Analysis of the structural organization of the human hand using anatomical network models

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SUMMARY

Despite the fact that morphogenetic mechanisms of transformation of the hand during ontogenesis are currently known, the question remains as to how its various anatomical parts are (metacarpal bones, phalanges of fingers) organized into a complex integrated structure. This question remains unanswered for several reasons, including the lack of consensus about conceptual definitions and approaches, including the lack of tools to assess and compare variations in different anatomical parts of the hand.

The aim of this study is to assess the structural organization of the metacarpal bones and phalanges of the fingers of the human hand by Anatomical Network Analysis (AnNA). In this study, the functions of the IGRAPH package in the R data analysis programming environment were used for AnNA. The modeling and layout of the network is performed using the Fruchterman-Reingold algorithm. The Spinglass algorithm is used to determine modularity in anatomical networks.

For AnNA, X-ray osteometric indicators of the length (joint length) of the metacarpal bones and phalanges of the fingers of 100 middle-aged men and 100 women without traumatic changes, deformities and developmental abnormalities were used. AnNA demonstrates that the organization of the elements of the rays of the hand is represented by two modules – the proximal, which includes (metacarpal bones and proximal phalanges) and the distal, which includes the middle and distal phalanges. When comparing the characteristics of the network models of the hands, it was found that in women the organization of the metacarpal bones and phalanges of the fingers is characterized by higher morphological integration and modularity (modularity 0.31) than in men (modularity 0.45).

Morphological modularity and integration are the organizing factors of the structure of morphological parameters of various parts of the hand. The structural organization of the hand is a system consisting of two modules – the proximal (metacarpal bones and proximal phalanges) and the distal (middle and distal phalanges).

Key words: Human hand – Structural organization – Network analysis – Morphological modularity – Morpho-logical integration.

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INTRODUCTION

The morphological substrate of the pentadactyly of the distal segments of the upper extremities of primates and in humans in particular are rays, each of which is formed by the metacarpal bone and the phalanges of its corresponding finger (Patel and Maiolino, 2016). The development and growth of the rays of the hand is determined by morphogenetic mechanisms that are uniform for all their elements in time and space (Glover et al., 2023). Subsequent ontogenetic transformations lead to the formation of the preaxial (I finger and I metacarpal bone) and postaxial (II–V metacarpal bones and II–V fingers) ray groups of the hand (Shubin and Alberch, 1986). However, despite the fact that the morphofunctional aspects are the same for each of the rays, the ratios of the elements of the postaxial group of the latter determine the morphological patterns of the hand: ectaxonic (the length of the IV ray prevails over the rest), paraxonic (the length of the III-IV rays prevails over the rest, while the length of these rays is the same) and mesaxonic (the length of the III ray prevails over the rest) (Preuschoft and Chivers, 1993).

Considering the above, the question arises as to how such a morphologically complex part of the human body as the hand evolved, taking into account the limitations caused by genetic factors, developmental factors, as well as locomotor functions, which has been the subject of study for many decades (Perepelkin et al., 2020). In the middle of the 20th century, the study of covariance (conjugate variation) of morphological features and the consequences of this for evolutionary diversification was developed within the framework of the general concept of “morphological modularity and integration” – i.e., the development of phenotypic structures of biological objects does not proceed in isolation, but is organized into modular units that are relatively independent of each other, while morphological features, the variability of which is due to embryogenetic or morphofunctional factors, have a high degree of integration and develop to some extent as a whole (Klingenberg, 2014). Taking into account the model of polygenic inheritance underlying the quantitative features of the skeleton, including the hand, as well as the existence of differential pleiotropic effects, it is assumed that variations in the comparison of genotype with phenotype can lead to the appearance of semi-autonomous “modules” that have a relatively stronger integration between morphological features within them. This concept is also closely related to the question of the ability of anatomical structures to respond to the selective pressure of environmental factors. For example, some authors argue that modularity provides flexibility of the anatomical structure, since the direction and magnitude of evolutionary changes between parts and within the structure can vary without compromising the function of the latter (Raff, 1996). However, other authors believe that higher integration within the anatomical structure contributes to its evolutionary transformations (Conaway and von Cramon-Taubadel, 2022). The study of structural organization is especially important for understanding the transformation of the hand, which differs among primates in the scale of morphological changes during their evolution (Chavez and Morrell, 2022).

