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Enthesis Size and Hand Preference: Asymmetry in Humans Contrasts With Symmetry in Nonhuman Primates

Lucyna A. Bowland[1,2] | Lesley H. Eason[2,3] | Lucas K. Delezene[2] | J. Michael Plavcan[2]

[1]Department of Anatomy, Arkansas Colleges of Health Education, Fort Smith, Arkansas, USA | [2]Department of Anthropology, University of Arkansas, Fayetteville, Arkansas, USA | [3]Congdon School of Health Sciences, High Point University, High Point, North Carolina, USA

Correspondence: Lucyna A. Bowland (lucyna.bowland@achehealth.edu)

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ABSTRACT

Objectives: Humans display species-wide right-hand preference across tasks, but this pattern has not been observed at comparable levels in nonhuman primates, suggesting the behavior arose after the panin-hominin split. Muscle attachment sites (entheses) are used to infer soft tissue anatomy and reconstruct behaviors within skeletal populations, but whether entheseal size asymmetry can reflect hand preference remains unclear. If entheseal asymmetry is linked to hand preference, we expect to see greater asymmetry in human hands, where hand preference is more pronounced, compared to nonhuman primates. We tested for bilateral asymmetry in the size of the opponens pollicis muscle flange using a sample of humans and catarrhine primates to determine if enthesis development can be a reliable indicator of hand preference.

Materials and Methods: We assess the asymmetry of the opponens pollicis enthesis between paired (left/right) first metacarpals using distance-based heat maps generated from three-dimensional models of *Homo sapiens* ($n = 85$ individuals), *Macaca fascicularis* ($n = 58$ individuals), *Gorilla* spp. ($n = 8$ individuals), and *Hylobates lar* ($n = 44$ individuals). Metacarpals were cropped to isolate the metacarpal shaft and capture the majority of the enthesis while eliminating variation from the metacarpal ends.

Results: We found right-directional asymmetry for humans; no significant differences are observed for *Hylobates*, *Macaca*, and *Gorilla*.

Conclusion: The opponens pollicis enthesis shows right/left hand bias in humans. The lack of significant asymmetry in nonhuman primates suggests entheseal development in these species does not reflect the same level of hand preference observed in humans. Nonhuman primates can serve as a baseline for studying enthesis asymmetry based on the size of the opponens pollicis enthesis.

1 | Introduction

1.1 | Hand Preference

Hand preference refers to the consistent, lateralized use of one hand over the other for skilled manipulative tasks (McGrew and Marchant 1997). Humans display a species-wide right-hand bias in skilled tasks (Marchant and McGrew 2013; McGrew and Marchant 1997; Stephens et al. 2016), with frequencies for right-hand dominance reported between 85% and 95% (Fitch and Braccini 2013; Papadatou-Pastou et al. 2020). Conversely, other primates do not exhibit species-level, or even population-level, handedness in wild populations, and only a weak bias (approximately 65%) in some captive populations (Hopkins et al. 2011), suggesting the species-level right-hand preference in humans arose after the panin-hominin split (Stephens et al. 2016). Lateralized hand use in humans has been linked to important evolutionary milestones, including the advent of stone tool use and manufacture and the role that possible visuo-cognitive functional asymmetries played in the rise of manual dexterity within the hominin lineage (Williams-Hatala et al. 2016; Stephens et al. 2016).

Considering the profound implications of hand preference for human evolution, it is important to evaluate the sensitivity of skeletal markers of hand preference. Muscle attachment sites (entheses) have been shown to serve as valuable indicators of lifetime muscle activity (Hawkey and Merbs 1995; Schlecht 2012; Foster et al. 2014; Karakostis et al. 2017, 2019a, 2019b). Advances in the study of entheseal morphology, particularly through techniques like the "Verified Enthesis-based Reconstruction of Activity" (VERA) approach (Karakostis and Lorenzo 2016 [outlined in detail in Karakostis and Harvati 2021; Karakostis 2023]), offer promising avenues for reconstructing past behaviors and understanding muscle synergies in skeletal assemblages (Karakostis et al. 2017; Bousquié et al. 2022; Buikstra 2023). In addition, recent studies on nonhuman models have advanced our understanding of entheseal morphology, with experiments on lab rats, house mice, and turkeys revealing the effects of muscle contraction and body size on entheseal development. For example, Karakostis et al. (2019b) showed significant changes in hind limb morphology in response to muscle stimulation in exercised versus non-exercised turkeys, while Castro et al. (2022) demonstrated that chronic exercise during ontogeny can influence enthesis morphology in house mice. These studies, alongside work on reindeer (Siali et al. 2024) and wild-type mice (Turcotte et al. 2022), highlight the utility of experimental models in refining methods for studying entheses and their relationship to muscle activity.

