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Phalangeal joints kinematics during Ostrich (*Struthio Camelus*) locomotion

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The ostrich is a highly cursorial bipedal land animal with a permanently elevated metatarsophalangeal joint supported by only two toes. Although locomotor kinematics in walking and running ostriches have been examined, these studies have been largely limited to above the metatarsophalangeal joint. In this study, kinematic data of all major toe joints were collected from walking to running during stance period in a semi-natural setup with selected cooperative ostriches. Statistical analyses were conducted to investigate the effect of locomotor gait on toe joint kinematics. The MTP3 and MTP4 joints exhibit the largest range of motion whereas the first phalangeal joint of the 4th toe shows the largest motion variability. The interphalangeal joints of the 3rd and 4th toes present very similar motion patterns over stance phases of walking and running. However, the motion patterns of the MTP3 and MTP4 joints and the vertical displacement of the metatarsophalangeal joint are significantly different during running from walking. This is probably because of the biomechanical requirements for the inverted pendulum gait at low speeds and also the bouncing gait at high speeds. Interestingly, the motions of the MTP3 and MTP4 joints are highly synchronised from slow to fast locomotion. This strongly suggests that the 3rd and 4th toes really work as an integrated system with the 3rd toe as the main load bearing element whilst the 4th toe as the complementary load sharing element with a primary role to ensure the lateral stability of the permanently elevated metatarsophalangeal joint.

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Abstract

The ostrich is highly cursorial bipedal land animal with a permanently elevated metatarsophalangeal joint supported by only two toes. Although locomotor kinematics in walking and running ostriches have been examined, these studies have been largely limited to above the metatarsophalangeal joint. In this study, kinematic data of all major toe joints were collected from walking to running during stance period in a semi-natural setup with selected cooperative ostriches. Statistical analyses were conducted to investigate the effect of locomotor gait on toe joint kinematics. The MTP3 and MTP4 joints exhibit the largest range of motion whereas the first phalangeal joint of the 4th toe shows the largest motion variability. The interphalangeal joints of the 3rd and 4th toes present very similar motion patterns over stance phases of walking and running. However, the motion patterns of the MTP3 and MTP4 joints and the vertical displacement of the metatarsophalangeal joint are significantly different during running from walking. This is probably because of the biomechanical requirements for the inverted pendulum gait at low speeds and also the bouncing gait at high speeds. Interestingly, the motions of the MTP3 and MTP4 joints are highly synchronised from slow to fast locomotion. This strongly suggests that the 3rd and 4th toes really work as an integrated system with the 3rd toe as the main load bearing element whilst the 4th toe as the complementary load sharing element with a primary role to ensure the lateral stability of the permanently elevated metatarsophalangeal joint.

Introduction

Ostrich (*Struthio camelus*) is acknowledged as the fastest and largest extant bipedal land animal also with extraordinary endurance during locomotion and can possibly run faster than antelopes of a comparable size (Schaller et al., 2009; Alexander et al., 1979; Abourachid and Renous, 2000; Schaller et al., 2009, 2011). The ostrich has been filmed running steadily for 30 minutes at a speed exceeding 50 km/h and moving at a speed of 70 km/h for short sprints, with a step length reaching up to 5m (Abourachid and Renous, 2000; Schaller et al., 2011). In addition, it was also reported that they are capable of cutting maneuvers with minimal changes of their leg kinematics and joint torques (Jindrich et al., 2007). Some studies showed that ostriches are highly adapted to very economic locomotion from slow walking to fast running (Rubenson et al., 2004, 2010).

Ostrich leg morphology may provide the mechanical foundation for this unique locomotor performance (Schaller et al., 2011). Compared to other large cursorial ratites, e.g. rhea (*Rhea spp.*), emu (*Dromaius novaehollandiae*), cassowary (*Casuarius spp.*), ostrich has the longest absolute hindlimbs that contribute to achieve great step lengths and step frequency (Gatesy and Biewener, 1991). In addition, the proportion of ostrich hindlimb bones and multi-jointed muscel-tendon system are highly adapted for locomotion. Their erect femurs increase the joint chain extension and symmetrical movement (Abourachid and Renous, 2000). Furthermore, the ligaments system and tendons in or near the hindlimb joints have the important functions for ostrich economic and fast locomotion. Ligamentous system of the intertarsal joint prevents tarsometatarsal rotations by providing a primary guiding function and ensuring joint coherence throughout range of motion. During stance phase, the extended intertarsal joint is sustained in the engaged state to provide additional support for body mass (Schaller et al., 2009). The distal part of their hindlimbs is primarily controlled by the long and stretched tendons; therefore, the metatarsophalangeal joint plays an important role in storing and releasing elastic energy, and absorbing shock during fast locomotion hence providing an energy-saving mechanism (Alexander 1984, 1985; Gatesy, 1991; Castanet et al., 2000; Almeida Paz et al., 2008).

The most distal part of ostrich hindlimbs has the distinctive morphology. All the other birds have three or four toes, while the largest avian biped ostrich has only two toes, the main 3rd toe and the lateral 4th toe. Another unique adaptation at the distal part of the hindlimb is the supra-jointed toe posture with the metatarsophalangeal joint and proximal phalanx of both toes being permanently elevated above the ground surface (Schaller, et al., 2011; Deeming, 2003). Pressure plate data suggested that both toes play a vital role in ostrich terrestrial locomotion with different load distributions in walking and running. The 3rd toe sustains most of the ground reaction force during locomotion and its claw provides the forces at push-off in fast locomotion. While the 4th toe functions as a lateral support during locomotion (Schaller et al., 2007, 2011; Schaller, N. U. Structural attributes contributing to locomotor performance in the ostrich (*Struthio camelus*), PhD Thesis, University of Heidelberg, Heidelberg, Germany, 2008.).

