Correlated evolution of brain regions involved in producing and processing facial expressions in anthropoid primates

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Anthropoid primates are distinguished from other mammals by having relatively large primary visual cortices (V1) and complex facial expressions. We present a comparative test of the hypothesis that facial expression processing coevolved with the expansion of V1 in anthropoids. Previously published data were analysed using phylogenetic comparative methods. The results of our study suggest a pattern of correlated evolution linking social group size, facial motor control and cortical visual processing in catarrhines, but not platyrrhines. Catarrhines that live in relatively large social groups tended to have relatively large facial motor nuclei, and relatively large primary visual cortices. We conclude that catarrhine brains are adapted for producing and processing complex facial displays.

Keywords: brain evolution; facial motor nucleus; neocortex; face perception

1. INTRODUCTION
Anthropoid primates exhibit a variety of adaptations in the visual system for high acuity that distinguish them from other mammals (Ross 2000; Kirk & Kay 2004). Anthropoids are also distinguished from other mammals by their use of complex facial expressions to facilitate social interactions (van Hooff 1967). Taken together, these observations have led some researchers to suggest a role for facial expression processing in the evolution of anthropoid visual systems, especially cortical visual areas (Allman 1977; Barton 1998).

Because the primary visual cortex (V1) is the earliest stage of visual processing in the cerebral cortex, it is important for basic analyses of spatial frequency, orientation and colour. Notably, V1 is relatively large in anthropoids when compared with other mammals. This is true whether V1 is scaled against body size, brain size or the size of other brain regions (Frahm et al. 1984; Bush & Allman 2004; Barton 2007). These scaling features represent possible neural adaptations for visual information processing in anthropoids that might be relevant to discriminating facial displays. Indeed, previous studies have noted a positive correlation between relative V1 volume and group size in anthropoids, indicating a possible social explanation for V1 expansion (Joffe & Dunbar 1997; Barton 1998).

Evolutionary links between V1 and facial expression may be approached by examining the facial motor nucleus. The facial nucleus is located in the brainstem and contains motoneurons that directly innervate the muscles of facial expression via cranial nerve VII. Thus, facial nucleus volume can be used as a proxy for facial motor control in comparative studies. A previous study examined the relationship between relative facial nucleus volume and social group size in primates, but did not find a statistically significant correlation (Sherwood et al. 2005). However, the relationship between facial nucleus volume and social group size has yet to be examined in anthropoids separately from other primates.

Our study provides a comparative test of the hypothesis that anthropoid primary visual cortices are adapted for processing complex facial expressions. This hypothesis makes two main predictions: (i) species that live in larger groups should have greater facial motor control and (ii) species with greater facial motor control should have enhanced cortical visual processing capabilities. To test these predictions, we examined the relationship between relative facial nucleus volume and social group size in anthropoids. Then, we examined the relationship between facial nucleus volume and V1 volume after controlling for the size of the rest of the brain.

2. MATERIAL AND METHODS
Brain component volumes and group size data for 23 non-human anthropoid species were taken from previously published sources (Frahm et al. 1984; Nunn & van Schaik 2001; Sherwood et al. 2005; de Sousa et al. 2010). We examined trait correlations using multiple regression analyses. Two sets of analyses were carried out: (i) we examined the relative volume of the facial nucleus in relation to group size; and (ii) we examined the volume of V1 in relation to facial nucleus volume after controlling for brain size. Separate regression models were generated for platyrrhines and catarrhines. We used medulla volume to adjust for size in analyses relating facial nucleus volume to group size (Sherwood et al. 2005). The volume of the rest of the brain (i.e. total brain volume–(neocortex + facial nucleus volume)) was used to control for size in analyses relating V1 volume to facial nucleus volume (Barton 1998). All data were log-transformed (natural) prior to analysis. Regression coefficients and associated standard errors were generated using a phylogenetic generalized least-squares (PGLS) approach (Martins & Hansen 1997). We used COMPARE 4.6b (Martins 2004) to perform PGLS regressions, based on a Bayesian estimate of phylogeny and associated branch lengths downloaded from the 10k Trees website (http://www.10ktrees.fas.harvard.edu/).

