

Neuroanatomical Basis of Facial Expression in Monkeys, Apes, and Humans

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INTRODUCTION

The face is a focal point for the expression of emotions and is central in mediating social exchanges among primates. Early researchers^{1,2} noted phylogenetic differences in the facial expressiveness of primates. More recently, psychobiological studies have suggested that great ape and human facial expression may constitute a mode for the communication of highly nuanced nonemotional signals not present in Old World monkeys.³ Despite these indications of phylogenetic differences in gestural communication, very little is currently known about the comparative neurobiology of facial expression.

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Here we report data from ongoing comparative quantitative neuroanatomic studies of the brain-stem facial nucleus and primary motor cortex face area in haplorhine primates (i.e., tarsiers, New World monkeys, Old World monkeys, apes, and humans). Using these data we test the hypothesis that great apes and humans differ from other haplorhines in the neural organization of motor face representation.

IS THE FACIAL NUCLEUS ENLARGED?

We calculated the planimetric volume of the facial nucleus in 49 haplorhine individuals (including 10 great apes and 4 humans), representing 30 different species. The facial nucleus was outlined in a stack of digital micrographs of Nissl-stained sections, and total volume was obtained according to the Cavalieri principle. To test whether the facial nucleus of great apes and humans is enlarged, we calculated a prediction equation from the rest of the haplorhine data by regressing log (facial nucleus volume) against log (medulla volume). As a group, the observed values for great apes and humans were significantly larger than predicted by the haplorhine regression line (FIG. 1a; paired samples *t*-test: $t = 4.175$, $P = 0.001$, d.f. = 14); on average, the facial nucleus of great apes and humans is 27% larger than expected for a haplorhine of the same medulla volume. When the independent-contrasts regression line is computed and mapped back onto the original data space to generate phylogenetically informed prediction intervals,⁴ however, only the orangutan point falls above the 95% prediction interval (FIG. 1b).

REORGANIZATION OF PRIMARY MOTOR CORTEX

The face area of primary motor cortex was investigated for phylogenetic differences in cytoarchitectural organization (FIG. 2a). Nissl-stained histological sections were analyzed from the region corresponding to the face representation of the right hemisphere from long-tailed macaque ($n = 3$), anubis baboon ($n = 1$), orangutan ($n = 2$), gorilla ($n = 2$), common chimpanzee ($n = 2$), and human ($n = 2$). Measurements of cortical layer width were performed from several locations and the percent of total cortical width represented by each layer was calculated. Compared to Old World monkeys, the motor cortex of great apes and humans has a significantly expanded layer III and a reduced layer V (FIG. 2b), although some overlap exists in the range of Old World monkey and orangutan values for layer III. Given that layer III is comprised predominantly of neurons forming corticocortical connections, this result suggests an increase in association networks in great apes and humans.

We pursued further the observation of increased thickness of layer III in great apes and humans by analyzing neuronal packing density in this layer us-

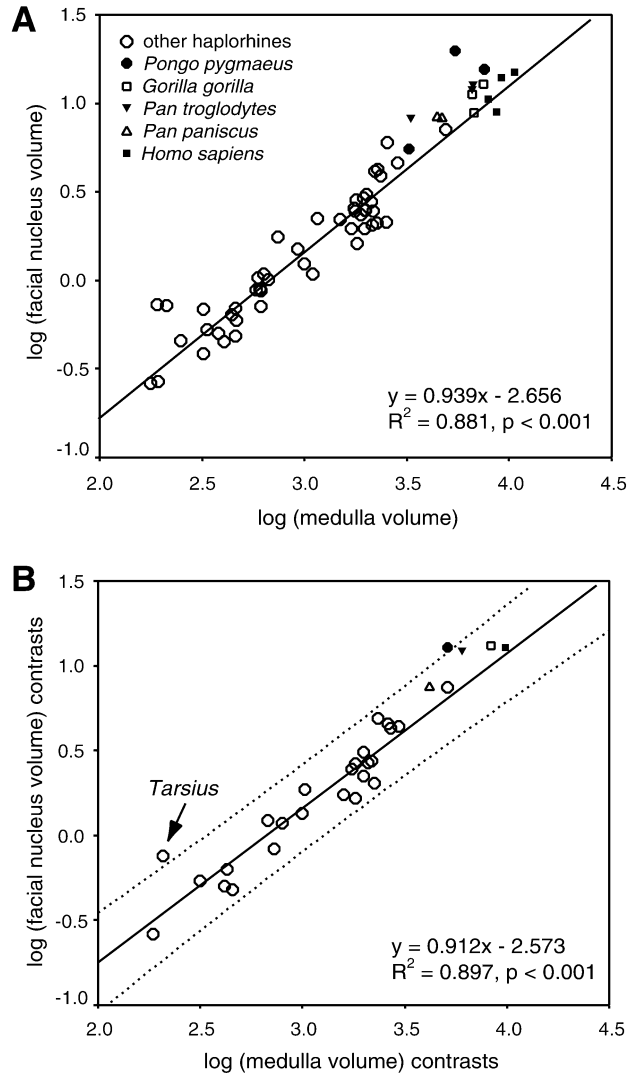


FIGURE 1. A double logarithmic scatterplot of facial nucleus volume and medulla volume is presented (a). The reduced major axis line was fit to the data from all haplorhines except great apes and humans. Independent contrasts of species means plotted in the original data space with 95% prediction intervals shown (b).

