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

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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 travelled distance (an index of ecological constraints) and population density (an index of social constraint). 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 clarifies 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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1. Introduction:

Numerous studies have addressed the mechanisms underlying the evolution of cognitive abilities in primates, using brain size as a proxy (Chambers, Heldstab, & O'Hara, 2021; A. R. DeCasien, Barton, & Higham, 2022; Powell, Isler, & Barton, 2017; Carel P. van Schaik, Triki, Bshary, & Heldstab, 2021). 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, 1993). Even if both of these hypotheses are supported by experimental evidence, they are often opposed, with the idea that one of them should have significantly more weight on brain evolution compared to the other (e.g. (Alex R. DeCasien, Williams, & Higham, 2017)). Critically, this apparent opposition between the 'social brain' and the 'ecological brain' is based on the assumption that the whole brain volume is a good proxy for overall cognitive abilities (Deaner, Isler, Burkart, & van Schaik, 2007; Falk & Gibson, 2001). In this framework, cognitive skills could allow to solve both ecological and social challenges, but one of these two factors (social or ecological) would have had more weight on the evolution of these skills across species.

Nevertheless, this assumption remains poorly specified from a psychological and a neurophysiological perspective. Indeed, from a neurobiological perspective, the idea that the social and ecological brain hypotheses should be in opposition appears counterintuitive, since recent studies have shown that, for the most part, the brain regions involved in social interactions vs. foraging were different. One one hand, imaging studies in humans have identified a set of specific brain regions (e.g., the temporo-parietal junction, TPJ) involved in social interactions (Stanley & Adolphs, 2013). The network of brain regions involved in social interactions is often referred to as the social brain, and recent comparative studies have shown that it exists in other primate species including macaques (Rushworth, Mars, & Sallet, 2013; Jérôme Sallet et al., 2011; Testard et al., 2022). On the other hand, foraging, which involves a complex spatio-temporal representation of food availability and values, would involve a distinct set of brain regions, including the hippocampus and the ventromedial prefrontal cortex (Lin, Horner, Bisby, & Burgess, 2015; Louail, Gilissen, Prat, Garcia, & Bouret, 2019; Vikbladh et al., 2019; Zuberbühler & Janmaat, 2010). However, the brain systems potentially involved in social cognition and foraging are probably not completely independent: several regions of the frontal lobe seem to be involved both in foraging and social interactions (Barbey et al., 2014; Gallagher & Frith, 2003; Kolling, Behrens, Mars, & Rushworth, 2012; Mansouri, Koechlin, Rosa, & Buckley, 2017; Rudebeck, Walton, Smyth, Bannerman, & Rushworth, 2006; Yoshida, Saito, Iriki, & Isoda, 2012). This partial overlap between the so called 'social brain' and the so called 'foraging brain' is in line with the idea that some cognitive operations are generic enough to be involved in multiple contexts (Garcia, Bouret, Druelle, & Prat, 2021). This is typically the case for executive functions, which allow to organize behavior over space and time to reach a goal, and rely upon several regions of the prefrontal cortex (Fuster, 2008; Luria, 1973). But the extent to which these functional networks identified in laboratory conditions apply to behavior in the wild often remains very speculative. Indeed, , even if the mapping between cognitive functions and specific brain regions has been a core issue for cognitive neurosciences for several decades, it has mostly been studied in laboratory conditions and in clinical settings (Passingham, Passingham, & Wise, 2012; Yechiam, Busemeyer, Stoof, & Bechara, 2005). But to what extent are these cognitive operations and their neural substrate identified in laboratory settings related to natural socio-ecological processes, and to the socio-ecological variability across species, based on their evolutionary history?

