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Evolutionary biology

Plain faces are more expressive: comparative study of facial colour, mobility and musculature in primates

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Facial colour patterns and facial expressions are among the most important phenotypic traits that primates use during social interactions. While colour patterns provide information about the sender's identity, expressions can communicate its behavioural intentions. Extrinsic factors, including social group size, have shaped the evolution of facial coloration and mobility, but intrinsic relationships and trade-offs likely operate in their evolution as well. We hypothesize that complex facial colour patterning could reduce how salient facial expressions appear to a receiver, and thus species with highly expressive faces would have evolved uniformly coloured faces. We test this hypothesis through a phylogenetic comparative study, and explore the underlying morphological factors of facial mobility. Supporting our hypothesis, we find that species with highly expressive faces have plain facial colour patterns. The number of facial muscles does not predict facial mobility; instead, species that are larger and have a larger facial nucleus have more expressive faces. This highlights a potential trade-off between facial mobility and colour patterning in primates and reveals complex relationships between facial features during primate evolution.

1. Introduction

The primate face is a complex morphological structure in which both external and internal parts function in tasks that are relevant for social interactions. Externally, facial features bear information that allows recognition of conspecifics, individuals within the social group and potential mates. This information is encrypted in traits such as the shape of facial parts, and the complexity and hues of its colour patterns [1,2]. Internally, the facial musculature and neural centres control how the external morphology is presented to other individuals through the production of facial expressions, which are important in communicating behavioural intentions within a social context (e.g. bared teeth communicate the intent to withdraw from an agonistic encounter [3]). Therefore, both internal and external facial structures are not only in close physical proximity, but are also tightly connected in function.

Facial coloration patterns evolved in tandem with sociality and sympatry in primates [4,5]. In most primate radiations, highly social and sympatric species evolved multi-coloured faces, while less social species tend to have less colourful faces [4]. Complex facial patterns potentially enable higher interindividual variation within social groups and among species, facilitating recognition at either of these levels. Facial expressions are also linked to sociality; highly gregarious species produce a wider variety of facial movements [6], which may function in group cohesion by enhancing communication during conflict management and bonding [6]. Facial expressions result from the action of facial muscles that are controlled by neural pathways (facial nucleus of the pons—cranial nerve

VII—and the primary motor cortex). Although the primate facial musculature is among the most complex across mammals, it is unclear if and how it has evolved in response to functional demands associated with ecology and sociality [7–9]. However, primate species with relatively large facial nuclei tend to have highly expressive faces [10].

To date, it is poorly understood if and how the functional connections between external and internal facial traits and intrinsic factors owing to phylogenetic inertia have impacted the evolution of primate facial diversity. If the evolution of facial displays has been primarily driven by social factors, then highly gregarious primates would be expected to possess both complexly coloured and highly expressive faces. Conversely, if external facial morphology influences the ability of primates to identify and detect facial expressions [11], there could be trade-off in the evolution of facial mobility (and its underlying features) and facial colour patterning. Here, we use a comparative approach integrating behavioural, morphological and neural data across 7–21 primate species (figure 1 and the electronic supplementary material) to test these hypotheses. We predict that species with a wider repertoire of facial expressions have evolved more plainly coloured faces to facilitate conveying the information contained in facial expressions. We also explore whether behavioural traits are more evolutionarily labile than morphological traits in this system [13], which could explain how differences in evolutionary patterns arise while still meeting functional demands. Primate faces are exceptionally variable and diverse, thus understanding the mechanisms driving their evolution can illuminate the origins of high phenotypic diversity.

2. Material and methods

For each species, we quantified facial colour patterns as facial colour pattern complexity (FCPC; the total number of uniquely coloured facial areas [5]; electronic supplementary material), using high-resolution, close-up photographs of male faces. Higher FCPC represents a more complexly patterned face. We estimated facial mobility at the species or genus level by applying a subset of the human facial action coding system ([14]; electronic supplementary material) to video recordings of facial activity during feeding in zoo animals [6]. We used anatomical dissections and high-resolution photographs to document the number of facial muscles [7,9]. Data on body mass, volumes of major orofacial motor nuclei (trigeminal, hypoglossal and facial) and medulla oblongata were collected from the literature [10,15].

