Structural Analysis of Network Models in Tetrapod Skulls [Thesis Summary]

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Background

Ever since classic anatomists like George Cuvier, Geoffroy St. Hilaire, or Richard Owen laid down the fundamental principles of comparative anatomy in the 19th century, connections among anatomical parts have been essential for the recognition of biological homologies. However, few studies have addressed the possibility of implementing an adequate methodological tool to use connections among parts to unveil problems in morphology; although Woodger, Rashevsky, Riedl, and, more recently, Rasskin-Gutman pointed in this direction.

In the last decades Network Theory has been developed as a novel conceptual and methodological framework to deal with the relational properties that emerge due to connections between parts in any organized system (e.g., robustness, self-organization, and modularity). Network analysis was readily applied to a wide range of complex biological systems, such as gene regulatory pathways, brain neuronal systems, or ecological communities. However, a seemingly natural arena to use this mathematical tool such as comparative anatomy has never been systematically studied using current network analysis tools.

Aims

The aim of my thesis is to carry out a comparative analysis of connectivity patterns in tetrapod skulls to assess problems on the evolution and ontogeny of morphological complexity, integration, and modularity. This kind of analysis can reveal key morphological properties of the skull that most common studies, based solely on shape and size, would keep unravel. Empirical and theoretical outcomes of this comparative analysis of skull networks have been used to assess how connectivity patterns affect the formation and evolution of the skull morphology in tetrapods.

Methods

I formalize the structure of connections in the skull (i.e., connectivity pattern) using network models, in which nodes and links represent bones and suture contacts, respectively. Thereby, skull networks were built for extant and extinct species, including some human newborn skulls with different craniosynostosis conditions.

These skull networks were analyzed using current network analysis methods and null models to reveal the properties of their morphological organization related to complexity, integration, and modularity. To this end, I also developed a complete framework of anatomical interpretations for the most common parameters used in networks analysis (e.g., density, clustering coefficient, and path length), which, in general, have been never applied in a morphological context. Finally, the results of skull networks analysis have been discussed in an evolutionary and developmental context.

Remarks

• Morphological complexity increases during evolution in tetrapod skulls, due to the random loss of poorly connected bones and the selective fusion of highly connected ones

• The organization of connectivity modules decreases in disparity during skull evolution, due to an increase in morphological integration of connectivity patterns.

• Bones within the same connectivity module share the same allometric growth pattern in humans; as a consequence, connectivity modules resemble units of allometric growth

• The analysis of network models in human skulls with craniosynostosis indicates that modifications of connectivity patterns due to premature fusion of bones have similar effects than those observed during the evolution of the tetrapod skull (e.g., changes in complexity, variations in modular organization). This further suggests a strong relation between bone fusion during development and skull evolution.

• Tetrapod skulls have occupied the space of possible forms following a directional pattern during their evolution; from forms with more bones and higher variability available, to forms with fewer bones and lower variability.

• The null model that better explains this directional pattern is based on structural constraints imposed by the bilateral symmetry of the skull and a growth rule to establish connections between bones based on geometric proximity (Gabriel rule).