Linking the evolution of two prefrontal brain regions to social and foraging challenges in primates

Authors:
Sebastien Bouret (1), Emmanuel Paradis (2), Sandrine Prat (3), Laurie Castro (3, 4), Pauline Perez (1), Emmanuel Gilissen (5,6), Cécile Garcia (4)

Affiliations

(1) Team Motivation Brain & Behavior, ICM, CNRS UMR 7225 - INSERM U1127 -UPMC UMRS 1127, Hôpital Pitié-Salpêtrière, 47 Boulevard de l'Hôpital, 75013 Paris, France.

(2) ISEM, Univ. Montpellier, IRD, CNRS, Montpellier, France

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

(4) UMR 7206 Eco-anthropologie, CNRS - MNHN – Univ. Paris Cité, Musée de l'Homme, 17 Place du Trocadéro, 75116 Paris, France.

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

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

ORCID:

SB: 0000-0003-2279-6161
EP: 0000-0003-3092-2199
SP: 0000-0003-3024-1959
CG: 0000-0002-2591-5245

Abstract

The diversity of cognitive skills across primates remains both a fascinating and a controversial issue. Recent comparative studies provided conflicting results regarding the contribution of social vs ecological constraints to the evolution of cognition. Here, we used an interdisciplinary approach combining comparative cognitive neurosciences and behavioral ecology. Using brain imaging data from 16 primate species, we measured the size of two prefrontal brain regions, the frontal pole (FP) and the dorso-lateral prefrontal cortex (DLPFC), respectively involved in metacognition and working memory, and examined their relation to a combination of socio-ecological variables. The size of these prefrontal regions, as well as the whole brain, was best explained by three variables: body mass, daily traveled distance (an index of ecological constraints) and population density (an index of social constraints). The strong influence of ecological constraints on FP and DLPFC volumes suggests that both metacognition and working memory are critical for foraging in primates. Interestingly, FP volume was much more sensitive to social constraints than DLPFC volume, in line with laboratory studies showing an implication of FP in complex social interactions. Thus, our data highlights the relative weight of social vs ecological constraints on the evolution of specific prefrontal brain regions and their associated cognitive operations in primates.

Keywords:
Primates, brain evolution, phylogenetic comparative studies, cognition, prefrontal cortex

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Introduction:

Numerous studies have addressed the mechanisms underlying the evolution of cognitive abilities in primates, using brain size as a proxy (Powell, Isler et al. 2017, Chambers, Heldstab et al. 2021, van Schaik, Triki et al. 2021, DeCasien, Barton et al. 2022). One of the major hypotheses, referred to as the 'social brain' hypothesis, proposes that social interactions require higher cognitive skills such that the complexity of social interactions played a central role in the increase in brain size during primate evolution (Dunbar 1998). Another major theory, referred to as the 'ecological brain' hypothesis, proposes that the increase in brain size and corresponding cognitive skills was driven by the need to build mental representations in order to forage efficiently (Milton 1981, Milton 1993). Critically, both of these theories are based on the assumption that the whole brain volume is a good proxy for overall cognitive abilities, and that these global abilities can benefit social interactions or foraging, across species in an evolutionary framework. But clearly, the level of precision of such neuro-cognitive scenario remains limited, given the precision with which neuroscience and psychology have characterized the brain functional anatomy and cognition, respectively.

Imaging studies in humans have identified a network of brain regions involved in social interactions, and this network is often referred to as the social brain (Stanley and Adolphs 2013). Recent comparative studies have shown that it also existed in macaques (Sallet, Mars et al. 2011, Rushworth, Mars et al. 2013, Testard, Brent et al. 2022). Along the same lines, laboratory studies have also proposed that a set of specific brain regions (e.g. cingulate cortex) was underlying foraging in humans and macaques (eg (Hayden, Pearson et al. 2011, Kolling, Behrens et al. 2012). These studies, however, have only been conducted in a handful of species and in very artificial conditions, such that the relation between these brain regions and natural behavior or evolution remains elusive. In terms of the cognitive processes involved, 'social interactions' and 'foraging' remain poorly specific and at least in primates, they probably involve myriads of more elementary cognitive operations. For example, social interactions involve some form of categorization of facial expressions and metacognition, and the brain regions associated with these elementary cognitive operations (e.g. frontal pole or temporo-parietal junction) are usually part of the 'social brain', i.e. the set of brain regions associated with social interactions (Gallagher and Frith 2003, Rushworth, Mars et al. 2013, Devaine, San-Galli et al. 2017, de Gelder and Poyo Solanas 2021, de Gelder 2023, Deen, Schwiedrzik et al. 2023). Along the same lines, foraging is thought to require mental spatio-temporal representations of food availability and values, and these elementary cognitive operations rely upon a distinct set of brain regions, including the hippocampus and the ventromedial prefrontal cortex (Zuberbühler and Janmaat 2010, Lin, Horner et al. 2015, Louail, Gilissen et al. 2019, Vikbladh, Meager et al. 2019). Finally, the brain systems potentially involved in social cognition and foraging partially overlap, especially in the frontal lobes (Gallagher and Frith 2003, Rudebeck, Walton et al. 2006, Kolling, Behrens et al. 2012, Yoshida, Saito et al. 2012, Barbey, Colom et al. 2014, Mansouri, Koechlin et al. 2017). This partial overlap between the networks referred to as the 'social brain' and the 'ecological brain' is in line with the idea that some elementary cognitive operations are generic enough to be involved in multiple contexts (Garcia, Bouret et al. 2021, Shultz and Dunbar 2022). This is typically the case for executive functions (e.g. working memory), which allow to organize behavior over space and time to reach a goal, and rely upon several regions of the prefrontal cortex (Luria 1973, Fuster 2008).

Given the complexity encountered in natural environments, it is hazardous to extrapolate these findings in artificial laboratory conditions and in a handful of species to the decision-making processes in both social and food dimensions occurring in wild primates, for which the diversity of social interactions (e.g. number of individuals an animal can remember, degree of social awareness i.e. knowledge and representation of the dominance hierarchy, kinship relations or friendship associations) and foraging behaviors (e.g. food processing techniques, knowledge of harvesting schedules, extractive foraging) require much more cognitive flexibility. One can wonder to what extent these neuro-cognitive concepts (i.e. elementary cognitive operation and their underlying cerebral substrate) can be used as theoretical bricks to understand the diversity of natural behaviors reported in the wild and their evolution across species.

In terms of evolution, the functional heterogeneity of distinct brain regions is captured by the notion of 'mosaic brain', where distinct brain regions could show a specific relation with various

socio-ecological challenges, and therefore have relatively separate evolutionary trajectories (Barton and Harvey 2000, DeCasien and Higham 2019). But these relations between specific brain regions and socio-ecological variables across species provide little insight into the cognitive processes that could be at play. Thus, it remains challenging to bridge the gap between 1) laboratory studies relating brain regions to elementary cognitive operations in individual species and 2) studies relating brain regions to socio-ecological challenges through an evolutionary scenario (i.e. across numerous species).

