Morphological integration and modularity of the human hand

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SUMMARY

Morphological modularity is a concept that refers to the level of covariance between the components of a structure. Morphological modules are independent subsets of correlated features; in particular, in the human hand, these are the metacarpus (metapodium) and fingers (acropodium). The human hand has been studied as an integral morphological structure for a long time, but its modularity has not been evaluated within the framework of an integrative approach. The aim of this study is to assess the hypothesis of modularity of the metapodium and acropodium of the human hand in the context of their spatial conjugacy using geometric morphometry. Using geometric morphometric methods to determine the shape and location, both modules were examined in samples from 100 digital X-ray images of the right hands of men and women, using 16 two-dimensional landmarks. The modules were compared using partial least squares analysis and the Escoufier coefficient (RV). Against the background of weak allometric effects (4.6-4.86%, $p<0.05$), there is a moderate correlation between the blocks of landmarks of the metapodium and acropodium ($RV=0.5$, $p<0.05$). Partial Least Squares analysis demonstrates that the shape of the hand is more influenced by the shape of the acropodium, and the change in the shape of the metapodium turned out to be more conservative than that of the acropodium. The observed integration of metapodium and acropodium into human hands in this study indicates the plasticity of the hand, especially its fingers in the context of the diversity of its shape.

Keywords: Human hand – Geometric morphometry – Morphological modularity – Morphological integration

INTRODUCTION

The human hand is functionally integrated as a whole, but its morphological integration is rather heterogeneous. The hand consists of several parts – metacarpus (metapodium) and fingers (acropodium)– which differ from each other in the context of development or function (Wagner and Chiu, 2001). This coordination into subunits or modules is known as morphological integration (Klingenberg and Marugán-Lobón, 2013). Integration and modularity relate to the degree of covariance between parts of a structure that represent separate areas from a developmental perspective (Adams and Felice, 2014). Some authors have proposed the metapodium and acropodium as two different human hand modules, since they are units whose parts are strongly integrated internally, but poorly integrated with each other, although hand modules can never be completely independent of each

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other (von Cramon-Taubadel, 2022). On the other hand, modules can limit or enhance the potential of the hand to evolve into new forms, which is probably observed during the evolution of thoracic limbs in primates and humans in particular. At the same time, the metapodium and acropodium form rays that determine the shape of the hand, while in various representatives of primates, including humans, the latter are characterized by a variety of forms (Patel and Maiolino, 2016).

Thus, the idea of the modular structure of the hand is of interest in the context of the form of the latter – whether the geometry of the metapodium and acropodium can change in space without any negative consequences for the structure of the hand as a whole. The hypothesis was that there may be an ontogenetic difference between these parts of the hand, and the shape of the acropodium will affect the variability of the shape of the hand to a greater extent than the metapodium, since it has a more complex structure.

The aim of this study was to assess whether the metapodium and acropodium are two spatially conjugate parts of the hand, corresponding to a single integrated block, or form two separate modules, by using Geometric Morphometry (GM).

MATERIALS AND METHODS

Sample

Digital images of radiographs of the right hands (anterior-posterior projection, fingers in the position of reduction) of 50 men (average age 46.3 ± 1.1 years) and 50 women (average age 49.2± 0.9 years) were taken from the archive of digital images of the Department of Radiation diagnostics of the Doctor Chuchkalov Ulyanovsk Regional Clinical Center of Specialized Types of Medical Care. The criteria for inclusion in the study: the absence of fractures of the metacarpal bones and phalanges of the fingers, developmental anomalies, deformities and bone and joint pathology.

Digitization and Landmarking

On each digital image of the radiograph, 16 landmarks were located using TPSDig2 v. 1.40, which represented the metapodium and acropodium modules (Fig. 1) (Rohlf, 2015).