Although a large number of studies have been conducted to investigate the ostrich hindlimb kinematics during locomotion (Haughton, 1865; Alexander et al., 1979; Alexander, 1985; Gatesy and Biewener, 1991; Abourachid and Renous, 2000; Jindrich et al., 2007; Rubenson et al., 2004, 2007, 2010; Watson et al., 2011; Smith et al., 2006, 2007, 2010, 2013; Schaller et al., 2009, 2011; Birn-Jeffery et al., 2014; Hutchinson et al., 2015), those kinematic analyses were mainly focused on hip, knee and ankle joints. So far, little is known about the relative motions of the 3rd and 4th toes intrinsic joints and the metatarsophalangeal joint during ostrich foot locomotion.

As the only body part in contact with the ground surface, the unique toe joint motions may play important biomechanical roles during locomotion. Therefore, a better understanding of the interphalangeal joint of toes and the metatarsophalangeal joint kinematics may provide valuable information to reveal the biomechanical mechanism underlying the extraordinary locomotor performance of ostriches. Our primary aims were to test the hypothesis that the 3rd and 4th toes work as an integrated whole, and motions of the metatarsophalangeal joint and the interphalangeal joints of the 3rd and 4th toes have significantly different patterns during walking and running gaits.

In this study, we examined the in vivo kinematics of all major joints of ostrich toes during walking and running using high speed videos and specially designed markers. This includes the interphalangeal joint motions within both toes, the relative motions between the first phalanx of the 3rd and 4th toe with respect to the tarsometatarsus, and the angle between the long axis of the 3rd and 4th toe over entire stance phases. Statistical analysis was also conducted to investigate the effect of locomotor speed on those joint motions. This study may further our understanding of the in vivo biomechanical function of ostrich toes and their contribution to the overall locomotor performance of ostriches.

Materials and Methods

Animals

Ten healthy sub-adult ostriches (*Struthio camelus*) with an average age of eight months were selected from the Ji'an breeder, Jilin province, P.R. China. The average mass and height of these ostriches are 84.5±2.12 kg and 2.11±0.01 m (displayed by means±S.D), respectively. The specimens were in excellent physical condition with the properly elevated metatarsophalangeal joints, without any form of surgical treatment or invasive physical manipulation, which representing the average body proportion and weight for ostriches of their age and sex (Deeming, 2003). These ostriches were kept in outdoor enclosure in daytime with unlimited access to food and water, and housed in an indoor enclosure at night. Each bird was trained to walk and run on a fenced-in corridor at least 30 minutes each time, twice per day over a month before data collection. After comprehensive comparison of representation and amenability, two tractable female sub-adult ostriches were selected as objects to complete all tests. All living and experimental conditions were approved by the Institutional Animal Care and Use Committee (IACUC, protocol number: 20140706) of Jilin University, P.R. China.

Experimental setup and trials

A 80m long runway fenced by 1.5m tall wire mesh was set up in the breeding field with a data acquisition area in the middle of 4m long and 1m wide zone (see Figure 1). At both ends of the runway, large spaces were provided for the ostriches to rest and eat. The area outside of the data acquisition zone was about 76m long and 2m wide with two "V" shape transition areas gradually connecting to the data acquisition zone, which helps guide the ostriches to naturally enter into the data acquisition area. A high-speed video system with three synchronised digital cameras (Casio Exilim EX-FH25, Tokyo, Japan; 240 frames s^{-1}) was placed around the central zone of the data acquisition area in a triangle shape with one camera positioned perpendicular to the sagittal plane of motion (see Figure 1).

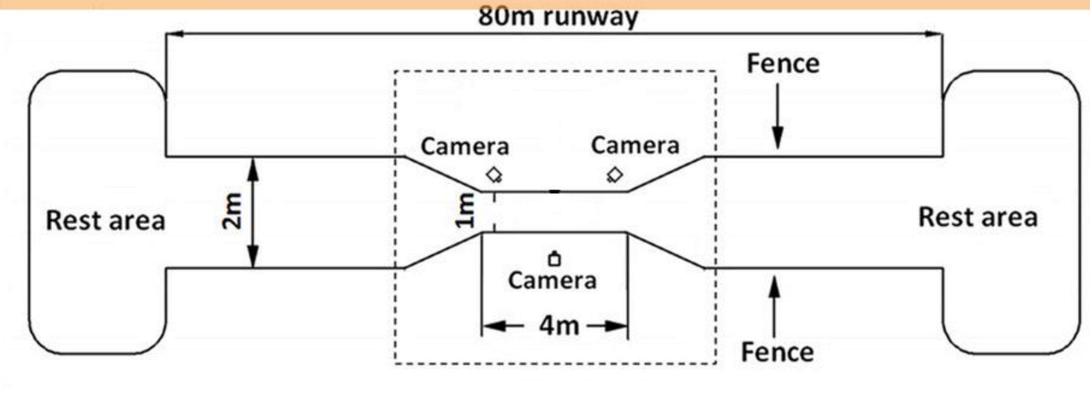

Figure 1. Schematic diagram of the experimental site of 80m long. The data acquisition area in the centre of the dotted box is of 4m long and 1m wide. Fences of 1.5m high were set on both sides of the runway. Three high-speed cameras were placed in the central data acquisition area in a triangular shape. Both ends of runway are rest areas for ostriches to rest and eat foods.

During measurements, ostriches were led by their breeders or experimenters, using positive reinforcement such as food rewards and vocal commands, with the goal of maintaining a steady speed across a straight distance of about 15 m. Experimenters randomly varied the speed from slow walking to fast running across trials and allowed ample rest and food between trials to prevent fatigue. Experiments were cancelled if animals showed fatigue that would cause discomfort or adversely affect our measurements. To minimise the interference of sunlight, one sunshade net was set on the top of the data acquisition zone.

