio VMPFC/brain hemisphere and the primary somatosensory**
 317 **cortex (S1) among our primate sample.** All measurements are expressed in mm³ and represent the
 318 average of one hemisphere only. For the sake of consistency, the cerebellum was systematically
 319 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

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3.2. Absolute volume of the brain

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

333 **Table 2.** Results of the best fitted generalized linear model examining the relationship between the
 334 absolute volume of the brain without cerebellum (n = 28), phylogeny, daily traveled distance and
 335 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

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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.

348 **Table 3.** Results of the best fitted generalized linear model examining the relationship between the
 349 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

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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.

364 **Table 4.** Results of the best fitted generalized linear model examining the relationship between
 365 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

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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.

376 **Table 5.** Results of the best fitted generalized linear model examining the relationship between the
 377 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

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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

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

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 390 **Table 6.** Results of the best fitted generalized linear model examining the relationship between
 391 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

393 4. DISCUSSION

394 This study provides specific models describing the influence of phylogeny and key socio-ecological
 395 variables on several brain regions. One of the aims of our study was to go beyond the use of the
 396 overall brain volume as a proxy to infer a global cognitive capacity (e.g. Benson-Amram et al.,
 397 2016, Lefebvre et al., 2004;), which is crude and can lead to misinterpretations (e.g. Healy & Rowe,
 398 2007; Logan et al., 2018). In line with our hypothesis, socio-ecological factors (diet quality and
 399 weaning age) implying a strong pressure from the environment to exhibit flexibility in foraging
 400 strategies had a specific influence on the VMPFC, a region associated with both episodic memory
 401 and decision-making. The influence of these factors was not detectable when using less specific
 402 regions (the whole gyrus rectus or the whole brain) or when using a control region not involved in
 403 executive functions (the primary somatosensory cortex, S1). The similarity across the socio-
 404 ecological factors influencing the size of these later regions is probably related to a global
 405 relationship between brain size and cognition/behavioral control (e.g. Deaner et al., 2007; Isler &
 406 van Schaik, 2014; Reader & Laland, 2002).

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

415 Besides phylogeny, brain size was also significantly related to ecology: bigger brains are associated
416 with longer distances traveled by day. This is in accordance with previous studies showing
417 associations between brain size and home range size (which is correlated with distances traveled by
418 day) (Gilissen, 2005; Powell et al., 2017). Our results are also somehow consistent with those
419 recently published by De Casien et al. (2017) who showed that, among primates, brain size was
420 related to dietary factors more than to social parameters; frugivorous primates having bigger brains
421 than folivorous ones. Although we found a better relationship between brain size and daily traveled
422 distance than diet quality, the two studies converge in showing that brain size seems to be better
423 predicted by feeding ecology than by group size. Moreover, when entered as a covariate, group size
424 — which has been used as a proxy for social complexity in primates (Dunbar, 1998) — has a
425 negative influence on brain size and its influence is one order of magnitude less (3% of the total
426 variance) than that of phylogeny (66%) and ecology (30%). This might look at odds with the Social
427 Brain hypothesis (Dunbar, 1998). This hypothesis suggests that social challenges favored the
428 evolution of larger brains, and especially larger neocortex size, with species living in larger groups
429 having bigger brains to deal with the associated complex social interactions (Barrett et al., 2003;
430 Dunbar & Shultz, 2007; van Schaik & Burkart, 2011). Cognitive adaptations are expected to
431 improve the effectiveness with which a species deals with social challenges (coalition formation,
432 social learning of skills...), and social factors have been suggested as selective forces to favor
433 increases in cognitive abilities (Street et al., 2017). Nevertheless, disentangling the respective role
434 of social factors and ecological factors involved in the increase of cognitive abilities remains tricky,
435 especially because some social factors, such as group size, are not independent from ecological
436 factors. Indeed, group size in primates is often limited by feeding competition, for example as group
437 size increases, there is an inevitable increase in scramble competition and consequently individual
438 daily traveled distance increases (van Schaik, 2016). Moreover, it appears that in more stable and
439 productive environment, groups of a given species tend to be larger (e.g. Chapman & Chapman,
440 2000; Emery Thompson, 2017). Consequently, the weak negative influence of group size (when
441 associated with other covariates such as phylogeny and daily traveled distance) that we reported is