Entheses not only provide insight into lifetime activity patterns but also offer a potential means of understanding skeletal indicators of hand preference. For instance, Stephens et al. (2016) found right-directional asymmetry in the trabecular loading patterns in the first metacarpal in humans, suggesting right-handedness is reflected in trabeculae. Additionally, Bousquié et al. (2022) used the VERA method to investigate the effect of biological factors on manual enthesis size in a South African skeletal sample that included individuals with both European and African ancestry. The study found that right-side manual entheses showed significant differences between ancestral groups, leading the authors to suggest that the results were not driven exclusively by systemic factors and could, at least in part, be explained by increased recruitment of the right hand compared to the left (i.e., right handedness).

1.2 | Understanding Hand Preference in Nonhuman Primates

The expression of hand preference is poorly understood in nonhuman primates. Most studies on nonhuman primates suggest that while a hand preference might exist for an individual, it is not species-wide and is dependent upon multiple factors, including the task at hand, complexity of the task, and posture, among others (McGrew and Marchant 1997; Meunier and Vauclair 2007; Fitch and Braccini 2013; Bardo et al. 2015; Stephens et al. 2016). Some authors (Warren 1980; Cashmore et al. 2008; Cashmore 2009; Uomini 2009) have proposed that any right-hand bias found within captive populations is simply an artifact of right-hand usage within the human caretakers present. However, Hopkins et al. (2011) found that orangutans (*Pongo* spp.) exhibited the lowest levels of hand preference, despite comprising the group with the highest number of captive-born apes across studies. This finding does not support the hypothesis that hand preference within captive populations is a learned behavior from right-handed caretakers.

Understanding the evolutionary origins of human handedness has proved difficult, though the available evidence does provide some insight. Archaeological studies often rely on accurately inferring striking preference during stone tool flake production (Stephens et al. 2016; Bargalló et al. 2017), but there is debate as to how informative lithic remains are in assessing handedness, as even experienced knappers tend to produce flakes differently across experiments (Cashmore 2009). Fossil evidence for handedness is scarce, as most fossil assemblages simply do not have enough postcranial remains from which to accurately infer handedness (Cashmore 2009; Stephens et al. 2016). However, evidence from labial striations on the anterior dentition suggests a right-directional bias within Neanderthal assemblages across sites. For example, Volpato et al. (2012) stated the Regourdou 1 Neanderthal was right-handed based on oblique striations on the anterior dentition, and Lozano et al. (2017) determined that 14 of the 18 Neanderthal specimens in their study were right-handed based on labial striations, while only one showed evidence for left-directional bias.

1.3 | Hand Use in Different Taxa Within Study

1.3.1 | *Homo sapiens*

Humans routinely perform complex grips in which the thumb opposes the fingers, allowing for forceful precision handling of objects. These grips are facilitated in part by derived thenar musculature, including the opponens pollicis, which has a larger physiological cross-sectional area (PCSA) in humans compared to other apes and, thus, can produce larger forces through the joint (Marzke 1997). During flexion and opposition, the first metacarpal is loaded by a combination of joint reaction forces and muscular tension (Stephens et al. 2016), meaning variation in loading patterns should be reflected based on the tenets of the mechanostat model (Frost 1987; Stephens et al. 2016). Since humans display a species-wide preference for right-handedness across populations (Papademetriou et al. 2005; Fitch and Braccini 2013), we predict asymmetrical loading patterns in the first metacarpal will reflect this behavior, regardless of geographic region of origin.

1.3.2 | Hylobates

Arboreal apes are important for lateralization studies because they often support their body mass with one or both hands (MacNeilage et al. 1987; Morino 2011). In particular, the unique nature of the hylobatid thumb makes it an ideal test for how possible adaptations for fine precision grasping, independent of handedness, influence asymmetry within the first metacarpal. It is likely that the structure of the hylobatid thumb is a consequence of their terminal branch feeding behavior, which involves reaching for food objects while suspended from the tree canopy. During foraging bouts, hylobatids use their thumbs to pluck food objects from terminal branches while keeping their long fingers wrapped around branches in a hook-like grip. The unique structure of the thumb allows hylobatids to hold a small food item firmly next to the palm, while keeping the long fingers free for travel (Prime and Ford 2016). However, hylobatid hand usage outside of locomotion is still largely understudied and poorly understood (Prime 2014). Even so, there is no evidence that hylobatids engage in any level of preferential hand usage that would result in asymmetrical manual enthesis development.