Marker placements and joint angles

Nine specially designed thermoplastic plates carrying nine retroreflective markers were firmly mounted at the major anatomical landmarks around the ostrich toes using double sided tapes (see Figure 2A). The marker locations were determined by palpation and referring to a three-dimensional (3D) geometric model of the tarsometatarsus bone and the phalanges of the 3rd and 4th toes, reconstructed from the CT images of a healthy adult female ostrich (Age: 3 years, Weight: 95kg, Height: 2.10m) left foot by using Mimics 10.0 software (Materialise, Leuven, Belgium) (see Figure 2B). Four markers were used for the 3rd toe at the dorsal base of the toenail (marker A), the joint between phalanges II and III (marker B), the joint between phalanges I and II (marker C), and the joint between phalanx I and tarsometatarsus (marker D). Whereas, three markers were placed on the 4th toe at the joint between phalanx I and tarsometatarsus (marker F), the joint between phalanges I and II (marker G), and the distal end of the 4th toe (marker H). Additionally, one marker was put on the anterior side of the tarsometatarsus bone proximal to the metatarsophalangeal joint (marker E). Here, the toenail, phalanges III and IV of the 3rd toe were considered as one segment (phalanges III in Figure 2B), and the phalanges II III IV and V of the 4th toe were assumed as one part (phalanges II in Figure 2B) because the relative motions among them are very small (Fowler et al., 1991).

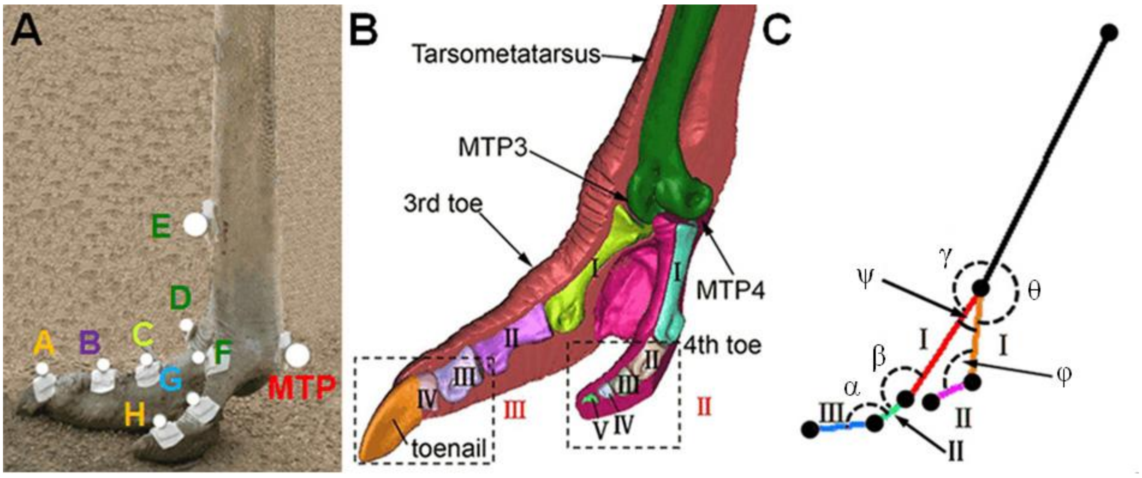

Figure 2. The reflective markers on ostrich foot and the toe joint angle measured. Nine reflective markers were placed at the major anatomical landmarks of ostrich toes (Figure 2A). The marker locations were determined by palpation and referring to a 3D geometric toe model reconstructed from the CT images of a healthy adult female ostrich (Age: 3 years, Weight: 95kg, Height: 2.10m) left foot (Figure 2B). Six toe joint angles were defined (Figure 2C): angle a between the phalanges II and Ⅲof the 3rd toe, angle b between the phalanges I and II of the 3rd toe, angle g between the tarsometatarsus and the phalanx I of the 3rd toe (MTP3 joint), angle q between the tarsometatarsus and the phalanx I of the 4th toe (MTP4 joint), angle j between the phalanges I and II of the 4th toe, and angle y between the 3rd and 4th toes.

The 3D coordinates of the nine retroreflective markers were measured at 240 Hz using a three-camera (Casio Exilim EX-FH25, Tokyo, Japan) motion tracking system (Simi Motion 2D/3D® 7.5 software, SIMI Reality Motion Systems GmbH, Germany). Two series of representative video frames recorded for walking and running respectively are shown in Figure 3. The marker data and joint kinematics were analyzed using Simi Motion 2D/3D® 7.5 software. The software allows for three-dimensional calibration, digitisation of bony landmarks and calculation of the segmental and joint kinematic parameters of interest (Stoessel and Fischer, 2012). The time histories of six joint angles were calculated, namely, angle α between the phalanges II and Ⅲ of the 3rd toe, angle β between the phalanges I and II of the 3rd toe, angle γ between the tarsometatarsus and the phalanx I of the 3rd toe (MTP3 joint), angle θ between the tarsometatarsus and the phalanx I of the 4th toe (MTP4 joint), angle φ between the phalanges I and II of the 4th toe, and angle ψ between the 3rd and 4th toes (see Figure 2C).

