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Neural connectivity and cortical substrates of cognition in hominoids

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Abstract

Cognitive functions and information processing recruit discrete neural systems in the cortex and white matter. We tested the idea that specific regions in the cerebrum are differentially enlarged in humans and that some of the neural reorganizational events that took place during hominoid evolution were species-specific and independent of changes in absolute brain size.

We used magnetic resonance images of the living brains of 10 human and 17 ape subjects to obtain volumetric estimates of regions of interest. We parcellated the white matter in the frontal and temporal lobes into two sectors, including the white matter immediately underlying the cortex (gyral white matter) and the rest of white matter (core). We outlined the dorsal, mesial, and orbital subdivisions of the frontal lobe and analyzed the relationship between cortex and gyral white matter within each subdivision.

For all regions analyzed, the observed human values are as large as expected, with the exception of the gyral white matter, which is larger than expected in humans. We found that orangutans had a relatively smaller orbital sector than any other great ape species, with no overlap in individual values. We found that the relative size of the dorsal subdivision is larger in chimpanzees than in bonobos, and that the ratio of gyral white matter to cortex stands out in *Pan* in comparison to *Gorilla* and *Pongo*. Individual variability, possible sex differences, and hemispheric asymmetries were present not only in humans, but in apes as well.

Differences in the distribution of neural connectivity and cortical sectors were identified among great ape species that share similar absolute brain sizes. Given that these regions are part of neural systems with distinct functional attributes,

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we suggest that the observed differences may reflect different evolutionary pressures on regulatory mechanisms of complex cognitive functions, including social cognition.

Keywords: Brain evolution; Frontal lobe; Temporal lobe; Apes; Humans; White matter; Cortex; Dorsolateral; Orbitofrontal; Mesial frontal; Morphometry; Magnetic resonance; Social cognition

Introduction

In a series of comparative neuroanatomical morphometric studies of the brains of humans and apes, we showed that human brain evolution and the evolution of complex cognitive capabilities cannot be simply attributed to an overall differential enlargement of the frontal lobe, as both humans and great apes share, relative to the rest of the brain, a large frontal lobe and frontal cortex (Semendeferi and Damasio, 2000; Semendeferi et al., 2002). While it is likely that the absolute size of the human brain is important for human cognition (Gibson, 2002; Passingham, 2002), the outstanding cognitive capabilities of humans may also be supported by discrete modifications in the relative size of specific neural systems that accompanied increases in the absolute size of the brain. In the study reported here, we tested the idea that certain subdivisions of the cerebrum involved in complex cognitive behaviors are differentially enlarged in humans, including sectors of the frontal cortex and subdivisions of the white matter in the frontal and temporal lobes. We also tested the idea that, during hominoid evolution, adaptive neural reorganizational events took place (Holloway, 1968) that are species-specific and possibly independent of changes in absolute brain size (Holloway, 1979, 2001).

We parcellated the white matter into two regions of interest. One was the gyral white matter (GWM), including the sector of the white matter immediately underlying cortical territories; the other region was the core, including all remaining white matter in the frontal and temporal lobes. This type of parcellation of the white matter is analogous to parcellation schemes adopted by other studies, with the gyral white matter corresponding closely to the overlying cortical parcellation unit of the outer zone of the white matter (Makris et al., 1997; Herbert et al., 2004). Furthermore, we identified the three major gross anatomical sectors in the frontal lobe (dorsal, mesial, orbital) and the amount of tissue devoted to gray, as opposed to white, matter (cortex and gyral white matter) within each sector. Enlarged gyral white matter in any region of interest for a given species may indicate increased interconnectivity within and between neighboring cortical regions, many of which are involved in complex cognitive behaviors. Specifically, we tested the hypothesis that humans have relatively more gyral white matter in the frontal and temporal lobes compared to other hominoids. We also tested the idea that orangutans have a smaller orbital frontal cortex than other apes, a hypothesis based on findings from our pilot study, discussed below. Additionally, we analyzed our regions of interest in search of possible asymmetries and sex differences.

Lesions in the frontal lobe were thought, until recently, to result in a generalized frontal lobe syndrome (Hecaen, 1964; Luria and Homskaya, 1964; Teuber, 1964), but systematic studies over the past two decades using the lesion method and imaging technology in humans, as well as a variety of experimental studies in rhesus monkeys, have demonstrated that this large cortical territory comprises anatomical subdivisions with rather distinct functional attributes. The dorsal sector of the frontal lobe is involved in perception, response selection, working memory, and problem solving (Owen, 1997; Bechara et al., 1998; Petrides, 2000; Pochon et al., 2001). It also includes territories activated during language production in humans (Foundas, 2001) and most of the primary motor and premotor cortices (Zilles et al., 1995). The mesial frontal cortex, including the anterior cingulate, is important for processing emotional stimuli