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Original article

Foot strike patterns and hind limb joint angles during running in Hadza hunter-gatherers

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Abstract

Background: Investigations of running gait among barefoot and populations have revealed a diversity of foot strike behaviors, with some preferentially employing a rearfoot strike (RFS) as the foot touches down while others employ a midfoot strike (MFS) or forefoot strike (FFS). Here, we report foot strike behavior and joint angles among traditional Hadza hunter-gatherers living in Northern Tanzania.
Methods: Hadza adults ($n = 26$) and juveniles ($n = 14$) ran at a range of speeds (adults: mean 3.4 ± 0.7 m/s, juveniles: mean 3.2 ± 0.5 m/s) over an outdoor trackway while being recorded via high-speed digital video. Foot strike type (RFS, MFS, or FFS) and hind limb segment angles at foot strike were recorded.
Results: Hadza men preferentially employed MFS (86.7% of men), while Hadza women and juveniles preferentially employed RFS (90.9% and 85.7% of women and juveniles, respectively). No FFS was recorded. Speed, the presence of footwear (sandals *vs.* barefoot), and trial duration had no effect on foot strike type.
Conclusion: Unlike other habitually barefoot populations which prefer FFS while running, Hadza men preferred MFS, and Hadza women and juveniles preferred RFS. Sex and age differences in foot strike behavior among Hadza adults may reflect differences in running experience, with men learning to prefer MFS as they accumulate more running experience.

Keywords: Barefoot; Biomechanics; Foot strike; Foraging; Running

1. Introduction

Like many other animals, humans employ a bouncing, mass-spring gait when running, with the hind limb storing and releasing elastic strain energy each step.[1,2] This spring-like behavior of the lower limb reduces the amount of muscle work required and improves running efficiency.[1–3] From a mechanical perspective, the two most important anatomical springs in the human leg are the Achilles tendon and the

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plantar arch; together, these structures store and return roughly half of the potential and kinetic energy lost each step during running.[1] These anatomical springs are most effective when runners land on the middle or front of the foot, allowing the Achilles tendon and plantar arch to stretch as the foot is loaded during early stance phase.[4] Landing on the midfoot or forefoot may also reduce the incidence of running-related injuries.[5] Nonetheless, many runners habitually heel strike,[6–8] landing on the rear portion of their foot, and the effects of training, footwear, and speed on foot strike patterns remain unclear. Here, we examine running mechanics among Hadza hunter-gatherers to assess foot strike patterns in an untrained, physically active, traditional population with minimal footwear.

Foot strike patterns have recently emerged in debates over the role of endurance running in human evolution. Endurance running has been cited by several researchers as a critical adaptation in the hominin lineage, marking a departure away from an ape-like, plant-based foraging ecology and toward a more active, omnivorous ecological strategy that included scavenging and hunting.[9–11] Bramble and Lieberman[11] noted that many of the anatomical features associated with effective endurance running in modern humans first appear in *Homo erectus* and proposed that key evolutionary changes seen in our genus followed the evolution of endurance running. Selection for endurance may have even played a critical role in the evolution of increased brain size.[12]

Subsequent work by Lieberman and colleagues[6] has suggested that the anatomical adaptations in the human foot are particularly advantageous during unshod running with a forefoot or midfoot strike (FFS, MFS). In a study of habitually barefoot Kenyan runners from the Kalenjin population, Lieberman and colleagues[6] noted that these renowned endurance runners tend to land on the front or middle of their foot while running. In contrast, habitually shod American runners tend to rearfoot strike (RFS). Lieberman and colleagues[6] hypothesized that the population difference in foot strike behavior was influenced by differences in footwear: barefoot running, common among Kalenjin individuals, allows runners to experience the high impact forces imparted by RFS and leads to the adoption of MFS or FFS. In contrast, conventional running shoes absorb much of the impact associated with RFS, and their elevated heel increases the likelihood and incidence of RFS. This hypothesis suggests that RFS has become more common with the development and popularity of modern athletic footwear, and that RFS should be rare or absent among unshod or minimally shod populations.