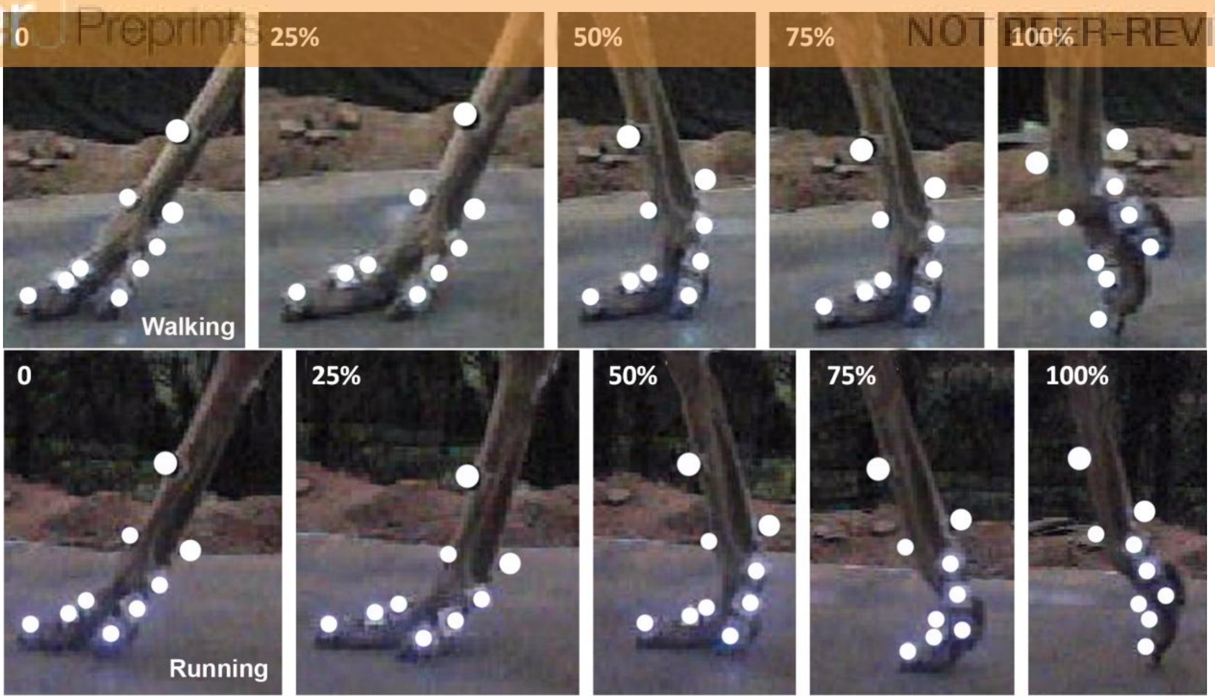

Figure 3. Two representative high speed video traces of toe motions during walking and running in stance phases. Time in each frame was indicated in millisecond. The traces started at touchdowns when the 3rd toe touched the ground at 0ms. In the walking trial, the mid-stance is at 921ms and the 3rd toe cleared off the ground at 1125ms. In the running trial, the mid-stance is at 246ms and the 3rd toe was off the ground at 346ms.

Animal forward velocity for each stride was measured by calculating the average MTP3 joint marker (marker D in Figure 2A) velocity. We defined steady state trials as those in which the absolute difference between the forward velocities at two consecutive touch downs was less than 20% of the average forward velocity. Trials with greater or smaller values of acceleration/deceleration were discarded. Froude numbers $Fr=v^2/(gh)$ and dimensionless speed ($u=Fr^{0.5}$) were calculated to normalize speeds (e.g. Alexander and Jayes, 1983). Gait parameters, including, cycle period, stance duration, swing duration, duty factor and stride length, were calculated for each steady state trial.

Statistical analysis

Statistical analyses were conducted to examine the differences in four gait parameters (stance and swing durations, cycle period and stride length), six key indicators (angle/displacement at touch-down, mid-stance, lift-off, maximum, minimum and range of motion) of the six toe joint angles and the vertical displacement of the metatarsophalangeal joint between walking and running gaits using Origin Pro 2015 software (OriginLab Corporation, Northampton, USA). In this study, trials with stance duration > 0.9s and duty factor > 0.5 were considered as walking gaits, whereas trials with stance duration < 0.9s and duty factor < 0.5 were regarded as running gaits (Schaller et al., 2011). We used one-way ANOVA statistical technique to analyze the effect of locomotor gait on each gait parameter or joint angle/displacement indicator (Schache, 2011; Stoessel and Fischer, 2012). Using the F-test to test whether these two variations are significantly different. Statistical significance level was considered as P<0.05.

Results

Gait parameters

Averages and standard derivations of key gait parameters, including stance duration, swing duration, cycle period and stride length of all walking and running gaits were listed in Table 1 separately. It can be seen that there were statistically significant differences in stance duration, cycle period and stride length between walking and running gaits. Ostriches use considerably shorter cycle periods and stance durations during running than those durin walking, whereas dramatically increase their stride lengths. This was consistent with previous observation (Abourachid and Renous, 2000). Interestingly, no statistically significant difference was found in swing duration between walking and running gaits.

Table 1. The key gait parameters during walking and running gaits

Gait parameters	walking (0.38−1.23m/s)	running (2.26−3.31m/s)
Number of trials	27	16
Average speed (m/s)	0.84±0.20	2.77±0.28
Froude numbers	0.06±0.03	0.66±0.13
Duty factor	0.74±0.09	0.45±0.03
Stance phase (second)	1.22±0.33*	0.34±0.03*
Swing phase (second)	0.44±0.16	0.42±0.02
Cycle period (second)	1.66±0.30*	0.76±0.03*
Stride length (metre)	1.33±0.16*	2.11±0.15*

Values are means ± S.D. Statistically significant speed effects are indicated by an asterisk ($P < 0.05$).