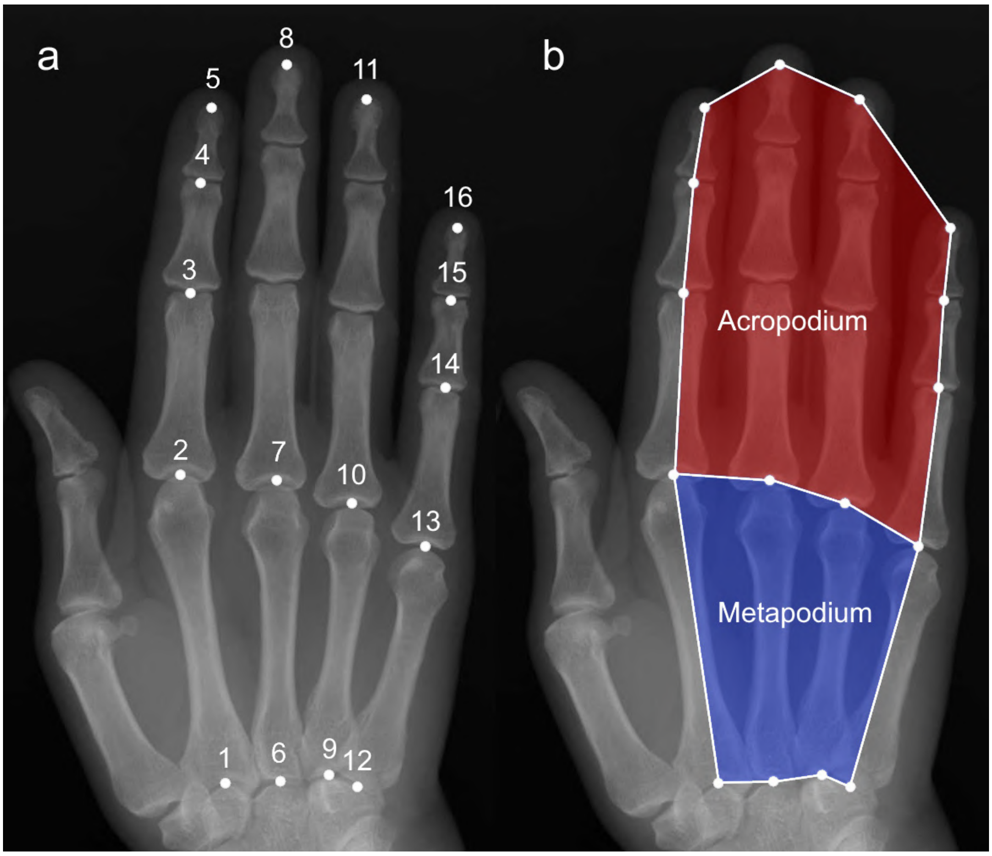

Fig. 1.- Landmark positions (**a**) and configuration of modules (**b**).

Geometric morphometric analysis

The two-dimensional coordinates of the metapodium (n=100) and acropodium (n=100) landmarks were subjected to Generalized Procrustes analysis (GPA) in order to optimally align the configuration of the landmarks in the general shape space and eliminate effects unrelated to the shape (position, orientation, scale) (Pavlinov and Mikeshina, 2002). As a result of the GPA for each configuration of landmarks, the Procrustean distance (the square root of the sum of the squares of the distances between the landmarks of this configuration) is obtained, which is a measure of the shape space and the centroid size (Centroid Size, CS is the square root of the sum of the squares of the distances between each landmark and the center of gravity, or- centroid), which is a size variable.

The evaluation of allometry (the relationship between shape and size) was carried out using multivariate regression of shape (Procrustean coordinates) as a dependent variable on size (CS) as an independent variable (Klingenberg, 2016).

Partial Least Squares analysis (PLS) was used to evaluate the interaction between modules, which allows us to study models of integration of parts within individual configurations of landmarks (Klingenberg and Marugán-Lobón, 2013). The average values of each individual's configurations were used to calculate covariance matrices between individuals. Since the degree of covariance between metapodium and acropodium is a criterion for assessing the integration and modularity of morphometric data, a measure for quantifying covariance between sets of landmarks is of critical importance. To estimate the strength of covariance between modules, the Escoufier coefficient (RV) was used, which is a multidimensional generalization of the square of the Pearson correlation coefficient (Adams, 2016). The RV coefficient is a scalar measure of the strength of the relationship between two sets of variables, which demonstrates the overall magnitude of the association between sets of variables relative to covariance within sets of variables (Klingenberg, 2009). Thus, RV values close to 0 indicate low covariance between sets of landmarks, and RV values close to 1 indicate a large covariance between them (Abdi and Williams, 2013).

MorphoJ 1.07a and OriginPro 2022 (Mann-Whitney test) were used for all statistical analyses (Klingenberg, 2011; Seifert, 2014).

RESULTS

As expected, the CS of the studied hand modules in men is larger than in women (U=2134, p<0.05), while the CS acropodium exceeds the size of the metapodium regardless of gender (U=2500, p<0.05) (Fig. 2).