1.3.3 | Gorilla

Gorillas use their hands to process a wide variety of foods, but feeding preferences differ between species and even within populations of the same species, partially because of the environmental differences between populations (Neufuss et al. 2019). *Gorilla beringei* often engages both hands, with one hand acting as a support while the other is processing food (Byrne and Byrne 1991), as opposed to lowland gorillas, which mostly consume fruits that do not require much manual processing (Doran and MacNeilage 1998). During feeding, *G. beringei* engages the first digit across several different grip types in which the thumb is strongly flexed, meaning the opponens pollicis is likely heavily recruited during feeding and foraging bouts, though empirical data is lacking (Bardo et al. 2017; Neufuss et al. 2019). Previous research has documented interspecific morphological variation in the postcranial skeleton of *Gorilla* spp. (Knigge et al. 2015), and we expect these morphological differences to be reflected in our sample.

1.3.4 | *Macaca*

Macaca fascicularis practices arboreal palmigrade locomotion, in which pressure is evenly distributed over the entire palm (Patel 2010); thus, locomotor habits should not induce asymmetric loading within *M. fascicularis* metacarpals. Outside of locomotion, decades of research (Helmkamp and Falk 1990; Fagot and Vauclair 1991; Fagot et al. 1991; Schmitt et al. 2008) on hand preference within *Macaca* spp. have failed to find evidence for population or species-wide hand preference (McGrew and Marchant 1997). Studies focusing on “task complexity” (Fagot and Vauclair 1991) have found that high-complexity, bimanual tasks tend to elicit a more asymmetrical hand use in macaques (Fagot et al. 1991); though, this finding is not universal, and many studies have found that, regardless of task complexity, there is no evidence for significant right-and-left-hand usage in any *Macaca* species (Schmitt et al. 2008).

1.4 | Study Aims

Building on the understanding that enthesis size reflects muscle recruitment, we expect to see significant asymmetry in entheseal size between the left and right hands in humans. Conversely, nonhuman primates do not exhibit species or even population-level handedness (McGrew and Marchant 1997; Stephens et al. 2016) and, thus, should not show asymmetrical manual entheseal development. The opponens pollicis muscle offers an ideal site for testing the hypothesis that enthesis development reflects repetitive muscle recruitment, as it is heavily used in many key grips employed during precision manipulation (Marzke 1997). The muscle inserts onto the radial aspect of the first metacarpal and is largely active during flexion and abduction of the thumb, as well as adduction when the thumb is in early stages of opposition (Maki and Trinkaus 2011).

To determine if hand preference influences entheseal size, we analyze the asymmetry of the opponens pollicis enthesis in humans, macaques, gibbons, and gorillas. We hypothesize that humans will exhibit right-directional asymmetry, reflecting the widespread right-hand dominance observed in the species. In contrast, we anticipate that other primates will not demonstrate significant directional asymmetry. By comparing entheseal size differences between the left and right hands in humans, using other primates as a referential baseline, we aim to determine if a consistent relationship exists between muscle recruitment and enthesis morphology across species.

2 | Materials and Methods

2.1 | Study Sample

All individuals within this study are adults, and both the right and left first metacarpal (Mc1) were measured for each individual. The *Ho. sapiens* sample (Table 1) ($n = 85$ individuals) is from the archaeological site of Merida (Tiesler et al. 2020), a late 18–19th century cemetery in Yucatan, Mexico ($n = 43$ individuals), and Mistihalj (Cowgill 2018), a 14–15th century site from Montenegro ($n = 42$ individuals). Both human samples are housed at the Peabody Museum in Cambridge, Massachusetts. The *Gorilla* spp. sample ($n = 8$ individuals) comprises two wild-shot *G. beringei* individuals from the Republic of Cameroon and six wild-shot *G. gorilla*, all housed at the Museum of Comparative Zoology at Harvard University. The *M. fascicularis* sample ($n = 59$ individuals) is from a captive breeding population at Wake Forest University in Winston-Salem, North Carolina. The *Hylobates lar* sample ($n = 45$ individuals), from Thailand, is housed at the Museum of Comparative Zoology at Harvard University.

2.2 | Surface Scanning

All specimens were scanned using an Einscan Pro HD scanner. Specimens were first scanned with the proximal facet occluding the turntable base to capture the metacarpal head morphology, then flipped so that the metacarpal head was occluding the turntable, and the proximal facet morphology could then be captured. The two sets of scans were then cleaned and merged using the Einscan Pro software (Shining 3D, 2022), and any additional hole filling or model cleaning was performed using the Geomagic Wrap software (Geomagic, 2013).

TABLE 1 | Comparison of asymmetry scores between the original values and those obtained from error analysis, along with the corresponding percent errors for each specimen.