Toe joint kinematics

Figure 4 showed the averages and one standard deviation zones of the six toe joint angles and the vertical displacements of metatarsophalangeal joint (α, β, γ, θ, φ, ψ, z) over the stance phases for all walking and running trials respectively. By comparing Figure 4A and B, it can be seen that the time trajectories of the angle α shared very similar patterns in the stance phases during walking and running. The second phalangeal joint of the 3rd toe extended about 10 degree immediately after the touch-down, and thereafter remained at about 165 degree throughout from early stance to late stance. This was followed by a swift flexion of about 35 degree and also a rapid protraction of about 20 degree just before lift-off. However, compared to walking gaits, it appeared that during running the joint extension in the early stance finished slightly later (at 20% of the stance phase), and the joint flexion and protraction in the late stance occurred earlier (at 70% of the stance phase).

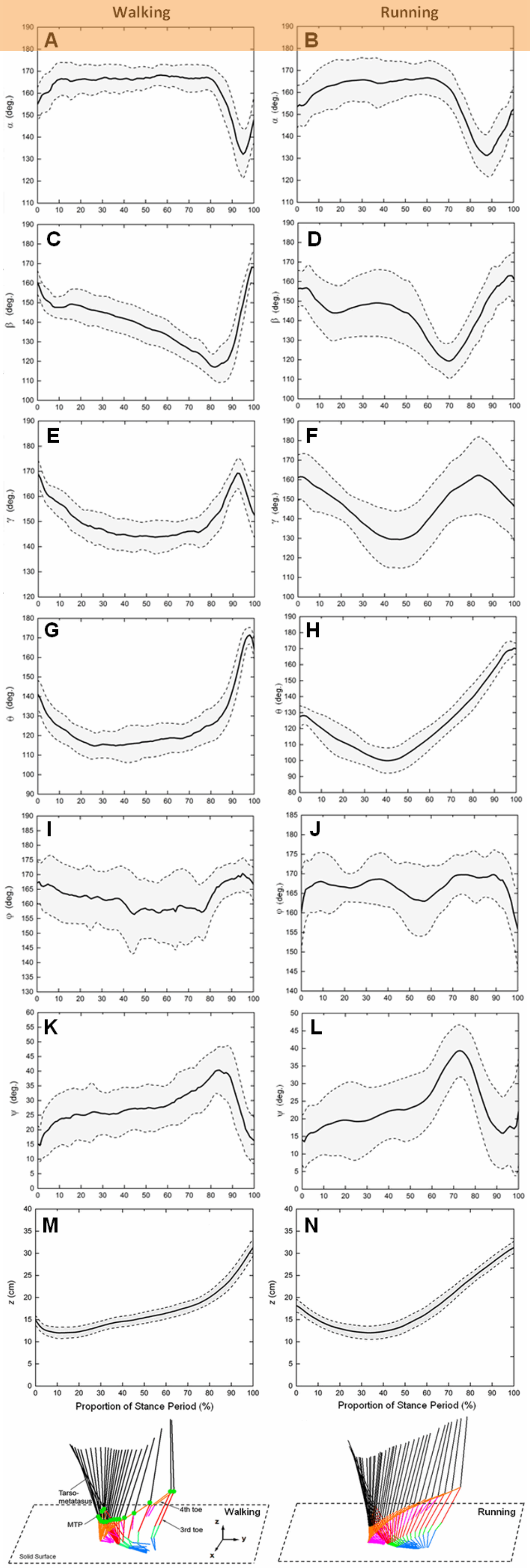

Figure 4. The averages and one standard deviation zones of the six toe joint angles and the vertical displacement of the metatarsophalangeal joint (α, β, γ, θ, φ, ψ, z) over the stance phases for all walking and running trials. Angle decrease represents flexion while angle increase indicates extension. Stick figure at the bottom fo Figure 4 shows the ostrich foot motion in stance phase and the green point indicates the metatarsophalangeal joint.

From Figure 4C and D, we can see that the angle β showed similar patterns in the stance phases of walking and running. The joint angle decreased after touch-down from about 160 degree to 120 degree or so at late stance. Thereafter, the joint extended swiftly back to about 160 degree just before lift-off. However, it's noteworthy that the joint flexed and extended much more radically in running than during walking, and high variability was observed from early stance to middle stance (from touch-down to 60% of stance phase).

The MTP3 joint angle γ was been shown in Figure 4E and F present noticeably different patterns during walking from running. In walking, the joint angle decreased gradually from touch-down to 30% of stance phase about 25 degree, and then remained steady till reaching 80% of stance phase. A sharp joint angle increased occurs just before lift-off with the MTP3 joint extended almost 60 degree. Whereas, in running there was no plateau stage in middle stance. The joint flexed gradually from touch-down to middle stance, and thereafter extended progressively to 210 degree at lift-off.

The MTP4 joint angle θ also showed different motion patterns during walking from running (see Figure 4G and H). In walking, the MTP4 joint flexed about 25 degree directly after touch-down, and remained reasonably steady from early stance through to late stance. Just before lift-off, a swift joint extension occured at the MTP4 joint reaching a nearly fully extended position at 170 degree. Whereas, in running gaits, there was no steady stage in the middle of stance phase. After touch-down, the MTP4 joint flexed gradually about 30 degree till middle stance, and thereafter followed by a progressive joint extension of 60 degree till lift-off.

The largest angle variability among all the six toe joints was observed at the angle φ. From Figure 4I and J, we can see that no apparent patterns presented for angle φ during both walking and running. The joint angle fluctuated around 165 degree though it appeared that larger variability occured during walking rather than running. While, angle ψ showed clear patterns over the stance phase (see Figure 4K and L). The joint between the two toes moved similarly during walking and running with a gradually increasing joint extension from touch-down to late stance followed by a swift joint flexion before lift-off. The average peak joint extension was about 39 degree for both walking and running.

