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Sexual Dimorphism and Laterality in the Evolution of the Primate Prefrontal Cortex

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Sexual dimorphism · Laterality · Prefrontal cortex · Primate · Anthropoid

Abstract

Social selective pressures are commonly considered as the main driving force of primate brain evolution. Primate social behaviour is, however, known to be sexually dimorphic, and no previous study has made a direct comparison between male and female brain structures across species. We quantify sex-specific evolutionary trends in the prefrontal cortex of anthropoid primates (including humans) to investigate how sexual selection has shaped brain evolution in primates. The prefrontal cortex is of particular importance to the investigation of sexual dimorphism in primate brain evolution because of its association to those cognitive capacities central to primate (and human) evolution: sociality and higher-order cognitive processing. Our results demonstrate sex-by-hemisphere differences in the evolution of the prefrontal cortex in humans and non-human anthropoid primates congruent with the principal selective pressures considered to underlie anthropoid behavioural evolution. Our findings further show how sexual selection can shape brain adaptation in primates and provide an evolutionary framework for interpreting sex and sex-by-hemisphere differences in cortical organization in humans and non-human primates.

Introduction

Sexual selection is known to play a dominant role in shaping the biology of organisms across the animal kingdom. Neuroanatomical [Cahill, 2006], neurochemical [Robinson et al., 1977], functional [Speck et al., 2000], and molecular [Isensee and Ruiz Noppinger, 2007] work on sex differences in the brain show that the mammalian neural system is no exception to this rule. Recent work on the evolution of gene expression relevant to the development of the primate occipital cortex [Reinius et al., 2008] implies a conserved signature of sexual gene expression dimorphism across primates, suggesting that at least some of the mechanisms for controlling sex biases in the primate brain are inherited [Jazin and Cahill, 2010]. In humans, structural dimorphism has been indicated for

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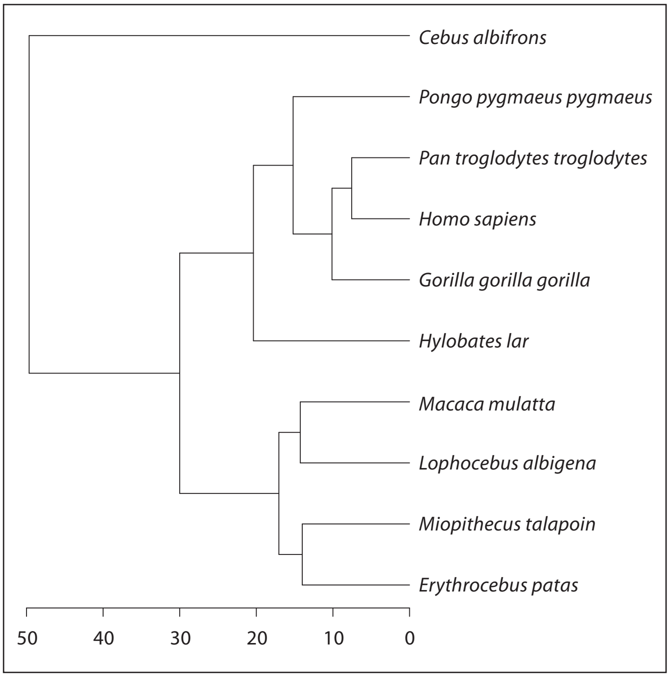

Fig. 1. Phylogenetic tree from species incorporated in the analysis [10kTrees Project: Arnold et al., 2010]. The tree axis indicates millions of years.

frontal [Zilles et al., 1996; Amunts et al., 2000; Goldstein et al., 2001] and occipital [Amunts et al., 2007] cortical areas, the amygdala, hypothalamus, and hippocampus [Goldstein et al., 2001], and the cerebellum [Raz et al., 2001].