In order to bridge this gap, we designed this study to derive and test predictions where a set of well-identified elementary cognitive operations and their associated brain regions (as studied in laboratory conditions) could be involved in more natural functions (as assessed in wild animals living in their natural environments). We focused on two well-known cognitive operations, both considered as executive functions, and involving distinct regions of the prefrontal cortex: metacognition, which involves the frontal pole (FP), and working memory, which involves the dorso-lateral prefrontal cortex (DLPFC), as demonstrated by extensive work in humans and macaques (Fuster 2008, Passingham, Passingham et al. 2012, Mansouri, Koechlin et al. 2017). Based on the literature, we hypothesized that FP and metacognition would be associated both with social interactions (by supporting theory of mind, the ability of an individual to conceptualize others' states of mind) and with foraging (by enabling complex planning) (Frith 2007, Fleming and Dolan 2012, Devaine, San-Galli et al. 2017, Mansouri, Koechlin et al. 2017). For example, group hunting, which involves both social and foraging functions, only occurs in a few primate species where metacognition is thought to be particularly developed (Boesch 1994, van Schaik 2016, Conard, Serangeli et al. 2020, Garcia, Bouret et al. 2021). Concerning the DLPFC, given its very clear implication in working memory and planning, we speculated that it would be critically involved in foraging. Its potential relation with social interactions, however, was less clear: on one hand, DLPFC is rarely associated with social interactions in laboratory studies, but on the other hand working memory and planning could readily be involved in complex social interactions in more natural conditions (Frith 2007, Fuster 2008, Passingham, Passingham et al. 2012, Sallet, Mars et al. 2013).

To evaluate the relevance of laboratory-based neuro-cognitive concepts for understanding which cognitive operations could be mobilized to overcome specific socio-ecological challenges in the wild and their variability across species, we addressed two central questions: 1) *to what extent does this functional mapping of prefrontal regions generalize across primates, and 2) to what extent does the functional mapping between brain regions and specific executive functions observed in laboratory relate to socio-ecological variables measured in natural conditions?*

To address these questions, we measured the volume of the two prefrontal regions of interest (FP and DLPFC) in 16 primate species and evaluated the influence of key socio-ecological factors on the size of these regions. Based on the known positive relation between the size of a given brain region (or the number of corresponding neurons), and the relative importance of its associated function, both within and across species, we assume that the size of each brain region can be taken as a proxy for the weight of its associated function on behavior (Barton and Harvey 2000, Maguire, Gadian et al. 2000, Sallet, Mars et al. 2011, Barks, Calhoun et al. 2014, Herculano-Houzel, Kaas et al. 2016, Herculano-Houzel 2017, DeCasien and Higham 2019, Louail, Gilissen et al. 2019, Ferrucci, Nougaret et al. 2022, Testard, Brent et al. 2022). These two regions were chosen and identified based on functional maps and reliable macroscopic landmarks, rather than cytoarchitectonic criteria, to maximize the reliability of the comparative approach (see also (Louail, Gilissen et al. 2019). Anatomical studies have shown that these regions and landmarks were relatively well conserved between humans and macaques, both in terms of cytoarchitectonics and connectivity profiles (Petrides, Tomaiuolo et al. 2012, Sallet, Mars et al. 2013, Amiez, Sallet et al. 2019). Finally, the cognitive functions in which they are involved appear relatively well conserved between macaques and humans (Fuster 2008, Mansouri, Koechlin et al. 2017). In addition to these two regions, we also used measures of whole brain volume as a reference to facilitate comparison with other studies that only use whole brain measures. The 16 primate species were chosen to cover a wide range of phylogenetic distances coupled to a diversity of socio-ecological variables. We compared the influence of several combinations of these socio-ecological variables on the variability in size of each brain region of interest, and interpreted it in the light of its known function in laboratory conditions. Thus, we could evaluate the strength of the relation between specific regions of the

prefrontal cortex and specific socio-ecological variables across species, as observed in the wild, thereby complementing laboratory studies and bridging the gap between cognitive neurosciences, behavioral ecology and primate evolution.

2. Material & Methods

Sample

Thirty one brain magnetic resonance (MRI) 3D reconstructions from 16 primate species (*Ateles fusciceps*, n=1; *Cebus capucinus*, n=1; *Cercopithecus mitis*, n= 1; *Gorilla gorilla*, n=5; *Gorilla beringei*, n=1; *Homo sapiens*, n=4; *Hylobates lar*, n=1; *Lagothrix lagotricha*, n=1; *Lophocebus albigena*, n=1; *Macaca fascicularis*, n=1; *Macaca fuscata*, n=4; *Macaca mulatta*, n=2*; Pan troglodytes*, n=5; *Pan paniscus*, n=1; *Papio papio*, n=1, *Pongo pygmaeus*, n=1) were used in this study. Japanese macaques (*M. fuscata*) and rhesus macaques (*M. mulatta*) were captive animals scanned at the National Institutes for Quantum and Radiological Science and Technology (Chiba, Japan) and at Brain and Spine Institute (Paris, France), respectively. *P. troglodytes* and *G. 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. The *P. paniscus* and *G. beringei* brains came from the Royal Museum for Central Africa (RMCA) (Tervuren, Belgium) and the Royal Belgian Institute of Natural Sciences (Bruxelles, Belgium). All the *Pan* and *Gorilla* specimens have been scanned at University of Leuven (KUL). The brain scans *A. fusciceps, C. mitis,* and *L. lagotricha* were obtained from the Primate Brain Bank, NIN Utrecht University. Finally, the remaining species (*C. capucinus*, *H. lar*, *L. albigena*, *P. pygmaeus*, *M. fascicularis, P. papio* and one specimen of *H. sapiens*) came from the brain catalogue website (https://braincatalogue.org), which gathers scans of specimens from the collections of the Muséum national d'Histoire naturelle (Paris). The three other *H. sapiens* brain scans were obtained from the Allen Institute (online brain atlas). All specimens were sexually mature at the time of scanning. The sexes of individuals were mostly unknown. Moreover, some specimens in the sample came from captivity. Thus, we neglected the effects of captivity and sex on brain/endocranium measurements, which were both shown to be very small compared to inter-species differences (Isler and van Schaik 2012).

Processing of brain MRI and measurements

Brain measurements (visualization, segmentation and quantification of brain tissues volumes) were processed using Avizo v9.0 software. The whole brain volume was measured in order to facilitate comparisons with the literature. The cerebellum was excluded from all brain measurements, because it was missing on some of the MRI scans (gorilla brains). Whole brain segmentation was performed using the semi-automated tool in Avizo that enables to select a material or structure according to a specific gray-level threshold. It was however necessary to bring some manual corrections, for example when the brain had a similar gray-level than an adjacent tissue. Segmentations of the frontal pole (FP) and the dorso-lateral prefrontal cortex (DLPFC) were carried out manually with the brush tool, slice by slice of the MRI scan.