Ideas about the morphological modularity, integration, and structural organization of the postcranial skeleton remain somewhat limited due to the difficulty of studying the many interactions between the bones of its various departments (Conaway and Adams, 2022). Moreover, due in no small part to the complexity of analyzing data sets and understanding them, most studies have focused on the skeleton of the girdle and the free part of the upper and lower limbs, with the exception of the distal segments (Conaway and von Cramon-Taubadel, 2022). Thus, the problem of the structure of the skeleton of the human hand in the context of architectonics and the organization of morphological indicators of its bones is relevant, which requires a new methodology based on the identification and comparison of morphological modularity and integration between the elements of the rays of the hand and their morphometric parameters in order to obtain a comprehensive assessment and an integrative look at the evolution and morphology of distal segments of the upper extremities.

One of the new powerful tools for studying patterns of interrelation between parts of the anatomical structure is Anatomical Network analysis

(AnNA) (Ziermann et al., 2021). Unlike quantitative morphometric methods, a unique feature of AnNA is a direct comparison of different parts of the studied object (McQueen and Towers, 2020). In particular, AnNA evaluates connectivity patterns using tools and statistics borrowed from network theory, formalizing parts of the studied object as nodes and connections between them as a network model to assess structural organization and identify patterns of integration and modularity between parts of the anatomical structure (Rasskin-Gutman and Esteve-Altava, 2009). It is noteworthy that AnNA represents a formal basis for the study of morphological organization, free from a priori assumptions and hypotheses about the development, functional and phylogenetic relationships between parts of anatomical structures (Diogo et al., 2018).

Using AnNA provides an opportunity to explore which patterns of integration/modularity have an impact on the structural organization of a person's hand.

The aim of this study was to study the structural organization of the elements of the rays of the human hand with the help of AnNA.

MATERIALS AND METHODS

Sample

In this work, we used the results of morphometry of certified digital radiographs of the hands of 200 people (100 men and 100 women) from the databases "Biometric description of X-ray osteometric signs of the metacarpal bones of the human hand" and "X-ray osteometric characteristics of the phalanges of the fingers of the human hand" (Ermolenko, 2021a, b). The average age of men was 46.3±1.1 years, the average age of women was 49.2±0.9 years (M±m).

AnNA

For the analysis, the indicators of articular length (the distance between the center of the articular area of the base and the point furthest from it on the head of the bone) of the metacarpal bones and phalanges of the fingers of the hand were used. Anatomical networks have been modeled as systems of connections between nodes, information about which is encoded in the form of adjacency correlation matrices: a square symmetric matrix where each row and column repre-

