Kinematic and dynamic aspects of chimpanzee knuckle walking - finger flexors likely do not buffer ground impact forces

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Abstract

Chimpanzees are knuckle-walkers, with forelimbs contacting the ground by the dorsum of the finger's middle phalanges. As these muscular apes are given to high velocity motions, the question arises how the ground reaction forces are buffered so that no damage ensues in the load bearing fingers. In literature, it was hypothesized that the finger flexors help buffer impacts because in knuckle stance the metacarpophalangeal joints (MCPJ) are strongly hyperextended, which would elongate the finger flexors. This stretching of the finger flexor muscle-tendon units would absorb impact energy. However, EMG studies did not report significant finger flexor activity in knuckle walking. While these data by themselves question the finger flexor impact buffering hypothesis, the present study aimed to critically investigate the hypothesis from a biomechanical point of view. Therefore, various aspects of knuckle walking were modeled and the finger flexor tendon displacements in the load bearing fingers were measured in a chimpanzee cadaver hand, of which also an MRI was taken in knuckle stance. The biomechanics do not support the finger flexor impact buffering hypothesis. In knuckle walking, the finger flexors are not elongated to lengths where passive strain forces would become important. Impact buffering by large flexion moments at the MCP joints from active finger flexors would result in impacts at the knuckles themselves, which is dysfunctional for various biomechanical reasons and does not occur in real knuckle walking. In conclusion, the current biomechanical analysis in accumulation of previous EMG findings suggests finger flexors play no role in impact buffering in knuckle walking.

Introduction

The African great apes: *Gorilla spp.*, *Pan troglodytes* (chimpanzee) and *Pan paniscus* (bonobo), are emblematic knuckle-walkers. In this distinctive locomotor mode, the hands contact the substrate with the dorsum of the middle phalanges (MP). To enable this, the proximal interphalangeal joints (PIPJ) are hyperflexed and the metacarpophalangeal joints (MCPJ) hyperextended (Inouye, 1994; Thompson et al., 2018; Thompson, 2020) (**Figure 1**)**.** The ground reaction forces generally do not apply at the proximal phalanx head but are distributed over the middle phalanx dorsum, which is covered by a thick skin pad (Matarazzo, 2008; Wunderlich and Jungers, 2009; Matarazzo, 2013). Between gorillas and chimpanzees, the hand position in knuckle walking differs. In captive chimpanzee observations, weight is mainly borne by digits 2, 3 and 4, and knuckle-walking positions vary over a spectrum between palms facing backwards or inwards (Wunderlich and Jungers, 2009; Thompson, 2020). However, gorillas more often use a palm-back position with loading of digits 2 to 5 (Inouye, 1994; Matarazzo, 2013; Samuel et al., 2018). In wild gorillas, a wider variability in hand postures has recently been documented, including fist walking (Thompson et al., 2018).

Even though in metacarpals and phalanges skeletal correlates with knuckle-walking have been studied extensively (Tuttle, 1967; Susman, 1979; Sarmiento, 1994; Richmond et al., 2001; Matarazzo, 2008), it remains unclear how impact energy during knuckle strike is buffered so that no finger damage occurs - given the large body size of the animals and speeds at which knuckle-walking can occur.

In 2018, Simpson *et al*. formulated the hypothesis that MCPJ hyperextension would elongate the finger flexors, which would buffer the ground reaction forces on the knuckle at ground contact: *'… Since even minor extension of a muscle belly increases its force output … hyperextension at the MCPJs in the African apes is an effective means of allowing the digital flexors to function as shock absorbers, often without significant energy expenditure.*' (Simpson et al., 2018).

Finger flexor buffering of impact by ground reaction forces extending the fingers is structural in digitigrades and especially terrestrial ungulates, where the large finger flexor tendons elastically elongate at impact, diminishing impact peak forces. However, the African great apes contact the ground by the dorsum of the middle phalanges, with hyperflexed PIPJ, which has no equivalent in digitigrades. Therefore, extrapolating finger flexor impact buffering as exists in digitigrades to knuckle walking is not self-evident.

The present study aims to evaluate the finger flexor impact buffering hypothesis, which Simpson and colleagues formulated without supporting evidence. If the flexor impact buffering hypothesis were correct, the following outcomes should be expected: (i) between ground strike and full load bearing stance, the finger flexors should undergo significant lengthening; (ii) during this phase, the finger flexors should exert large forces, actively or passively by being stretched, as without large forces no finger flexor impact buffering could occur.

Electromyographic (EMG) studies of finger flexors in knuckle walking have consistently measured very low activity throughout the gait cycle - in stance and swing phases alike - in chimpanzees (Susman and Stern, 1979; Thompson et al., 2019) as well as in gorillas (Tuttle et al., 1972). While this lack of EMG activity by itself renders the finger flexor impact buffering hypothesis unlikely, it does not explain why finger flexor activity would be so low. The present study analyses knuckle walking biomechanics to help answer this question.

Methodologically, the kinematics and some force aspects of knuckle walking were modeled and experimentally tested in a fresh-frozen chimpanzee hand, of which also an MRI in knuckle walking position was made. Investigated were (i) the general conditions for stable placement of the fingers at strike, (ii) the finger flexor length changes that occur during knuckle strike, relative to estimated flexor resting lengths, and (iii) the biomechanical implications of using large finger flexor forces during knuckle strike and stance. In terms of nomenclature, the term 'stance phase' will indicate the ground contact phase of the walking cycle, while 'knuckle stance' will indicate the finger position itself, static or during the stance phase, as indicted by the context.

Some general observations on finger positions during knuckle walking

As an introduction to the biomechanical models, some basic aspects of knuckle walking are here considered. A straight articular chain aligning ground contact at the proximal phalanx (PP) head with MCPJ, wrist and (fore)arm is unsuited for dynamic locomotion (**Figure 2**, A). The small ground contact area would lead to high tissue pressure at impact even with a thick skin pad; the more so because a straight joint chain does not buffer impact energy. Maintaining the neutral MCPJ position would require constant muscle effort. Even more trivial, the longest finger would support all load, as the shorter fingers would not reach the ground (**Figure 2**, B). To allow the shorter fingers reaching the ground, the MCPJ must hyperextend and the PIPJ flex (**Figure 2***,* C). The MCPJ and PIPJ in the longest finger D3 will be more hyperextended and hyperflexed, respectively, than in the shorter fingers, at least with vertical metacarpals (**Figure 2**, C). From observation of knuckle-walking chimpanzees, it seems that a distinction can be made between 'high' and 'low' knuckle walking positions of the hand. High stance is with three supporting fingers and the PP of the shortest finger quasi vertical or even slightly flexed (**Figure 2**, C, D). Low stance is with the PIPJ of the longest finger at maximum flexion. High and low stances have different spacing of ground contacts (arrows in **Figure 2**, D and F). Therefore, a high stance cannot change into a low stance without ground contacts shifting to closer alignment, meaning that with high ground friction, fingers will have to be lifted and repositioned. Maximum PIPJ flexion is likely limited by extra-articular bone contact at the PIPJ (**Figure 2**, E, arrow). In that case, when in low knuckle stance body weight is supported by the MP, high forces at this bone contact might occur. Indeed, the bone contact point then becomes a pivot between the ground reaction force at the MP and the PIPJ ligaments as constraining elements. Then why does low knuckle stance not lead to damage at the extra-articular PIPJ bone contacts? Or does the volume of the soft tissues enclosed between PP and MP (palmar finger skin, fat pads, tendons) limit maximal PIPJ flexion, diminishing the extra-articular bone contact forces? While these questions were not the subject matter of the present study, they illustrate that knuckle walking is not a straightforward matter and that impact energy buffering is a relevant question. The specific question here considered is whether the finger flexors have a role in impact buffering.