Of course, the precision with which these cognitive operations and their neurobiological substrate have been defined in laboratory conditions is quite challenging to achieve in wild conditions, and even more so when they must be compared across species (but see Janmaat et al, 2021). 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 & Harvey, 2000; Alex R. DeCasien & Higham, 2019b). What remains challenging, however, is to bridge the gap between brain structures and functions associated with specific cognitive operations in labora-

tory conditions and brain functions in natural conditions, when facing real socio-ecological challenges. Again, in laboratory conditions, cognitive operations are captured very precisely but their relation to socio-ecological challenges remains, at best, speculative. In order to bridge this gap, it seems essential to derive predictions where a set of well identified cognitive operations and their associated brain regions studied in laboratory conditions could be involved in more natural conditions as assessed in wild animals evolving in their natural environments (Barks et al., 2014)(A. R. DeCasien et al., 2022; Janmaat et al., 2021; Louail et al., 2019).

For this study, 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 involving the dorso-lateral prefrontal cortex (DLPFC). First, metacognition might be critical both for social interactions by supporting theory of mind (the ability of an individual to conceptualize others' states of mind) and for foraging by enabling complex planning (Devaine et al., 2017; Fleming & Dolan, 2012; Frith, 2007; Mansouri 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; Conard, Serangeli, Bigga, & Rots, 2020; Garcia et al., 2021; C. P. van Schaik, 2016). Secondly, given the very clear role of DLPFC in working memory and planning, we could speculate that it is critically involved in foraging, but its role in complex social interactions is less clear: on one hand, it is not often 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 et al., 2012; J. Sallet et al., 2013).

In order to bridge the gap between these brain regions (and their functions) defined in laboratory conditions and potential neuro-cognitive operations that evolved across primates to adapt to their specific socio-ecological challenges in the wild, 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 conditions translate to 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 relative size of each brain region can be taken as a proxy for its associated function (metacognition for FP and working memory for DLPFC) (Barks et al., 2014; Barton & Harvey, 2000; Alex R. DeCasien & Higham, 2019a; Ferrucci et al., 2022; Herculano-Houzel, 2017; Herculano-Houzel, Kaas, & de Oliveira-Souza, 2016; Louail et al., 2019; Maguire et al., 2000; Jérôme Sallet et al., 2011; Testard 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 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 (Amiez et al., 2019; Michael Petrides, Tomaiuolo, Yeterian, & Pandya, 2012; J. Sallet et al., 2013). Finally, the cognitive functions in which they are involved appear relatively well conserved between macaques and humans (Fuster, 2008; Mansouri 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 Museum 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 Museum 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 & 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) (Ongür, Ferry, & Price, 2003; Ramnani & Owen, 2004; Semendeferi, Armstrong, Schleicher, Zilles, & Van Hoesen, 2001; Tsujimoto, Genovesio, & Wise, 2011). Besides cytoarchitectonic landmarks, the frontal pole can also be identified based on connectivity patterns: it receives projections from the temporal superior cortex (M. Petrides, 2005) and has connections with the superior temporal sulcus (J. Sallet et al., 2013). We also used the probabilistic maps of the frontal pole proposed by John et al. (John et al., 2007) and Bludau et al. (Bludau 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 (Borden, Stefan, & Forseen, 2015; Saleem & Logothetis, 2007) 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.