Specimen	Original asymmetry score	Error analysis asymmetry score	Percent error
1	0.13867736	0.14278883	−2.9214667
2	0.43839955	0.43356968	1.1078067
3	0.10405209	0.10082803	3.1472676
4	0.01873696	0.01912757	−2.0631843
5	0.08104825	0.08295808	−2.3289658
6	−0.08036849	−0.08207983	−2.1069309
7	0.12383531	0.12773730	−3.1020837
8	0.05200717	0.04713915	9.8198681
9	−0.07155815	−0.07205387	−0.6903595
10	−0.12218641	−0.13482190	−9.8327510

2.3 | Heat Map Generation

Heat maps were generated using CloudCompare v2.12.3 (CloudCompare, 2023). Right specimens were first mirrored to reflect the left side, then the right side was translated and rotated to overlap the left side in 3D space using the "translate/rotate" tool in CloudCompare. Bounding boxes of the two meshes were then matched using the "Match Bounding Box Center" tool for preliminary alignment of the meshes in 3D space. Meshes were then fine registered using the iterative closest point (ICP) algorithm, which randomly samples vertices of each mesh and matches the closest vertices between meshes (Rusinkiewicz and Levoy 2001; random subsample of 50,000 vertices). Distance between the specimens was calculated by taking the nearest vertices between meshes and computing the average Euclidean distance between corresponding vertices of the two meshes. All measurements obtained are in millimeters (mm).

2.4 | Model Segmentation and Error Analysis

After alignment, meshes were divided using the segmentation tool in CloudCompare. With the metacarpals in palmar view, meshes were sectioned to isolate the metacarpal shaft from the proximal and distal epiphyses. Using the CloudCompare software, meshes were positioned in the anatomical position in palmar view. In this view, a line was drawn mediolaterally just inferior to the palmar condyles and extended superiorly to encompass the metacarpal head, delineating the distal extent of the segmented shaft portion. The metacarpal head was then segmented out from the rest of the mesh. This process was repeated for the proximal end, with the line being drawn mediolaterally across the widest points on the metacarpal base, delineating the proximal extent of the segmented shaft portion. These locations are based on landmarking locations on the first metacarpal, outlined in more detail in Bowland et al. (2021). After segmenting out the distal and proximal ends of the metacarpal, the resulting mesh consisted of just the metacarpal shaft. All subsequent analyses were performed on the isolated shafts of each specimen.

The metacarpal shaft was isolated to ensure the asymmetry values reflect the opponens pollicis enthesis and are not driven by possible variation in the proximal or distal end (Figure 1). Though this study design excludes a portion of the enthesis insertion, the results demonstrate that capturing the entire insertion area is not necessary to detect a clear directional signal in enthesis-based studies.

Heat map generation and segmentation, as described in Sections 2.3 and 2.4, were carried out by one author (LAB). These procedures were then repeated for 10 individuals from the *Ho. sapiens* sample ($n = 5$ from each population) to assess error and repeatability.

2.5 | Statistical Analyses

After isolating the shaft, asymmetry scores were calculated using the weighted mean averages of the distances between the right and left sides. To calculate the weighted average, distances were binned into eight categories. For each bin, (1a) multiply the number of values by the median of each bin and (1b) repeat the calculation for each bin; (2) sum the values calculated in 1b for all bins, and (3) divide the result from step two by the total number of observations across all bins. The formula can be expressed as follows, with N being the total number of individuals, m_i being the median of bin I, and O_i being the total number of observations in bin i.

1. $\text{Value}_i = N \times m_i$ Repeat for each bin i
2. $\text{Sum\_Values} = \sum_i \text{Value}_i$
3. $\text{Average\_Value} = \text{Sum\_Values}$