The frontal pole is the most rostral part of the prefrontal cortex. Cytoarchitectonic studies indicate that it strongly overlaps with Brodmann area 10 (BA 10) (Semendeferi, Armstrong et al. 2001, Ongür, Ferry et al. 2003, Ramnani and Owen 2004, Tsujimoto, Genovesio et al. 2011). Besides cytoarchitectonic landmarks, the frontal pole can also be identified based on connectivity patterns: it receives projections from the temporal superior cortex (Petrides 2005) and has connections with the superior temporal sulcus (Sallet, Mars et al. 2013). We also used the probabilistic maps of the frontal pole proposed by John et al. (John, Yashavantha et al. 2007) and Bludau et al. (Bludau, Eickhoff et al. 2014). We delimited the frontal pole according to different criteria: it should match the functional anatomy for known species (macaques and humans, essentially) and be reliable enough to be applied to other species using macroscopic neuroanatomical landmarks. We integrated these criteria and the data from the literature on brain atlases of rhesus macaques and humans (Saleem and Logothetis 2007, Borden, Stefan et al. 2015) to define visible limits of the frontal pole, as shown in Figure 1. The anterior limit of the frontal pole was defined as the anterior limit of the brain. The cingulate sulcus represented the posterior limit. The ventral limit was set as the dorsal limit of the gyrus rectus. Finally, the dorsal limit was defined as the fundus of the superior frontal sulcus in humans and apes, or the principal sulcus in monkeys. We chose this very conservative dorsal limit in monkeys to avoid any overlap with what could be considered as part of the

DLPFC (typically, BA9). However, we are aware that several studies in macaques suggest that the frontal pole in monkeys might extend more dorsally (Tsujimoto, Genovesio et al. 2011, Sallet, Mars et al. 2013). Thus, we also conducted a series of measures with a less conservative dorsal limit for the frontal pole (see supplementary material section 4).

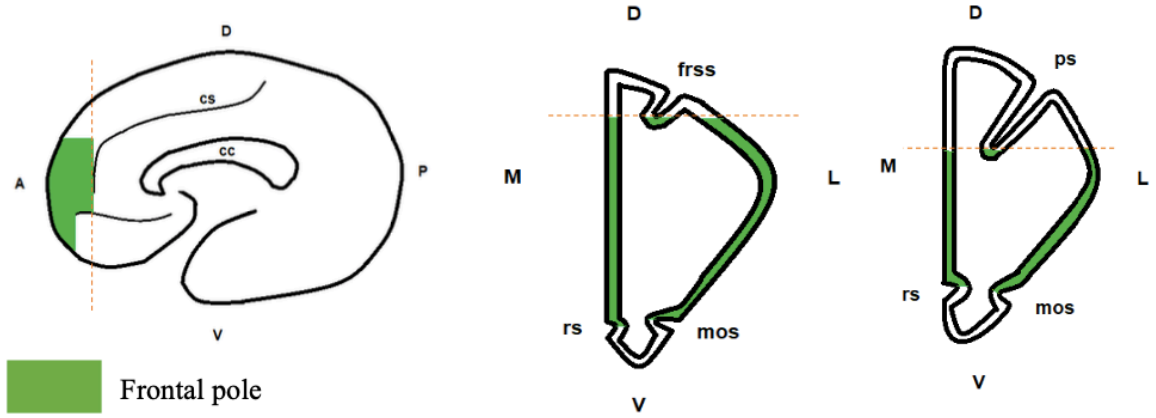
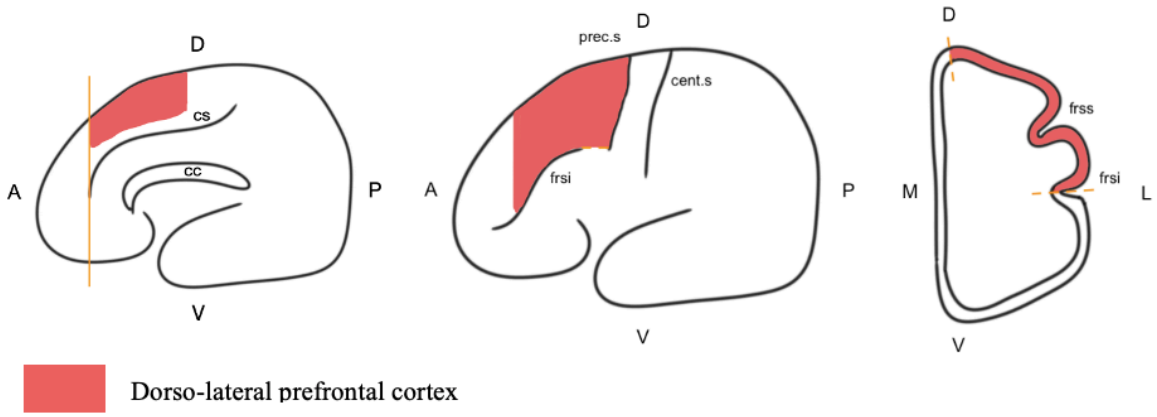


Figure 1. *Boundaries of the frontal pole. From left to right: sagittal view, coronal view for great apes and humans, coronal view for monkeys. Frontal pole is in green. Abbreviations: cs: cingulate sulcus; cc: corpus callosum; rs: rostral sulcus; mos: medial-orbital sulcus; frss: superior frontal sulcus; ps: principal sulcus; D: dorsal; V: ventral; M: medial; L: lateral; A: anterior; P: posterior.*

Similarly, the dorso-lateral prefrontal cortex was measured by combining functional and anatomical data from the literature to identify reliable macroscopic landmarks (Levy and Goldman-Rakic 2000, Passingham and Sakai 2004, Passingham, Passingham et al. 2012, Petrides, Tomaiuolo et al. 2012, Sallet, Mars et al. 2013). Given the major difference in sulcal organization between monkeys and greats apes, we used different landmarks, shown on figures 2a and 2b. DLPFC comprises portions of middle frontal gyrus and superior frontal gyrus in great apes and lies in and around the principal sulcus in macaques. Then, the ventral limit was set as the fundus of the principal sulcus for monkeys, and the frontal inferior sulcus for apes and humans. The anterior limit of the DLPFC was defined as the posterior limit of the frontal pole, which was the cingulate sulcus. For apes and humans, the posterior limit was defined as the precentral sulcus, whereas in monkeys it was defined as the end of the arcuate sulcus. Finally, the medial limit was designated as the inter-hemispheric sulcus.