A key question is to what extent sexual differentiation in neural structures can be explained by environmental and/or behavioural selective pressures. In phylogenetic comparative investigations of brain structure evolution (modelling phenotype evolutionary patterns along the branches of a phylogenetic tree), there is a strong tradition of relating variation in quantitative aspects of brain structures (e.g. relative size, white/grey matter ratio) to behavioural variation, evidenced by empirical support across the animal kingdom [DeVoogd et al., 1993; Huber et al., 1997; Dunbar and Shultz, 2007a; Iwaniuk and Wylie, 2007; Smith et al., 2010]. The argument is that the internal organization of an animal's brain reflects its adaptation to the behavioural requirements of a particular niche [Barton and Harvey, 2000; de Winter and Oxnard, 2001]. Variation in the internal organization of the brain is then regarded as the result of selective pressures acting on neural circuits supporting behaviour that increases an individual's fitness [Barton and Harvey, 2000]. This 'mosaic' or 'niche adaptationist' approach to brain structure evolution predicts that, where there is sexual differentiation in behavioural selective pressures, sexual differentiation of relevant neural structures is likely to occur [Lindenfors et al., 2007] and, vice versa, that sexual differentiation between neural structures reflects sexual differentiation in associated behavioural selective pressures. In primates, behaviour has long been suggested to be sexually dimorphic [Emlen and Oring, 1977], but no investigation has made a direct comparison between male and female brain structures across a range of different species.

Previous comparative investigations on the nature of sex biases in the brain either compared distantly related species (humans, rodents, worms, flies), few closely related species (humans to no more than 2 non-human primates), or aggregated male and female brain data across many species. A comparative investigation of sex-specific brain structures across a broader sample of different species of the same radiation (e.g. primates) will provide further information on the nature of neural adaptation by sexual selection. Here, we investigate the evolution of relative prefrontal volumes and white/grey matter ratios in males versus females in 32 individuals across 10 primate species (humans, 4 apes, and 5 monkeys). According to the niche adaptationist hypothesis of brain structure evolution, the primate prefrontal cortex is a likely candidate for sexually dimorphic evolution because of its association to social behaviour [Dunbar and Shultz, 2007a; Adolphs, 2009; Powell et al., 2010] and the observation that primate social behaviour is subject to sex-specific selection pressures [Emlen and Oring, 1977; Plavcan and van Schaik, 1992, 1997; Lindenfors et al., 2004]. We investigate sex-specific prefrontal evolutionary patterns separately for each hemisphere considering evidence for sex-by-hemisphere differences in prefrontal function in humans [Tranel et al., 2005] and hemisphere differences in the evolutionary pattern of relative prefrontal cortex volume in anthropoid primates [Smaers et al., 2011].

Materials and Methods

Brain Data

We examined 32 individuals (9 humans, 11 apes, and 12 monkeys) from 10 anthropoid species (fig. 1). For each species, both male and female individuals were available. Brain data came from the Stephan, Zilles, and Zilles-Amunts collections [Zilles et al., 2011] housed at the C. & O. Vogt Institute for Brain Research (University of Düsseldorf, Düsseldorf, Germany). The following individuals were used (* indicates females): *Homo sapiens* (collection numbers pm2, pm4, pm6, pm7, pm13, pm1*, pm8*, pm9*, pm10*), *Pan troglodytes* (280, 497*), *Gorilla gorilla* (375, 8214*),