Owing to strong phylogenetic signal in our data ($\lambda = 1$; [12,16,17]), we used phylogenetic generalized least square (PGLS) regressions to test for associations among phenotypic traits while accounting for phylogeny. We investigated whether FCPC evolved in tandem with facial mobility and number of facial muscles through a PGLS regression with these as predictor variables. We determined the best predictors of facial mobility through a PGLS model including the number of facial muscles and the volume of each orofacial motor nucleus as predictor variables. Because larger primates have more expressive faces [18] and the volume of cranial nuclei scales positively with brain size [10], we also conducted these PGLS regressions including log-body mass and medulla oblongata volume in the models. Finally, to test whether the evolution of behavioural traits is more labile than morphological traits, we compared background rates of evolution for facial mobility, FCPC and number of facial muscles using the package AUTEUR [19].

3. Results

We found that species with more uniformly coloured faces have wider ranges of facial movement; conversely, species with complexly coloured faces have lower facial mobility (PGLS $\beta = -0.484 \pm 0.174$, $p = 0.022$, $t = -2.775$, d.f. = 12). This relationship is robust after accounting for body mass ($\beta = -0.725 \pm 0.276$, $p = 0.0277$, $t = -2.625$, d.f. = 12). There was no significant relationship between facial colour patterning and the number of facial muscles ($\beta = 0.200 \pm 0.454$, $p = 0.669$, $t = 0.440$, d.f. = 12) or body mass ($\beta = 1.485 \pm 1.121$, $p = 0.215$, $t = -1.324$, d.f. = 12).

Our analyses confirmed that larger primates have more expressive faces ([18]; $\beta = 4.310 \pm 1.018$, $p = 0.002$, $t = 4.233$, d.f. = 12). Facial mobility is also well predicted by the volume of the facial nucleus ($\beta = 0.482 \pm 0.049$, $p = 0.0002$, $t = 9.927$, d.f. = 7) and the medulla oblongata ($\beta = 0.001 \pm 2.4 \times 10^{-4}$, $p = 0.669$, $t = 0.037$, d.f. = 7), but not the trigeminal motor nor the hypoglossal nucleus, nor the number of facial muscles ($p > 0.05$ in all cases). When size is included in PGLS regressions explaining mobility, these do not yield significant results ($p > 0.05$). Across the three major characters studied, the background rate of evolution was highest for the facial nucleus volume (0.288), followed by facial mobility (0.036), colour patterning (FCPC; 0.029) and, lastly, the number of facial muscles (0.009).

4. Discussion

Faces convey a breadth of social signals through coloration and expressions. Our results indicate a significant association in the evolution of facial colour patterns and facial mobility within a subset of primate species. Supporting our hypothesis, plainly coloured faces evolved in tandem with enhanced ability for facial expressions. It is thus possible that there is a trade-off in the evolution of these two types of facial cues; while complex facial colour patterns may be beneficial for advertising identity [4,5], a highly ‘cluttered’ face may mask the visibility of facial expressions used to convey behavioural intention. At a neural level, although there is some degree of separation between the mechanisms for recognition of identity and expression, these complex tasks involve the concerted action of potentially overlapping functional components [20], which could explain part of this result.

Reliance on facial colour patterns or facial expressions for communication may be differentially selected across primate lineages based on the species’ habitat, social systems or traits inherent to the organisms such as body size. Even though facial patterning is not related to size, we confirmed that larger primates, which have a larger facial nucleus, tend to have more expressive faces. Evolution of differences in body size can constitute a line of least resistance that could facilitate the evolution of differences in these and many other functional traits [21]. The evolution of larger bodies, potentially coupled with increased reliance on vision for other ecological tasks (e.g. finding food and avoiding predators), may have potentiated a higher use of facial expressions that was not possible at smaller body sizes owing to physical constraints on the perception of facial movements. Facial expressions are likely more difficult to discern by smaller than larger species, because smaller mammalian eyes have lower visual acuity [18,22,23]. This