3. RESULTS
The amount of variance explained ($R^2$) was greater than 90 per cent in all PGLS regression models (see electronic supplementary material). Medulla volume was strongly correlated with facial nucleus volume in catarrhines ($b = 1.07; t_{11} = 11.89; p < 0.001$) and platyrrhines ($b = 0.93; t_6 = 7.75; p < 0.001$). Catarrhines exhibited a significant positive correlation (figure 1) between group size and facial nucleus volume after controlling for medulla volume ($b = 0.17; t_{11} = 2.83; p = 0.016$). However, this effect was absent from platyrrhines ($b = -0.03; t_6 = -0.30; p = 0.774$).
The results of our study suggest a pattern of correlated evolution linking group size, facial motor control and cortical visual processing in catarrhine primates. Species that live in relatively large social groups tend to have relatively large facial motor nuclei, and species with enlarged facial nuclei had relatively large primary visual cortices. These results mirror previous findings that species characterized by relatively large primary visual cortices. These results suggest that catarrhine brains are adapted for processing facial expressions and that while most catarrhines rely on facial displays to some degree, the same cannot be said for most platyrrhines, with the exception of a few taxa. Platyrrhines may rely more heavily on olfactory signals instead of visual signals (Barton 1998). Taxonomic differences between catarrhines and platyrrhines may also exist in the organization of connections between regions of facial motor representation in the neocortex. Specifically, in Japanese macaques (Macaca fuscata), many neurons of the supplementary motor area (SMA) project to the orofacial region of primary motor cortex (Tokuno et al. 1997), while relatively few neurons in the SMA of owl monkeys (Aotus trivirgatus) make these projections (Stepniewska et al. 1993). Moreover, compared with the broad region of SMA that can evoke orofacial movements in macaques (Godschalk et al. 1995), electrical surface stimulation of the SMA in squirrel monkeys (Saimiri sciureus) have been described as 'subtle' and 'not sustained as in macaques' (Marriott & Salzen 1978). On the other hand, some New World species do have complex facial displays (Moynihan 1967; Moynihan et al. 1993). Moreover, compared with catarrhines, platyrrhines do not exhibit signs of selection for facial expression processing. This implies a fundamental difference between infraorders with regard to facial expression. It has been suggested that platyrrhines in general have fewer and less complex facial displays than catarrhines (Moynihan 1967; Eisenberg 1976; Weigel 1979). In particular, marmosets and tamarins (Callitrichinae) have been described as 'poker-faced' with regard to facial expression (Moynihan 1967). Similarly, the facial displays of squirrel monkeys (Saimiri sciureus) have been described as 'subtle' and 'not sustained as in macaques' (Marriott & Salzen 1978). On the other hand, some New World species do have complex facial displays (Moynihan 1967). Capuchins (genus Cebus), in particular, exhibit catarrhine-like patterns of facial expression (De Marco et al. 2008). It seems that while most catarrhines rely on facial displays to some degree, the same cannot be said for most platyrrhines, with the exception of a few taxa. Platyrrhines may rely more heavily on olfactory signals instead (Barton 2006). Taxonomic differences between catarrhines and platyrrhines may also exist in the organization of connections between regions of facial motor representation in the neocortex. Specifically, in Japanese macaques (Macaca fuscata), many neurons of the supplementary motor area (SMA) project to the orofacial region of primary motor cortex (Tokuno et al. 1997), while relatively few neurons in the SMA of owl monkeys (Aotus trivirgatus) make these projections (Stepniewska et al. 1993). Moreover, compared with the broad region of SMA that can evoke orofacial movements in macaques (Godschalk et al. 1995), electrical surface stimulation of the SMA in squirrel monkeys (Saimiri sciureus) have been described as 'subtle' and 'not sustained as in macaques' (Marriott & Salzen 1978). On the other hand, some New World species do have complex facial displays (Moynihan 1967). Capuchins (genus Cebus), in particular, exhibit catarrhine-like patterns of facial expression (De Marco et al. 2008). It seems that while most catarrhines rely on facial displays to some degree, the same cannot be said for most platyrrhines, with the exception of a few taxa. Platyrrhines may rely more heavily on olfactory signals instead (Barton 2006).
monkeys does not evoke orofacial movements (Welker et al. 1957). Similarly, intracortical microstimulation of only a small region of SMA in owl monkeys evokes orofacial movement (Gould et al. 1986). These data further support our conclusion that catarrhines, but not platyrrhines, have co-evolved visual and motor neural systems specifically relevant to the use of complex facial expressions.