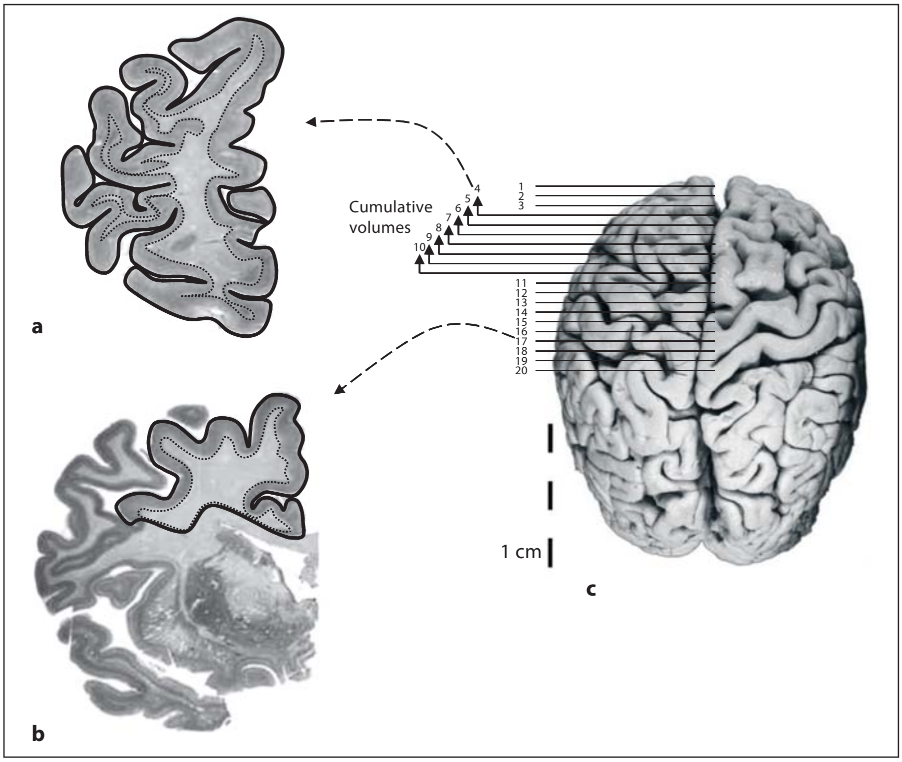

Fig. 2. For each individual, the cortical areas anterior to the border between area 3 and area 4 are delineated in each hemisphere using 20 equidistant sections. Cumulative volumes are computed for the 10 most anterior sections, and allometric trends are investigated at each interval. **a**, **b** The 4th and 17th sections of individual pm10 (human female). **c** Dorsal view of the brain with an approximation of section intervals for the left hemisphere.

Pongo pygmaeus (297, 597, 8538, 459*), *Hylobates lar* (1203, 397*, 81146*), *Cercocebus albigena* (242, 221, 99*), *Erythrocebus patas* (1545, 1341*), *Miopithecus talapoin* (1171, 1201*), *Macaca mulatta* (448, 516*, 114*), and *Cebus albifrons* (1200, 6062*).

Prefrontal Delineation Procedure

To investigate variation in prefrontal cortex volume across species, we employed a bootstrap approach based on the cytoarchitectonic delineation of the frontal lobe [Smaers et al., 2011] (fig. 2). The frontal lobe is defined as the part of the neocortex anterior to the boundary between area 4 and area 3 (this boundary is defined based on cell shape, cell density, cell size, presence of granular layer IV, diffuseness of white/grey matter border, and lamination patterning) [Smaers et al., 2010]. The bootstrap approach consists of considering cumulative volumes along the anterior axis of the frontal lobe [Smaers et al., 2011]. For each hemisphere, coronal sections at 20 equidistant intervals between the area 4-area 3 boundary and the most anterior end of the neocortex were used to compute frontal lobe volumes. For each individual and for each hemisphere, cumulative volumes were then computed along the 10 most anterior intervals (considered to comprise those frontal areas where the prefrontal is located). This approach computes volumetric estimations at 10 intervals along the anterior axis of the frontal lobe such that the volume at each interval includes the volume of more anterior intervals (i.e. cumulative volumes). To investigate variation in prefrontal volume across species, we analyzed cumulative volumes along all 10 intervals so that a detailed overview of volumetric evolutionary trends along the anterior axis of the frontal lobe was revealed. Cumulative volumes along the first 3 intervals were not considered to avoid volumetric estimations based on too few sections. Tables 1 and 2 indicate the scaling coefficients (slopes and intercepts of the regressions of prefrontal volume to rest of brain volume and of prefrontal white to grey matter volume; slopes indicate the amount of change in one variable compared to another; differences between intercepts indicate whether one variable indicates a higher or lower value compared to another variable) for intervals 4 through 10; figure 2 provides an overview by indicating scaling coefficients and individual residuals averaged over intervals 4 through 7.

Statistical Procedure

Comparative phylogenetic methods are tools to infer evolutionary trends based on extant variation and phylogenetic relatedness. We used the phylogenetic generalized linear model (PGLM) as described by Freckleton et al. [2002] and as implemented in the *CAIC* package in *R* [R Development Core Team, 2010]. To take into account topological and branch length uncertainty in tree estimation, we ran all analyses across 10,000 trees from a posterior probability distribution of a Bayesian tree estimation (10kTrees Primates: Version 2 [Arnold et al., 2010]). Values presented thus represent averaged values across 10,000 phylogenetic regressions. All scaling coefficients are based on nonhuman primate data. Plots represent individual data points calculated based on PGLM scaling coefficients and residuals. To assess whether particular individuals are aligned with the overall allometric trend, residual values were determined relative to the 95% confidence intervals of the PGLM regression. All analyses were performed separately for each hemisphere to allow estimating allometric scaling differences between hemispheres.

