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METACARPOPHALANGEAL JOINT LOADS DURING BONOBO LOCOMOTION: MODEL PREDICTIONS VS. PROXIES

Alexander Synek[1*], Szu-Ching Lu[2,3], Sandra Nauwelaerts[4,5], Dieter H. Pahr[1,6], Tracy L. Kivell[2,7]

[1] Institute of Lightweight Design and Structural Biomechanics, TU Wien, Vienna, Austria
[2] Animal Postcranial Evolution Laboratory, Skeletal Biology Research Centre, School of Anthropology and Conservation, University of Kent, Canterbury, UK
[3] Laboratory for Innovation in Autism, School of Education, University of Strathclyde, Glasgow, UK
[4] Department of Biology, University of Antwerp, Wilrijk, Belgium
[5] Center for Research and Conservation KMDA, Astridplein, Antwerpen, Belgium
[6] Department of Anatomy and Biomechanics, Karl Landsteiner Private University of Health Sciences, Krems an der Donau, Austria
[7] Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

* Corresponding author:
asynek@ilsb.tuwien.ac.at

Abstract

The analysis of internal trabecular and cortical bone has been an informative tool for making inferences about behavior in extant and fossil primate taxa. Within the hand, metacarpal bone architecture has shown to correlate well with primate locomotion, however the extent of morphological differences across taxa is unexpectedly small given the variability in hand use. One explanation for this observation is that the activity-related differences in the joint loads acting on the bone are simply smaller than estimated based on commonly-used proxies (i.e. external loading and joint posture), which neglect the influence of muscle forces. In this study, experimental data and a musculoskeletal finger model are used to test this hypothesis by comparing differences between climbing and knuckle-walking locomotion of captive bonobos (*Pan paniscus*) based on (1) joint load magnitude and direction predicted by the models and (2) proxy estimations. The results showed that the activity-related differences of predicted joint loads are indeed much smaller than the proxies would suggest, with joint load magnitudes being almost identical between the two locomotor modes. Differences in joint load directions were smaller but still evident, indicating that joint load directions might be a more robust indicator of variation in hand use than joint load magnitudes. Overall, this study emphasizes the importance of including muscular forces in the interpretation of skeletal remains and promotes the use of musculoskeletal models for correct functional interpretations.

Keywords: musculoskeletal, joint load, bone, primate, hand, metacarpal

Background

Bone is a living tissue that adapts to external mechanical loading [1]. As bone preserves in the fossil record, the interpretation of fossil bone morphology, and particularly internal trabecular and cortical bone, has become an informative tool for making inferences about the behavior of human ancestors (hominins). Within the hand, variation in metacarpal trabecular morphology has been shown to correlate with distinct types of primate locomotion, such as knuckle-walking and suspension [2,3], which can then be used to infer locomotor behavior in fossil specimens. However, although differences in metacarpal trabecular architecture were found across taxa, the extent of these differences was surprisingly small given the variation in hand postures used during different types of locomotion [4]. Possible reasons for these limited differences include insufficient sensitivity of the morphometric methods used [5] and/or the nature of bone remodeling in which bone might adapt to infrequent, high-magnitude loading or to frequent, low-magnitude loading [6,7]. Alternatively, differences in loads acting on the metacarpal during various primate locomotor modes may be simply smaller than expected.

Expectations of activity-related differences in bone loading are usually driven by quantitative observations of joint angles (e.g. kinematics from video) and external loading (e.g. substrate pressure or force). Tested hypotheses typically assume that joint load direction roughly coincides with joint posture, and that external loading directly correlates with the joint load magnitude. For example, with regards to the hand, during knuckle-walking in which directly applied high substrate forces are incurred primarily by the middle phalanx [8,9], it was assumed that large joint loads would be experienced at the dorsal surface of the metacarpal head during the typical hyperextended metacarpophalangeal (MCP) joint posture [2,10,11]. In contrast, climbing and suspensory locomotion was assumed to cause smaller joint loads at the volar aspect of the metacarpal head due to potentially lower external forces [2] and typically flexed-finger grasping postures [2,12].

Measuring joint posture and external finger loading is often the only ethical and logistical method to estimate joint load direction and magnitude in living animals. However, these proxies exclude the role of muscle forces that have been shown through biomechanical analyses to contribute substantially to joint loading of hand and finger joints (e.g. [13,14,15]). It remains unclear whether differences in MCP joint loading during knuckle-walking versus climbing are as pronounced as the proxy estimations suggest.