Figure 4M and N showed the average and one standard deviation zone of the vertical displacements of the metatarsophalangeal joint over stance phases for all walking trials and for all running trials respectively. It can be seen that markedly different patterns were present during walking compared to running. In walking, the metatarsophalangeal joint moved downwards towards the ground surface about 3.0 cm just after touch-down, and thereafter went smoothly upwards about 20 cm before lift-off. Whereas, during running, the joint only moved downwards slightly about 6.2 cm from touch-down to near middle stance, and then kept going upwards before lift-off about 20 cm.

Effect of locomotor gait

The results of the statistical analyses examining the effect of locomotor gait on the six key indicators (angles/displacements at touch-down, mid-stance, lift-off, maximum, minimum and range of motion) of the six toe joint angles and the vertical displacement of the metatarsophalangeal joint were listed in Table 2 and Figure 5. Among all the six toe joints, the MTP3 and MTP4 joints showed the largest ranges of motion. Whereas, angle φ had the smallest range of motion. As shown in Table 2 and Figure 5, no statistically significant differences were found for the six key indicators of angles α, β, φ, ψ between walking and running gaits. There were statistically significant differences were found for the range of motion of angle β and the lift-off angle of φ. A slightly larger range of motion of the first phalangeal joint angle of the 3rd toe (angle β) presented during walking than running. In addition, the first phalangeal joint of the 4th toe (joint angle φ) flexed much more at lift-off during running than walking.

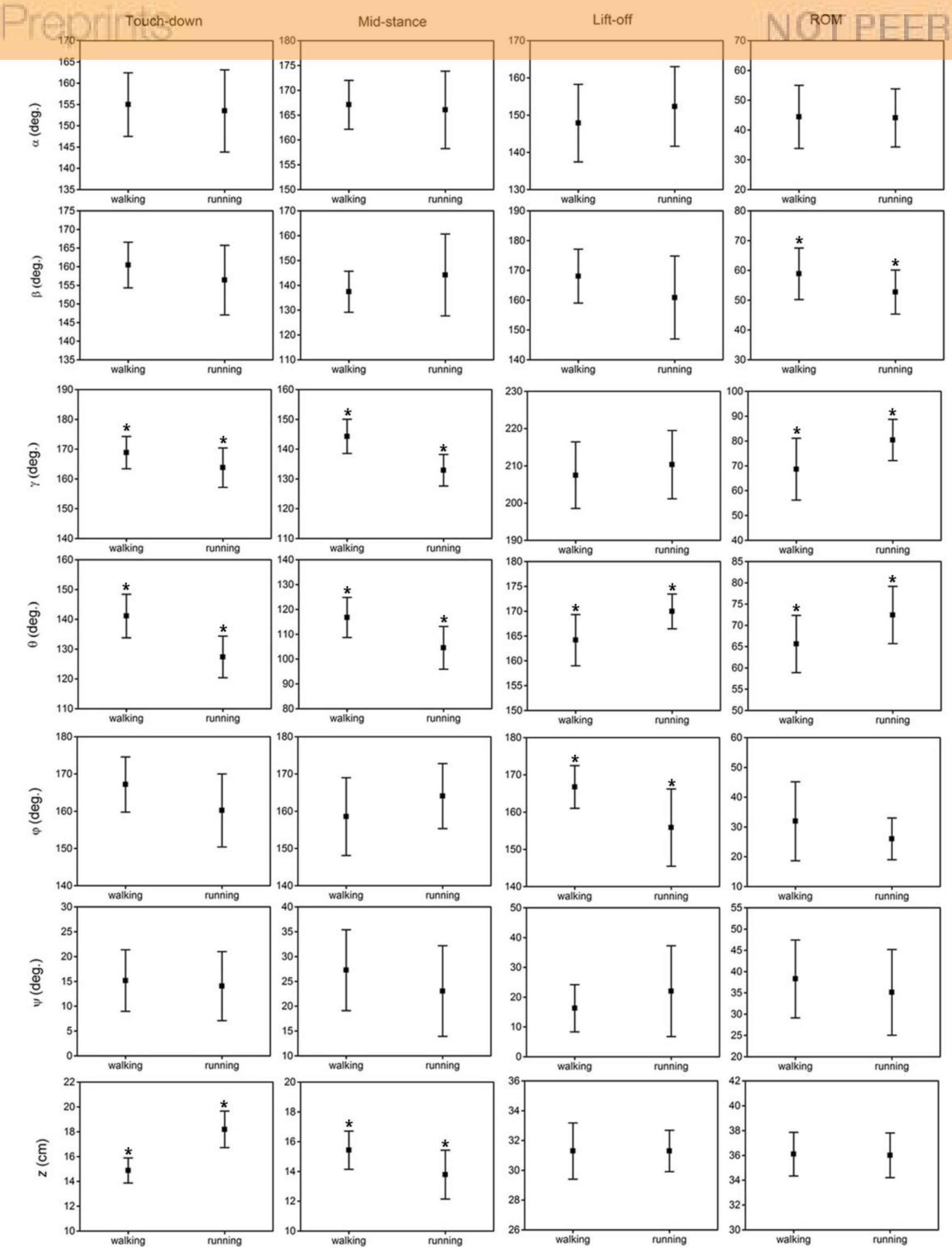

Figure 5. The averages and standard deviations of the six toe joint angles and the vertical displacement of the metatarsophalangeal joint at touch-down, mid-stance, lift-off and also the ranges of motion during walking and running.