442 difficult to interpret, especially because when considered individually, group size positively affects
443 all brain measures. Thus, given these limitations and our limited sample (5 species), the putative
444 effects of group size must be treated cautiously, and testing the Social Brain hypothesis would
445 require clarifying the prediction regarding the influence of sociality on specific vs. generic
446 cognitive skills, as well as the corresponding brain regions. Lastly, it should be kept in mind that
447 group size could be a very crude (or even inaccurate) measure of social complexity, and more work
448 is necessary to find a better proxy of the quality of social interactions (e.g. social network size). For
449 example, larger group size may not always be associated with a corresponding increase of
450 differentiated relationships at the individual level (Bergman & Beehner, 2015; De Casien et al.,
451 2017; Dunbar & Schultz, 2007). Thus, this measure (even if largely used in primate studies) could
452 inaccurately capture what the Social Brain hypothesis actually entails and refining this hypothesis
453 would also benefit from a clarification of the specific social and cognitive processes at play.
454 Nevertheless, whatever the relation between group size and social skills and whatever the
455 limitations of our study, feeding ecology remains a better predictor of brain volume compared to
456 group size in our sample. Thus, even if the ecological and social hypotheses are not mutually
457 exclusive (Rosati, 2017), our work reinforces the idea that ecological parameters, and particularly
458 those related to foraging, could have played a stronger role than sociality in the evolution of overall
459 brain volume (home range size: Clutton-Brock & Harvey, 1980; Powell et al., 2017; ephemeral food
460 resources: Milton, 1981, 1988; extractive foraging: in van Schaik, 2016).

461 Given the limitations of whole brain measures, we designed this study to capture the relation
462 between specific cognitive operations and key socio-ecological factors by measuring the volume of
463 a specific brain region, the VMPFC, which is associated with decision-making and valuation based
464 on episodic memory (e.g. Barron et al., 2013; Rushworth et al., 2012; San-Galli et al., 2016).
465 Indeed, these processes are thought to be crucial for behavioral flexibility and acquisition of food
466 resources or “foraging cognition” among primates (Cunningham & Janson, 2007; Noser & Byrne,
467 2007; Rosati, 2017; Zuberbühler & Janmaat, 2010). To our knowledge, our study is the first to
468 focus on this specific brain region at the interspecific level, and we demonstrate that this approach
469 provides a significant insight into the relationship between cognition, neuroanatomy and ecology. In
470 fact, the best model to capture the difference in size of the VMPFC across species included not only
471 phylogeny and group size (as it was the case for the whole brain and other control regions’ size),
472 but also diet quality and weaning age. This clearly suggests that coping with these socio-ecological
473 factors would involve the cognitive operations in which the VMPFC plays a critical role. Primate
474 species with a more diversified diet, including fruits and/or animal items, should require a solid
475 capacity of selecting which course of action to take based on expected costs and benefits, compared
476 to species which have an easier access to resources such as leaves and stems. Thus, the cognitive

477 operations involving the VMPFC (selecting actions based on memorized information and according
478 to a specific context) may have been favored among primates that forage in complex and variable
479 environments for ephemeral or seasonal food resources such as fruits. The negative influence of
480 weaning age on the VMPFC that we reported could be interpreted along the same lines: all other
481 things being equal, being weaned earlier could mean that animals must start earlier to make
482 appropriate foraging decisions, in part by selecting the right food and the right way to obtain it. In
483 other words, the VMPFC might provide the cognitive tools to survive both when animals need to
484 obtain diverse food resources from a rich environment and when they must learn to forage on their
485 own earlier in their life. Even if similar arguments had been already advanced based on experiments
486 in individual species (rhesus macaques: San-Galli et al., 2016 or humans: Rushworth & Behrens,
487 2008), the present work is the first direct demonstration of a relationship between a specific brain
488 region and a set of specific ecological variables across several primate species.