a)



b)

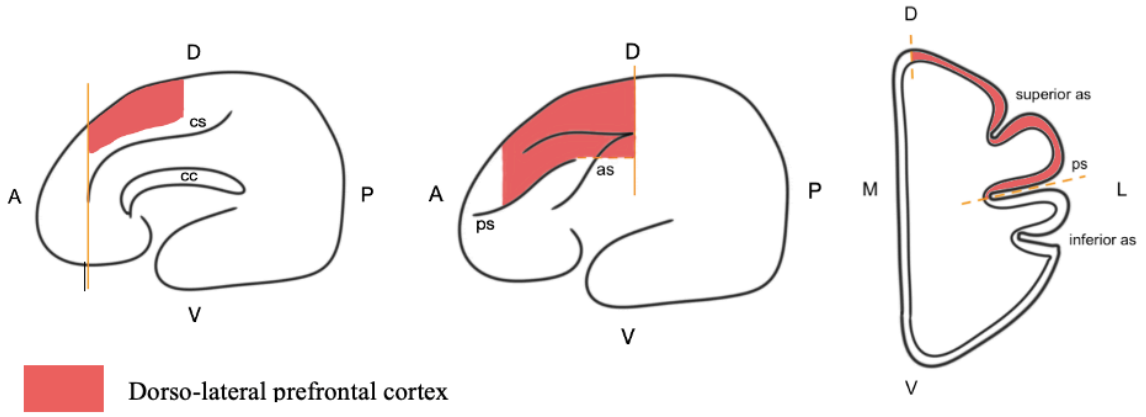


Figure 2. *Boundaries of the dorso-lateral prefrontal cortex*

*a**) for great apes and humans.** From left to right: sagittal view, external view, coronal view. Abbreviations: cs: cingulate sulcus; cc: corpsus callosum; frsi: frontal inferior sulcus; frss: frontal superior sulcus; cent.s: central sulcus; prec.s: precentral sulcus; A: anterior: P: posterior; D: dorsal; V: ventral; L: lateral; M: medial.*

*b**) for monkeys.** From left to right: sagittal view, external view, coronal view. Abbreviations: cs: cingulate sulcus; cc: corpsus callosum; ps: principal sulcus; as: arcuate sulcus; A: anterior: P: posterior; D: dorsal; V: ventral; L: lateral; M: medial.*

Socio-ecological and phylogenetic data

Eleven socio-ecological variables were selected for the analyses, gathered in different categories: body condition (body mass), diet (dietary quality index and tool use), movements and ranging behavior (daily traveled distance), social parameters (group size, population density, social system), and variables related to reproduction and life-history traits (mating system, mate guarding, seasonal breeding, and weaning age). Each variable was assessed based on the literature on wild populations, whenever possible, which was the case in a vast majority of cases (and otherwise specified, see below). We verified that these variables showed minimal correlation (see supplementary material section 2).

The dietary quality index (DQI) was used to characterize the richness of the dietary spectrum and was calculated from the formula DQI = 1s + 2r + 3,5a, where s is the percentage of plant structural parts in the diet, r the percentage of plant reproductive parts and a the percentage of animal preys (Sailer, Gaulin et al. 1985). Thereby, a low index (around 100) characterizes folivorous diets, while a high index (around 200) characterizes more diversified diets (including animals and fruits). Tool use represented the occurrence and complexity of using objects in feeding contexts. We took the

definition of St Amant and Horton (St Amant and Horton 2008) which states that "tool use is the exertion of control over a freely manipulable external object (the tool) with the goal of (1) altering the physical properties of another object, substance, surface or medium (the target, which may be the tool user or another organism) via a dynamic mechanical interaction, or (2) mediating the flow of information between the tool user and the environment or other organisms in the environment." It includes notions of control over an object and goal. The presence or absence of tool use in feeding contexts for species in the wild was assessed from literature. Daily traveled distance was expressed in kilometers. Regarding social parameters, group size was defined as the mean social group size of a species. We also used population density (number of individuals per km^2) in order to bring spatial precisions over the group size variable. Group size and population density data were collected and compiled from several primary and secondary sources (see supplementary material section 1). For group size and population density of *Homo sapiens*, we took an average between industrialized societies and hunter-gatherers societies. Social system was defined using the four-way categorization scheme typically used in primate studies and included solitary, pair-living, polygyny and polygynandry (see also (DeCasien, Williams et al. 2017). Mating system categories included spatial polygyny (among solitary species, agonistically powerful males defend mating access to several females), monogamy (one male is socially bonded to one breeding female), polyandry (one female is simultaneously bonded to multiple males), harem polygyny (one male is simultaneously bonded to multiple breeding females) and polygynandry (multiple males and multiple females breed within the same group, but no lasting bonds are formed) (Clutton-Brock 1989). Mate guarding is defined as a female monopolization over an extended period of time to secure paternity (Manson 1997) and is characterized by male attempts to associate and copulate with a female during the presumptive fertile period (Manson 1997, Dixson and Oxford University Press. 2012). This categorical variable was divided into two categories: species using mate guarding and those that do not usually show this behavior. Finally, in order to account for differences in lifespan between study species, the weaning age was calculated as a percentage of maximum lifespan. For some missing values from wild studies, data were taken from studies in captivity and compared to data related to close species (in the wild and in captivity). This method was applied for the weaning age and the dietary quality index of *Papio papio*, with other species of baboons. Moreover, the absence of tool use for *Lophocebus albigena* was inferred from the absence of published papers or other forms of communication on this subject.

The phylogenetic tree was obtained from the 10ktrees website (https://10ktrees.nunn- lab.org/Primates/downloadTrees.php, version 3). This version (Arnold, Matthews et al. 2010) provides a Bayesian inference of the primate phylogeny based on collected data for eleven mitochondrial and six autosomal genes from GenBank across 301 primate species.

Statistical analysis

We used a phylogenetic generalized least squares (PGLS) approach to evaluate the joint influence of socio-ecological variables on the neuro-anatomical variability across species (Grafen 1989). This approach allowed us to take into account the phylogenetic relation across species when evaluating the influence of socio-ecological variables on their neuroanatomy.

To identify the combination of socio-ecological variables that best predicted the size of a given brain region, given the phylogenetic relations across species, we fitted neuro-anatomical data with several PGLS models, each reflecting a specific combination of socio-ecological variables. Brain measurements and body mass were log10-transformed before analyses. For the same model several correlation structures were used: standard Brownian, Pagel's (Pagel 1999), and OU-based (Martins and Hansen 1997) and were compared based on the smallest AIC values (Akaike 1974). For a given correlation structure, the effects of the social and ecological variables were assessed with likelihood-ratio tests. All analyses were performed with ape (Paradis and Schliep 2019).