Multidimensional regression of the coordinates of the Scroll depending on CS showed that that al-

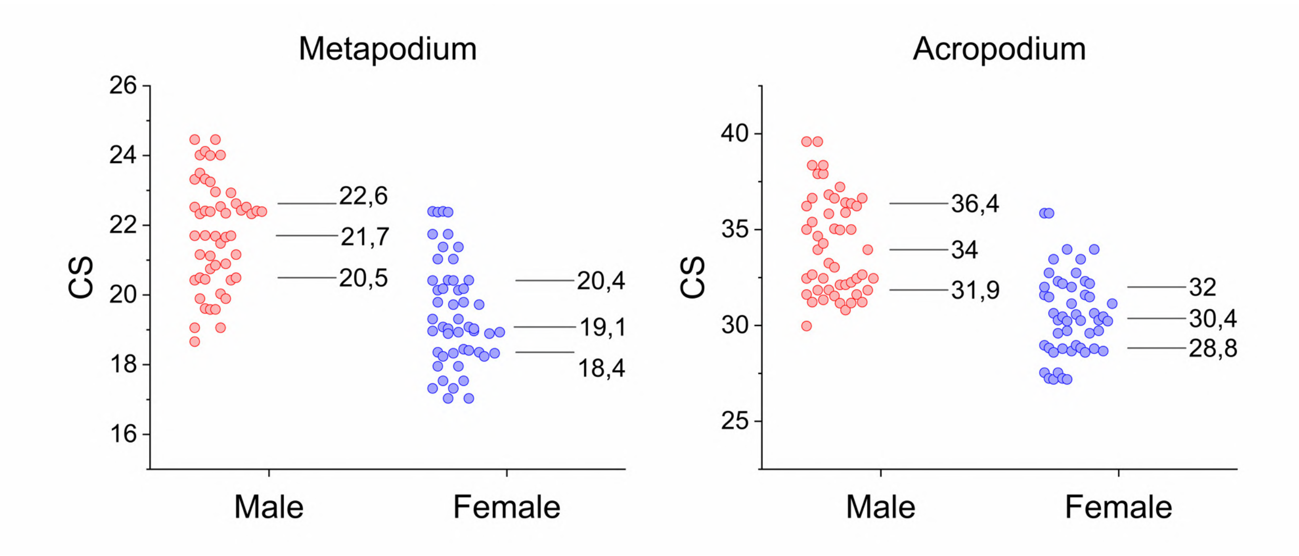

Fig. 2.- Plots of CS (Me, 25-75%).

lometry is statistically significant (10,000 random permutations). Metapodium accounted for 4.6% (p=0.0013), and acropodium accounted for 4.86% (p=0.0021) of the shape change explained by size.

The PLS results demonstrate a moderate degree of correlation between the two reference blocks (RV=0.5, p<0.0001, 10000 rounds of randomization) and the hypothesis of no covariance was rejected, which indicates the relationship between the modules. For the entire dataset, the first axis (PLS1) describes 75.2% of the total square of the covariance, indicating that it represents the main covariance of the two modules. PLS demonstrates that the shape of the hand is more influenced by the shape of the acropodium, and the change in the shape of the metapodium turned out to be more conservative than that of the acropodium (Fig. 3, Table 1).

DISCUSSION

In this study, the GM method was used to determine whether the two parts of the hand – metapodium and acropodium – are morphologically integrated or independent of each other, since integration determines the degree of their structural connection, which is significant in the context of hand morphogenesis (Adams and Felice, 2014). One of the aspects of morphological integration is that high integration of modules leads to a decrease in the diversity of the structure that these modules form, since non-weak integration between modules allows the latter to change more freely; within the framework of variation they do not have a negative impact on the structure as a whole (Zelditch and Goswami, 2021). The observed integration of the metapodium and acropodium into human hands in this study indicates the plasticity of the hand, especially its