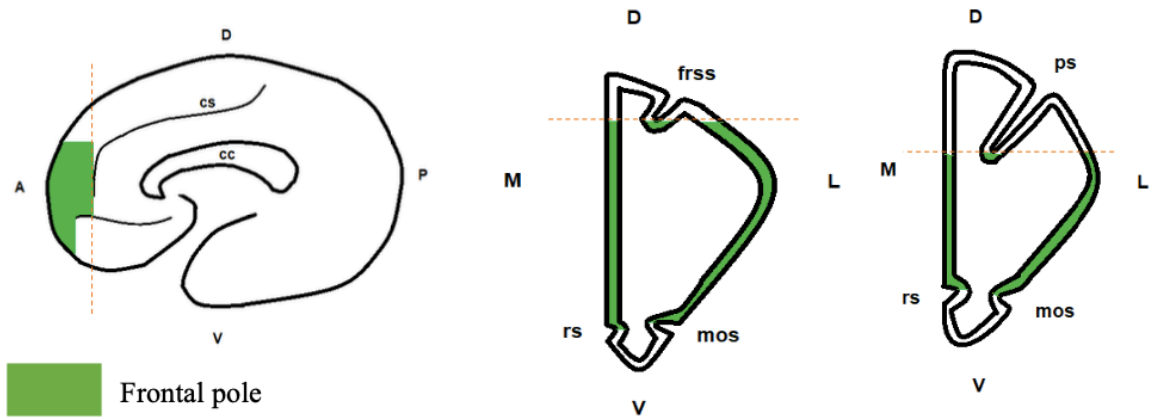


Figure 1. *Boundaries of the frontal pole. From left to right: sagittal view, coronal view for great apes and humans, coronal view for monkeys. Frontal pole is in green. Abbreviations: cs: cingulate sulcus; cc: corpus callosum; rs: rostral sulcus; mos: medial-orbital sulcus; frss: superior frontal sulcus; 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 & Goldman-Rakic, 2000; Passingham et al., 2012; Passingham & Sakai, 2004; Michael Petrides et al., 2012; J. Sallet 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.