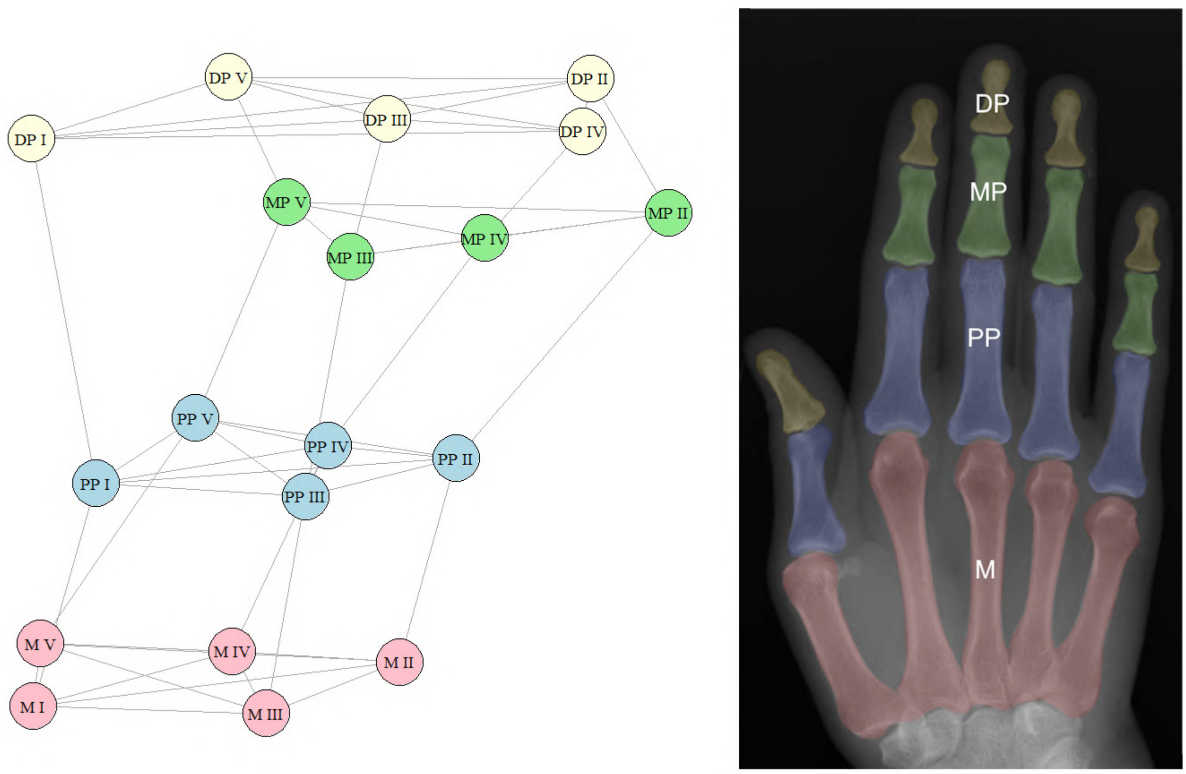

Fig. 1.- The scheme hand, formalized in the form of a network.

sent one anatomical part. For the hands (pastern and distal part of the hand (fingers)) men and women have built network models in which nodes represent bones (Fig. 1).

The measure of quantification of the connection between nodes was the weight of the connection. The nodes are arranged using the Fruchterman-Reingold algorithm. To determine modularity in anatomical networks, the Spinglass algorithm was used, the implementation of which is based on paired interactions in the system based on the assumption that the connections between nodes are in similar "spin" states, which determines the morphological context of modularity (Yan et al., 2016). In this study, the functions of the IGRAPH package in the R data analysis programming environment were used to build the network (Csardi and Nepusz, 2006). The quantitative assessment of the main network parameters included: connection density (the number of existing connections relative to the total maximum possible in accordance with the total number of nodes), the average clustering coefficient (the arithmetic mean of the clustering coefficient of all nodes in the network), the average distance between nodes (the average value of the sum of the distances between two nodes in the network), modularity (the value of indicating how well the network parts (modules) are separated from each other), heterogeneity of compounds (the ratio between the standard deviation and the average value of compounds).

RESULTS

Anatomical networks representing the hands of men and women were analyzed (Fig. 2).

Analysis of the relationship between nodes within the module and between nodes of modules of each module, regardless of gender and body side, demonstrates the absence of grouping within each module, which allows us to distinguish two modules. Module 1 (proximal) included the I-V metacarpal bones and the proximal IV fingers. Module 2 (distal) included the middle phalanges of the II-V fingers and the distal phalanges of the I-V fingers (Fig. 3).

The name of each module refers only to the anatomical area it occupies, and excludes any interpretation related to development and function. The