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

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

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

515 Altogether, it seems reasonable to conclude that the specific cognitive operations associated with
516 the VMPFC are strongly related to an increase in dietary quality and potentially to the complexity
517 of associated foraging strategies. Our results are in line with several studies that emphasize the key
518 influence of feeding ecology on evolution of primate cognition (De Casien et al., 2017; Powell et
519 al., 2017; Rosati, 2017; Schuppli et al., 2016b; Zuberbühler & Janmaat, 2010). Even if the primate
520 species tested in our study spanned a large range of brain sizes found in living primates (suggesting
521 that the results may reflect a general pattern for Old World primates, at least), our conclusions must
522 be taken with caution given our small sample size, and our analysis should be extended to more
523 primate species. In addition, our study confirms that the relationship between feeding ecology and
524 cognition is strong enough to be detected by using such a crude proxy for cognitive skills as brain
525 size (cf. the positive effect of daily traveled distance not only on the whole brain but also on the
526 gyrus rectus and on the somatosensory cortex). The exact cognitive operations and the
527 neuroanatomical substrates underlying this relation, however, still needs to be established. Our
528 work provides a significant step in that direction, by demonstrating that the relationship between
529 ecology, neurobiology and cognition can be better captured with a more specific brain measure, and
530 presumably a more specific cognitive operation. The strong modulation of VMPFC size by the diet
531 quality paves the way for a more specific exploration of the neurobiological and cognitive
532 operations underlying foraging. Conversely, this works also provides a critical insight into the
533 ecological function of distinct brain systems, complementing the studies conducted in laboratory
534 settings (Kolling et al., 2012; San-Galli et al., 2016). More generally, the capacity to guide behavior
535 in complex and variable environment in order to fulfill energetic requirements may have had a
536 major impact on primate evolution. Together with previous studies (Foley & Lee, 1991; Reader &
537 Laland, 2002; Zink & Lieberman, 2016), we suggest that foraging strategies, together with
538 extractive abilities (e.g. tool use), manipulative complexity and food processing techniques played a
539 primary role in the evolution of cognition in hominids (i.e. *Pongo*, *Pan*, *Gorilla* and *Homo*
540 including their immediate ancestors). Efficient foraging and associated behavioral and technical
541 innovations (van Schaik, 2016) may have been particularly favored among hominin species (i.e.
542 modern humans, their direct ancestors, and their extinct relatives) who complexified foraging
543 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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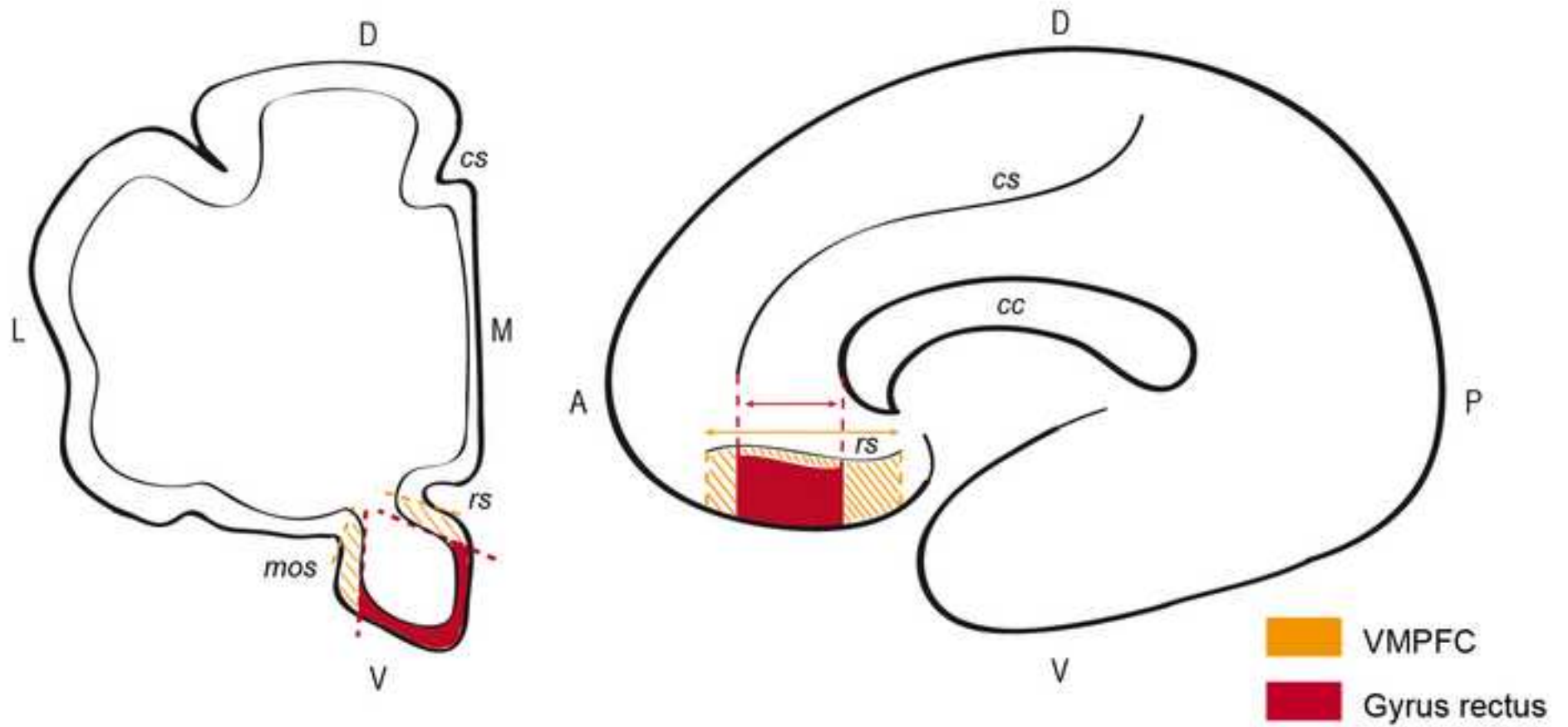