Table 1. Slopes of PGLM regressions of prefrontal volume to rest of brain and of prefrontal white matter to grey matter volume in both hemispheres

		Volume left			Volume right			White/grey left			White/grey right		
		slope	min	max	slope	min	max	slope	min	max	slope	min	max
Male	Interval 4	1.23	1.03	1.43	1.17	1.04	1.29	1.28	1.10	1.46	1.24	1.07	1.41
	Interval 5	1.23	1.06	1.39	1.18	1.05	1.30	1.27	1.10	1.45	1.26	1.11	1.40
	Interval 6	1.23	1.09	1.37	1.18	1.06	1.31	1.26	1.11	1.42	1.25	1.10	1.40
	Interval 7	1.22	1.09	1.35	1.17	1.03	1.30	1.24	1.09	1.39	1.19	1.03	1.35
	Interval 8	1.17	1.05	1.29	1.13	0.99	1.26	1.20	1.03	1.37	1.16	1.00	1.31
	Interval 9	1.17	1.03	1.31	1.12	0.98	1.26	1.19	1.03	1.34	1.18	1.05	1.32
	Interval 10	1.16	1.03	1.29	1.13	0.99	1.26	1.21	1.07	1.36	1.20	1.06	1.33
Female	Interval 4	1.06*	0.88	1.24	1.14	0.81	1.47	1.47**	1.13	1.81	1.39*	1.07	1.72
	Interval 5	1.08*	0.93	1.23	1.11	0.81	1.41	1.41	1.12	1.71	1.39*	1.12	1.65
	Interval 6	1.07**	0.93	1.22	1.07*	0.80	1.35	1.37	1.10	1.63	1.47**	1.22	1.73
	Interval 7	1.06**	0.92	1.20	1.05*	0.79	1.31	1.36	1.12	1.60	1.43**	1.20	1.66
	Interval 8	1.05**	0.91	1.19	1.03	0.79	1.27	1.29	1.06	1.52	1.39**	1.15	1.63
	Interval 9	1.04*	0.90	1.18	1.02	0.80	1.24	1.26	1.03	1.49	1.35**	1.07	1.63
	Interval 10	1.04*	0.91	1.17	1.02	0.82	1.23	1.27	1.03	1.52	1.29	1.00	1.59

Values indicate average scaling coefficients across 10,000 trees. ‘min’ and ‘max’ indicate the 95% confidence interval. Significance values (* $p < 0.10$; ** $p < 0.05$) indicate where females are significantly different from males.

Table 2. Intercepts of PGLM regressions of prefrontal volume to rest of brain and of prefrontal white matter to grey matter volume in both hemispheres

		Volume left			Volume right			White/grey left			White/grey right		
		intercept	min	max	intercept	min	max	intercept	min	max	intercept	min	max
Male	Interval 4	–5.71	–6.70	–4.71	–5.31	–5.93	–4.70	–1.79	–1.96	–1.61	–1.71	–1.86	–1.55
	Interval 5	–5.26	–6.07	–4.45	–4.93	–5.53	–4.33	–1.73	–1.92	–1.55	–1.62	–1.77	–1.46
	Interval 6	–4.91	–5.60	–4.23	–4.61	–5.23	–4.00	–1.66	–1.86	–1.47	–1.54	–1.74	–1.35
	Interval 7	–4.55	–5.19	–3.90	–4.24	–4.89	–3.58	–1.57	–1.78	–1.35	–1.40	–1.63	–1.17
	Interval 8	–4.07	–4.63	–3.50	–3.80	–4.46	–3.15	–1.43	–1.70	–1.16	–1.27	–1.52	–1.02
	Interval 9	–3.85	–4.53	–3.17	–3.56	–4.24	–2.88	–1.31	–1.58	–1.04	–1.24	–1.47	–1.01
	Interval 10	–3.63	–4.27	–2.99	–3.41	–4.07	–2.75	–1.32	–1.59	–1.05	–1.23	–1.49	–0.97
Female	Interval 4	–4.88	–5.76	–4.00	–5.09	–6.66	–3.52	–1.55**	–1.82	–1.27	–1.58*	–2.12	–1.05
	Interval 5	–4.59	–5.32	–3.87	–4.61	–6.03	–3.18	–1.53**	–1.78	–1.27	–1.53	–1.96	–1.10
	Interval 6	–4.23**	–4.92	–3.54	–4.21	–5.50	–2.91	–1.50*	–1.77	–1.23	–1.44	–1.67	–1.21
	Interval 7	–3.88**	–4.56	–3.19	–3.81	–5.03	–2.60	–1.39*	–1.68	–1.11	–1.35	–1.59	–1.11
	Interval 8	–3.57*	–4.25	–2.88	–3.47	–4.60	–2.34	–1.23	–1.54	–0.93	–1.26	–1.54	–0.97
	Interval 9	–3.31	–3.99	–2.64	–3.21	–4.25	–2.17	–1.14	–1.48	–0.79	–1.19	–1.55	–0.82
	Interval 10	–3.14	–3.78	–2.50	–3.06	–4.02	–2.10	–1.14	–1.54	–0.75	–1.15	–1.65	–0.66