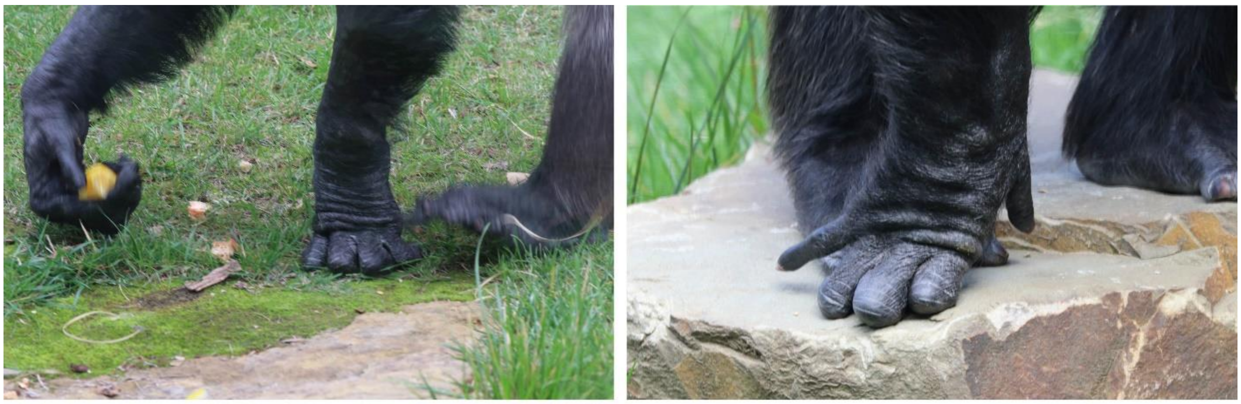

Figure 1. Low stance knuckle walking. In both cases index and middle fingers are load bearing (which requires wrist ulnar deviation): PIPJ in flexion end-positions, MCPJ likely in maximum hyperextension. Ring fingers are likely not load bearing: PIPJ are not in flexion end-position and MCPJ not at hyperextension limit. Ground contacts occur at middle phalanx, not at the proximal phalanx heads. (Photographs courtesy Marie Vanhoof - chimpanzee colony at Antwerp Zoo, Belgium)

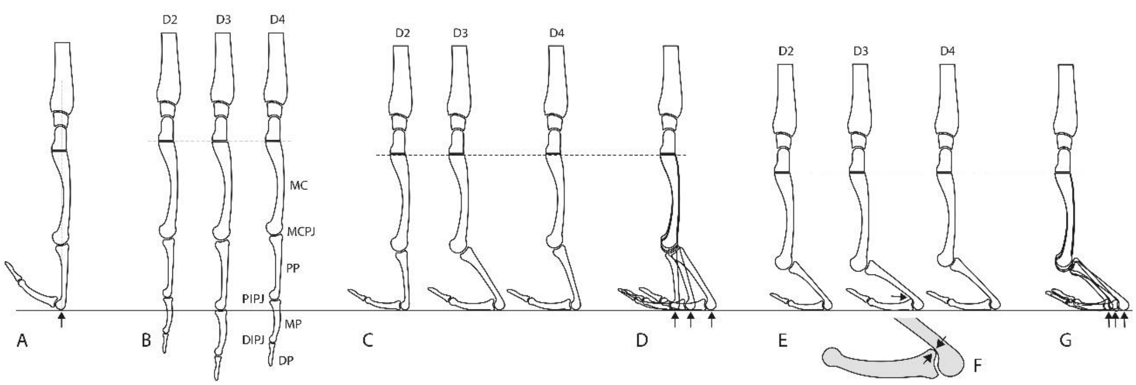

Figure 2. Knuckle stance basic postures. A. Straight knuckle chain. B. Segment proportions obtained from X-ray and MRI . Middle finger (D3) is longest, D2 shortest although its metacarpal is slightly longer than D4. C. To allow D2 reaching the ground, the MCPJ of D3 and D4 must hyperextend. C, D. High knuckle stance. D: combined positions of C. E-G. Low knuckle stance with vertical metacarpals. E. Individual finger positions. $PIPJ_3$ maximally hyperflexed, likely limited by extra-articular bone contact (D3, arrow, detail in F). $PIPJ_2$ and PIP_4 likely not maximally flexed. G. Low stance, combined positions of E. Arrows in D and G show differences in ground contact positions between high and low stance. MC, PP, MP, DP: metacarpal, proximal, middle and distal phalanges. MCPJ, PIPJ, DIPJ: metacarpophalangeal and proximal and distal interphalangeal joints.

Materials and methods

This study presents biomechanical models and experimental kinematic measurements of a chimpanzee hand. The biomechanical models are presented in the results section. In the following, the material and methods of the experiments are described.

Specimen and preparation for experiments

A fresh-frozen left-hand specimen from a 46-year-old female chimpanzee (*Pan troglodytes*), deceased by natural causes, was provided by the Ghent University Faculty of Veterinary Medicine. The hand was obtained disarticulated at the elbow, with radius and ulna intact. The specimen was thawed at room temperature before starting the dissection. All extrinsic finger tendons proximal to the wrist were dissected from their muscle tissue, which was then completely removed from ulna and radius. The flexor retinaculum and wrist tendon compartments were kept intact. The flexors carpi radialis and ulnaris (FCR, FCU), extensors carpi radialis longus, brevis and ulnaris (ECRL, ECRB, ECU), and the tendons of superficial (FS) and deep flexors (FP) of index, middle and ring fingers (D2, D3, D4) were knotted by a 'strangling' sailor's knot to 1.1 mm Dyneema strings (sk99 fiber, Liros GmbH, Berg, Germany – breaking strength 2400N) actuated by weight balanced pulleys. The high string stiffness and strength, 24 times the maximum tendon loads of 100N in experiments, ensured negligible string strain. The strangling knot is stable for tendon diameters greater than the string diameter and exhibits no slippage and very little creep when preloaded well in excess of the experimental forces.

Radiological investigations

X-ray A palmar-dorsal and a 45-degree side view X-ray of the entire hand were taken. The X-ray revealed a grossly consolidated fracture proximal-dorsal at the middle phalanx of D3 (**Figure 3**, A). Surprisingly, this fracture allowed apparently normal PIPJ motion until full flexion, but did limit PIPJ extension to about 10 degrees flexion.

MRI of low knuckle stance MRIs were taken of the hand with D2, D3 and D4 in low knuckle stance. The purpose was visualizing (i) the PIPJ angles at flexion end-positions, (ii) whether extra-articular bone contacts determined the PIP end-positions, and (iii) the internal position of the finger flexor tendons. To obtain an immobile low knuckle stance during the MRI recordings, all finger and wrist tendons were individually connected under tension proximal to the forearm bones or to stiff rubber bands connected to the forearm bones, as follows (**Figure 3**). The radius and ulna were proximally tightly bound together by a Dyneema string, called the base string, wired through drilled holes. The base string also served to attach the tendon strings and rubber bands that fixed the finger and wrist positions. The wrist flexor strings were connected directly to the base string with the wrist in neutral position. The wrist extensors were tensed using rubber bands attached to the base string. This kept the wrist by antagonistic tension immobile during MRI recording. Digits D2-D4 were forced into low knuckle stance by tensed rubber bands around the MPs, attached by strings to the base string. To stabilize this construct, the finger strings were constrained at the dorsum of the wrist by an annular string. The superficial and deep flexor tendons of D2 to D4 were individually connected to rubber bands at the base string, ensuring that the tendons ran under tension in their pulleys. For reference, an MRI was also taken of a human female hand specimen, similarly mounted in a low knuckle stance position. This specimen was embalmed according to the Thiel method, which preserves soft tissue suppleness (Ottone et al., 2016). Both the chimpanzee and human hand were scanned with a 3 Tesla Siemens PrismaFit MRI scanner in the Ghent Institute for Functional and Metabolic Imaging. The specimen was placed in a 64-channel head coil, with the palm of the hand facing down, stabilized by sandbags. Two main MRI parameter settings were used, MRI_s1 and MRI_s2, detailed in the Supplementary Materials.

Joint angles obtained from the MRI Comparative measurements of the PIPJ angles in maximum flexion were obtained for D2, D3 and D4 from the chimpanzee and human MRIs. The joint angles were measured between lines through the MCPJ and PIPJ, and the PIPJ and DIPJ estimated joint centers (**Figure 5**, row 2, D2). While MCPJ$_2$ was likely close to the hyperextension end-position, MCPJ$_3$ and MCPJ$_4$ were not, so their angles in the MRI have no special significance.

Bone profiles For the models further presented, bone profile outlines were obtained from the MRI, meaning that the model illustrations should be in realistic proportions.

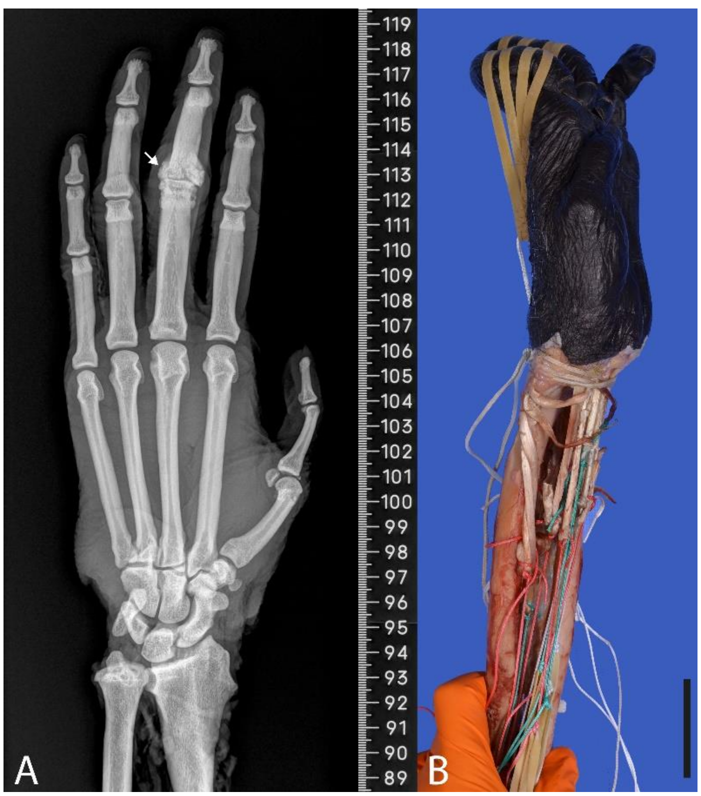

Figure 3. A. X-Ray of the female chimpanzee left hand used in experiments. Arrow: grossly consolidated fracture at the dorsal base of the middle phalanx. The fifth metacarpal head is markedly smaller than the load bearing metacarpals MC2-MC4.
B. Chimpanzee hand mounted for low knuckle stance MRI. Strangling knots rigidly connect tendons to strings. Interposed rubber bands consolidate the finger positions and tense the tendons. Measure bar: 50mm.