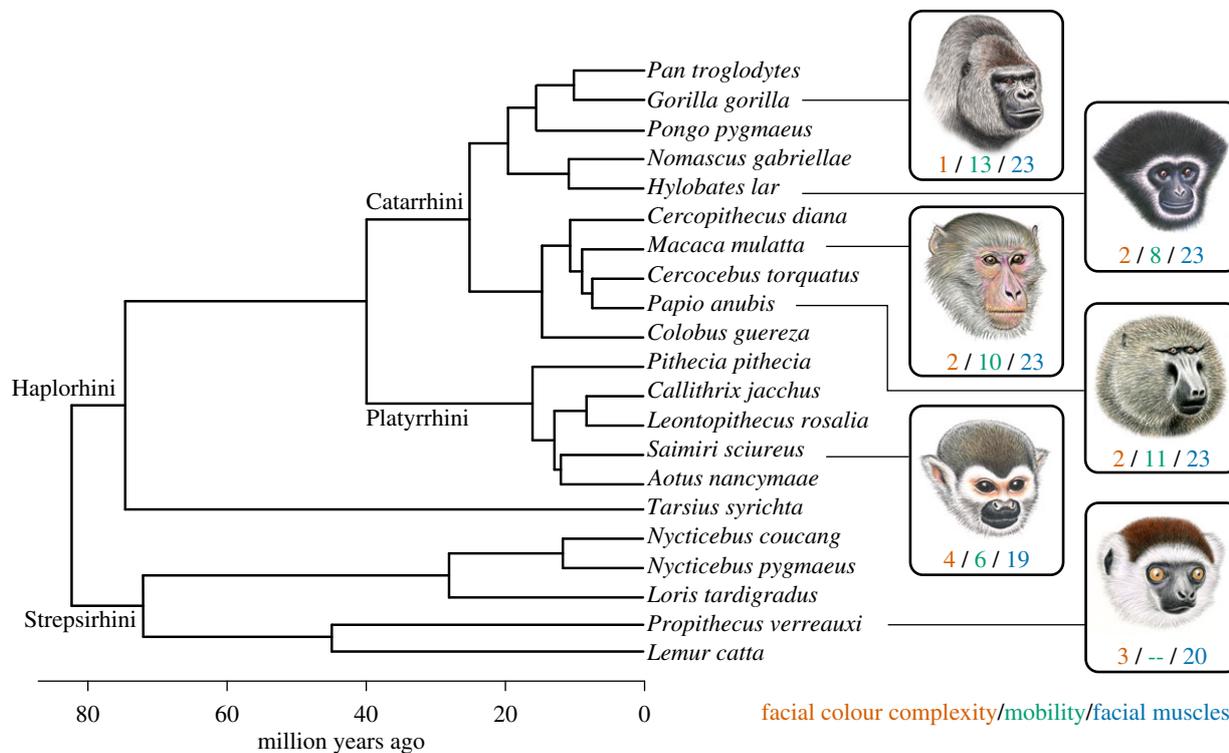


Figure 1. Phylogeny of species included in this study [12] with examples illustrating major trends in facial colour pattern complexity, mobility and facial muscles. Species that are larger and have more plainly coloured faces tend to have more facial expressions. Illustrations copyright 2012 Stephen D. Nash/IUCN/SSC Primate Specialist Group (with permission). (Online version in colour.)

could explain why larger species (e.g. apes) have more expressive faces, whereas smaller primates (e.g. marmosets) are more 'poker-faced' and rely on colourful facial patterns for communication [18].

Although the evolution of facial mobility is closely associated with external morphology and body mass, it is not directly related to the number of muscles that produce facial movements. Facial muscle number is, in fact, the slowest evolving trait in our dataset and has strong phylogenetic inertia [9]. In sharp contrast, the volume of the facial nucleus has evolved most rapidly. Changes in facial mobility via changes in facial nucleus volume and body mass, instead of muscle morphology, highlight an emphasis on the evolution of motor control of muscles instead of new divisions of pre-existing musculature. The faster evolution of the resulting behavioural traits (facial mobility) than morphological traits

(musculature and colour) fits the hypothesis that behavioural traits are more labile [13]. The rapid evolution of facial coloration could be explained by the fact that dramatic changes in the distribution of colour pigments and hair patterning can arise from point mutations within pigment pathways [24].

Our study has identified the patterns of evolution and potential trade-offs among some of the most important features used by primates in social communication. While there is outstanding diversity and intraspecific variation of facial traits across primates, simple organismal features such as body mass seem to have a strong connection with what types of facial cues evolve for communication and how. Future studies should experimentally address the relative contribution of the different aspects of facial diversity in social communication across primate species that have different ecologies.

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