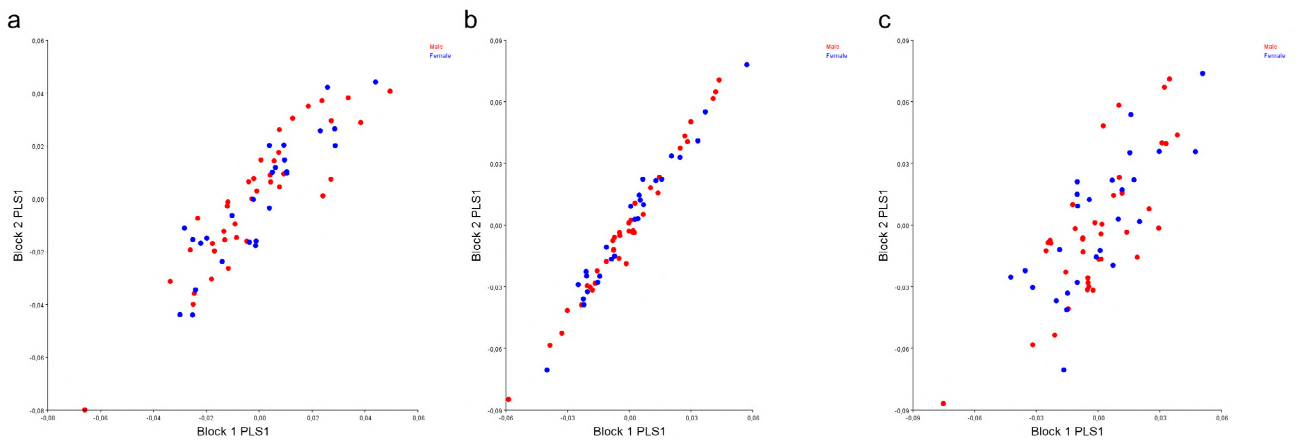

Fig. 3.- Results of two-block PLS (scatter plot of the PLS1). Hand (Block 2)/Metapodium (Block 1) (**a**). Hand (Block 2)/Acropodium (Block 1) (**b**). Acropodium (Block 2)/Metapodium (Block 1) (**c**).

Table 1. Angular comparison of hand shape vectors and covariance between two blocks of modules.

Integration	**Angular value**	**p-value**
Shape – Hand/Metapodium	26.9°	<0.00001
Shape – Hand/Acropodium	4,65°	<0.00001

fingers in the context of the diversity of its shape (Patel and Maiolino, 2016). Integration between the metapodium and acropodium in the aspect of hand shape disproportions in humans is more pronounced than in other primate species, which can be explained by the relatively independent ability to change during locomotor adaptation of the upper limbs (von Cramon-Taubadel, 2022). In the evolutionary context, one of the aspects of the phylogenetic transformation of the shape of the hand due to changes in proportions between the metapodium and acropodium is biomechanical – progressive functional improvement of the functions of the hand (thumb opposition, precision finger grip of small objects) (Patel and Maiolino, 2016; von Cramon-Taubadel, 2022). The results of testing alternative hypotheses demonstrate that a high degree of integration between modules leads to a smaller transformation of the shape of the biological object as a whole, while less integrated modules cause greater variability in shape (Klingenberg and Marugán-Lobón, 2013).

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REFERENCES

ABDI H, WILLIAMS LJ (2013) Partial least squares methods: partial least squares correlation and partial least square regression. *Methods Mol Biol*, 930: 549-579.

ADAMS DC (2016) Evaluating modularity in morphometric data: Challenges with the RV coefficient and a new test measure. *Methods Ecol Evol*, 7(5): 565-572.

ADAMS DC, FELICE RN (2014) Assessing trait covariation and morphological integration on phylogenies using evolutionary covariance matrices. *PLoS One*, 9(4): e94335.

KLINGENBERG CP (2009) Morphometric integration and modularity in configurations of landmarks: Tools for evaluating a priori hypotheses. *Evol Dev*, 11(4): 405-421.

KLINGENBERG CP (2011) MorphoJ: an integrated software package for geometric morphometrics. *Mol Ecol Resour*, 11(2): 353-357.

KLINGENBERG CP (2016) Size, shape, and form: concepts of allometry in geometric morphometrics. *Dev Genes Evol*, 226(3): 113-137.

KLINGENBERG CP, MARUGÁN-LOBÓN J (2013) Evolutionary covariation in geometric morphometric data: analyzing integration, modularity, and allometry in a phylogenetic context. *Syst Biol*, 62(4): 591-610.

PATEL BA, MAIOLINO SA (2016) Morphological diversity in the digital rays of primate hands. In: Kivell T, Lemelin P, Richmond B, Schmitt D (eds). *The Evolution of the Primate Hand. Developments in Primatology: Progress and Prospects*. Springer, New York, pp 55-100.

PAVLINOV IJA, MIKESHINA NG (2002) Principles and methods of geometric morphometrics. *Zh Obshch Biol*, 63(6): 473-493.

ROHLF FJ (2015) The tps series of software. *Hystrix, It J Mamm*, 26: 9-12.

SEIFERT E (2014) OriginPro 9.1: scientific data analysis and graphing software-software review. *J Chem Inf Model*, 54(5): 1552.

VON CRAMON-TAUBADEL N (2022) Patterns of integration and modularity in the primate skeleton: a review. *J Anthropol Sci*, 100: 109-140.

WAGNER GP, CHIU CH (2001) The tetrapod limb: a hypothesis on its origin. *J Exp Zool*, 291(3): 226-240.

ZELDITCH ML, GOSWAMI A (2021) What does modularity mean? *Evol Dev*, 23(5): 377-403.