ing the optical fractionator technique (Fig. 2c). Species mean layer III neuronal density and brain weight were not correlated ($r = -0.84$, $P = 0.12$); however, we found that densities were lower in layer III of great apes and humans compared to Old World monkeys ($t = 5.31$, d.f. = 10, $P < 0.01$), revealing increased space for interconnections among neurons. Taken together with

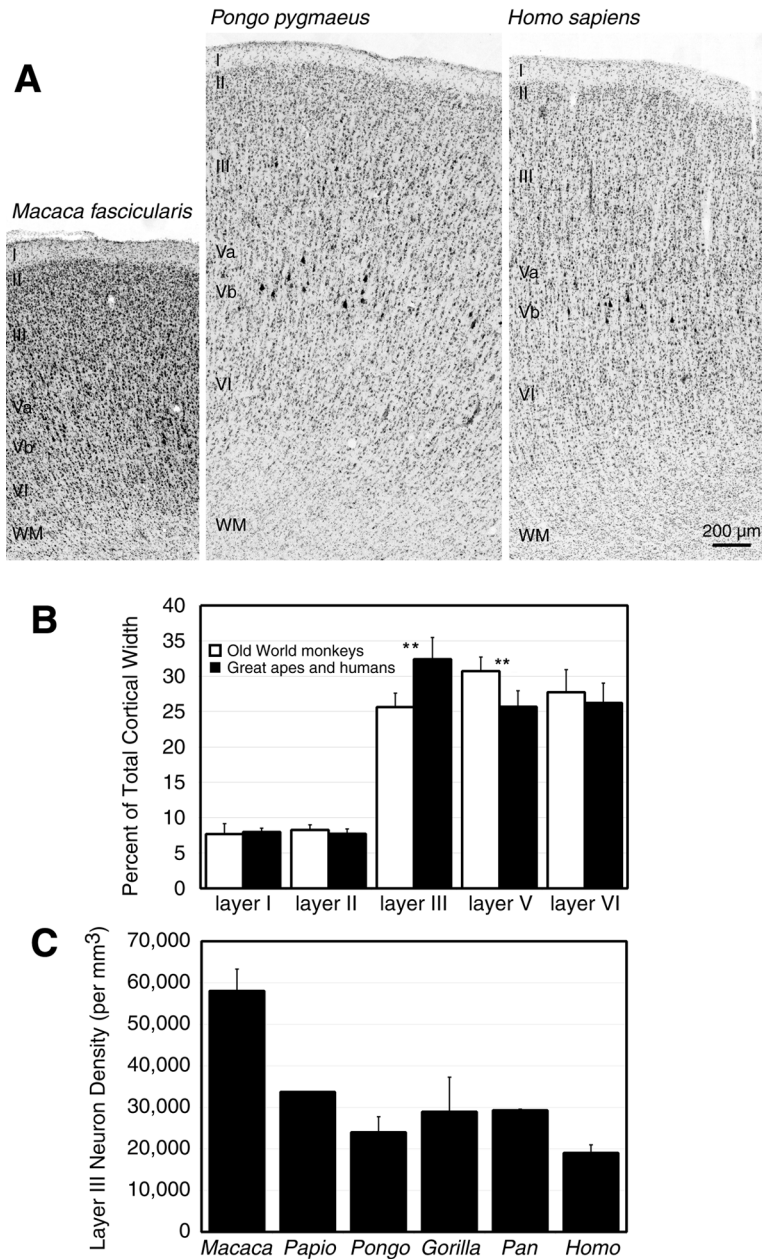


FIGURE 2. Cytoarchitecture of face area of primary motor cortex in representative catarrhine primates is shown (a). Bar graphs show phylogenetic comparisons of relative laminar widths (b) and neuronal densities (c) in primary motor cortex (mean \pm 2 SEM). Asterisks indicate statistically significant contrasts at $P < 0.01$.

the observation that neuropil volume increases in supragranular cortical layers of primary visual cortex through primate phylogeny,⁵ this suggests a general evolutionary trend in the primate cerebral cortex for increasing neuropil in supragranular cortical layers.

CONCLUSIONS

The data reported here indicate that the facial motor system of great apes and humans is evolutionarily derived in comparison to other primates. The evidence for microstructural reorganization of primary motor cortex face area may constitute a substrate for the strengthening of corticocortical integration from orbital, insular, ventral premotor, supplementary motor, cingulate motor, and parietal areas.⁶ These modifications of motor face representation may underlie the evolution of flexible and subtle facial movements among humans and our close relatives, the great apes.

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