Values indicate average scaling coefficients across 10,000 trees. ‘min’ and ‘max’ indicate the 95% confidence interval. Significance values (* $p < 0.10$; ** $p < 0.05$) indicate where females are significantly different from males.

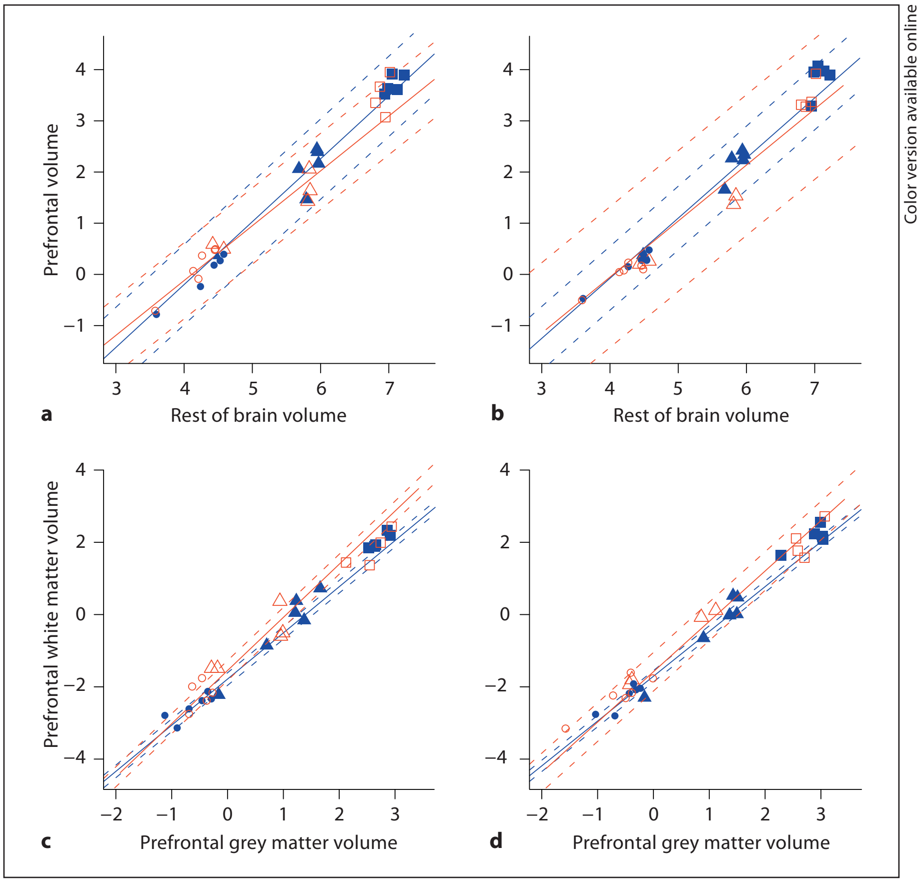

Fig. 3. PGLM regressions of prefrontal volume to rest of brain volume for the left (**a**) and right (**b**) hemisphere and prefrontal white to grey matter volume for the left (**c**) and right (**d**) hemisphere. Scaling coefficients and individual values represent values averaged over intervals 4, 5, 6, and 7 of the anterior axis of the frontal lobe (see text). Open (red; colours refer to online version only) symbols represent females, and closed (blue) symbols males. Squares represent humans, triangles non-human apes, and circles monkeys. The slope and 95% confidence interval indicated in red are for females, and blue ones are for males.