Measuring flexor tendon displacements between finger positions

Experimental set-up (**Figure 4**) The radius and ulna were fixed, each by two 4 mm self-tapping orthopedic screws, in supination position into a massive frame ensuring immobility during experiments. To measure the flexor tendon displacements, the flexor strings were guided into a parallel arrangement in the horizontal plane. Marker sutures were needled into the strings and a measuring rod as scale was positioned parallel in the plane of the strings. A photo camera (Nikon D7000, 105 mm Nikkor macro lens) positioned perpendicular to the tendon plane recorded all suture positions together with the scale. Rubber bands pulling the individual pulley wheels kept all strings under sufficient tension to prevent tendons from becoming slack during tests, even when not actively loaded.

Measuring tendon displacements with joint angle changes In the set-up, the wrist could be moved freely and was positioned by its five tendons, controlled by pulleys. Strong antagonistic co-contractions of the wrist tendons before locking their pulleys allowed to rigidly put the wrist in any desired position. Tendon displacement-joint position relationships were obtained in D2 to D4 for the nine finger positions given in **Figure 9**. The positions 1, 2, 3 and 9 were likely beyond the *in vivo* physiological range of the finger flexor muscle fiber lengths, but were possible to achieve as the tendons were unattached to muscles. The *in vivo* physiological range of tendon displacements was estimated to allow the joint ranges between positions 4 and 8. In human, with fully flexed fingers, active finger flexor insufficiency occurs at about 25° to 40° wrist flexion. However, the chimpanzee MCPJ and PIPJs flex further than in human, so the finger flexor tendon displacements between full finger extension and flexion are proportionally greater. Therefore, *in vivo* active finger flexor insufficiency with fully flexed fingers may occur already with neutral wrist (this is further modeled in the Supplementary Materials). The *in vivo* maximum physiological elongation of the flexors was estimated to occur at about -25° degrees wrist extension with all finger joints in neutral extension. The measurements proceeded as follows. The wrist was positioned by the wrist flexors as described. Fingers D2 to D4 were manually put and held in the desired position by one investigator. A second investigator then manually checked all flexor tendons individually by tugging their pulleys to ensure no slack remained in any tendon. Photographs were taken of the tendon marker positions together with the scale, and of the hand-finger positions in profile. In this way, all nine finger positions were systematically documented. From the hand profile photographs, the wrist and index (D2) joint angles were measured as the angles between the lines going through the estimated joint centers (**Figure 9**), using Adobe Illustrator software. The D3 and D4 fingers were held in the same position as D2, but as this was done manually likely small unsystematic variations in their joint angles occurred relative to the index position. As the results show, these variations were minor and did not affect the general consistency of the measured finger flexor tendon displacements.

Measuring tendon displacements in knuckle stance The low knuckle position (**Figure 9**, pos. 6) was measured as follows. The wrist was first put in neutral extension and rigidly fixed by its tendons. A vertical ground plate on a heavy sledge sliding on the frame was pushed towards the hand, with D2 through D4 positioned in MCPJ hyperextension and PIPJ flexion (**Figure 4**). The sledge was advanced until the PIPJ of D3 was in its flexion end-position and the sledge could not be pushed more proximally. In that position the flexor tendon positions were recorded. The PIPJ of D2 and D4 were then not fully in their flexion end-positions (**Figure 2**, E), but close enough to produce realistic tendon position estimates.

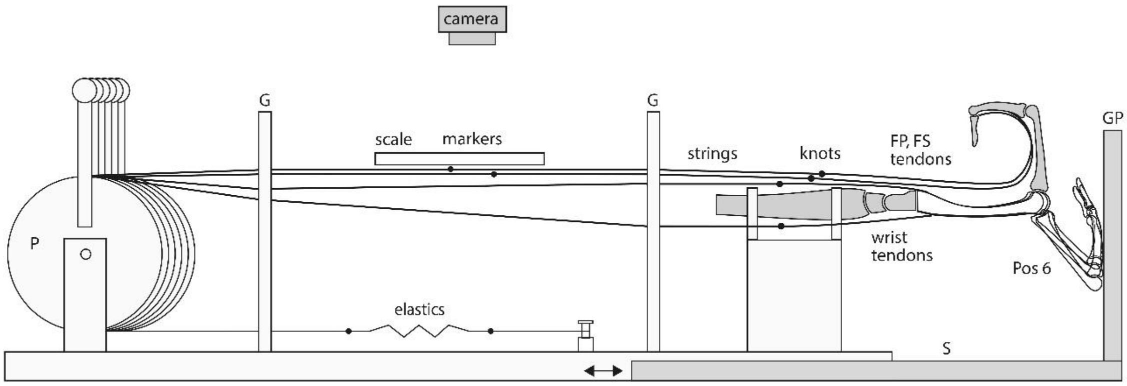

Figure 4. Set-up for measuring flexor tendon displacements. Tendons individually actuated by pulley wheels (P) were knotted to strings passing through appropriate guides (G). The flexor tendon strings of D2 to D4 were guided parallel in the horizontal plane. A camera photographed markers sutured to the tendon strings with a horizontal scale in the tendon plane in sight. Elastics at the individual pulleys kept the tendon strings under tension. The wrist was positioned by the wrist tendons. For low knuckle stance measurements (**Figure 9**, position 6), a ground plane (GP) on a heavy sledge (S) was pushed towards the hand until the target knuckle stance position was reached.

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Results

Comparative MRI of chimpanzee and human in low knuckle stance

Joint ranges MRIs of chimpanzee and human fingers D2, D3 and D4 in simulated knuckle stance are shown in **Figure 5**. In chimpanzee and human alike, maximum PIPJ flexion seems limited by extra-articular bone contact at the PIPJ (**Figure 5**, rows 1 and 2, large long arrows). Maximum PIPJ flexion was 17° to 25° greater in chimpanzee than in human (for PIPJ2 to PIPJ4: 144°, 144°, 153° versus 122°, 127°, 128°, respectively). Despite the fracture in chimpanzee D3, maximum $PIPJ_3$ flexion was equal to $PIPJ_2$. The chimpanzee MCPJ cartilaginous surface extended far more dorsally than in human, so that even at -53° hyperextension the bone contact in the $MCPJ_2$ was still between cartilage surfaces. Generally, as measured during the finger positioning (**Figure 9**), chimpanzee flexion ranges in finger joints and wrist were about 20° or more greater than in human. The wrist passive flexion limit, without forcing, was 123° in the chimpanzee specimen. Maximum passive index $MCPJ_2$ flexion was 145°and $MCPJ_2$ hyperextension -61°.

Flexor tendon curvatures At the PIPJs, the chimpanzee FP tendons bent almost 180° degrees, with the greatest curvatures distal at the A2 pulley and especially proximal at the A4 pulley, schematized in **Figure 6**. The FS tendons, which consist at PIPJ level of two thin broad parallel tendon bands, were not consistently visualized by the MRI. Their curvature at A4 was likely less than the FP curvature. In human, the FP tendon curvatures were smoother, which correlates with the relatively shorter phalanges and the less flexed PIPJ end-positions.

Fingernail skin indentation The deep flexors were pulled taut by rubber bands. Even though the rubber band forces were not large, the chimpanzee DIP joints flexed and the fingernails indented the skin (**Figure 5**, row 1 , D2, D3, arrows at fingernails).