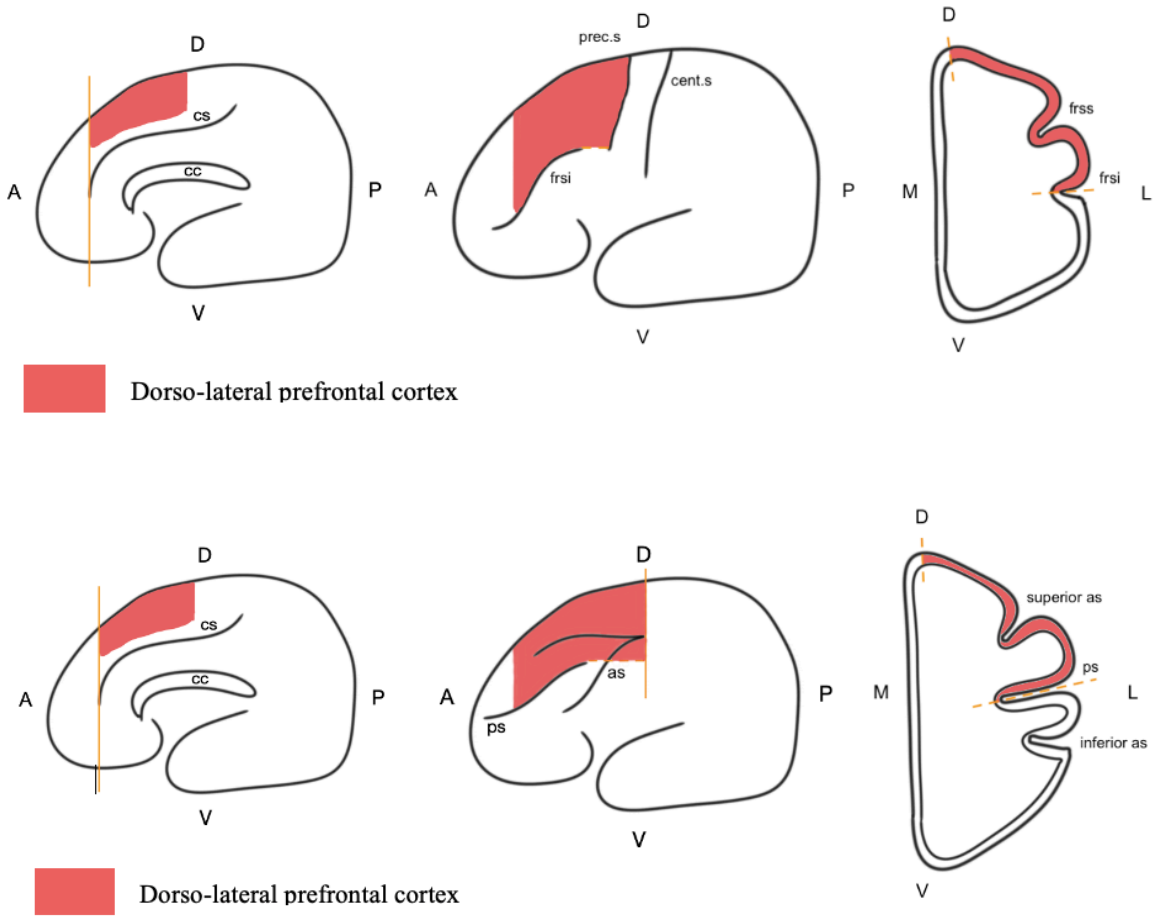


Figure 2. *Boundaries of the dorso-lateral prefrontal cortex*

*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 data 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, Boster, & Kurland, 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 con-

texts. We took the definition of St Amant and Horton (St Amant & 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 supplemantary material, SI 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 (Alex R. DeCasien 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 (Dixson & Oxford University Press., 2012; Manson, 1997). 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, & Nunn, 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 & 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 & Schliep, 2019).

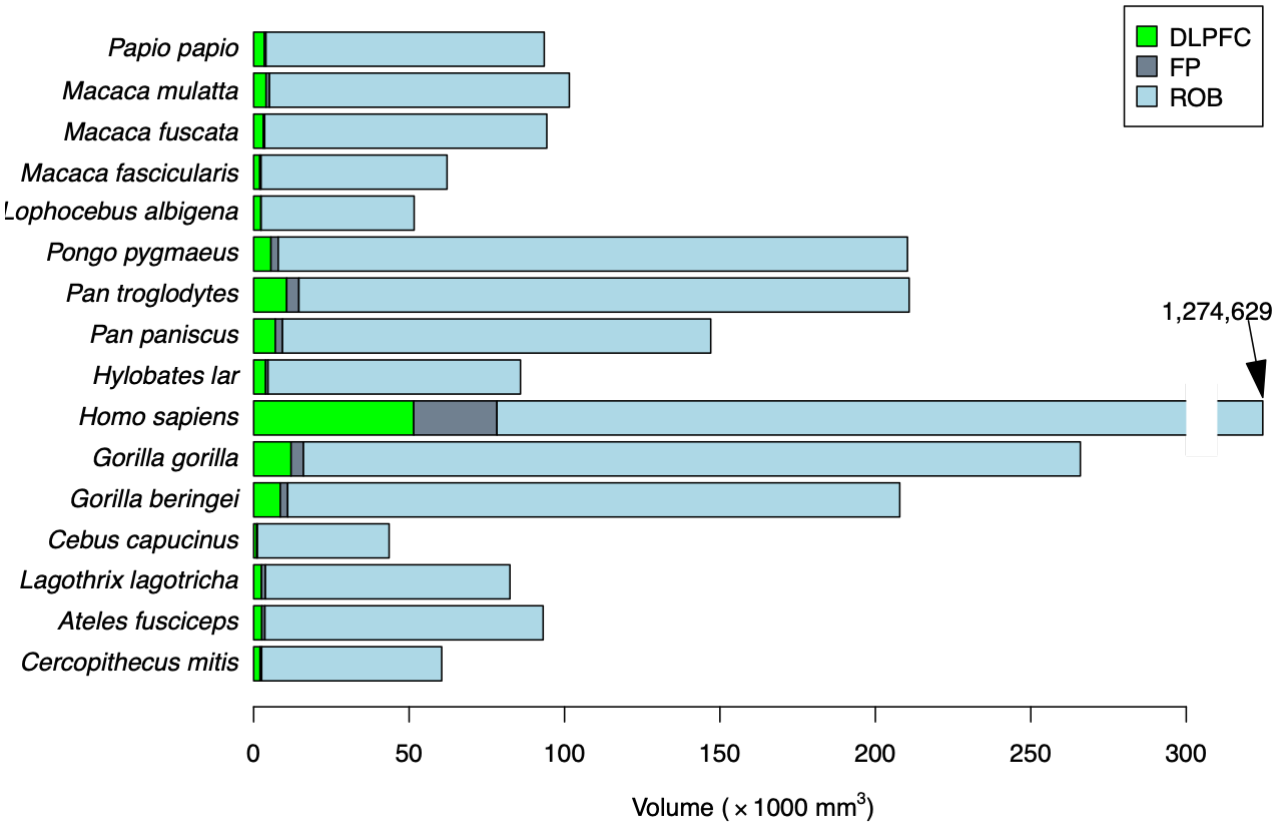
Because of the relatively small number of species in our sample, we assessed the reliability of the inferred models with a "leave-one-out" procedure: we removed one species from the data and the phylogenetic tree and re-fitted the model selected previously. This was repeated for each species.