More recently, Hatala and colleagues[8] studied foot strike and impact forces at different running speeds in 38 habitually unshod adults from the Daasanach population of Northern Kenya. The Daasanach are traditional pastoralists; they typically walk long distances to tend herds, gather water, and in other daily tasks, but run much less than the Kalenjin. In contrast to the Kalenjin, Hatala and colleagues[8] found that the Daasanach often RFS, and that running speed affects foot strike behavior. At speeds less than 5.01 m/s, the Daasanach used RFS at a higher frequency than MFS or FFS. Between 5.01 and 6 m/s, frequencies of MFS and FFS were similar, while MFS was the predominant pattern at speeds greater than 6.01 m/s. These results indicate that not all unshod populations prefer to MFS or FFS while running, and that training, experience, and speed may affect foot strike patterns.

Yet another pattern of foot strike use is reported for the Tarahumara, a minimally shod population of traditional farmers living in the Sierra Madre Occidental of Northwestern Mexico.[13] The Tarahumara are renowned endurance runners, running 75 km or more in traditional ball games and, in recent years, competing in ultramarathons.[14] Tarahumara traditionally wore simple rawhide sandals (*huaraches*), and many continue to do so today, although some have adopted conventional running shoes.[13] Lieberman[13] reported that 89% of Tarahumara who wear conventional shoes habitually RFS, while Tarahumara who wear traditional *huaraches* tend to MFS or FFS.

In this study we examined foot strike patterns and running kinematics among traditional Hadza hunter-gatherers in Northern Tanzania. As described in detail elsewhere,[15] traditional Hadza subsist almost entirely on wild foods, hunting and gathering each day on foot and with simple hand tools. Traditional Hadza have no agriculture, livestock, or machinery. Women typically walk 6 km each day gathering wild berries, tubers, and other plant foods, while men walk an average of 11 km per day, hunting small and large game with bow and arrow, and gathering honey.[15,16] The landscape they inhabit is semiarid savannah with a patchy mix of forest and grassland cover; the ground is often rocky, and low craggy hills are common. While the Hadza are highly active, they rarely run.[15]

Musiba and colleagues[17] conducted a study of walking gait and foot dimensions among traditional Hadza. As discussed in that report, Hadza adults typically wear simple sandals made from repurposed tire rubber, common throughout East Africa. These sandals have relatively thin ($\sim$1 cm) soles that offer protection from sharp rocks and thorny plants but do not provide any cushioning or elevate the heel. Traditional Hadza can therefore be categorized accurately as “minimally shod”, and their feet display many of the same features (e.g., splayed toes, greater foot width) evident in habitually unshod populations.[17,18] While Musiba and colleagues[17] did not examine running, self-selected speeds during walking trials reported for Hadza adults (1.15 m/s) were relatively fast compared to other traditional, unshod populations, and the Hadza also used greater stride frequencies and stride lengths.

We used high-speed digital video to analyze foot strike patterns and limb-segment angles of Hadza adults and juveniles running at a range of speeds. Our objectives were to determine the frequency of RFS, MFS, and FFS among the Hadza, to investigate the effects of speed and age on foot strike patterns, and to compare these data to published values for the Kalenjin and Daasanach. We predicted that the Hadza, who lack the training and experience in endurance running common among the Kalenjin, would exhibit foot strike patterns more similar to the Daasanach.

2. Materials and methods

2.1. Subjects

In May and June 2010, we recruited 26 Hadza adults ($n = 15$ males, body mass: 50.4 ± 4.2 kg, height: 158.0 ± 6.4 cm, hip height: 84.8 ± 4.0 cm; $n = 11$ females, body mass: 45.9 ± 6.0 kg, height: 150.0 ± 7.0 cm, hip height: 83.5 ± 4.0 cm) and 14 Hadza juveniles (9 males and 5 females, mean age: 8.6 years, range 5−14, body mass: 20.3 ± 5.9 kg, height: 111.1 ± 21.4 cm, hip height: 58.2 ± 9.0 cm) in two camps (Setako and Sengeli) to participate in walking and running trials, as part of a larger study on Hadza energy expenditure.[16] Body mass and height were measured using a digital scale and stadiometer, respectively. Hip height was measured as the distance from the greater trochantor to the ground while standing unshod. Prior to the study, human research permissions were obtained from all legally cognizant institutional and governmental agencies, including the Tanzanian Council for Science and Technology and National Medical Research Institute. Verbal informed consent and, for juveniles, verbal parental consent, was obtained prior to participation. Communication was conducted in Swahili, in which the Hadza are generally fluent.