$\sum_i O_i$

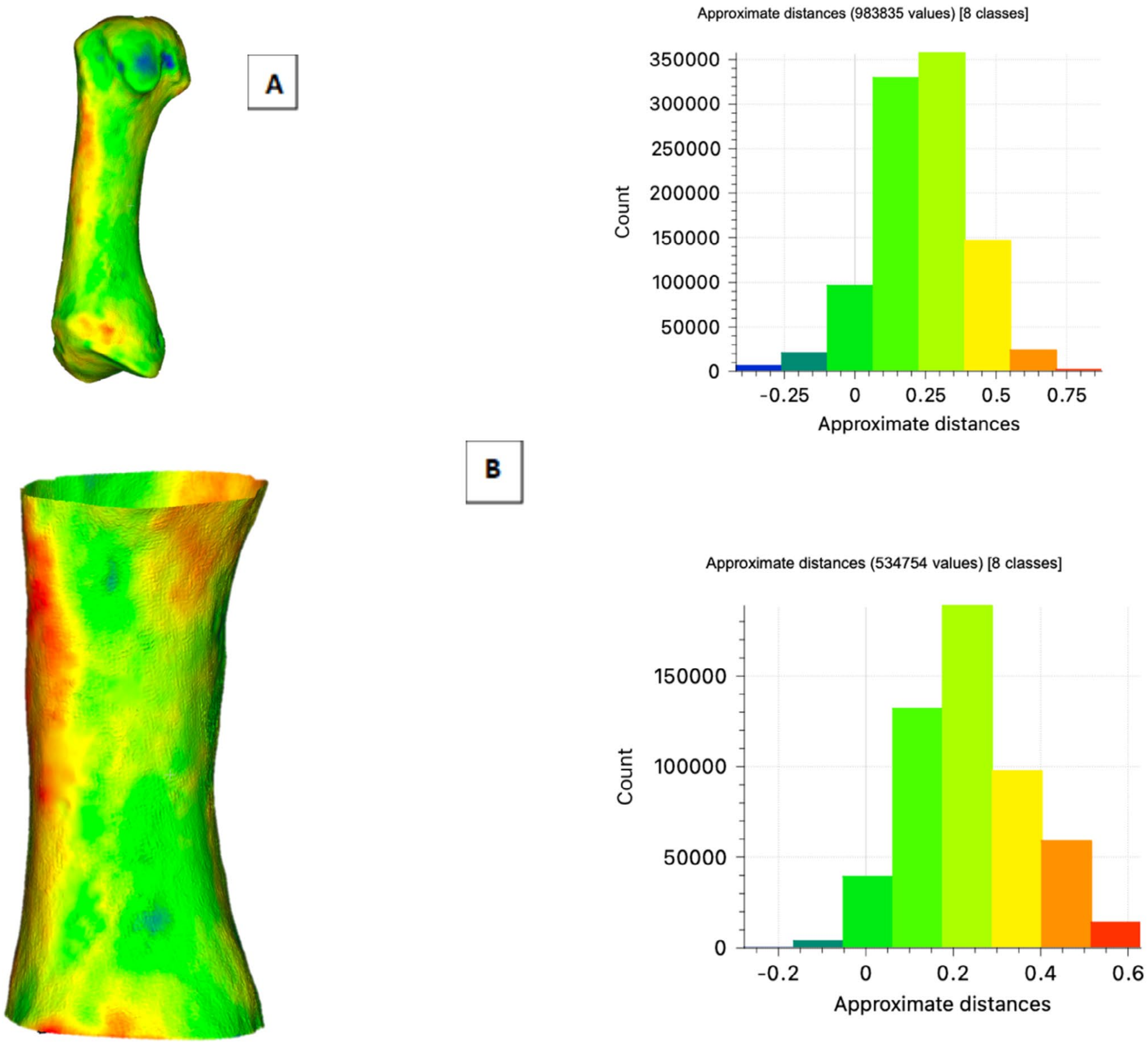

FIGURE 1 | Left: (A) CloudCompare heat map of a *Ho. sapiens* specimen showing differences between sides before (left) and after (right) segmenting the shaft to isolate enthesis variation. (B) shows the accompanying histogram for each specimen showing the values of the root mean square (RMS) in millimeters, with a red line indicating 0 (i.e., no difference between the size of the left and right sides). Positive values indicate right-directional asymmetry, while negative values indicate left-directional asymmetry. Images by Lucyna Bowland from the Peabody Museum of Archaeology and Ethnology, Harvard University, 968-10-40/N8978.0.

A Shapiro–Wilks test determined that the data are not normally distributed ($p < 0.01$). Thus, a nonparametric Mann–Whitney *U* test was performed to determine statistical significance. When significant differences were found, a Wilcoxon post hoc test was used to determine pairwise differences between taxa. Males and females were analyzed together as no significant differences in asymmetry were found between sexes.

3 | Results

Hypothesis: The OP enthesis can assess levels of asymmetry between the right and left sides of the body in humans and nonhuman primates, with greater asymmetry expected in humans than in nonhuman primates.

3.1 | Error Analysis

A paired *t*-test revealed no significant differences ($p = 0.299$; $t = 1.12$) between the weighted asymmetry scores of the two samples included in the error analysis, while the reported mean percent error values of the two samples are reported in Table 2.

3.2 | Asymmetry Between Taxa

Ho. sapiens is significantly different from the other three taxa (*Gorilla* spp., *Hy. lar*, and *M. fascicularis*) in terms of asymmetry between the right and left sides, while there are no statistically significant differences between *Gorilla*, *Hylobates*, and *Macaca* when compared to each other (Table 3). Species averages for the

TABLE 2 | Sex-based distribution of each taxon used in this study.

Taxon	Male	Female	Sex unknown	Total
Macaca fascicularis	24	21	14	59
Hylobates lar	25	20	0	45
Homo sapiens				
Merida	19	23	1	43
Mistihalj	23	16	3	42
Gorilla gorilla	4	2		6
Gorilla beringei	2	0		2
				197

weighted asymmetry scores are shown in Table 3 and further underlie these results, showing that, on average, *Macaca* show no evidence of asymmetry and *Hylobates* show very minor right-directional asymmetry.