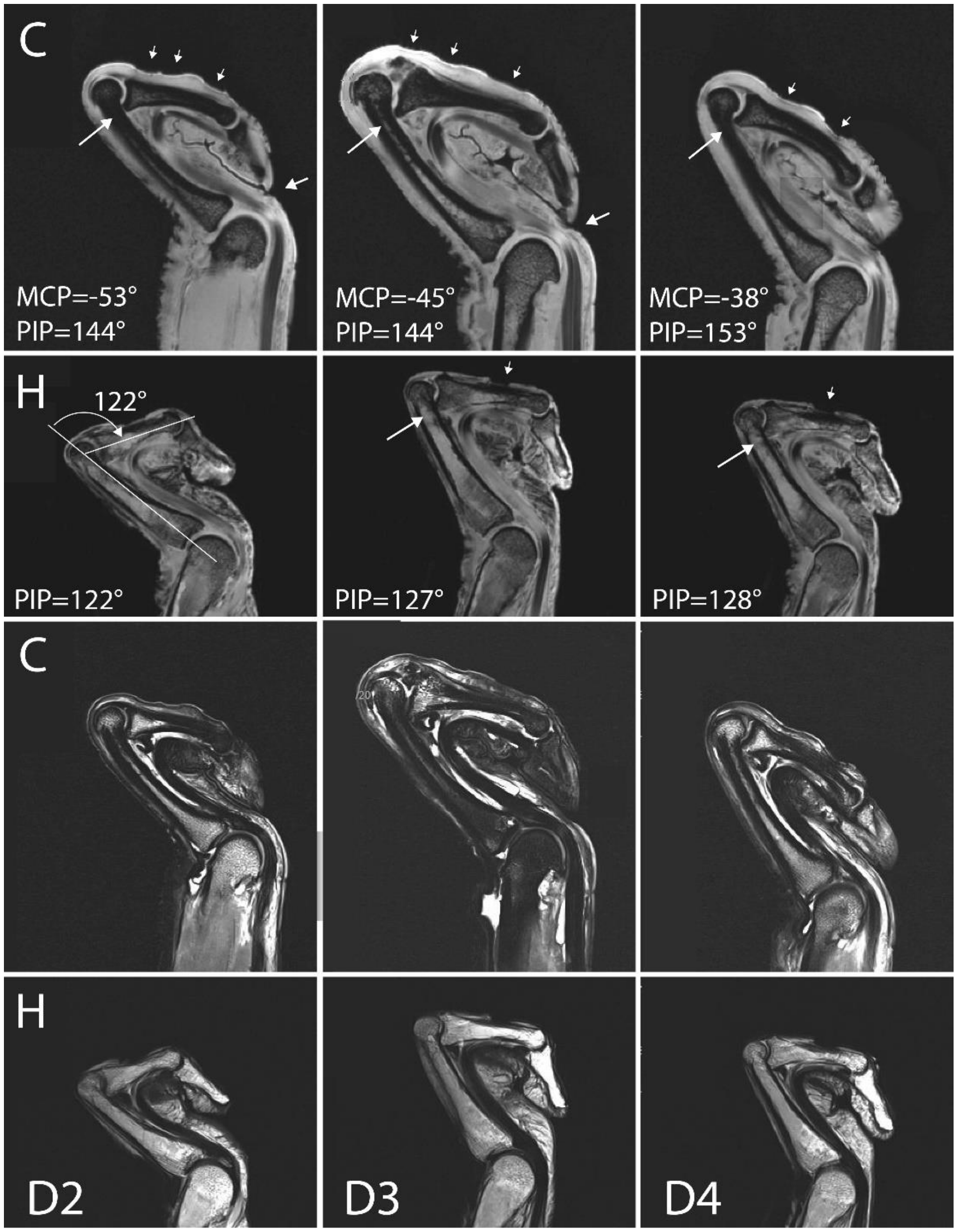

Figure 5. MRI of fingers D2-D4 in chimpanzee (C: rows 1 and 3) and human (H: rows 2 and 4) as fixed in **Figure 3**. Top two rows: MRI_s1 settings, showing bone and cartilage. Bottom two rows, MRI_s2 settings, showing flexor tendons in black. Chimpanzee-human differences: relative length of phalanges; maximum PIP flexion angles 17° to 25° greater in chimpanzee; extended dorsal cartilage and joint surface in chimpanzee MCPJ. In chimpanzee, the thick skin pad covering the proximal phalanx head and middle phalanx was barely indented by the rubber bands forcing the PIPJ in flexion end-positions (row 1, small arrows). In human, the rubber bands squeezed the fluid from the thin dorsal skin, which shows up as skin gaps (row 2, small arrows). D2, D3, top row, short large arrows: fingernails indenting palmar skin at MCPJ. Long large arrows, rows 1 and 2: extra-articular bone contact at the PIPJ. The chimp MCPJ are not in hyperextension end-positions (manually verified).

Figure 6 Chimpanzee finger flexors and pulleys in maximum PIPJ flexion (schematic from MRI). The main pulleys are annular pulleys A2 and A4 (human nomenclature), A3 is a lesser pulley. Tendon stress concentrates where tendons are maximally bent. A. Deep flexor (FP) stress concentrates at the distal edge of A2 and the proximal edge of A4. B. Superficial flexor (FS) stress concentrates distal at A2 but less at A4, because FS inserts at the level of A4.

Model analysis

High knuckle stance has passive stability but seems not suited for habitual knuckle walking

A high knuckle stance should - theoretically - have an intrinsic passive stability when three fingers of unequal length, with the longest in the middle, contact the ground with sufficient friction (**Figure 7**). The body weight will force the metacarpal heads (MCH) to move along circular trajectories of different radii centered at the PIPJ (**Figure 7**, A). These relative MCH motions would strain the (inter)metacarpal ligaments, which at some point would prevent further motion. Indeed, a full collapse from high stance into PIPJ flexion end-positions without shifting knuckle ground contacts would lead to relative MCH displacements that should exceed the lengths of the intermetacarpal ligaments (**Figure 7**, B). The passive stability derived from intermetacarpal ligament strain would increase with increasing differences between the MCH trajectories, e.g., when the middle phalanges are not positioned fully in parallel or when the MCPJ of one of the shorter fingers would be slightly flexed (**Figure 7**, C). A three-finger high stance cannot shift into a low stance unless the ground contact points shift into a closer alignment (Figure 7, D). Functionally, a high stance would somewhat elevate the upper body. However, a high stance seems not suited for habitual knuckle walking because the PP heads would be the prime load bearing ground contact points. Indeed, since the PIPJs are not in end-positions, any load sharing by the middle phalanges would create PIPJ flexion moments that could only be balanced by the PIPJ extensors, which would be too weak to consistently do so. In habitual knuckle walking the middle phalanges rather than the PP heads are load bearing. This indicates that high stance would rather be reserved for static positions. Hence, in the further analysis of knuckle walking only low stance will be considered, where (some) PIPJs are in end-positions.

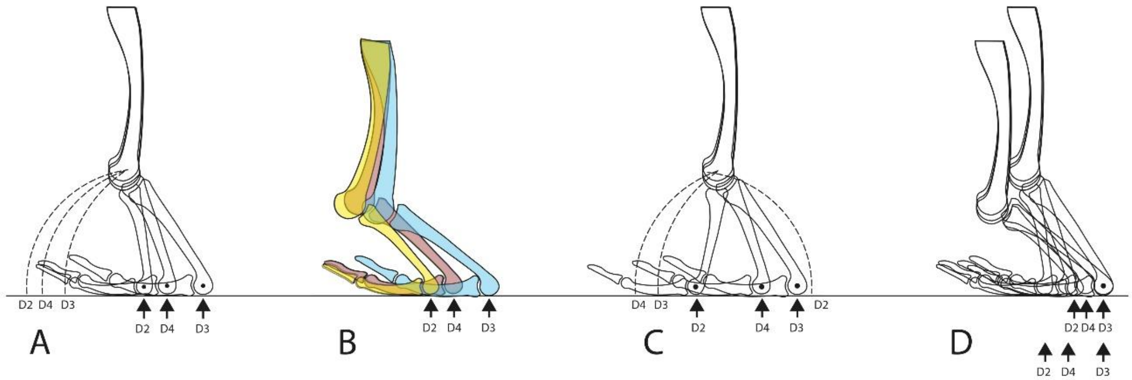

Figure 7. High knuckle stance with three supporting fingers - model of passive stability. A. The metacarpal heads (MCH) move on circle arcs centered at the PIPJ (dotted lines). B. Moving from high stance into low stance without ground shifts would force the MCH into positions as depicted, likely exceeding inter-metacarpal ligament lengths. C. High stance passive stability should increase when conflicts between the MCH trajectories increase, as happens when putting one finger with slightly flexed MCPJ. D. Transition of high to low stance without relative MCH displacements requires closer realigning of ground contacts.