Table 2. The six indicators (angles/displacements at touch-down, mid-stance, lift-off, maximum, minimum and range of motion) of the six toe joint angles and the vertical displacement of the metatarsophalangeal joint

Kinematic parameters	Touchdown		Mid-stance		Liftoff		Maximum		Minimum		Range of motion	
	Walking	*Running*	*Walking*	*Running*	*Walking*	*Running*	*Walking*	*Running*	*Walking*	*Running*	*Walking*	*Running*
α(degrees)	155±7	153±10	167±5	166±8	148±10	152±11	168±4	166±5	132±10	131±9	36±11	35±10
β(degrees)	160±6	156±9	137±8	144±17	168±9	161±14	168±5	163±8	117±7	119±9	51±9*	43±7*
γ(degrees)	169±5*	164±7*	144±6*	133±5*	207±9	210±9	207±9	211±9	143±6*	131±5*	63±13*	80±8*
θ(degrees)	141±7*	127±7*	117±8*	105±9*	164±5*	170±4*	171±4	170±4	114±6*	100±8*	56±7*	72±7*
φ(degrees)	167±7	160±10	159±10	164±9	167±6*	156±10*	170±3	169±2	156±13	155±8	13±12	13±7
ψ(degrees)	15±6	14±7	27±8	23±9	16±8	22±15	40±8	39±9	14±5	13±6	25±9	25±10
z (cm)	14.9±1.0 *	18.2±1.5*	15.4±1.3*	13.8±1.6*	31.3±1.9	31.3±1.4	31.3±1.8	31.3±1.4	11.9±1.2	12.0±1.5	19.4±1.8	19.3±1.8

Values are means±S.D. Statistically significant speed effects are indicated by an asterisk ($P < 0.05$).

Statistically significant differences were found in several key indicators of angle γ, θ, and also the vertical displacement of the metatarsophalangeal joint between walking and running trials. This was consistent with the distinct patterns we observed in Figure 4. The MTP3 joint flexed much more at touch-down, mid-stance, and uses a larger range of motion during running compared to walking. The MTP4 joint presented a more flexed positions at touch-down and mid-stance, and a more extended position at lift-off during running. This led to a larger range of motion at the MTP4 joint in running trials. For the vertical displacement of the metatarsophalangeal joint, though very similar ranges of motion were used during walking and running, the metatarsophalangeal joint was at a statistically higher position at mid-stance during walking.

Discussions

This study presents the first toe joint kinematic analysis for overground walking and running ostriches. Reliable data on major toe joint angle trajectories and metatarsophalangeal vertical displacement were obtained base on a large number of trials, allowing interpretation of toe function in this flightless, cursorial bird with a unique elevated metatarsophalangeal joint supporting only by two toes. Having chosen two genetically unrelated subjects of the same sex and very similar age and size, the consistency of inter-individual results in walking and running trials accurately document a generalized pattern in ostrich locomotion.

Rough skins, sturdy ligaments, fascia and lumpy fat pads envelop the metatarsophalangeal joints, toe skeleton and interphalangeal joints to ensure structural integrity, seemingly providing limitation on toe mobility (Schaller et al., 2011). However, our study reveal that almost all the six major toe joints present notably large motions from slow to fast locomotion. The MTP3 and MTP4 joints exhibit the largest range of motion among all the six toe joints with an average range of motion about 70 degree in walking and a higher motion range of 80 degree during running. The smallest range of motion is found at the first phalangeal joint of the 4th toe, but still has an average range of about 30 degree. This suggests that the toes might play an active role in force and power generation, and also energy saving for walking and running ostriches.

Two toes as an integrated whole

The 3rd toe and claw essentially forming an extension of the tarsometatarsal limb sustain most of the impact force at touch-down and ensure stable load bearing and grip during stance phase (Schaller et al., 2011). During walking and running, just after touch-down, simultaneous flexions at the first phalangeal joint of the 3rd toe and the MTP3 joint, and also an extension at the second phalangeal joint of the 3rd toe occurs implying compliance at the interphalangeal joints of the 3rd toe is used to moderate ground impact at touch-down. Thereafter, the second phalangeal joint remains fully extended in contact with the ground surface whereas the first phalangeal joint flexes gradually till late stance. Interestingly, the angle α and β show statistically very similar motion patterns during running compared to walking. Since no intrinsic muscles exist in ostrich toes (Gangl et al,. 2004), this suggests that the tensions at the toe flexor tendons are well tuned by some of the tendons crossing the different joints come from the same digital flexor muscle during running, not only to counteract the higher ground reaction forces but also to regulate the interphalangeal joint motions.

The first phalangeal joint of the 4th toe presents the largest motion variability among all the six toe joints examined in this study with no obvious patterns found during walking and running. This appears to support the previous hypothesis that the 4th toe acts as a stabiliser to compensate uneven ground surface and adjust potential body imbalance (Schaller et al., 2011). This seems further supported by the result that the deviation of the motion range of the joint angle φ during walking is almost twice higher than that of running. Slow moving may need a greater level of neural control and muscular regulation of the ground contact elements. The angle ψ shows very similar pattern during walking and running implying the high stiffness of the interphalangeal ligaments connecting the 3rd and 4th toes. Over most of the duration when the 4th toe is in contact with the ground during walking, the average ψ angle is only about 25 degree. This is much lower than the maximum angle (34 degree) determined by a fresh anatomical dissection study (Schaller et al., 2011) and also the in vivo maximum value (46±8 degree) recorded in this study. The average ψ angle further drops to about 20 degree during running. This strongly suggests that the body stabilisation function of the 4th toe due to its lateral orientation may not be as pronounced as proposed by the previous study (Schaller et al., 2011) especially for fast locomotion. The major function of the 4th toe might be to offset the ground impact and reaction forces during early and middle stances, thereby to provide extra support for the lateral stability of the elevated metatarsophalangeal joint as the body weight transfers laterally.

