Differences in the 2nd to 4th digit length ratio in humans reflect shifts along the common allometric line

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Ratios often lead to biased conclusions concerning the actual relationships between examined traits and comparisons of the relative size of traits among groups. Therefore, the use of ratios has been abandoned in most comparative studies. However, ratios such as body mass index and waist-to-hip ratio are widely used in evolutionary biology and medicine. One such, the ratio of the 2nd to the 4th finger (2D : 4D), has been the subject of much recent published research in humans and animals. Most studies agree that 2D : 4D is sexually dimorphic. In men, the 2nd digit tends to be shorter than the 4th, while in women the 2nd digit tends to be of the same size or slightly longer than the 4th. Nevertheless, here we demonstrate that the sexes do not greatly differ in the scaling between the 2nd and 4th digit. Sexual differences in 2D : 4D are mainly caused by the shift along the common allometric line with non-zero intercept, which means 2D : 4D necessarily decreases with increasing finger length, and the fact that men have longer fingers than women. We conclude that previously published results on the 2D : 4D ratio are biased by its covariation with finger length. We strongly recommend regression-based approaches for comparisons of hand shape among different groups.

Keywords: 2D : 4D; allometry; morphometrics; sexual dimorphism

1. INTRODUCTION
It has been known for a long time that ratios between two measurements of body parts can change with the alterations in size of the organs involved or general body size. This observation crystallized into the concept of ‘allometry’, which was defined concisely by Levinton (1988) as ‘the relationship between changes in shape and overall size’. The concept was first coined in their seminal work by Huxley & Teissier (1936) (for a historical overview, see Gayon 2000). Throughout the following decades, it was documented many times that ratios often lead to biased or even opposite conclusions concerning the actual relationships between the examined traits and comparisons of the relative size of traits among groups (sexes, populations or species; e.g. Poehlman & Toth 1995). Therefore, the use of ratios was widely abandoned in most comparative studies, at least in morphometrics. It is thus surprising that many ratios such as body mass index and waist-to-hip ratio are widely used in evolutionary biology and medicine. One such, the 2D : 4D ratio, i.e. the ratio of the length of the 2nd finger (index finger) and to the length of the 4th finger (ring finger) in humans has undergone a marked increase in interest. The first article concerning the 2D : 4D ratio was published by Manning et al. (1998) and has been cited 207 times during the last 10 years. In this period, more than 300 other papers on this topic were published, three of which were co-authored by one of us (Flegr et al. 2005, 2008; Lindová et al. 2008). More recently, research on the 2D : 4D ratio has been extended to animals (for references, see Voracek & Loibl 2009). Many results were reviewed in two monographs devoted exclusively to the 2D : 4D ratio (Manning 2002, 2008). The researchers explored the relationship between the 2D : 4D ratio and a wide variety of human characteristics, including personality traits, reproductive success and sexual performance, sexual orientation, hand preference, verbal skills, physical and mental health and diseases and musical and sporting talents. While the connection between many of the examined characteristics to 2D : 4D is questionable, most studies agree that 2D : 4D is sexually dimorphic: in men, the 2nd digit tends to be shorter than the 4th, and in women, the 2nd digit tends to be of the same size or slightly longer than the 4th, although the sexes overlap to a great extent (Manning et al. 1998). Studies suggest that the 2D : 4D ratio is affected by exposure to androgens while in the uterus and that the 2D : 4D ratio can be used as an indicator of prenatal androgen exposure (Manning et al. 1998; cf. Puts et al. 2004, 2008; experimentally supported in rats by Talarovcová et al. 2009).

However, as mentioned earlier, one of the problems with ratios is that they often covary with organ or body size. For example, in the case of the linear relationship between variables, the ratio (y/x) is not dependent on size only when the intercept b of the equation y = ax + b is zero. In a wild bird species, Garamszegi et al. (2007) have shown that 2D and 4D scale allometrically with other body parts and with each other. If the allometric slopes are different for different digits the 2D : 4D ratio may be affected. They recommended that studies of 2D : 4D should also consider absolute digit lengths. We agree—in the present communication we explore the extent to which the 2D : 4D in humans is influenced by its covariation with finger length and whether an allometry-based approach for comparisons of hand shape among different groups, e.g. the sexes, gives the same results as the ratios.