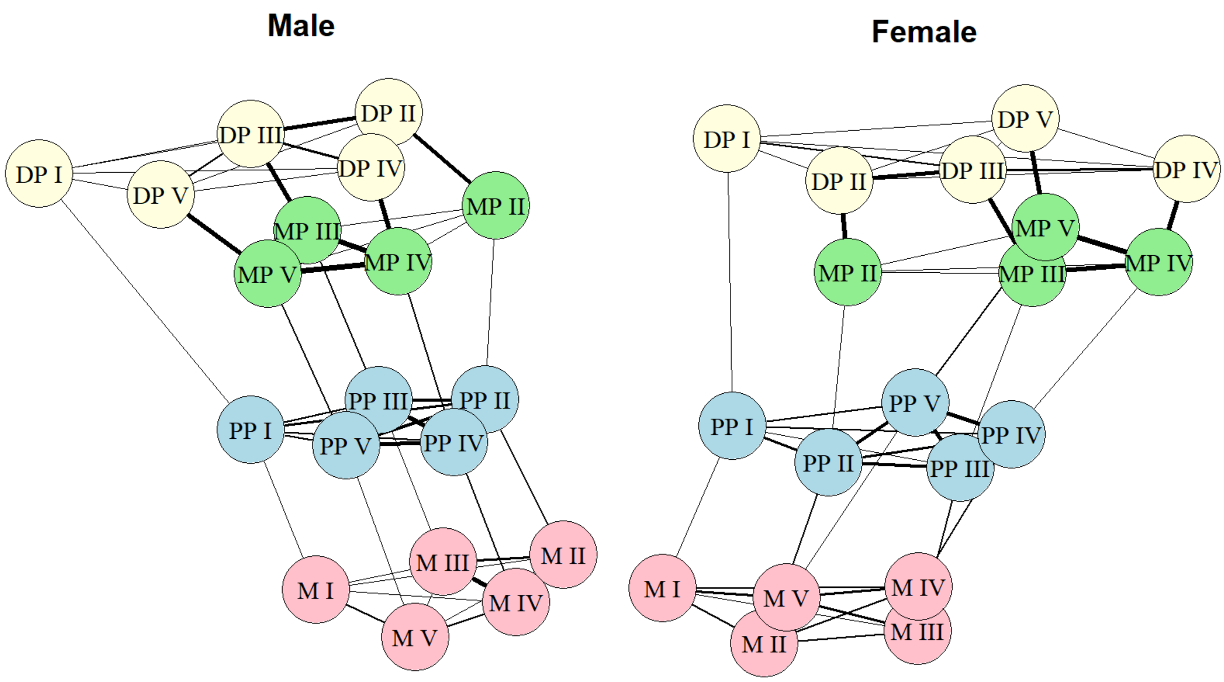

Fig. 2.- Network hand models.

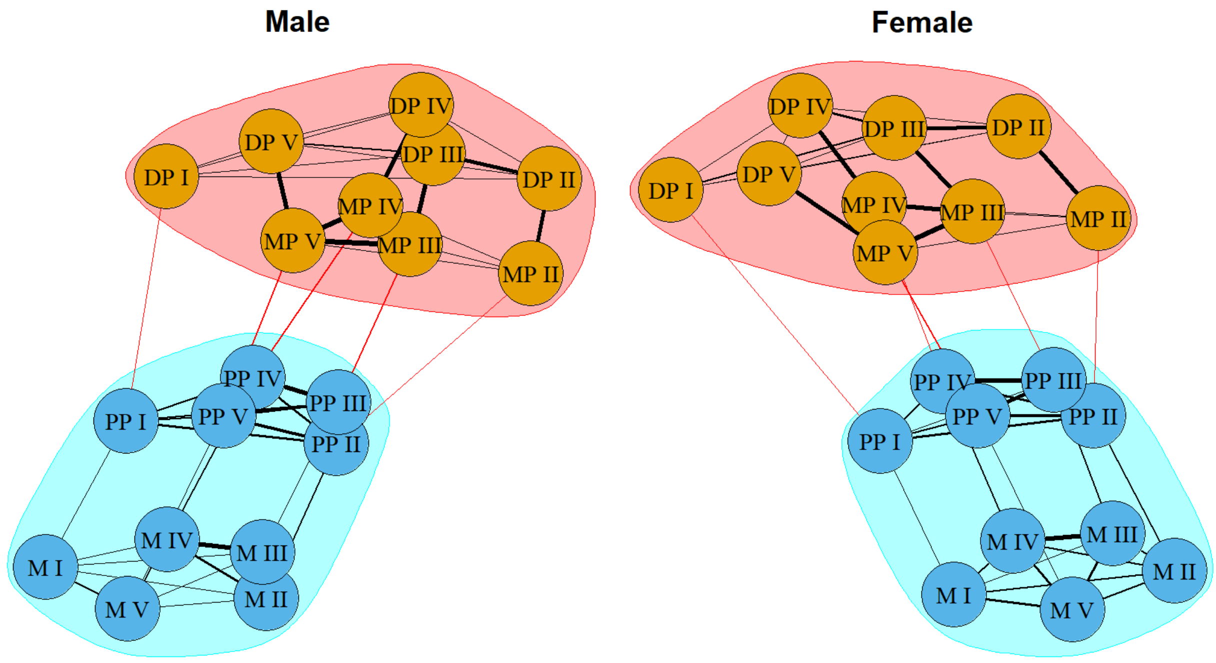

Fig. 3.- Hand modules.

analysis of network models of the hands demonstrates that in women, if compared with men, the organization of the metacarpal bones and phalanges of the fingers is characterized by higher morphological integration and modularity (Table 1).