Figure2

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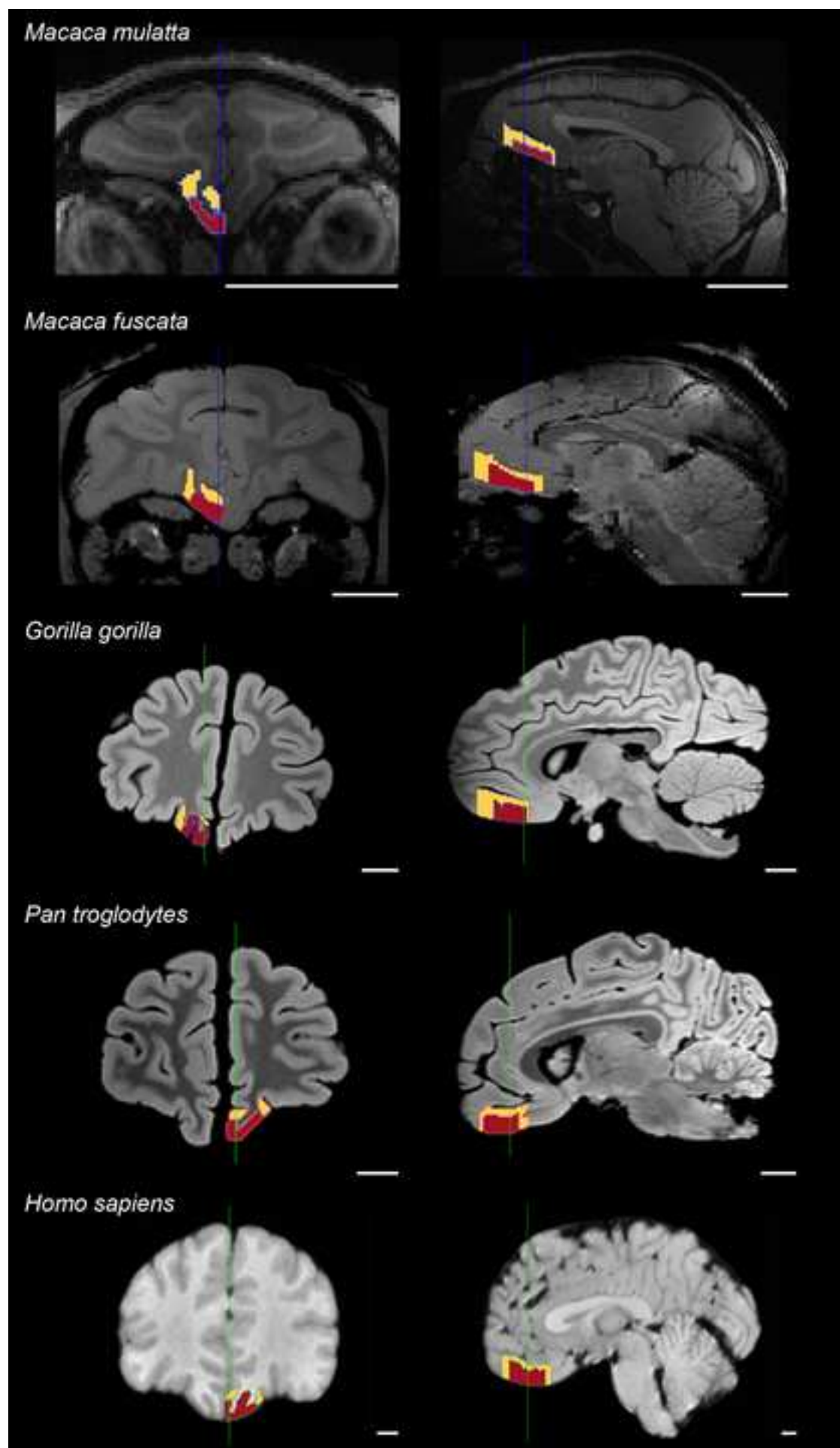


Figure3
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