2. MATERIAL AND METHODS
Using univariate ANOVAs, we tested sexual dimorphism in the 2D : 4D ratio in three datasets, of the measurements taken from 245 biology students of our University, 238 children of an elementary school and 117 members of the adult population (for detailed methodology see Flegr et al. 2005, 2008; Holub et al. 2008; Lindová et al. 2008). In the case of the 245 biology students for which results of the serological test for toxoplasmosis were available, we also tested for the effect of Toxoplasma infection on the 2D : 4D ratio (documented in Flegr et al. 2005). Next, we fitted the full-factorial GLM model with the length of the 2nd finger as a dependent variable, the length of the 4th finger as a covariate, sex and eventually Toxoplasma infection status as factors, and searched for a significant
Table 1. Effect of sex and toxoplasmosis estimated with both the traditionally used ANOVA method and the recommended full-factorial GLM model. The left part of the table shows results of ANOVAs with dependent variable 2D : 4D ratio and factors sex (lines 1, 2, 5, 6, 7 and 8) or sex and toxoplasmosis (lines 3 and 4). The right part of the table shows the results of the full-factorial GLM model with length of the 2nd finger as a dependent variable and sex, length of the 4th finger (lines 1, 2, 5, 6, 7 and 8) or sex, toxoplasmosis and length of the 4th finger (lines 3 and 4) as factors or covariate. The second column shows the number of subjects in the first group (males or Toxoplasma-negative and Toxoplasma-free subjects) and in the second group (females or Toxoplasma-infected subjects). The third column shows arithmetic means for the 2D : 4D ratio in the first group and the second group, respectively.

<table>
<thead>
<tr>
<th>Dataset, Factor Tested, Hand</th>
<th>n1/n2</th>
<th>( \text{mean 1/mean 2} )</th>
<th>ANOVA</th>
<th>Full-factorial GLM</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Biology students, sex, right hand</td>
<td>104/193</td>
<td>0.972/0.986</td>
<td>12.60 &lt;0.0001 0.041 0.94</td>
<td>1.44 0.232 0.005 0.22</td>
</tr>
<tr>
<td>2. Biology students, sex, left hand</td>
<td>104/193</td>
<td>0.979/0.985</td>
<td>2.25 0.135 0.008 0.32</td>
<td>1.34 0.248 0.005 0.21</td>
</tr>
<tr>
<td>3. Biology students, Toxoplasmosis, right hand</td>
<td>201/44</td>
<td>0.982/0.977</td>
<td>0.97 0.325 0.004 0.17</td>
<td>0.537 0.464 0.002 0.11</td>
</tr>
<tr>
<td>4. Biology students, Toxoplasmosis, left hand</td>
<td>201/44</td>
<td>0.984/0.971</td>
<td>6.51 0.011 0.026 0.72</td>
<td>0.148 0.700 0.001 0.07</td>
</tr>
<tr>
<td>5. Elementary school students, sex, right hand</td>
<td>131/107</td>
<td>1.001/1.011</td>
<td>4.36 0.038 0.018 0.55</td>
<td>2.67 0.104 0.011 0.37</td>
</tr>
<tr>
<td>6. Elementary school students, sex, left hand</td>
<td>131/107</td>
<td>1.003/1.023</td>
<td>15.49 0.0001 0.062 0.97</td>
<td>0.66 0.797 &lt;0.0001 0.06</td>
</tr>
<tr>
<td>7. General population, sex, right hand</td>
<td>50/67</td>
<td>1.002/1.015</td>
<td>3.15 0.079 0.027 0.42</td>
<td>1.18 0.279 0.01 0.19</td>
</tr>
<tr>
<td>8. General population, sex, left hand</td>
<td>50/67</td>
<td>0.995/1.012</td>
<td>5.92 0.016 0.049 0.68</td>
<td>3.25 0.074 0.028 0.43</td>
</tr>
</tbody>
</table>

3. RESULTS

We found significant \( (p < 0.05) \) sexual dimorphism in the 2D : 4D ratio concerning at least one hand in all three of our datasets (table 1). In accordance with previously published results, men tend to have a lower 2D : 4D ratio than women in all cases (table 1). Also, we confirmed the significant differences between Toxoplasma-negative and Toxoplasma-positive individuals in the left-handed 2D : 4D ratio (cf. Flegr et al. 2005).