Biomechanical conditions for safe knuckle strike

In knuckle walking, prior to ground strike, the hand must be positioned so that the ground reaction forces have extension moments at the MCPJ (**Figure 8**, A). Large MCPJ flexion moments from ground reaction forces would cause the MCPJ to collapse into full flexion, since the finger extensors would be too weak to balance such moments (**Figure 8**, A, a). Ground reaction force MCPJ extension moments can be realized by different combinations of (fore)arm, wrist and MCPJ angles. With a protracted forearm, the wrist and MCPJ could be in neutral positions (**Figure 8**, A, b). To the degree that the forearm is put down vertically with vertical metacarpals, the wrist and/or MCPJ must be hyperextended (**Figure 8**, A, c-e). When the MCPJ is sufficiently hyperextended, the wrist can be straight or even slightly flexed (**Figure 8**, A, e). Even with hyperextended MCPJ, an oblique impact force can cause an MCPJ flexion moment (**Figure 8**, A, f). Just before ground strike, to allow good middle phalanx ground placement, the PIPJ must be sufficiently flexed. It may not be necessary to position the middle phalanx fully horizontally before impact, as the ground reaction forces will further flex an already flexed PIPJ.

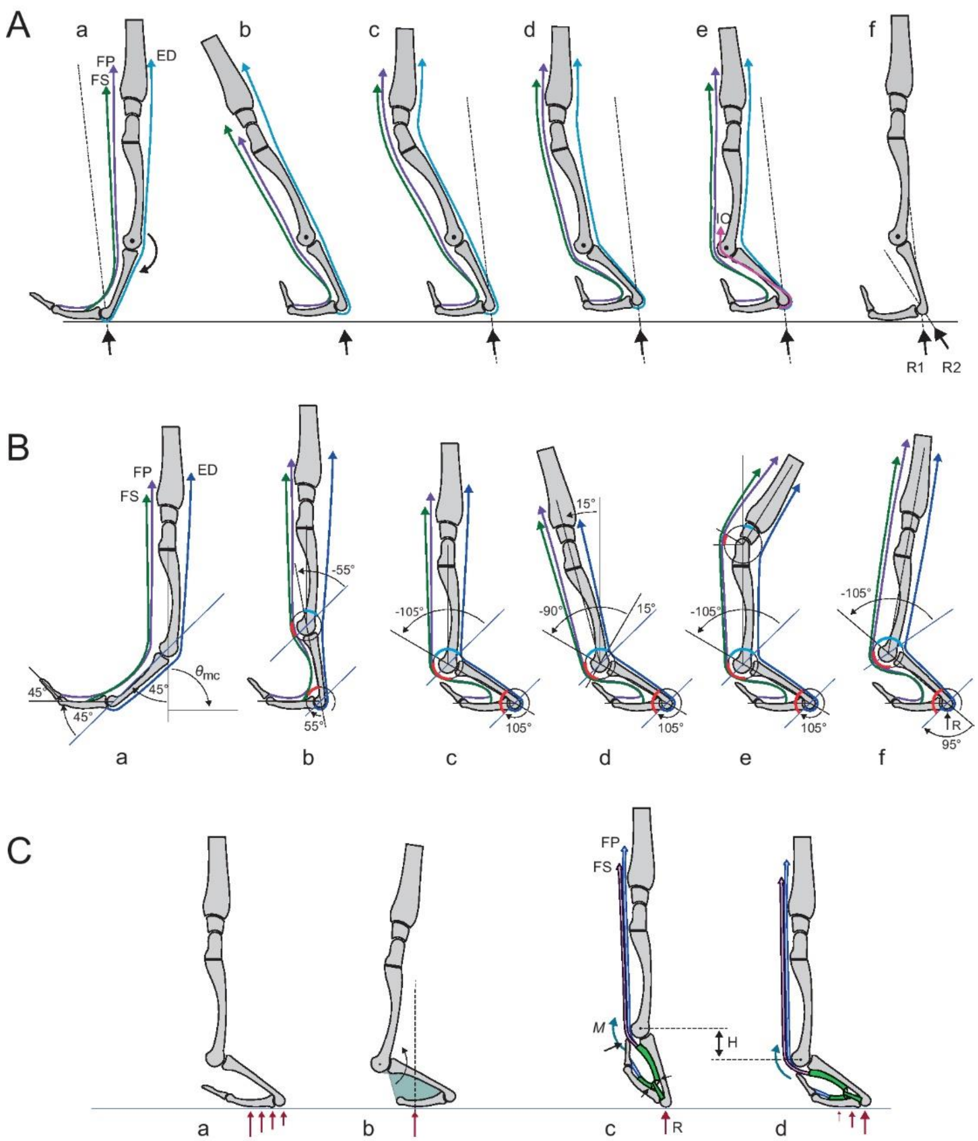

Figure 8. A. MCPJ ground reaction force moments at impact. (a) An MCPJ flexion moment will likely cause collapse into MCPJ flexion, as the finger extensors are likely too weak to prevent this. (b – e) Different positions of forearm, wrist and MCPJ realizing an MCPJ extension moment. (b) Protracted forearm with neutral wrist and MCPJ. (c) Wrist extension. (d) Combination of wrist and MCPJ extension. (e) Wrist slightly flexed with hyperextended MCPJ. (f) Safe knuckle strike depends on the ground reaction force direction. Force R1 results in safe placement. Force R2 causes MCPJ flexion collapse. FP, FS, ED, IO: deep flexor, superficial flexor, extensor digitorum, interosseous tendons.

B. Finger flexor length changes between finger positions. Circles represent the mean tendon moment arms. Joint angles positive for flexion. (a) Position FJ_{45} with finger joints at 45°, neutral wrist. (b) High knuckle stance. From a→b, MCPJ extends -55° and PIPJ flexes 55°. With equal MCPJ and PIPJ moment arms, equal but opposite flexor lengths are taken up or given free at MCPJ and PIPJ, respectively (with static DIP joint), so that the finger flexors remain isometric. MCPJ, blue circle arc: flexor lengths taken up at MCPJ when extending from (a). MCPJ, red arc: blue arc rotated to flexion side of the MCPJ, for visual effect. PIPJ, red circle arc: flexor length given free when PIPJ flexes from (a). (c) Low knuckle stance. From a→c, MCPJ extends -105° and PIPJ flexes 105°, so that the finger flexors remain isometric. From b→c, MCPJ extends -50° and PIPJ flexes 50°, meaning the flexors remain isometric from high to low stance. (d-f) Stance phases with palm backwards. (d) Knuckle strike in low stance. The MCPJ hyperextension angle is smaller than in (c); the PIPJ angle is equal. Therefore, the finger flexors are shorter than in FJ_{45}. (e) At the end of the stance phase, the wrist could in principle hyperextend, lengthening the flexors beyond FJ_{45} length, but such wrist extension was experimentally not observed (see text). (f) With MCPJ in hyperextension end-positions, decreasing the metacarpal angle with the horizontal would extend the PIPJ and shift the ground reaction forces R to the knuckles. The finger flexors then become longer than in FJ_{45}.

C. Flexor force considerations in knuckle walking. (a, b) Single finger, all muscles inactive. (a) At knuckle impact, the PIPJ will collapse into the flexion end-position. (b) With the PIPJ in end-position, the ground reaction force extension moment will force the MCPJ into the hyperextension end-position. (c, d) Hypothetical finger flexor impact buffering model, single finger. Transition from high (c) to low stance (d) leaves the impact buffering height H for negative work decelerating metacarpal descent. However, a large MCPJ flexion moment *M* can only arise after the interphalangeal joints are in end-positions. Then the ground reaction force R would impact the knuckle itself. Large FP forces would create tendon stress at the flexor pulley edges (c, small arrows), while DIPJ flexion could drive the finger nails into the palmar MCPJ skin (c, large arrow).

Finger muscle action preceding knuckle strike

Low stance strike Biomechanically, MCPJ hyperextension with PIPJ flexion immediately prior to impact requires forces in both the finger extensors and finger flexors. The extensors hyperextend the MCPJ, while the flexors must keep the PIPJ from extending too much. EMG studies of the finger flexors show consistent finger extensor activity in the second half of the swing phase prior to strike, ending at 5% to 10% of stance phase, but no finger flexor activity (Thompson et al., 2019) (with additional personal communication). From this, it can be concluded that the flexor tonus forces and some flexor stretching by the MCPJ hyperextension suffice to flex the PIPJ sufficiently for safe knuckle placement at strike. However, the EMG data were obtained in chimpanzee walking in controlled conditions. In fast running or skirmishing, where the hand must be placed stably on the ground in a much shorter time interval, it may well be that the preparation for a stable strike requires active co-contraction of the finger flexors with the finger extensors.

High stance placement While the biomechanical conditions for low stance strike preparation are relatively mild (sufficient MCP hyperextension and PIPJ flexion), high stance requires putting three fingers simultaneously at the ground with the MCPJ at rather precise angles near neutral extension. Achieving such precise MCPJ angles prior to hand placement would require a controlled flexor/extensor moment equilibrium at the MCPJ and therefore – at least theoretically – co-contractive flexor-extensor activity.