Results

For the analyses on prefrontal volume, we regressed volumes of subsequent intervals along the anterior axis of the frontal lobe (cytoarchitectonically defined as the border between areas 3 and 4) to rest of the brain volume [Smaers et al., 2011]. Left prefrontal volume follows different allometric trends in males versus females (table 1, 2). This difference is mainly driven by relatively larger left prefrontal volumes in female compared to male smaller-brained anthropoids (monkeys) (fig. 3a; table 2). In terms of right prefrontal cortex volume, males significantly hyperscale to rest of brain volume, while females scale isometrically (table 1). This trend is explained mainly by the increased right prefrontal investment in male versus female chimpanzees and gorillas (fig. 3b).

For the analyses on prefrontal white/grey matter ratio, we regressed white matter volume to grey matter volume along subsequent intervals of the anterior axis of the frontal lobe. The non-human anthropoid pattern indicates an increased investment in white over grey matter in females relative to males as brain size increases (table 1, 2). Humans, however, do not follow this trend: females evolve less and males more white/grey matter volume than predicted for a non-human anthropoid female/male with the brain size of a human, resulting in a monomorphic human pattern (fig. 3c, d).

Discussion

We compared changes in relative prefrontal cortex volumes of the left and right hemispheres between males and females across 10 primate species and found that the two hemispheres of the prefrontal cortex indicate different sex-specific allometric trends. Left prefrontal cortex volumes follow a sex-specific allometric trend (table 1, 2; fig. 3), mainly driven by relatively larger left prefrontal volumes in female compared to male smaller-brained anthropoids (monkeys) (fig. 3a). In larger-brained anthropoids, males seem to catch up with females in terms of relative left prefrontal volume. For right prefrontal volumes, males significantly hyperscale to the rest of the brain volume, while females scale isometrically (table 1). This trend appears to be explained mainly by the increased right prefrontal investment in male versus female chimpanzees and gorillas (fig. 3b). Humans follow this trend for increased right prefrontal volume in males relative to smaller-brained (male) primates, although results are not fully conclusive: a high cluster of 5 human individuals with increased right prefrontal cortex volumes comprises 4 males, while a low cluster of 4 individuals comprises 3 females (fig. 3b).

For the white/grey matter ratio (fig. 3c, d), results indicate an evolutionary trend for humans to become more monomorphic in both the left and right prefrontal cortex. The non-human anthropoid pattern indicates an increased investment in white over grey matter in females relative to males as brain size increases, but humans are indicated to not follow this trend. Instead, human females evolve less and males more white/grey matter volume than predicted for a non-human anthropoid female/male with the brain size of a human, resulting in a monomorphic human pattern. This trend is particularly pronounced in the left hemisphere. For females, 3 out of 4 individuals indicate a white/grey matter ratio that is lower than expected for a non-human primate of their brain size. For males, all individuals indicate a white/grey matter ratio that is higher than expected. This result contextualizes previous reports of significant lateralization in white/grey matter ratio based on a predominantly male sample [Smaers et al., 2011]. Larger sample sizes for other species will be needed to establish whether this is a pattern that is unique for humans among anthropoids.

In terms of brain structure evolution, our results thus demonstrate sex-by-hemisphere differences in the evolution of the prefrontal cortex in humans and non-human anthropoid primates, suggesting sexual selection has influenced prefrontal cortex evolution in a hemisphere-specific way. These results demonstrate that sexual dimorphism and laterality are important factors underlying divergent brain evolution in primates.

Additionally, these results may help elucidate elements of brain-behaviour evolution in primates. Considering substantial evidence in different orders for an association between variation in brain organization and behavioural capacity within and across species [DeVoogd et al., 1993; Huber et al., 1997; Barton and Harvey, 2000; Maguire et al., 2000; de Winter and Oxnard, 2001; Iwaniuk and Wylie, 2007; Shultz and Dunbar, 2010; Smith et al., 2010; Bickart et al., 2011], divergent patterns of brain adaptation may be considered as biological markers of past and current behavioural selective pressures and used to make inferences on the behavioural selective pressures underlying primate diversity.