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 weight (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 weight of daily traveled distance and population density (0.007 +/- 0.003).

Table 1: Estimated coefficients of socioecological variables for the whole brain volume.

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

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 (SI 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 variables related to both social (population density) and ecological (daily traveled distance) variables. The weight of the ecological variable, however, seems to be 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 (SI section 3). The values of estimated coefficients, all positive, are provided in the 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.

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

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

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 loose significance ($p>0.05$). As can be seen in the supplementary material (SI 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.

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 (SI section 3). The values of estimated coefficients, all positive, are provided in the table 3.

Table 3: Estimated coefficients of socioecological variables for the DLPFC volume.

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

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 loose 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, SI 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 FP and the DLPFC. 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 travelled 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 their known cognitive functions in laboratory conditions.

First, we need to consider two methodological questions:
1) How reliable is the difference 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. By contrast, for the DLPFC, the effect of population density failed to reach significance ($p=0.07$) and its beta weight was one order of magnitude smaller than that of daily traveled distance. Finally, this relatively weak influence 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. This is 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 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. (Alex R. DeCasien & Higham, 2019b), 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 et al., 2016; Herculano-Houzel, 2017).Typically, 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 & 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 (Alex R. DeCasien & Higham, 2019a; Louail et al., 2019; Maguire et al., 2000; Testard 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 et al., 2012); but see (A. R. DeCasien et al., 2022). Importantly, more precise quantitative studies showed the fraction of neurons in the prefrontal cortex, 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, Wong, & Kaas, 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, rather than in an increase in the ration 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 (Boorman, Behrens, Woolrich, & Rushworth, 2009; Gallagher & Frith, 2003; Genovesio, Wise, & Passingham, 2013; Koechlin, 2016; Passingham & Sakai, 2004; Preuss & 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. 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 specific functional areas. As for our previous study using a similar approach, this method was reliable enough to capture meaningful and specific effects of interests (Louail 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, could reliably be extrapolated to other species (Amiez et al., 2019; Bludau et al., 2014; J. Sallet et al., 2013). 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 & Harvey, 2000; Alex R. DeCasien & Higham, 2019b; Louail et al., 2019; Maguire et al., 2000). Again, we assume that the size of a brain region is a good proxy for the number of neurons allocated to a given function (given the macroscopic connectivity pattern of the region and its local anatomo-functional features), given the known positive relaiton between number of cortical neurons and cognitive skills in primates (Herculano-Houzel, 2017, 2018). 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, & Fichtel, 2020), and cognitive abilities associated with foraging are likely to play a role in social foraging tactics too (Street, Navarrete, Reader, & Laland, 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 et al., 2021). Thus, our work indicates not only 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, 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, and even more so 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 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 (Fleming & Dolan, 2012; Frith, 2007; Jérôme Sallet et al., 2011; Testard 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 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 (A. R. DeCasien et al., 2022; Smaers et al., 2021; Carel P. van Schaik et al., 2021), 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 explain the evolution of brain size and then 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 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 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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