We also calculated standardized coefficients, to facilitate comparison. Standardized coefficients were calculated by the product of the coefficient estimated by PGLS with the ratio of the standard-deviation of the predictor on the standard-deviation of the response.

Because of the relatively small number of species in our sample, we assessed the reliability of the inferred models with a "leave-one-out" procedure: we removed one species from the data and the

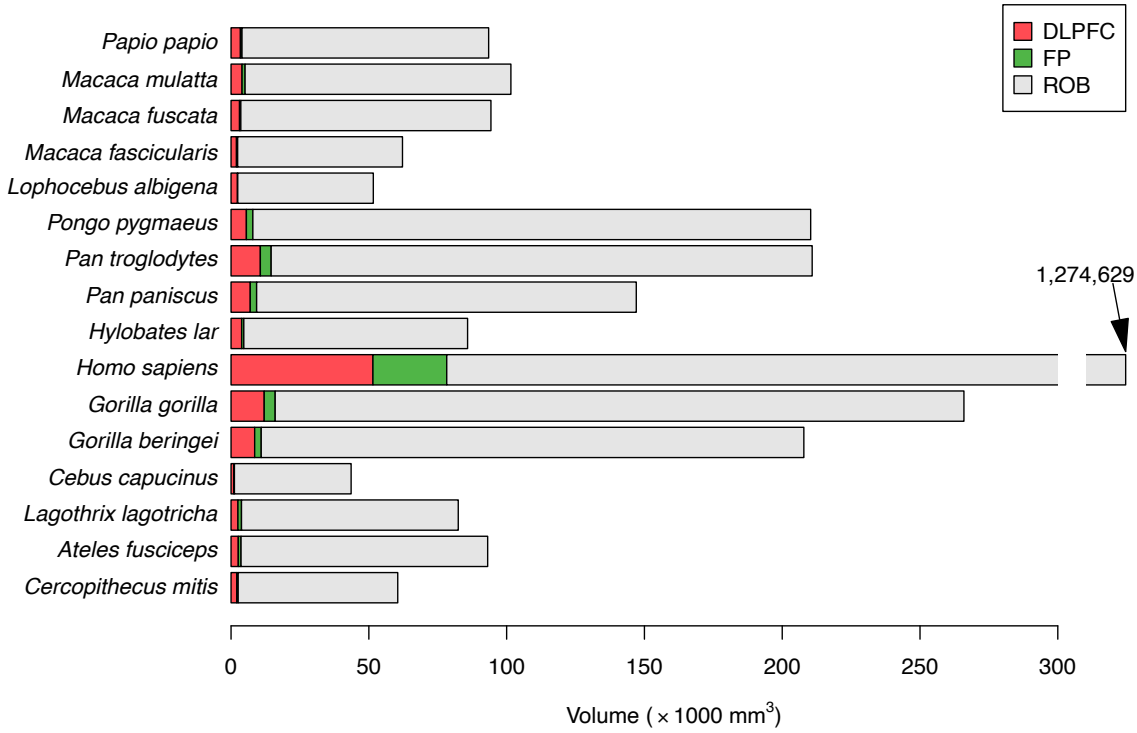
phylogenetic tree and re-fitted the model selected previously. This was repeated for each species. The details of this procedure are provided in supplementary material, section 6.

3. Results

1) Neuroanatomical measures

The average size of the regions of interest (whole brain, FP and DLPFC) are shown on figure 3. As expected, all these measures were highly correlated (all r=0.99, Pearson correlation). Not only the volumes of DLPFC and FP, which are two neighboring regions of the prefrontal cortex, but also each of these regions and the whole brain.

Figure 3. *Average values of the 3 regions of interest. Each line provides the cumulated volumes of the dorso-lateral prefrontal cortex (DLPFC, green), the frontal pole (FP, grey) and the rest of the brain (ROB, blue), such that the size of each bar represents the whole brain volume. Note: for Homo sapiens, the bar has been truncated, since its value was out of scale with the other species.*



2) Influence of socio-ecological variables on whole brain volume

We used a model-comparison approach to select the best combination of socio-ecological variables accounting for the variability in whole brain size across species using PGLS. Details of the different models are provided in supplementary material (SI section 3).

The best model explaining the volume of the whole brain is the one that includes body mass, daily traveled distance, and population density. The values of the estimated coefficients are provided in table 1. These three variables have a positive influence on the volume of the whole brain. Even if all three factors had a significant effect, their influence on the whole brain volume seemed to differ: there was an order of magnitude between the estimated beta (i.e. contribution) of body mass (0.47 +/- 0.15) and that of daily traveled distance (0.05 +/- 0.01). There was also an order of magnitude between the estimated beta of daily traveled distance and population density (0.007 +/- 0.003). Note that the standardized beta (see methods) is also greater for daily traveled distance than for population density (see supplementary material section 5).

Table 1: Estimated coefficients of socio-ecological variables for the whole brain volume.

Predictor	Beta (estimate)	Beta (Std. Error)	Standardized beta	t-value	p. value
Intercept	4.26	0.24		17.8	0
Body mass (log)	0.47	0.15	0.71	3.10	0.009
Daily Traveled Distance	0.05	0.01	0.42	4.08	0.002
Population density	0.007	0.003	0.35	2.35	0.036

We evaluated the robustness of the influence of these socio-ecological variables on whole brain volume using a « leave-one-out » procedure. Thus, each model was tested 16 times (one per species removed) and we evaluated the reliability of each variable after each species was removed. The details of this analysis are provided in the supplementary material (section 4). The influence of body mass was very robust, in that it remained significant for all models where one species was removed. Daily traveled distance remained significant for all models but one, whereas population density lost significance ($p>0.05$) for four models where one species was removed, even if in all cases the estimated coefficient remained positive. Thus, the influence of body mass and daily traveled distance are very robust for the combination of species used for the analysis. It is less the case for population density, even if based on model comparison this variable plays a significant role in increasing the volume of the whole brain.

In summary, this analysis indicates that the volume of the whole brain across primates is positively modulated by body mass, as well as social (population density) and ecological (daily traveled distance) variables. The weight of the ecological variable, however, seems to be slightly stronger and more reliable than the weight of the social variable.

3) Influence of socio-ecological variables on Frontal Pole volume

As for the whole brain, the best model accounting for the volume of the frontal pole is the one that includes body mass, daily traveled distance and population density. Details of the different models are provided in supplementary material (section 3). The values of estimated coefficients, all positive, are provided in table 2.

As for the whole brain, the largest effect is body mass (0.69 +/- 0.23), then daily traveled distance (0.07 +/- 0.02) and population density (0.011 +/- 0.004). By comparison with the whole brain, however, the coefficients for daily traveled distance and population density have the same order of magnitude such that their impact on the volume of the frontal pole seems to be equivalent. Note that the standardized beta for daily traveled distance is smaller than for population density, whereas it was the opposite for the whole brain, i.e. bigger for daily traveled distance compared to population density.