Finger flexor lengths in knuckle stance relative to the finger flexor insufficiency limits

In knuckle stance with horizontal middle phalanx, the MCPJ and PIPJ angles and the metacarpal angle θ_{mc} relate as:

$$\theta_{\mathrm{mcp}} = \theta_{\mathrm{mc}} - \theta_{\mathrm{pip}}$$

Eq. 1

with θ_{mcp} and θ_{pip} measured from neutral position, positive for flexion, and θ_{mc} measured from the metacarpal dorsum to the ground (**Figure 8**, B). When the finger changes from high to low knuckle stance while the metacarpal angle remains constant ($\Delta\theta_{\mathrm{mc}} = 0$), the MCPJ and PIPJ joints hyperextend and flex, respectively, by equal but opposite angles:

$$\Delta\theta_{\mathrm{mcp}} = -\Delta\theta_{\mathrm{pip}}$$

Eq. 2

Fingers can change positions without finger flexors changing length ($\Delta L_{\mathrm{FP}} = \Delta L_{\mathrm{FS}} = 0$), by interchanging finger flexor tendon lengths over the individual joints. The kinematics of these position changes are described by:

$$\Delta L_{\mathrm{FP}} = r_{\mathrm{Pw}}.\Delta\theta_{\mathrm{w}} + r_{\mathrm{Pmcp}}.\Delta\theta_{\mathrm{mcp}} + r_{\mathrm{Ppip}}.\Delta\theta_{\mathrm{pip}} + r_{\mathrm{Pdip}}.\Delta\theta_{\mathrm{dip}} = 0$$
$$\Delta L_{\mathrm{FS}} = r_{\mathrm{Sw}}.\Delta\theta_{\mathrm{w}} + r_{\mathrm{Smcp}}.\Delta\theta_{\mathrm{mcp}} + r_{\mathrm{Spip}}.\Delta\theta_{\mathrm{pip}} = 0$$

Eq. 3

with $\Delta\theta_i$ the joint angle changes in radians and, for simplicity, r_{P} and r_{S} constant, being the mean moment arms of FP and FS at wrist and finger joints. With constant wrist angle ($\Delta\theta_{\mathrm{w}} = 0$), the MCPJ and PIPJ joint positions with isometric finger flexors are given by:

$$\Delta\theta_{\mathrm{mcp}} = -\frac{r_{\mathrm{Ppip}}}{r_{\mathrm{Pmcp}}}.\Delta\theta_{\mathrm{pip}} - \frac{r_{\mathrm{Pdip}}}{r_{\mathrm{Pmcp}}}.\Delta\theta_{\mathrm{dip}}$$
$$\Delta\theta_{\mathrm{mcp}} = -\frac{r_{\mathrm{Spip}}}{r_{\mathrm{Smcp}}}.\Delta\theta_{\mathrm{pip}}$$

Eq. 4

At the chimpanzee PIPJ there is considerable flexor tendon bowstringing as evidenced by the MRI (**Figure 5**), while in knuckle stance the MCPJ flexor moment arms are minimal as the tendons are pulled against the hyperextended MCPJ joint surface. Therefore, the mean finger flexor moment arms at MCPJ and PIPJ should not differ much over the range between high and low stance:

$$r_{\mathrm{Pmcp}} \cong r_{\mathrm{Ppip}}$$
$$r_{\mathrm{Smcp}} \cong r_{\mathrm{Spip}}$$

Eq. 5

so that with a constant DIPJ angle ($\Delta\theta_{\mathrm{dip}} = 0$), the isometric finger flexor length conditions of Eq. 4 reduce to

$$\Delta\theta_{\mathrm{mcp}} \cong -\Delta\theta_{\mathrm{pip}},$$

Eq. 6

meaning that the finger flexors remain approximately isometric in all motions where the MCPJ and PIPJ have equal but opposite rotations with a constant wrist angle. Importantly, since Eq. 6 equals Eq. 2, moving from high to low knuckle stance will not significantly change finger flexor lengths. Two reference positions can be defined: $FJ_{45}[\theta_{wrist} = 0°, \theta_{mcp} = 45°, \theta_{pip} = 45°]$ (finger joints flexed by 45°) and $MCP_{90}[0°, 90°, 0°]$ (straight finger flexed 90° at MCPJ). From low knuckle stance (LKS), the joint angle changes to these positions are:

$$\begin{array}{llll} LKS = [0°, -60°, 150°] & \to FJ_{45} & [0°,\ 45°,\ 45°] & \Delta\theta_i = [0°,\ 105°, -105°] \\ LKS = [0°, -60°, 150°] & \to MCP_{90} & [0°,\ 90°,\ 0°] & \Delta\theta_i = [0°,\ 150°, -150°] \end{array}$$

Eq. 7

Eq. 6 holds for both finger position changes, so that FJ_{45} and MCP_{90} have approximately the same flexor tendon lengths as low knuckle stance (for FP when the DIPJ angle remains constant). Regarding the finger flexor impact buffering hypothesis, the following can be concluded.

1. From high to low knuckle stance, with static wrist and DIPJ, the finger flexors do not significantly change lengths.
2. The isometric finger flexor position MCP_{90}, with fully flexed MCP joint, demonstrates that the finger flexor lengths in low knuckle stance are not in the range where passive stretching forces can be important. Rather, the isometric flexor position FJ_{45} demonstrates that the finger flexors should be closer to resting lengths. The transition from position FJ_{45} to high or low knuckle stance without changes in finger flexor lengths is graphically represented in **Figure 8**, B, a-c.

The finger flexor lengths from knuckle strike to lift-off in palm-back position are hypothesized in **Figure 8**, B, d-f. At knuckle strike (**Figure 8**, B, d), the MCPJ will likely be less hyperextended than in neutral low stance (**Figure 8**, B, c) because of the protracted forearm, meaning that the flexor lengths should even be shorter and therefore further removed from passive stretching forces than in position FJ_{45}. Towards mid-stance (**Figure 8**, B, c), by the increasing MCPJ hyperextension as the metacarpals become vertically aligned, the flexors would lengthen to the lengths in FJ_{45}. Near lift-off, wrist extension with static PIPJs might lengthen the finger flexors beyond FJ_{45} length (**Figure 8**, B, e), but wrist extension was found to rather decrease in the last 20% of stance phase (Thompson 2020). At lift-off, with decreasing metacarpal angles with the horizontal, increases in MCPJ hyperextension would not be possible with MCPJ already in end-positions, so that instead the PIPJ would extend and, since these joints are then not in end-positions anymore, the ground reaction forces would shift to the knuckles (**Figure 8**, B, f). With palms facing medially, the finger flexor lengths would remain fairly constant at the FJ_{45} lengths throughout the stance phase, since ulnar to radial wrist deviation with constant wrist flexion-extension angle would not substantially change finger flexor lengths. In conclusion, with palms facing backwards, the finger flexors would be more contracted than the FJ_{45} length at knuckle strike, would be at about FJ_{45} length in mid-stance and could only be slightly lengthened beyond the FJ_{45} length near lift-off. With medially oriented palms, the finger flexors would remain at about FJ_{45} lengths throughout the entire stance phase. In none of these positions, the finger flexors would be elongated to lengths resulting in important passive stretching forces.

Measurements of finger flexor length changes with joint rotations

The experimentally measured finger flexor tendon displacements between positions 1 through 9 are presented in **Figure 9** (the numerical values are tabled in the Supplementary Materials). This includes positions beyond those achievable within the flexor's physiological contractile ranges. The active insufficiency limit (maximum contraction) was estimated at position 4, with wrist neutral and all finger joints maximally flexed. The passive insufficiency limit (maximum elongation) was estimated at position 8, with MCPJ, PIPJ and DIPJ neutral (0°) and the wrist -28° hyperextended. From position 4 to position 8, the FP and FS length changes were in D2, D3, D4: 72, 87, 78 mm and 66, 72, 65 mm, respectively. The relatively large differences of 15 mm and 9 mm in the FP length changes in D3 versus D2 and D4, respectively, correlate to differences in the FP moment arms. The MRI (**Figure 5**, top row) shows that the FP $PIPJ_2$ moment arm is the smallest and the FP $PIPJ_3$ moment arm the largest. However, different DIPJ angles in position 4 may also have contributed, as the fingers were manually positioned and the DIPJ angles were not precisely controllable with all fingers deeply flexed in the loose skin of the hand palm. The FS length changes in D2, D3 and D4 matched more closely, with a maximum difference of about 7 mm. The flexor elongations in D3 with extended $PIPJ_3$ will be an underestimation, given the $PIPJ_3$ extension deficit of about 10° caused by the MP_3 fracture (**Figure 3**). Position 6 is low knuckle stance with wrist neutral, $PIPJ_3$ maximally flexed and the MCPJs hyperextended correspondingly. The FP lengths of D2-D3-D4 in this low knuckle stance were a consistent 0.53 to 0.54 fraction of the estimated FP contractile ranges. The FS lengths in D2, D3 and D4 were 0.59, 0.65 and 0.55 of the estimated FS contractile ranges. Although the active and passive insufficiency limits were assumptions, these experimental data suggest that the flexor lengths in knuckle stance are rather close to the middle of the physiological range and certainly not in the range where passive stretching forces would become important. A full explanation of the estimation of the finger flexors' insufficiency limits and contractile ranges is provided in the Supplementary Materials.