The goal of this study is to investigate activity-related differences of MCP joint loads of captive bonobos (*Pan paniscus*) during knuckle-walking and climbing via musculoskeletal modelling and to compare these to the differences observed in the respective proxies. Specifically, we hypothesize that: (H1) the difference in the model-predicted MCP joint load magnitudes between knuckle-walking and climbing is smaller than the difference in the proxy estimations of MCP joint load magnitude (i.e. total external loading) between these two activities, and (H2) the difference in the model-predicted MCP joint load directions between knuckle-walking and climbing is smaller than the difference in the proxy estimations of MCP joint load direction (i.e. MCP joint posture) between these two activities.

Methods

Experimental data acquisition and processing

Finger loading and kinematics during knuckle-walking and vertical climbing were assessed based on previously presented experimental data [16]. In brief, hand pressures and kinematics during vertical climbing and arboreal knuckle-walking were collected from eight adult captive bonobos using a pole instrumented with a Novel® S2119 pressure mat (Novel GmBH, Munich, Germany) (Figure 1). To capture finger kinematics, three video cameras (Basler AG, Ahrensburg, Germany) were used to record the hands in contact with the substrate. Flexion-extension angles of the MCP, proximal interphalangeal (PIP) and distal interphalangeal joint (DIP) were evaluated at the moment of peak pressure using still images from the cameras and the video digitization software DLTdv3 [17]. Normal forces acting on each finger segment (proximal, middle, distal phalanx) were calculated from the pressure mat data matched with still images of hand position on the mat. Since the proximal and distal phalanges were not in contact with the substrate during knuckle-walking, it was assumed that no external forces were acting on this finger segments.

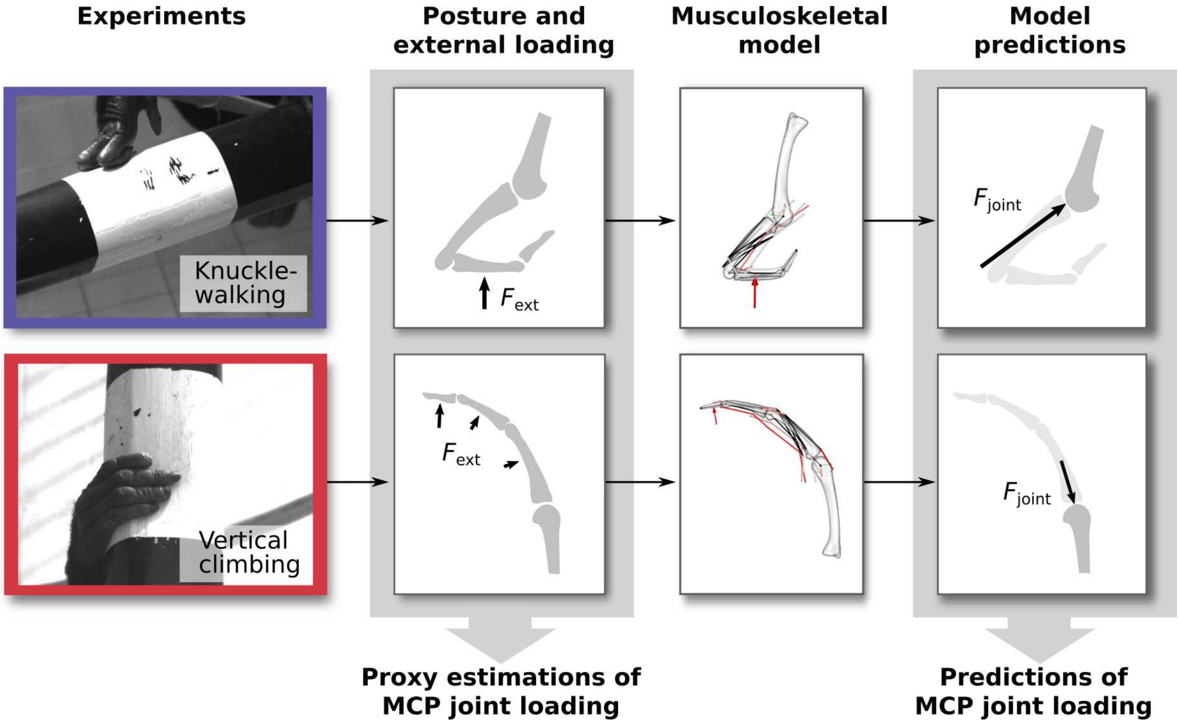

Figure 1: Overview of the study design. Activity-related differences of MCP joint loading predicted by musculoskeletal models (center, right) were compared to estimations based on proxies obtained from experiments (left).