As indicated in the methods section, we also conducted an analysis using a less conservative evaluation of FP volumes in monkeys. As shown in supplementary material (section 4), the relative weight of population density decreased when adding cortical regions dorsal to the principal sulcus. Thus, when using a less conservative estimate of the FP volume, its relation with socio-ecological variables was closer to that of the whole brain.

Table 2: Estimated coefficients of socioecological variables for the Frontal Pole volume.

Predictor	Beta (estimate)	Beta (Std. Error)	standardized beta	t-value	p. value
Intercept	1.87	0.37		5.08	0
Body mass (log)	0.69	0.23	0.66	2.96	0.012
Daily Traveled Distance	0.07	0.02	0.36	3.62	0.004
Population density	0.011	0.004	0.38	2.62	0.022

As for the whole brain, we evaluated the reliability of the model's variables using a "leave-one-out" procedure at the species level. The results of this analysis were similar to what we reported for the whole brain: the influence of body mass remained significant whatever the species removed, only one species caused daily travelled distance to lose significance and three species caused population density to lose significance ($p>0.05$). As can be seen in the supplementary material (section 4), however, the decrease in the weight of the estimated coefficient for population density was less dramatic for these three species, compared to what we observed for the whole brain. As specified in the method section, we also conducted an analysis where the dorsal limit of the frontal pole was less conservative, to include a part of the brain which might belong to the FP but also to the DLPFC (see results in supplementary material, section 4).

Altogether, these data indicate that the volume of the frontal pole across primates is positively modulated by body mass as well as by both population density and daily traveled distance, in line with the idea that it is affected by both social and ecological components. By comparison with the whole brain, the relative influence of the social (Population density) and ecological (Daily Traveled Distance) variables are more balanced.

4) Influence of socio-ecological variables on Dorso-Lateral Prefrontal Cortex volume

As for the whole brain and the frontal pole, the best model for the DLPFC is the one that includes body mass, daily traveled distance and population density. Details of the different models are provided in supplementary material (section 3). The values of estimated coefficients, all positive, are provided in table 3.

Table 3: Estimated coefficients of socio-ecological variables for the DLPFC volume.

Predictor	Beta (estimate)	Beta (Std. Error)	standardized beta	t-value	p. value
Intercept	2.78	0.28		9.99	0
Body mass (log)	0.47	0.18	0.62	2.67	0.021
Daily Traveled Distance	0.047	0.014	0.35	3.3	0.006
Population density	0.006	0.003	0.30	2.01	0.067

As for the whole brain and the frontal pole, the largest effect is body mass (0.47 +/- 0.18), followed by daily traveled distance (0.047 +/- 0.01). Even if the best model for DLPFC includes population density, its influence was very small (0.006 +/- 0.003) and failed to reach significance (p=0.067). The « leave-one-out » procedure confirmed the reliability of the model for body mass (with no species causing that variable to lose significance when removed) and that of daily traveled distance (only one species causing that variable to lose significance when removed). The influence of population density only reached significance for two of the models where one species was removed, but it failed to reach significance for all other combinations tested (n=14), as it was the case for the original one with all 16 species. Details of this analysis can be found in the supplementary material, section 4. In other words, the relative weakness of the influence of population density compared to that of other variables is relatively reliable across the combinations of species used for the tests.

In summary, the volume of the DLPFC across primates is also positively modulated by body mass as well as by both ecological (daily traveled distance) and social (population density) variables, but the influence of the later appears much weaker than that of the former.

4. Discussion

We evaluated the influence of eleven socio-ecological variables on the size of the whole brain as well as two specific brain regions involved in executive functions: the frontal pole and the dorsolateral prefrontal cortex. All together, our results showed that all three cerebral measures strongly correlated and were influenced by the same set of socio-ecological variables: body mass, daily traveled distance and population density. As expected from evidence suggesting brain-body covariation (Martin 1981), body mass had a strong and reliable influence on all brain measures. Daily traveled distance, a proxy for how challenging is foraging, also had a clear positive influence on all brain measures. Finally, population density, a proxy for how challenging and complex are social interactions, was generally less powerful at explaining neuro-anatomical variability, but it was also the variable showing the greatest difference in effect size across brain regions. For the FP, the influence of population density was similar to that of daily traveled distance, but it was much weaker for the whole brain, and it even failed to reach significance for the DLPFC. Thus, our data are generally compatible with the idea that the evolution of executive functions relying upon FP and DLPFC is driven both by ecological and social constraints. Critically, however, the relative influence of these constraints seems to vary across regions, in line with our hypothesis based on the cognitive functions with which they are associated in laboratory conditions. Thus, neuro-cognitive entities as defined in laboratory conditions can readily be articulated with socio-ecological processes in the wild, in order to better understand primate cognition and behavior in natural conditions.

First, we need to consider two methodological questions:
1) How reliable is the difference we reported between brain regions? Even if the same combination of variables accounted for the relative size of all three brain measures, there was a difference in the weight of population density, proxy for social challenges, across the three regions. Indeed, for the FP, the effect of population density was as strong as that of daily traveled distance: both were significant, and their effect size (beta weight) was of the same order of magnitude. Also, they showed a similarly small sensitivity to the « leave-one-out » procedure. Finally, standardized beta weights for population density were greater than for daily traveled distance. By contrast, for the DLPFC, the effect of population density failed to reach significance ($p=0.07$), its beta weight was one order of magnitude smaller than that of daily traveled distance and standardized beta weights for population density were smaller than for daily traveled distance. Finally, this relatively weak influence of population density on DLPFC volume was confirmed by the “leave-one-out” procedure, since the effect of population density on the size of the DLPFC was reliably marginal across all combination of species used to fit the model. Interestingly, the whole brain volume (which is strongly correlated with both FP and DLPFC) seems to show an intermediate tendency: even if the effect of population density appears smaller than that of daily traveled distance (beta weight is one order of magnitude smaller), it is clearly significant, and the « leave-one-out » procedure indicated that it was only slightly less reliable than daily traveled distance, with a significant decrease in model fit quality for four vs. one combination of species. Altogether, this indicates that even if the influence of population density cannot be ruled out for any of the three brain measures, it appears quantitatively smaller for the DLPFC than for the FP. Note that the relative weight of population density also decreased (relative to that of daily traveled distance) when we used a less conservative estimate of FP volumes, which included a dorsal part potentially overlapping with the DLPFC. This is also compatible with the fact that the influence of population density seems to be of intermediate magnitude in the whole brain, which includes both FP and DLPFC.
2) To what extent do these conclusions depend upon the specific sample of species used here? The results of the « leave-one-out » analysis showed that our sample, even if relatively limited, was sufficient to evaluate the relative weight of socio-ecological variables on specific brain regions in primates. Interestingly, the relation between brain region volumes and socio-ecological variables was not completely independent from the sample of species, as previously shown in a study conducted on a larger sample (Powell, Isler et al. 2017). In line with the main analysis (PGLS with all species included), the influence of body mass and daily traveled distance appears very reliable (no more than one species caused the model to fail when removed). The influence of population density appeared less reliable, since it was sensitive to the removal of up to three-four species (as a function of brain region, see previous paragraph). But the influence of individual species is nearly