In our datasets, a linear relationship exists between the length of the 2nd and of the 4th digit in mm (figure 1). Interestingly, both sexes and groups with different Toxoplasma-status evidently shared the same allometric line. The full-factorial GLM model determined that only the effect of the length of the 4th finger was significant. Neither sex nor Toxoplasma infection (in the case of the biology students), and/or their interactions with the covariate were significant (table 1). The intercepts \( b \) of the common allometric lines were in all cases significantly larger than zero (range 6.45–14.59, \( p < 0.003 \) in all cases). Therefore, the ratio of the 2nd to the 4th finger must necessarily decrease with increasing finger length. We can thus conclude that the trend for lower 2D : 4D ratio in certain subpopulations (men or Toxoplasma-infected subjects) is then an epiphenomenon of longer fingers in these subpopulations in comparison with other subpopulations (women or Toxoplasma-free subjects). For example, a two-sample \( t \)-test confirmed a pronounced sexual dimorphism in the length of the right 4th finger in the biology students \( (t = 13.97, p < 0.00001) \); in children of an elementary school \( (t = 3.11, p = 0.002) \) and in the members of the adult population \( (t = 7.40, p < 0.001) \).
4. DISCUSSION

We demonstrated that neither sexes nor groups with different Toxoplasma status differ in the scaling between the 2nd and the 4th digit, and that the differences between groups in the 2D : 4D ratio are mainly caused by the shift along the common allometric line. The correct answer to the question why men and women (or Toxoplasma-infected subjects and Toxoplasma-free subjects, and probably also heterosexuals and homosexuals, less fertile women and more fertile women, etc.) have different 2D : 4D ratio seems to be, because the representatives of the former groups usually have larger hands and longer fingers. Long-fingered women tend to have more ‘man-like’ and short-fingered men more ‘woman-like’ 2D : 4D ratios. Nevertheless, we have to note that our comparisons between sexes suffer from the fact that the sexes do not totally overlap in the extent of finger length (i.e. all individuals with the longest fingers are men and all individuals with the shortest fingers are women; see e.g. figure 1). We are thus forced to compare allometric lines between sexes somewhat beyond the extent of the data for each sex.

Our study deals with differences in the 2D : 4D ratio among individuals within a single developmental stage, i.e. at the level described by static allometry. In contrast to ontogenetic allometry (the growth trajectory of one organ relative to another during the growth of a single individual), there is no conceptual reason why the allometric line should go through the origin in the case of static allometry (e.g. Singleton et al. 2007). Here, we demonstrated the non-zero intercepts in static allometries of the length of 2nd finger to the length of the 4th finger among humans in three different ontogenetic stages (children, students, older adults). The automatic consequence of these non-zero intercepts is the scaling of the 2D : 4D ratio with finger length. These non-zero intercepts influence comparisons of the 2D : 4D ratio between groups with different finger lengths (e.g. sexes) and between individuals with different finger length within groups. Future studies on the scaling of hand shape should focus on ontogeny and ontogenetic allometries of the 2D : 4D ratio to understand the mechanism forming the static allometries in finger lengths. The results published up to now have concentrated on static allometries, although some of them described the 2D : 4D ratio at early ontogenetic stages (e.g. foetuses, children: Malas et al. 2006; McIntyre et al. 2005, 2006). In summary, we conclude that the widely used 2D : 4D ratio is, at least in humans, highly influenced by different finger lengths. Moreover, because it is a ratio, it is much less precisely measurable than the finger length itself (Voracek et al. 2007). We do not claim that earlier published results on the 2D : 4D ratios are wrong. We argue instead, that the interpretation of observed effects is partly misleading, as the results are biased by the existence of covariation with finger length. Instead of investigating the effect of a given factor (sex, fertility, sexual orientation, etc.) on the 2nd and 4th finger using ANOVA or t-tests, proper analysis requires a full-factorial ANCOVA. Our results suggest the existence of a common effect of studied factors on just a single variable, the length of fingers. The new interpretation of observed phenomena suggest that in order to search for physiological mechanisms, we have to ask how the studied factors influence length of fingers, instead of how the factors differently influence the length of the 2nd and 4th finger.

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