Resampling of the experimental data

Due to the low number of available trials (Table 1) and missing data due to obstructed views, each joint angle and each finger segment load was modelled as a random variable and 100 trials for each activity were randomly sampled from these variables. Joint angles were assumed to be normally distributed and finger segment loads were assumed to follow gamma distributions [18]. The parameters of the distributions were obtained by fitting probability density functions to the experimental data with custom Python scripts (Table 1). During knuckle-walking, DIP and PIP joint angles could only be evaluated in one trial. Hence, the measured value was assumed to represent the mean and the standard deviation was set to the mean standard deviation of all measured joint angles.

Locomotor mode	Variable	Joint angles (°)			Finger segment loads (N)		
		DIP	PIP	MCP	Distal	Middle	Proximal
Knuckle-walking	μ	60.39	128.32	-45.15	-	-	-
	σ	6.33	6.33	7.30	-	-	-
	k	-	-	-	-	6.66	-
	θ	-	-	-	-	4.45	-
	n	1	1	5	-	11	-
Vertical climbing	μ	18.52	45.43	28.40	-	-	-
	σ	3.18	5.22	7.64	-	-	-
	k	-	-	-	2.24	0.24	0.26
	θ	-	-	-	5.44	15.10	1.21
	n	8	8	8	23	23	23

Table 1: Experimental data and parameters of fitted distributions. μ and σ are the mean and standard deviations of normal distributions, k and θ are the shape and scale parameters of the gamma distributions, and n is the original sample size. Positive angle values refer to palmarflexion. Distal and proximal finger segment loads during knuckle-walking were assumed to be zero and are therefore omitted.

Musculoskeletal modelling

A validated 3D musculoskeletal model of the third digit of a bonobo [13] was used to predict MCP joint loads based on the joint angles and finger segment loads (Figure 1). In brief, the model comprised three movable segments (distal phalanx, middle phalanx, proximal phalanx) interconnected by three joints (DIP, PIP, MCP). The finger was actuated by six muscles, namely the flexor digitorum profundus (FDP), flexor digitorum superficialis (FDS), extensor digitorum communis (EDC), the lumbrical (LU), and interossei muscles positioned radially (RI) and ulnarly (UI) around the third digit. Tendon paths were modelled by via points to compute posture-specific moment arms and the extensor mechanism was included using the common Winslow's rhombus assumption [19,13].

The MCP joint loads were computed at the moment of peak pressure as the sum of external forces and muscle forces (see Supplementary Material S1 for details). External forces were applied at the center of each finger segment (Figure 1) and muscle forces were obtained by solving an optimization problem that minimizes the total muscle stress. Constraints in the optimization ensured that the muscle forces satisfy the torque equilibrium conditions and remain within physiological boundaries, i.e. forces must be larger than zero and below the muscle specific maximum force (see Supplementary Material S1 and [13]). Passive muscle forces and other passive components (e.g. ligaments, soft tissue contact) were not implemented explicitly as the required parameters are not yet available. To compensate for these missing modelling details, reserve actuators were implemented [20]. These reserve actuators generate torques at each joint but do not contribute to joint loads. Their contribution was limited to 10% of the torque generated by external forces except for the PIP joint in knuckle-walking, where extension torque was assumed to be generated by contact between the middle and proximal phalanx rather than muscle forces. Except for the PIP joint during knuckle-walking, the reserve actuator torque contributions remained small during the simulations of both knuckle-walking (mean: 0.06%) and climbing (mean: 0.07%).

Output variables and statistics

Activity-related differences were assessed in terms of predicted MCP joint load magnitude (F_{Joint}) and joint load direction relative to the metacarpal bone (φ) as well as respective proxies, i.e. total external finger loading ($F_{\mathrm{ext,tot}}$) and MCP joint angle (α_{MCP}). Cliff's delta d was used as a robust measure of effect size [21] to judge the relevance of the differences in relation to the variability. d ranges from -1 to 1 and can be used to categorize effects into negligible ($|d|<0.147$), small ($|d|<0.330$), medium ($|d|<0.474$), and large ($|d|\geq0.474$). Additionally, muscular effort of each activity was evaluated as the ratio of total muscle force ($F_{\mathrm{mus,tot}}$) to total external force ($F_{\mathrm{ext,tot}}$) and the muscle force patterns were compared.