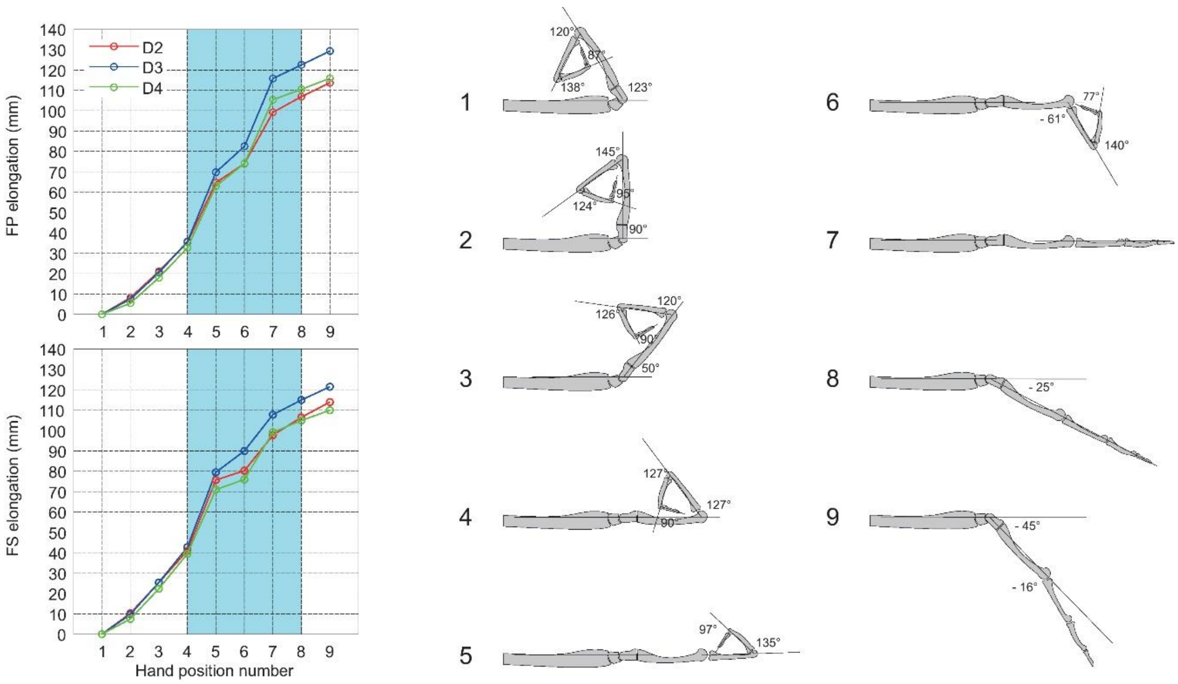

Figure 9. Deep (FP) and superficial (FS) flexor elongations in index, middle and ring fingers (D2, D3, D4) between finger positions 1 and 9. The joint angles in these positions were obtained from profile photographs (summary Table in Supplementary Materials). Positions 1, 2, 3 and 9 likely exceeded the flexors' physiological contractile ranges, which were estimated to be between positions 4 and 8 (blue areas). Position 6 is low knuckle stance with neutral wrist.

Deep flexor fingernail clawing in low knuckle stance

In low knuckle stance, with relaxed FP, the horse-shoe shaped fingernail edges were close to or even in contact, but remained tangent to the palmar MCPJ skin (**Figure 10**, A, B). However, with FP forces, the DIPJ flexed readily up to 60° and the sharp distal nail edges almost perpendicularly impressed the skin distal at the MCPJ (**Figure 5**, D2, D3, top row; **Figure 10**, C, D). To achieve this, no large FP forces were required: a tendon force of about 50 N sufficed to leave a deep skin nail impression. Therefore, at least in this specimen, the FP could not be strongly active in low knuckle stance, lest the palmar skin at the MCPJs would be injured by the fingernails.

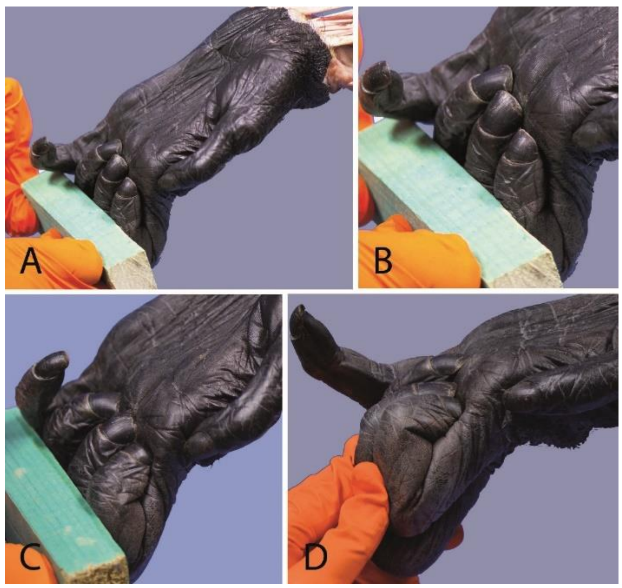

Figure 10. Fingernail positions in low knuckle stance. A, B: Relaxed deep flexors (FP). A. PIPJ hyperflexion brings the horse-shoe shaped fingernail edge close to or even in contact with the skin. With relaxed FP, nail-skin contact does not harm the skin. B: Detail of A. C, D: Active FP. The PIPJ are manually flexed, but the DIPJ are flexed by pulling the FP tendons. C: With flexed DIPJ, the fingernails incise the skin just distal to the MCPJs. Even with moderate FP forces, the nails left a marked skin impression, suggesting that with large FP forces the nails would damage the skin. D: Detail of C.

Impact buffering by negative work at the MCPJ by active finger flexors is not mechanically functional

The data above supported that in knuckle stance the finger flexors are not at lengths were passive-elastic forces would become sufficiently important to absorb knuckle impact energy. However, this leaves the possibility of finger flexors actively buffering knuckle strike impact by negative work at the hyperextending MCPJ. This possibility will be analyzed below. First, as a reference, low knuckle stance with inactive flexors is considered.

Low knuckle stance with inactive flexors

Consider a single finger. When put down unsupported by muscle action, the PIPJ would collapse into the flexion end-position (**Figure 8**, C, a). In PIPJ end-position, the PP and MP form a fixed unit that hinges at the MCPJ (**Figure 8**, C, b). Because of the ground reaction force extension moment at the MCPJ, this unit

would rotate, increasing MCPJ hyperextension until the hyperextension end-position. Hereby the GRF contact point shifts distally along the curved MP bone so that the PP head might not be in ground contact anymore.
Consider a three-finger low knuckle stance and assume that all finger joints have equal motion ranges. Then, with vertical MC, only D3, being the longest finger, will reach both the MCPJ and PIPJ end-positions. D2 and D4, being shorter, will not reach their PIPJ end-positions and therefore also not their MCPJ end-positions, meaning that without active muscle forces, D2 and D4 could not be load bearing. By this analysis, in low knuckle stance with equally mobile joints and no muscle activation, no three fingers can be load bearing at the same time. To make another finger load bearing with D3, the wrist must radially or ulnarly deviate until D4 or D2 reaches the PIPJ end-position (**Figure 1**). For palms facing medially, from strike to lift, the hand may roll laterally over the fingers, from ground contact by D4-D3 at strike to D2-D3 at lift-off.