3.3 | Opponens Pollicis Enthesis Asymmetry Between Primate Taxa

Results from the Kruskal–Wallis test for specimen differences, as well as the species averages based on asymmetry scores by taxon, demonstrate that humans are more asymmetrical than other primates in their opponens pollicis enthesis (Table 4). The species average for *Ho. sapiens* is much higher than that of the other taxa (Figure 2), indicating the asymmetry within the taxon is right-directional. To determine whether the values seen in *Ho. sapiens* are significantly asymmetrical, the weighted asymmetry scores were plotted with a 95% confidence interval to determine if values fall outside of the expected range of variation (Figure 3). *Hylobates* and *Macaca* have a mean of 0, or nearly 0, and the values for both taxa are largely concentrated around 0. *Gorilla* shows more variation than the other two nonhuman primate taxa, but this is likely an effect of sample size ($n = 8$) and is mainly driven by a single outlier; removing the outlier also removes the variation within the taxon (Figure 4).

4 | Discussion

We hypothesized that the species-wide right-hand dominance present in modern humans would be reflected as right-directional asymmetry in opponens pollicis enthesis size and that nonhuman primates would not evince directional asymmetry. We found that modern humans show right-directional asymmetry in the opponens pollicis enthesis size, reflecting the species-wide preference for right-hand dominance within the taxon. Conversely, we found that nonhuman primates do not display asymmetry in the opponens pollicis muscle enthesis size, reflecting the primary use of their hands for locomotion, as opposed to manual precision grasping.

TABLE 3 | Results of a Kruskal–Wallis test with a Wilcoxon post hoc and a Bonferroni correction.

Homo sapiens—Gorilla	***Hylobates—Gorilla***	***Macaca-Gorilla***	***Hylobates-Homo sapiens***	***Macaca-Homo sapiens***	***Macaca-Hylobates***
0.0804	1 (Not sig.)	1 (Not sig.)	**0.0001**	**0.00**	0.8131 (Not sig.)

Note: Data are from the specimen shaft averages from the CloudCompare data. Significant differences are shown in bold.

TABLE 4 | Species weighed averages for the CloudCompare shaft data.

Human	*Gorilla*	*Macaca*	*Hylobates*
0.20	−0.04	0.00	0.02

Note: Negative values indicate left-directional asymmetry, while positive values indicate right-directional asymmetry.

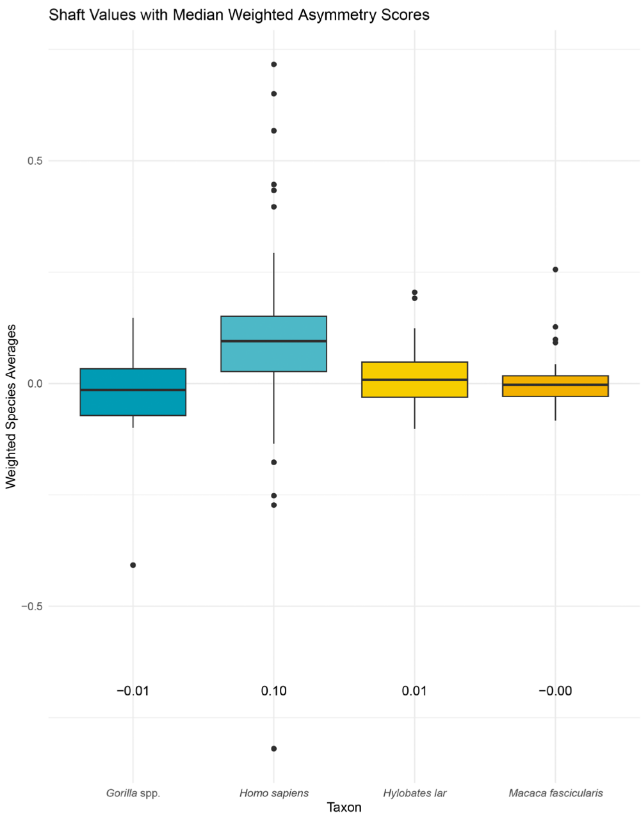

FIGURE 2 | Boxplot with median weighted asymmetry score listed below each taxon.

However, while humans displayed right-directional asymmetry in the opponens pollicis enthesis size, as predicted, the degree of asymmetry was not consistent with the reported approximately 90% frequency of right-handedness within modern humans (Papademetriou et al. 2005; Bousquié et al. 2022). This implies that although the size of the enthesis reflects muscle recruitment, it is not the only factor influencing enthesis size, and other variables must be accounted for when using entheses as a proxy for hand preference.