Although the interphalangeal joints of the 3rd and the 4th toes present distinct motion patterns in stance phases of walking and running, the two major joints (MTP3 and MTP4

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joint) connecting the two toes to the tarsometatarsus share highly similar patterns for both slow (see Figure 4E and G) and fast locomotion (see Figure 4F and H). The average trajectories of angles γ and θ are almost perfectly in phase over the entire stance phases. This strongly suggests that the 3rd and 4th toes actually move as an integrated whole from slow to fast locomotion. This synchronous pattern is more pronounced during running when the 4th toe lies more closely to the 3rd toe due to a smaller average ψ angle during most of stance phase. Moreover, from our high speed videos of running trials, we found that after the 4th toe clears off the ground, it aligns in a line and almost forms a single segment with the 3rd toe at push-off. This highly concerted toe motion is probably an emerging result of the dynamic interaction of the proximal leg musculature, the distal passive ground contact apparatus and the external environment. The leg muscles of ostriches are highly concentrated at the proximal joints resulting in a low moment of inertia with respect to the proximal joints. This enables ostriches to achieve high step frequency energy efficiently (Schaller et al., 2011; Haughton, 1865). The permanently elevated metatarsophalangeal joint further increases the leg length thereby leading to higher stride length (Rubenson et al., 2007; Schaller et al., 2011). Even though no intrinsic muscles are present to delicately regulate the toe motions (Gangl et al,. 2004), our toe joint motion data strongly suggests that the toe joints are appropriately controlled by well-tuned tensions at toe flexor and extensor tendons. Indeed, the ostrich toes can be considered as a passive mechanism well regulated by distal limb tendons to work as an integrated whole to generate ground reaction forces, attenuate ground impacts and accommodate ground surfaces whilst ensuring the stability of the elevated metatarsophalangeal joint from slow to fast locomotion.

Different strategies at slow and fast locomotion

Our measurement data indicates that significantly different time history patterns are used by ostriches in the vertical displacement of the metatarsophalangeal joint and also the joint motions at MTP3 and MTP4 joints during running compared to walking. This is supported by the statically significant differences found in a number of key indicators of the displacement z, angle γ and θ. In most of stance phase of walking (10% − 80%), the metatarsophalangeal joint only moves slightly upwards mainly due to the flexion of the first phalangeal joint of the 3rd toe because both the MTP3 and MTP4 joints and also the second phalangeal joint of the 3rd toe remain almost stationary over this period. Whereas, during fast locomotion, typical compression and rebounding patterns are observed in the vertical displacement of the metatarsophalangeal joint. This is probably due to the substantially distinct flexion and extension patterns at MTP3 and MTP4 joints at fast locomotion implying different neuromuscular control strategy is used compared to slow moving.

Previous study revealed that ostriches use an inverted pendulum gait at slow locomotion (Rubenson et al., 2004). The out-of-phase pattern in the fluctuations of the potential and kinetic energies allows for a high percentage of mechanical energy recovery at slow speeds, which are typical of walking in bipedal species (Cavagna et al. 1976, 1977; Heglund et al. 1982; Muir et al. 1996). Whereas, at fast locomotion (including grounded running and aerial running), ostriches tend to use a bouncing gait by using the legs as a springy mechanism to store and regain energy characterized by a marked reduction in the phase difference between the potential and kinetic energies (Rubenson et al., 2004). The distinct toe joint motions at slow and fast locomotion observed in this study are probably the direct result of the selective use of those two distinct energy strategies at different speed ranges. At low speeds, the metatarsophalangeal joint only moves slightly over most of the stance phase (10% − 80%) by mainly using the first interphalangeal joint motion at the 3rd toe. This is probably because of the constant leg length requirement of the inverted pendulum gait. However, at high speeds, the metatarsophalangeal joint presents a typical loading and rebounding pattern over the stance phase by mainly using the significant flexion and extension motions at the MTP3 and MTP4 joints possibly regulated by the stretched toe flexor tendons. This suggests that at fast locomotion the toes also work as a springy element in series with the proximal limb to attenuate ground impact, generate supporting forces and also save metabolic energy cost.

Perspectives

The gait measurements in this study was conducted on solid level ground surface in order to record simultaneous pressure plate data. Future work involves the investigation of the toe-joint motions when moving on rough terrain at slow and fast speeds, and also during sideways maneuvers. This would enable us to inspect gait motions and foot biomechanics of ostriches when moving in an experimental setup closer to their natural habitat. In addition, how does ostrich foot generate sufficient braking and propulsive forces on granular media is of high interest to us. Moreover, the tendon driven passive mechanism design of the ostrich toe complex with a unique supra-jointed posture might inspire development of innovative bi-pedal robots capable of running fast and economically as ostriches.

Conclusion

All the six major toe joints investigated in this study show noticeable motions from slow to fast gaits. The MTP3 and MTP4 joints present the largest range of motion whereas the first phalangeal joint of the 4th toe exhibits the largest motion variability. The interphalangeal joints of the 3rd and 4th toes show very similar motion patterns during walking and running. However, the MTP3 and MTP4 joints motions and also the vertical displacement of the metatarsophalangeal joint present significantly different patterns during running from walking. This is probably due to the biomechanical requirement for the inverted pendulum gait at low speeds and also the bouncing gait at high speeds.

Indeed, the motions of the MTP3 and MTP4 joints are highly synchronised across the entire speed range examined in this study. This strongly indicates that the 3rd and 4th toes actually work as an integrated whole with the 3rd toe as the primary load bearing element whilst the 4th toe as the complementary load sharing element mainly to ensure the lateral stability of the permanently elevated metatarsophalangeal joint.

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