impossible to interpret, because no apparent obvious pattern emerges. Indeed, the species without which the model failed was not always the same (e.g. humans and baboons have very distinct values for population density, 56 vs. 7.5). Note, however, that getting clear intuitions from the data remains difficult because the PGLS includes the covariance induced by phylogeny to the linear relation across variables. We see no reason to exclude humans (as done in previous studies e.g. (DeCasien and Higham 2019), because even if the brain of *Homo sapiens* is much bigger than others, a general biological law describing the relation between socio-ecology and the brain in primates should apply to humans (Gabi, Neves et al. 2016, Herculano-Houzel 2017). Moreover, even if the human brain is much bigger than that of other primates, the global organization of the frontal cortex appears qualitatively similar in humans and other primates (Sallet, Mars et al. 2013, Gabi, Neves et al. 2016, Herculano-Houzel, Kaas et al. 2016, Barrett, Dawson et al. 2020, Roumazeilles, Eichert et al. 2020). One potential issue with humans is the difficulty to evaluate socio-ecological variables, given that modern human populations show a tremendous geographical variability in terms of socio-ecological variables. But the same problematic applies to other modern primate species (including those confronted to intense anthropization of their habitat) (Beauchamp and Cabana 1990). Thus, the actual potential limitation (which concerns all species) is the reliability with which socio-ecological variables were estimated for each species, given the amount of intra-specific variability. Note, there is also a significant amount of intra-specific variability at the level of the brain, both in humans and non-human primates, but this intra-specific variability was shown to be negligible compared to inter-specific variability (Maguire, Gadian et al. 2000, DeCasien and Higham 2019, Louail, Gilissen et al. 2019, Testard, Brent et al. 2022). Thus, we acknowledge that intra-specific variability could introduce noise in the inter-specific relation between brain measures and socio-ecological variables, but the fact that clear relations could be established with our sample indicates that this source of intra-specific variability was limited enough relative to the inter-species relation between neuroanatomical measures and socio-ecological variables. In other words, the error with which these variables were estimated at the level of individual species was small enough to allow us to study the relation of interest across species, and from that perspective, there is no reason to exclude any species from that analysis and our sample appears reliable enough to characterize the relation between neuroanatomical features and socio-ecological variables across primates.

Our results provide an original insight on the existing debate on the source of inter-species variability in cognitive abilities, as measured using brain volumes, and on the main socio-ecological variables that affect the evolution of specific brain regions. Given that all three brain measures were highly correlated, it is not surprising that their variability across species is predicted by the same model, i.e. the same combination of socio-ecological variables. This is in line with the intuition that across primates the major difference in brain volumes is often accounted for by a difference in size of the prefrontal cortex (Passingham, Passingham et al. 2012); but see (DeCasien, Barton et al. 2022). Importantly, more precise quantitative studies showed that the fraction of neurons in the prefrontal cortex (PFC), relative to the whole brain (8%) was well conserved across primates, such that the key difference across species is not the proportion of prefrontal neurons, but its absolute number (Herculano-Houzel, Collins et al. 2007). In other words, the strong development of executive functions in species with larger prefrontal cortices is related to an absolute increase in number of neurons in the PFC, rather than in an increase in the ratio between the number of neurons in the PFC vs the rest of the brain. In that frame, it seems more appropriate to use absolute measures rather than relative measures, to evaluate the weight of each brain region and its corresponding cognitive function on behavior.
In addition, the exact boundary between FP and DLPFC as functional entities remains difficult to assess, even if the functions attributed to these two regions are clearly distinct (Gallagher and Frith 2003, Passingham and Sakai 2004, Boorman, Behrens et al. 2009, Genovesio, Wise et al. 2013, Koechlin 2016, Preuss and Wise 2021). Our aim here was clearly not to provide a clear identification of anatomical boundaries across brain regions in individual species, as others have done using much finer neuro-anatomical methods. Such a fine neuro-anatomical characterization appears impossible to carry on for a sample size of species compatible with PGLS. More importantly, we make no claim about specific mapping between the regions measured here and either the specific cognitive operations of interest (metacognition vs working memory) or the socio-ecological va-

riables (e.g. social or foraging complexity). First, we are aware of the complexity of identifying neural processes underlying such high level cognitive functions, and even in well controlled laboratory conditions the exact boundaries of cortical regions remains challenging (Petrides 2005, Sallet, Mars et al. 2013, Mansouri, Koechlin et al. 2017). Rather, as specified in the methods, we tried to maximize the reliability of the landmarks that could be identified in all species to compare the relative size of areas that are essentially used as proxies for their known function, as defined in laboratory conditions in macaques and humans. The underlying assumption that we used was that the functional anatomy of the prefrontal cortex was conserved enough in primates such that traits that were common between humans and macaques were also shared with other primates (Sallet, Mars et al. 2013, Bludau, Eickhoff et al. 2014, Amiez, Sallet et al. 2019). Note that studies conducted in marmosets confirm that the functional anatomy of the primate prefrontal cortex is relatively well conserved (Dias, Robbins et al. 1996, Roberts, Tomic et al. 2007). Of course, the neural mechanisms underlying metacognition and working memory are extremely complicated and they involve myriads of other brain regions (e.g. temporal and parietal cortices, as well as subcortical systems), but the contribution of the FP to metacognition and of the DLPFC to working memory is so strong and reliable in humans and laboratory primates that it seems reasonable to assume that, given the relative level of conservation of prefrontal cortex anatomical organization across primates, FP and DLPFC should also play a key role in metacognition and working memory in other primate species, at least those studied here. As for our previous study using a similar approach, this method was reliable enough to capture meaningful and specific effects of interests (Louail, Gilissen et al. 2019). Thus, even if we make no strong claim regarding the specific boundaries of FP and DLPFC, the anatomo-functional difference between these regions, as characterized in a few species used in laboratory experiments is reliable enough to be captured by the variability in socio-ecological variables in a larger set of primates.