Overall, larger-brained primates are faced with the challenge to rear increasingly expensive, slow-growing, and high energy-consuming offspring. To meet this challenge, primates are generally considered to resort to 'social' solutions. According to the 'Social Brain Hypothesis', creating complex social societies (involving pair bonding, cooperation, deception, alloparenting, etc.) provides primates with effective means of realizing such high-quality energetic networks [Dunbar and Shultz, 2007a, b]. The adaptive advantage of creating more complex social societies is to afford raising offspring with larger brains (in turn associated to adaptive fitness [Sol et al., 2008]). As societies become more complex, fitness payoffs will be determined more by long-term payoffs than immediate personal payoffs, resulting in a strong selective pressure for higher-order cognitive capacities and an associated investment in those brain structures supporting these cognitive capacities [Dunbar and Shultz, 2007a]. Because of the inevitability that females bear the energetic costs of gestation and lactation (resulting in sex-specific energetic expenditure strategies [Key and Ross, 1999]) and the fact that male reproductive success is primarily determined by access to females [Emlen and Oring, 1977], it has been argued that primate sociality inherently involves sex-specific behavioural pressures [Emlen and Oring, 1977; Lindenfors et al., 2004].

The increased left prefrontal volume in female compared to male smaller-brained primates can be understood in the context of evidence for an association between the left hemisphere and the production of positive emotions and approach behaviour relevant to affiliative interactions and social bonding [Davidson et al., 1990]. Overall, forging a large quantity of social bonds is considered to underlie female rather than male primate evolution [Lindenfors, 2005]. Our result that female primates indicate larger left prefrontal volumes than males in smaller-brained primates aligns with this prediction. The fact that males catch up with females in terms of left prefrontal volume in larger-brained primates may indicate that larger-brained primate males are faced with an increased pressure to forge lasting social interactions in order to successfully face the higher-order cognitive challenge involving long-term fitness payoffs of rearing increasingly larger-brained, high energy-consuming, and slow-growing offspring.

The increased right prefrontal volume in male compared to female larger-brained primates may be understood considering evidence for a link between the right hemisphere and the control of negative emotions in the context of agonistic interactions [Casperd and Dunbar, 1996; Wallez and Vauclair, 2011]. Larger-brained primates are faced with more complex higher-order social environments where competition for access to females may be expressed in more subtle behavioural cues, prompting increased selective pressure on higher-order interpretations and expressions of agonistic behaviour. In humans, a link between testosterone levels [Mazur and Booth, 1998] and associated traits such as facial masculinity [Quist et al., 2011] with perceived dominance suggests sex-specific (male-biased) cognitive investment in terms of dominance hierarchy recognition. The results of our human sample seem to point in a similar direction in terms of the evolutionary pattern of the right prefrontal cortex, although these results are not fully conclusive: a high cluster of 5 human individuals with increased right prefrontal cortex volumes comprises 4 males, while a low cluster of 4 individuals comprises 3 females (fig. 3b).

It is clear that precise behavioural interpretations of macro-evolutionary patterns of brain structure evolution involve inherent flaws but may be considered as building blocks in wider theories of brain-behaviour evolution. Future investigations should aim to increase the resolution of brain-behaviour studies both in terms of the delineation of precise brain areas and the description of cross-species behavioural capacities.

In conclusion, our results demonstrate sex-by-hemisphere differences in the evolution of the prefrontal cortex in humans and non-human anthropoid primates congruent with the principal behavioural selective pressures considered to underlie anthropoid evolution: sex-specific social pressures associated to successful mating and rearing strategies in a complex social setting involving long-term fitness payoffs [Emlen and Oring, 1977; Lindenfors et al., 2004, 2007; Lindenfors, 2005; Dunbar, 2007; Dunbar and Shultz, 2007a]. Our results thus suggest that behavioural selective pressures are a significant factor in controlling how sexual selection shapes brain adaptation in anthropoid primates.

Empirically, the current results provide an evolutionary framework for interpreting sex and sex-by-hemisphere differences in cortical organization in humans and non-human primates [Amunts et al., 2000, 2007; Tranel et al., 2005; Liu et al., 2009], inform us on the possible ways in which great ape brains are different from monkey brains, increase our understanding of how social behaviour influences primate adaptation [Dunbar and Shultz, 2007a], and provide further support for the mosaic hypothesis of brain evolution [Barton and Harvey, 2000; de Winter and Oxnard, 2001]. Methodologically, our results demonstrate that the standard approach in comparative brain research of aggregating male and female conspecific data and making inferences based on information from one hemisphere only confounds sex- and hemisphere-specific evolutionary trends, and thereby limits functional and evolutionary behavioural interpretations. Overall, our results help elucidate the different evolutionary mechanisms underlying species diversity in neural adaptation.

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