Results

The measured total external finger loading (i.e. proxy for MCP joint load magnitude) was considerably larger during knuckle-walking than during climbing (difference of means: 15.04N, |*d*|=0.75; see Figure 2a). Similarly, activity-related differences of MCP joint posture (i.e. proxy for MCP joint load direction) were also large (difference of means: 73.61°, |*d*|=1.00; see Figure 2a).

In contrast, musculoskeletal model predictions of MCP joint load magnitudes showed that differences between knuckle-walking and climbing were negligibly small (difference of means: -8.21 N, |*d*|=0.09; see Figure 2b). Differences in predicted joint load vector directions between the activities were clear (|*d*|=1.00) but the extent of differences (mean: 48.67°) was smaller than expected from the respective proxy. The direction of predicted joint loads were coincident with MCP joint angle during knuckle-walking but were more acute than the MCP joint angle during climbing (Figure 2b).

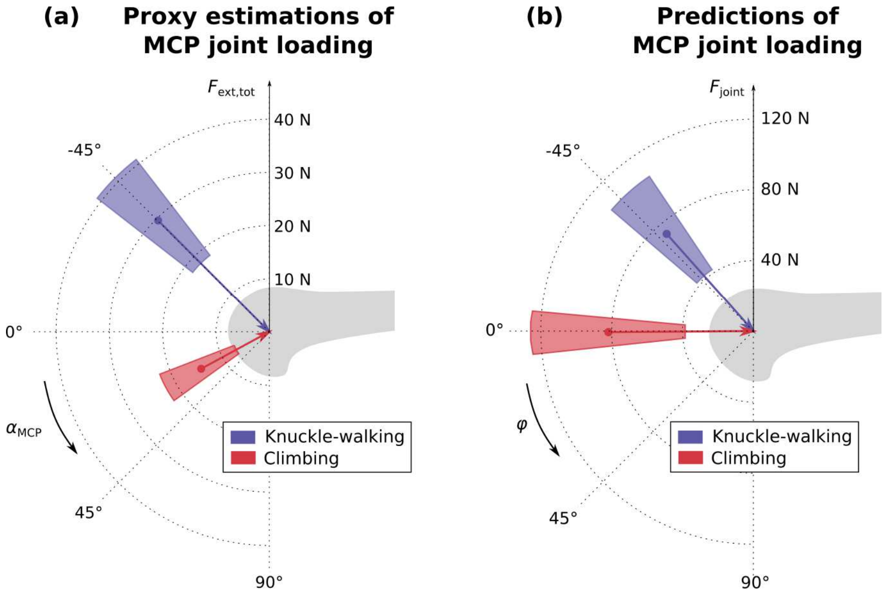

Figure 2: Activity-related differences of (a) proxy estimations of MCP joint load magnitude and direction and (b) respective predictions computed using musculoskeletal models.

Muscular effort ($F_{mus,tot}$/$F_{ext,tot}$) was approximately three times higher during climbing when compared to knuckle-walking (Table 2). During knuckle-walking, the muscle force was predominantly produced by the FDS muscle while force contributions of all other muscles remained small. Climbing required force contributions predominantly from extrinsic flexors (FDP, FDS), but also internal flexors (RI, LU, UI) and co-contraction of extrinsic extensors (EDC).

Locomotor mode	**$F_{mus,tot}$/ $F_{ext,tot}$ (-)**	**F_{FDP} (N)**	**F_{FDS} (N)**	**F_{EDC} (N)**	**F_{RI} (N)**	**F_{UI} (N)**	**F_{LU} (N)**
Knuckle-walking	1.90±0.57	0.87±0.48	50.13±25.77	0.00±0.00	5.60±2.97	0.00±0.00	0.21±0.42
Climbing	6.85±1.16	45.87±24.40	24.46±16.47	5.72±9.44	17.15±14.31	5.10±9.65	0.55±1. 03

Table 2: Activity-related differences of muscular effort ($F_{mus,tot}$/$F_{ext,tot}$) and individual muscle forces. All values are given as mean±standard deviation.