Biomechanical implications of Impact buffering by negative work of active finger flexors

Consider a single finger. Impact buffering by active flexors would imply the following. The finger contacts the ground with the MCPJ in minimal hyperextension (**Figure 8**, C, c). Large finger flexor forces create a large MCPJ flexion moment that by negative work over a buffering height H slows the descent of the metacarpal into low knuckle stance (**Figure 8**, C, d). However, finger flexors cause flexion moments also at the PIPJ (and DIPJ), which the PIPJ extensors (extensor and interossei) would not be able to oppose, being much weaker than the flexors and having smaller PIPJ moment arms. Therefore, large flexor MCPJ flexion moments could not build up before the PIPJ and DIPJ are in flexion end-positions. For effective finger flexor impact buffering, an MCPJ flexion moment must already exist at impact, meaning that (i) until the moment of impact, the finger extensors would need to strongly co-contract with the flexors, to prevent the MCPJ flexing into a fist and (ii) the interphalangeal joints would be in flexion end-positions at impact (**Figure 8**, C, c). The finger would then impact the ground by the proximal phalanx head itself, where the skin is maximally stretched. Impacts at stretched skin on the small knuckle contact area would lead to great tissue stresses, predisposing to tissue injury. The matter becomes even more compounded when three fingers are involved. Flexor impact buffering would imply that the hand would contact the ground in a high knuckle stance with fully flexed interphalangeal joints. However, lowering the hand with three fingers in high knuckle stance into low stance is not possible without shifting the knuckles over the ground (**Figure 7**, D). This would have to happen against high friction since the knuckles are at that moment load bearing. Finally, the large MCPJ flexion moments required for impact buffering would make fast knuckle-walking prone to tripping at slippery or unstable ground, such as mud. Indeed, these large MCPJ flexion moments would be balanced only by the ground reaction forces. However, to achieve a functional buffering height *H* (**Figure 8**, C, c-d), at impact the MCPJ cannot be very hyperextended, meaning that the angle of the shortest finger would be almost neutral (**Figure 7**, A). At unstable ground, the small MCPJ ground reaction force extension moment arms in the shortest finger(s) would not provide stable extension moments to counterbalance the large MCPJ flexion moments. Therefore, the smallest finger(s) would be prone to slip into MCPJ flexion, destabilizing the stance or pulling the other finger(s) with them into a fist (since the interphalangeal joints would be already flexed), tripping the animal. In conclusion, these arguments suggest that large finger flexor forces at impact do not lead to biomechanically stable functionality.

FP tendon-pulley stress In PIPJ-DIPJ end-positions, the FP is almost double folded at the PIPJ, creating tendon stress concentrations at the A2 and A4 pulley edges (**Figure 5**, **Figure 6**). Therefore, high FP forces in low knuckle stance as would be required for flexor impact buffering would predispose to FP tendon tissue damage at the pulley edges. This fact, in accumulation with possible nail impact at the palmar MCPJ skin (**Figure 10**), suggests that large FP forces with interphalangeal joints in end-positions would be dysfunctional.

Superficial flexor The FS does not flex the DIPJ. Its tendon bending is similar to FP at the A2 pulley, but will likely be less at the A4 pulley because the FS inserts into the MP at the level of A4. Therefore, in principle the FS would be somewhat better suited for active impact buffering, if it could be independently activated from FP. However, this does not diminish the above general biomechanical arguments against strong finger flexor forces in knuckle strike.

Discussion

Summary

This study investigated whether in knuckle walking the finger flexors could function as shock absorbers of knuckle strike impact, as stated by (Simpson et al., 2018). Therefore, kinematic and dynamic implications of this hypothesis were considered. Modelling and experimental testing (**Figure 9**) determined that the finger flexors in low (and high) knuckle stance are not stretched to lengths where passive stretching forces would become important. Finger flexor elongations by MCPJ hyperextension of up to -60° are more than reversed by PIPJ flexion till about 150°. This left the possibility of impact buffering by negative work from finger flexors actively counteracting the hyperextending MCPJ. However, the flexors can only produce large MCPJ flexion moments when the interphalangeal joints are locked in flexion end-positions. In consequence, multiple biomechanical arguments pointed consistently to the dysfunctionality of using large finger flexor forces in knuckle stance. Large FP forces with the PIPJ in end positions would, by strongly flexing the DIPJ, push the fingernails into the palmar skin at the MCPJ – at least, this happened in all load bearing fingers (D2-D4) of the investigated hand specimen (**Figure 10**). Large FP forces would also cause local tendon stress at the flexor pulley edges (**Figure 6**). Even if the FS could be activated independently of FP to produce MCPJ flexion moments, the knuckles, not the middle phalanges, would impact the ground, which in real knuckle walking does not happen. Moreover, impact buffering by negative work would require striking the ground in high knuckle stance and transitioning to low stance, during which the knuckles would need to shift their ground positions. Large MCPJ flexion moments at impact would destabilize knuckle strike at slippery terrain.

The biomechanical dysfunctionality of large flexor forces during knuckle strike and stance is corroborated by the absence of flexor EMG activity (Susman and Stern, 1979; Thompson et al., 2019). Since the finger flexors are not at passive forces stretching lengths, the large forces necessary for finger flexor impact buffering could only come from finger flexor activations, which EMG proves are not present. From these accumulated arguments, it must be concluded that finger flexor forces are generally not involved in impact buffering of knuckle strike.

The analysis pointed out other aspects, amongst others that in low knuckle stance on a flat surface, with fingers of different lengths and equal joint ranges, and with the longest finger in the middle, only two fingers can be truly load bearing at the same time (either D2-D3 or D3-D4). This agrees with observations in captive chimpanzees using the combinations D2-D3 or D3-D4 in terrestrial knuckle walking (Matarazzo, 2008; Wunderlich and Jungers, 2009; Matarazzo, 2013; Thompson, 2020). Of course, in a natural environment chimpanzees seldom travel on flat terrain, leading to more variable loading of D2, D3 and D4 (e.g., knuckle walking along arboreal substrates). In gorillas, metacarpal and finger lengths are more equal across digits, including D5, and load bearing is more distributed over all fingers, which correlates with greater body weight (Matarazzo, 2008; Wunderlich and Jungers, 2009; Matarazzo, 2013).

Study limitations

Experimentally, the study was limited by the availability of only one chimpanzee hand. Access to great ape specimens is strongly restricted and we were fortunate to obtain one hand. The (consolidated) fracture at the middle finger's PIPJ did not seem to affect the joint motion range, except for the mentioned slight extension deficit. Finger fractures are common in captive and wild apes (Jurmain, 1997; Carter et al., 2008) and given the paucity of specimens it would be unreasonable not to use this finger. However, the kinematics of tendon/joint motions depend only on the joint ranges and the integrity of the flexor pulleys, which was verified by the MRI (**Figure 5**) and confirmed by dissection after experiments. The results were consistent for the three fingers D2, D3 and D4, and we did not expect to obtain fundamentally different kinematic relationships if more specimens would be measured. A second limitation was that all models were two-dimensional, while the MCPJ has three rotational degrees of freedom. However, MCPJ abduction and/or axial rotation of the PP in knuckle stance will not substantially change finger flexor lengths, since the finger flexors have no significant MCPJ moment arms for ab/adduction. Therefore, the 2D kinematic models and measurements of finger flexor lengths remain relevant for real 3D MCPJ knuckle stances.

High and low knuckle stance

By theoretical considerations and observation, two stable knuckle stances were identified: high and low. Low stance derives its intrinsic stability from the PIPJ end-positions. High stance, in which no joint is in an end-position, has three supporting fingers and derives its stability from diverging kinematic paths of the metacarpal heads that strain the (inter)metacarpal ligaments (**Figure 7**). Since the PIPJ are not in end-positions, high stance cannot load the middle phalanges, as the relatively weak PIPJ extensors would then need to balance the MP ground reaction forces. Therefore, all load concentrates at the knuckles themselves, making high stance unsuited for habitual knuckle walking. However, in static postures high stance may be useful in enhancing upper body height. High stance cannot be reduced to low stance without the knuckles shifting relative to each other, so these are fundamentally different support modes that require different finger positioning preparations. For low stance it suffices to sufficiently hyperextend and flex the MCPJ and PIPJ, respectively, before strike. EMG – obtained in controlled knuckle walking - shows that this necessitates finger extensor activity but no significant finger flexor activity (Susman and Stern, 1979; Thompson et al., 2019), leading to the conclusion that finger flexor tonus forces and stretching by the hyperextending MCPJ suffice to sufficiently flex the PIPJ for stable touch-down in normal walking. The finger preparation for high stance should be more specific, as three fingers need to be stably placed in a relatively specific configuration. Therefore, finger positioning for put-down in high stance would require controlled flexion-extension equilibria at the MCPJ, meaning that the finger flexors and extensors would need to be co-active. However, this hypothetical finger flexor EMG activity would be difficult to verify experimentally, as high stance would be used incidentally and in static support, and therefore cannot be systematically investigated like low stance at walking platforms.

Remaining questions

The MRI shows that both in chimpanzee and human, the PIPJ flexion end ranges are limited by extra-articular bone contacts, created by the base of the middle phalanx abutting on the proximal phalanx shaft proximal to the PIPJ. In chimpanzee, these PIPJ flexion end-positions are systematically reached in locomotion, including vigorous movements such as running or skirmishing. Yet, even in a 46-year-old specimen, no bone abrasion, cortex thickening or osteophyte formation signatory of bone stress can be observed at the extra-articular PIPJ bone contacts. This suggests that, even if the PIPJ are in end-positions in low knuckle stance, buffering of the extra-articular bone contact forces might exist, possibly by the soft tissues enclosed between the proximal and middle phalanges: skin, palmar fat pads of the fingers and the flexor tendons. Investigating this further seems pertinent to fully understanding the biomechanics of knuckle walking, especially regarding the question of how knuckle strike impact forces are buffered, as the present study argues that neither by passive strain or action the finger flexors can do so.

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