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Multimodal analysis of the macaque frontal lobe reveals novel prefrontal areas

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Classical cytoarchitectonic maps of the macaque prefrontal cortex [1,2,3], based on qualitative analyses, differ in the number and extent of areas they display. Thus, the present research aims to characterize prefrontal areas based on a multi-modal approach based on quantitative cyto- and receptor architectonic analysis to create statistically testable parcellation [4] that can be transformed into stereotaxic space. The brain of an adult Macaca mulatta (ID: DP1, obtained from Prof. Deepak N. Pandya) was processed for cytoarchitectonic analysis, and those of three adults Macaca fascicularis (ID: 11530, 11539, 11543; obtained from Covance Laboratories, Münster, Germany) for combined cyto- and receptor architectonic analyses. Serial coronal sections (20μm thick) were processed for the visualization of 14 receptor binding sites or of cell bodies according to established protocols [5]. Resulting autoradiographs were digitized to obtain receptor densities by densitometric analysis and, finally, visualized as receptor fingerprints [5]. Resulting maps are used as seed regions to perform functional connectivity analyses of openly available MRI datasets [6] from the NHP data sharing consortium PRIME-DE to characterized identified areas by their functional connectivity pattern. Functional data were preprocessed using the Human Connectome Project-style pipeline for Nonhuman Primate as described previously [7]. Finally, multivariate analyses also included agranular frontal areas identified in the same macaque brains [8], providing a comprehensive insight into the hierarchical organization within the primate frontal lobe. A hierarchical cluster and principal component analyses were conducted to determine the degree of similarity of receptor fingerprints within primate cortex. Euclidean distances between areas were computed as a measure of (dis)similarity, and the Ward linkage algorithm was chosen as the linkage method. The number of stable clusters was determined by a k-means analysis and confirmed by the elbow method [8]. Figure 1A shows a map of the entire frontal lobe, displayed on the Yerkes 19 surface. Within the prefrontal region, 35 cyto- and receptor architectonic areas were identified, including novel subdivisions of Walker's areas 10, 9, 8B and 46 (Fig.1A). Multimodal receptor and functional connectivity analyses revealed a rostro-caudal trend in dorsal (areas 9 and 8B) and lateral (areas 46) prefrontal cortex. I.e., subdivisions of 9 (Fig.1B) and a46, located more rostrally, were characterized by bigger fingerprints and displayed limited functional connectivity with their neighboring areas, possibly suggesting that these areas are affected by a lower signal-to-noise ratio [9]. The opposite trend holds for caudally positioned subdivisions of 8B (Fig.1B) and p46. Further, multivariate analysis of receptor densities revealed five clusters segregated into two main groups (Fig.1C). Group A included the most rostral prefrontal areas and all orbital areas; group B comprised caudal prefrontal areas, which are further segregated from primary motor areas.
This study characterizes in detail the anatomical, neurochemical and functional connectivity of the primate prefrontal cortex, based on quantitative data. Taken together, it provides a comprehensive insight into the microstructural and molecular organization of the primate frontal cortex underlying brain function, and a sound basis for assessing homologies with the human brain. Our data will be publicly available for the entire scientific community.

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