Table 1. Parameters of anatomical network models of the hand.

Parameter	Male	Female
Number of nodes	19	
Number of connections	63	
Connection density	0.18	0.15
Clustering coefficient	0.43	0.47
Average distance between nodes	0.41	0.75
Modularity	0.31	0.45
Heterogeneity of compounds	0.79	0.64

Thus, we observe distinct proximal and distal modules in the human hand.

DISCUSSION

The obtained results demonstrate the possibilities of AnNA for studying the structural organization of the human hand. In previous studies, it was shown that differences in the structural organization of the hand in primates and humans in particular lie in the plane of differences between the morphometric parameters of the ray elements, which manifests itself in various proportional ratios between the metacarpal bones and phalanges of the fingers, identified using classical morphometry methods (Preuschoft and Chivers, 1993; Patel and Maiolino, 2016). Thus, the use of AnNA is an important step in assessing the structural organization of the hand in humans.

In this study, anatomical network models of the human hand were created. Despite the fact that the metacarpal bones and phalanges of the fingers are closely evolved modules of the hand, the results obtained confirm the hypothesis of an integration gradient in the postcranial skeleton (Chavez and Morrell, 2022). The development, growth and differentiation of the skeleton of the hand have a genetic determination and occur simultaneously in three planes as a continuum. These coordinated development processes ensure the integration of hand segments (Glover et al., 2023). Thus, the development of the structures of the proximal module (metacarpal bones and proximal phalanges) and distal modules (middle and distal phalanges) are regulated jointly, which leads to highly coordinated anatomical and functional relationships (Perepelkin et al., 2020).

The stronger relationships between the elements of each of the anatomical modules of the hand are consistent with its morphogenesis relative to the radiolateral (transverse) axis, which is due to the high proliferative activity of mesodermal cells forming a zone of polarizing activity located postaxially on the most distal part of the rudiment of the hand (McQueen and Towers, 2020).

In several anatomical studies, AnNA was used for comparative assessment, modeling of the development, functioning, and evolution of various morphological systems of the postcranial skeleton (Diogo et al., 2018; Ziermann et al., 2021). However, the research of the human hand with the help of AnNA focused on the analysis of the relationship of bone structures with tendons and muscles, while the structural organization was not considered in the context of organic integrity. The allocation of a two-level structure in the organization of the hand in the form of proximal and distal morphological modules possibly reveals the evolutionary aspect of the transformation from a hand with a force grip (the length of the fingers exceeds the length of the metacarpal bones), which is necessary for locomotion in lower primates to a hand with a precision grip (metacarpal bones and proximal phalanges provide the grip force, while the middle and distal phalanges play a role in precision grip), which is observed in higher primates, including humans, when manipulating objects.

Thus, a network model of the hand was built, which, apparently, reflects in the form of a network the morphogenetic effects underlying the coordinated development of human hand segments. The results of the study confirm that AnNA is an important tool for studying the distal segments of the human postcranial skeleton.

The results obtained cannot be considered in the context of the existence of a relationship between modularity and the complex structure of the skeleton of the hand from a morphological point of view. At the same time, attempts to limit the definition of the complexity of the structure of the skeleton of the hand confirm the positive feedback between modularity and structure. However, this thesis should be considered with some caution, due to the small number of metacarpal bones and phalanges of fingers in humans.

The results of the study demonstrate that the determining factors of the structural organization of the hand are morphological integration and modularity. This is the first study using AnNA to assess the structural organization of the hand based on radiography data. AnNA can be used to study the anatomical variability of the skeleton of the hand in terms of morphological modularity and integration.

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