As such, we suggest a threshold needs to be surpassed for remodeling to be significant enough to be useful for reconstructing hand preference. These findings are in line with previous research into the topic, as others exploring the factors influencing bone remodeling have also discussed such a threshold. Lanyon et al. (1982) referred to it as the "optimum customary strain level," in which increased strain leads to increased bone deposition. This level is not constant and varies by skeletal location and is influenced by systemic factors, including age, genetic background, and the type of strain (such as frequency).

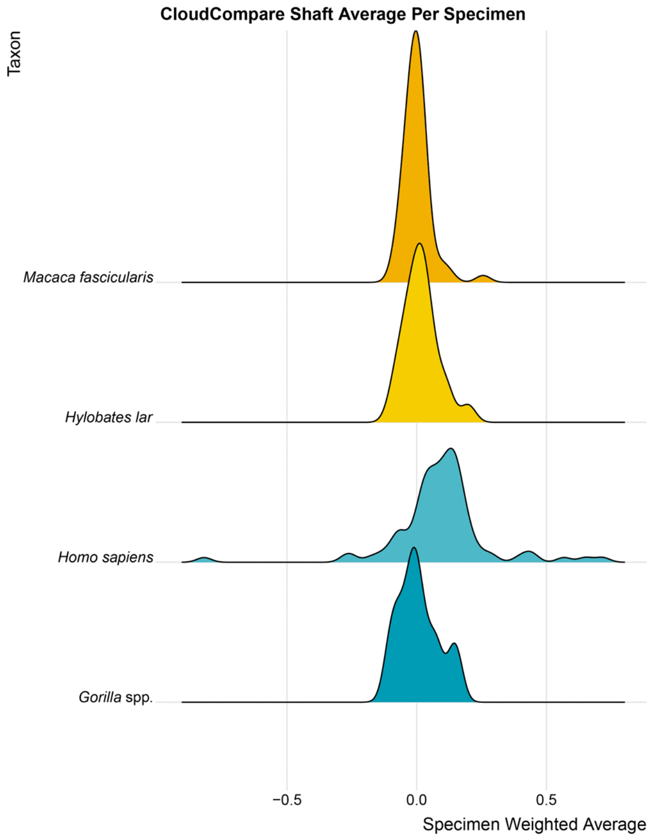

FIGURE 3 | A ridge plot showing asymmetry scores per specimen. Negative values indicate left-directional asymmetry, while positive values indicate right-directional asymmetry.

As such, disentangling load magnitude from frequency is difficult to do from bony morphology alone (Ruff et al. 2006). Perhaps most relevant to this study is that adult bones are ones that are already adapted to loading, meaning strains developed during more common activities would be "residual" strains that are less likely to stimulate modeling/remodeling. This could explain why the right-directional signal seen within the modern human populations is not as strong as could be expected based on right-handed frequency data. These points all underscore the complexity of understanding the relationship between strain, bone remodeling, and muscle recruitment in skeletal populations.

Another challenge that arises when interpreting findings from this study is the complex nature of handedness within modern humans. This study assumed a binary distribution of right/left hand preference within the populations based on published frequencies (Papademetriou et al. 2005; Papadatou-Pastou et al. 2020), but it is likely that human handedness is a continuous, rather than discrete, variable. The field of handedness studies is known for notorious variation in methodology that complicates comparing results across studies. There are many moderating factors that affect the estimate of frequencies, including reporting methods (self-reported vs. directed options) and different classification schemes across studies. For example, some studies offer participants the choice of identifying as simply either right- or left-handed, while some offer as many as seven different classifications and include the option of being "mixed" or ambidextrous (Papadatou-Pastou et al. 2020). The variability