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In summary, we are aware of the limitations of our study in terms of anatomical specificity, but these measures appear robust enough to draw original conclusions regarding the relation between functions attributed to FP and DLPFC (metacognition and working memory) in laboratory conditions and socio-ecological variables across 16 primate species. As we and others have done before (within and across species), we assume that the size of a given brain region provides a good proxy of the strength of its influence (through its known function) on behavior (Barton and Harvey 2000, Maguire, Gadian et al. 2000, DeCasien and Higham 2019, Louail, Gilissen et al. 2019). Again, we assume that the size of a brain region is a good proxy for the number of neurons allocated to its function, given the known positive relation between number of cortical neurons and cognitive skills in primates (Herculano-Houzel 2017, Herculano-Houzel 2018). Here, we restricted our analysis to a set of specific functional regions, namely the FP and the DLPFC, which implies that a given region and the neurons that it contains are characterized by a relatively homogenous connectivity pattern and physiological features, as demonstrated by converging evidences from anatomy, physiology, imaging and behavioral tests in laboratory animals (see methods for further details). In that frame, the difference in size of these brain regions across species could readily be used as proxies for the relative importance of their corresponding functions (namely, metacognition for the FP and working memory for the DLPFC). Again, we clearly make no strong claim regarding the exact boundaries of the regions of interest, and their relations with existing laboratory studies in humans or macaques. Rather, we wanted to assess the relation between neuro-cognitive entities (e.g. FP/metacognition vs. DLPFC/working memory) and socio-ecological variables, based on the assumption that the more a given cognitive function would be required to face a given socio-ecological challenge in a given species, the bigger the corresponding brain region would be. From that perspective, these data provide a new insight into the function of the FP and the DLPFC in primates.

The stronger sensitivity of the frontal pole to the variable 'population density' is reminiscent of the social brain hypothesis, i.e. the idea 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 (Dunbar 1998). Critically, the size of the frontal pole and the corresponding development of metacognitive skills is not exclusively related to population density (proxy for social interactions) but also to daily traveled distance (proxy for foraging

complexity). Thus, these data are also compatible with the ecological brain hypothesis (Milton 1981). This dual relation between frontal pole size, social and ecological constraints might be accounted for by the fact that in the wild, social and ecological constraints remain strongly related, even if we did not find strong correlations between those factors in our data set. In reality, it is difficult to treat ecological and social factors as if they were disconnected (Henke-von der Malsburg, Kappeler et al. 2020), and cognitive abilities associated with foraging are likely to play a role in social foraging tactics too (Street, Navarrete et al. 2017). Indeed, greater population density implies a greater inter-individual competition for food, and thus potentially increases in daily traveled distances, and/or the development of sophisticated foraging skills to deal with the increase in scramble competition. But from a cognitive point of view, this also implies that the benefits associated with increased FP volume, and presumably an increase in metacognitive skills, could be related to both social and ecological functions. Indeed, as pointed out earlier, the development of executive functions in general, and metacognitive skills in particular, could have been a critical leverage to allow the development of both complex social interactions (through the use of Theory of Mind) and complex foraging (through flexible, context-dependent planning) (Garcia, Bouret et al. 2021, Shultz and Dunbar 2022). Thus, our work indicates that the notions of 'social brain' and 'ecological brain' should not be mutually exclusive, even when considering specific brain regions. Rather, we confirm intuitions based on laboratory studies that the frontal pole, through its role in metacognition, belongs to both sets of brain regions defined as the social brain and the ecological brain, respectively. Further work would be needed to capture the metacognitive processes underlying social and foraging processes in the wild, as well as their interactions.

The size of the DLPFC, which we used as a proxy for working memory and planning skills, showed a significant relation with daily traveled distance (proxy for foraging complexity), and to a lesser extent with population density (proxy for social complexity). This suggests that the cognitive functions at play in the DLPFC, i.e. working memory and planning, are critical for foraging in primates, especially when they need to travel long distances, and presumably have to deal with more complex navigation strategies. This is clearly in line with the global idea of the ecological brain hypothesis, but here we provide a critical insight into the specific neuro-cognitive operations associated with foraging strategies. The weaker influence of population density, a marker of social complexity, might be surprising at first sight, because a priori working memory and planning could also be strongly involved in complex social interactions (Garcia, Bouret et al. 2021). But it is in line with laboratory data showing that social interactions seem to rely much more upon rostro-medial prefrontal regions compared to DLPFC (Frith 2007, Sallet, Mars et al. 2011, Fleming and Dolan 2012, Testard, Brent et al. 2022). In other words, this work confirms the specificity of the 'social brain'' as defined in laboratory conditions as a set of structures specifically involved in social interactions (Frith 2007, Rushworth, Mars et al. 2013). Critically, again, social and ecological functions are tightly intermingled in primates' natural environment and more specific studies would be needed to clarify how DLPFC-related functions such as working memory are involved in natural conditions, when animals need to face both ecological and social challenges.

This new set of results can be integrated in the general framework of the primate mosaic brain evolution, i.e. the different distinct structures varying in size both within and between species, and reflecting selection for cognitive skills. In line with recently published papers (Smaers, Rothman et al. 2021, van Schaik, Triki et al. 2021, DeCasien, Barton et al. 2022), we argue that the relation between ecology, neurobiology and cognition can be better captured with more specific brain measures, and more specific cognitive operations, than by using the traditional measures of relative brain size alone. We believe that comparisons between brain regions have the potential to identify which patterns of brain region evolution can provide insights into the evolution of cognition. Our new set of results are in agreement with a previous study we conducted on another brain region, the ventromedial prefrontal cortex (VMPFC), critically involved in value-based decision making (Louail, Gilissen et al. 2019). This study was conducted on 29 brain scans from only five species, such that we could not use a PGLS and instead included phylogenetic distance as a co-regressor, along social and ecological variables. As we did here, we also identified the combination of socio-ecological variables that best predicted neuro-anatomical variability across species. Interestingly, the pattern reported for the whole brain was similar to that of the current study and, the weight of

the ecological variable (daily traveled distance) was one order of magnitude greater than the influence of the social variable (group size). As it was the case here, VMPFC and whole brain volumes were strongly correlated (r=0.99), but the size of the VMPFC was predicted by a distinct set of ecological variables (dietary quality and weaning age), with little modulation by group size. Thus, our results from these two combined studies suggest that specific neuro-cognitive entities, established in laboratory studies and defined by a conjunction of specific brain regions and cognitive operations, can be related to specific socio-ecological challenges that animals face in natural conditions.

In conclusion, our results confirm that the size of specific brain regions can be related to socio-ecological variables through the cognitive operations relying on these regions in laboratory conditions. Thus, our approach aiming at articulating cognitive operations reported in laboratory settings with real socio-ecological challenges should provide a clear insight into the neuro-cognitive operations at play in the wild, as well as their evolution in primates. Conversely, integrating realistic socio-ecological challenges can provide a strong insight into the evolution of specific brain functions in primates. Of course, we would need to provide a clearer model regarding how facing socio-ecological challenges can rely upon specific and dynamic cognitive operations, but we believe that this is a critical first step that helps building a common theoretical framework to cross boundaries across behavioral ecology and cognitive neurosciences.

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