Discussion and conclusions

This study investigated how activity-related differences in MCP joint load magnitude and direction in the bonobo third digit may vary between commonly used proxies (external finger load and joint posture) versus a musculoskeletal model that incorporated muscular force as well. Results supported both of our hypotheses; activity-related differences in model-predicted MCP joint load magnitudes (H1) and directions (H2) were smaller between knuckle-walking and climbing than those estimated from the respective proxies. Indeed, model-predicted MCP joint load magnitudes during knuckle-walking and climbing were surprisingly similar.

Predicted muscle forces showed that the negligible difference between activity-related MCP joint load magnitudes is due to the reduced muscular effort during knuckle-walking when compared to climbing. This result is biomechanically reasonable assuming that the external load's line of action passes closely through the MCP joint (Figure 1) and effectively reduces the required joint torque to maintain equilibrium [22]. This is also confirmed by electromyographic studies reporting limited digital flexor muscle activity (FDS and FDP) during knuckle-walking [23]. The model predictions show that muscle forces are still required to maintain joint torque equilibrium during knuckle-walking (see FDS muscle force in Table 2), but this force likely represents a passive force due to the muscle stretch in the hyperextended MCP joint rather than an active contribution. In contrast to knuckle-walking, both extrinsic flexors show much higher levels of activity to maintain the grasping force during climbing and suspension [23]. Thus, since muscular forces outweigh external forces [13], joint load magnitudes at the MCP joint between knuckle-walking and climbing are more similar than proxies would suggest.

In addition, the results showed that the MCP joint load direction is not necessarily coincident with external joint posture. Specifically in climbing finger postures, the joint load direction is more aligned with the long axis (i.e. diaphysis) of the metacarpal than the measured (i.e. instantaneous) joint angle would suggest (Figure 2). This could be explained by the extrinsic flexor activity, which causes shear forces on the base of the proximal phalanx [24,14].

Some limitations of this study should be mentioned. First of all, passive muscle forces and soft tissue contact were not explicitly modelled. As a result, the muscle forces should be interpreted as total force (i.e. active plus passive) rather than active force alone, and the torque at the PIP joint during knuckle-walking had to be modelled using reserve actuators. Secondly, the kinematic data were evaluated from still images using image digitization software rather than using markers. However, applying markers to the bonobo hands was ethically and logistically unfeasible for this study. Thirdly, the resolution of the pressure mat was too coarse to evaluate and apply a pressure distribution on each phalanx. Instead, resultant normal forces were computed and applied to the phalanx centroids. Shear forces acting on the finger might also influence the joint load vector but could not be included in this study since only pressure data was available. Fourthly, this study was conducted only on the third digit, only for two specific locomotor activities (vertical climbing, knuckle-walking), and based on a small experimental dataset especially for knuckle-walking. Finally, evaluations were performed quasi-statically at the point in time when peak substrate pressure was measured rather than dynamically during a full motion sequence. Substrate pressures and muscle activity vary in course of the motion sequence and the point in time of peak substrate pressure might not be coincident with that of peak muscle activity.

Despite these limitations, this study has important implications for how we interpret function from bony morphology, especially in the fossil record. Soft tissues typically do not fossilize and data on muscular activity is ethically and logistically challenging to collect on non-human primates and especially apes. Thus, the effect of muscular force on joint load and ultimately bony morphology is often of limited consideration. This study demonstrates the critical influence of muscular force on joint load magnitude and direction. For example, the negligible differences in MCP joint load magnitude between bonobo knuckle-walking and climbing helps to explain the greater similarity in trabecular structure between African and Asian apes than would be predicted from hand posture and (presumed) locomotor substrate forces [2,3,25]. Our results also help to explain the smaller than expected differences in mean joint load vector magnitudes and directions at the MCP joint across great apes predicted by inverse bone remodeling methods [26].

Although methods like inverse bone remodeling [26] or more holistic measures of trabecular structure [25] appear sensitive enough to reveal differences in hand loading across great apes, caution must be applied when reconstructing behavior from the fossil record, particularly from isolated skeletal elements. This study suggests that joint load direction and, in turn, related measures of bone structure, such as degree of anisotropy or principle trabecular orientation [7], may be more a reliable indicator of variation in hand use in fossil taxa than joint load magnitude.

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