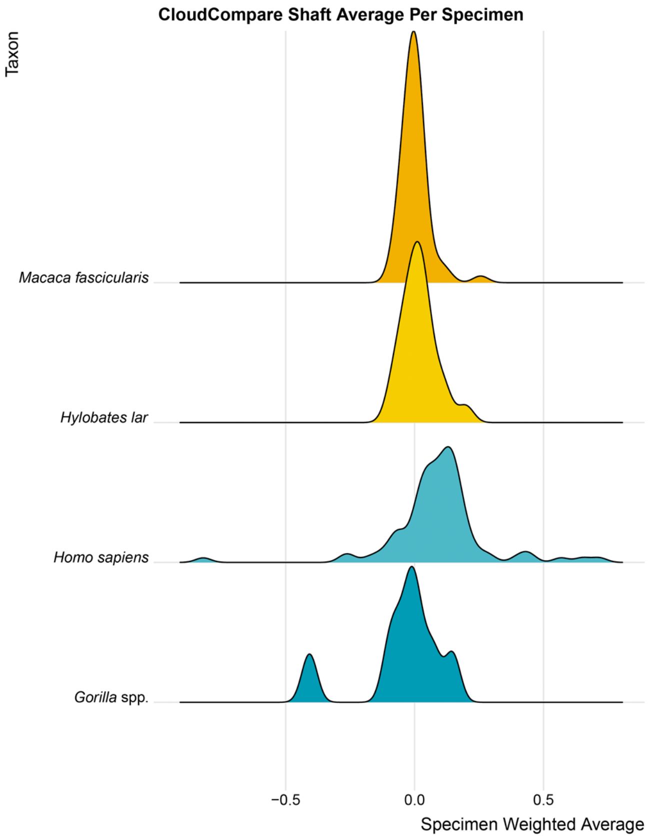

FIGURE 4 | A ridge plot showing asymmetry scores per specimen with the *Gorilla* outlier removed, showing the original variation within the taxon that is driven by an outlier (*Gorilla* $n = 7$). Negative values indicate left-directional asymmetry, while positive values indicate right-directional asymmetry.

in study methodologies and the complex, continuous nature of handedness highlight the need for more nuanced approaches and consistent classification systems in future research.

It is also important to note that the human samples in this study came from disparate ancestral regions and time periods (e.g., 15th-century Eastern Europe and 19th-century Yucatán), which may influence the results. Although demographic data for both populations are limited, some available information may provide further insight into the issue. The Mistihalj sample is composed of Vlahks, an indigenous Balkan ethnic group that regularly engaged in pastoral activities and who were "highly active, robust people" (Cowgill 2018, 81). In contrast, while little information is available for the historical Merida sample, it is composed of individuals from the Yucatan, which have historically been of shorter stature and known to suffer from stunted growth patterns (Tiesler et al. 2020). Future research using these methods will benefit from focusing on samples with better-documented information, such as age at death, sex, and occupation, to provide a more comprehensive understanding of possible observed patterns (Karakostis et al. 2017). Incorporating these variables will help refine interpretations and strengthen the findings of future studies.

Culture is another confounding factor in assessing handedness, as rates of right/left handedness have been shown to differ slightly across cultures. European samples have a higher average frequency of left-handedness (11.1%) than those from Sub-Saharan Africa (7.7%) or eastern Asia (5.7%). This discrepancy could be due to multiple factors, including genetic or cultural biases, though higher rates of non-right-handedness in the more "Westernized" Hong Kong (8%) could imply the lower rates seen in other eastern Asian countries could be due to increased cultural pressure against left-handedness (Papadatou-Pastou et al. 2020; Zheng et al. 2020). In summary, accurately assessing handedness within human populations is very difficult due to heterogeneity in study designs and the complex interplay of genetic and cultural factors that determine hand preference. Despite these obstacles, cross-cultural studies consistently indicate that left-handedness within modern human populations is approximately 10%. Therefore, while it is important to note that handedness encompasses more than simple right- or left-dominance, the results of this study underscore the potential for using entheses to infer hand preference and activity patterns across species.

5 | Conclusion

This study assessed whether the opponens pollicis muscle enthesis could accurately capture asymmetry that reflects hand preference between humans and nonhuman primates. Right-directional asymmetry is observed within modern humans, reflecting the species-wide preference for right-hand dominance. Conversely, nonhuman primates displayed symmetry in opponens pollicis enthesis size, underscoring the lack of documented handedness in nonhuman primates and demonstrating that these techniques are an appropriate metrological baseline that can capture entheseal (a)symmetry in humans and nonhuman primates. This novel methodology is particularly useful when the enthesis area is difficult to delineate, as often occurs in many nonhuman primates. The results of this study align with previous research (Bousquié et al. 2022) that identified differences between the right and left side manual entheses in modern humans. The findings of this study contribute to the growing body of literature supporting the use of entheses as a tool for inferring activity patterns across species (Karakostis et al. 2019a; Castro et al. 2022; Karakostis 2023; Siali et al. 2024). Future research would benefit from including more comprehensive demographic data and incorporating additional skeletal evidence, such as trabecular distribution patterns, studies on which (Stephens et al. 2016, 2018; Dunmore et al. 2023) have produced results similar to those presented here.

Author Contributions

Lucyna A. Bowland: conceptualization (lead), data curation (lead), formal analysis (lead), funding acquisition (lead), methodology (lead), writing – original draft (lead), writing – review and editing (equal). **Lesley H. Eason:** formal analysis (supporting), methodology (supporting), software (supporting), writing – review and editing (supporting). **Lucas K. Delezene:** formal analysis (supporting), project administration (supporting), writing – review and editing (supporting). **J. Michael Plavcan:** conceptualization (supporting), methodology (supporting), project administration (lead), resources (supporting), supervision (lead), validation (lead), writing – review and editing (lead).

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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