2.2. Experimental setup

In each Hadza camp we established a clear, level pathway for walking and running trials. Other than clearing small shrubs and loose rocks, no alteration was made to the trackway; its surface generally consisted of hard and dry soil of mixed sand and silt common to that region. A high-speed digital camera (Exilim F1; 300 fps; Casio America, Dover, NJ, USA) was placed 7.5 m from the track and oriented perpendicular to the direction of travel in order to capture kinematics in the sagittal plane. For 11 adult subjects, running trials were recorded during respirometry trials designed to measure energy expenditure (oxygen consumption and carbon dioxide production; see Pontzer et al.[16] which reports energetics data for walking trials). Subjects in these trials wore a Cosmed k4b2 (COSMED USA Inc., Chicago, IL, USA) respirometry unit in a light chest harness, as well as a light plastic mask, to collect and measure expired air. During these respirometry trials, subjects were asked to run at slow ("pole pole" in Swahili), medium ("kati kati"), and fast ("haraka") speeds for 2−3 min each, completing 2−3 laps of the 200-m trackway at each speed. Speeds were calculated by timing these laps with a stopwatch, and a researcher (HP) paced each subject to maintain a constant speed. Most subjects (9/11) chose to wear their sandals during respirometry trials; the other two ran barefoot. Respirometry results were reported previously.[16]

All other running trials were recorded during short ∼7−10-m bouts along a portion of the trackway, without respirometry equipment. No direction was given regarding running speed; subjects chose their own speed. These "short bouts" were begun several meters out of frame so that the subject was at a steady speed during video capture. Subjects were barefoot during these short-bout trials. Four adults completed both respirometry and short-bout trials. Two adults (men) performed additional short-bout trials shod. Combining respirometry and short-bout trials, we collected a total of 66 foot strike recordings.

All video analysis was performed using Kinovea software version 0.8.15 (http://www.kinovea.org/). Running speeds were calculated using the autotrack feature, calibrated using a 1- or 2-m scale bar placed along the trackway for all bouts. Because the scale bar was placed along the side of the trackway farthest from the camera, this method overestimates true running speed: the subject, running in front of the scale bar (i.e., between the scale bar and camera, Fig. 1), will appear to run faster than she is actually traveling. To account for this difference, we compared speeds calculated from video to those calculated using a stopwatch for a set of 13 respirometry trials. As expected, we found that video-based estimates of running speed were 13.4% ± 8.1% faster than speeds calculated using a stopwatch. This comports with the camera's angle of view

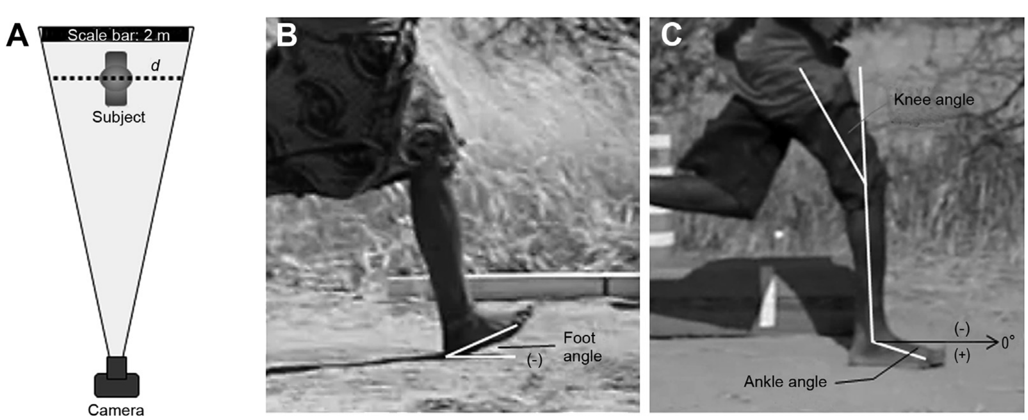

Fig. 1. (A) Schematic aerial view of the camera and trackway setup. Given the distance between the camera and the scale bar (7.5 m), the camera's angle of view (26°), and the positioning of the subject between the scale bar and camera, the sighted distance d is approximately 13% shorter than the scale bar distance of 2 m. As a result, speeds calculated using the scale bar were ∼13% faster than the actual speed measured using a stopwatch. Speeds were corrected for subsequent analyses. (B) A Hadza woman using a rearfoot strike. Foot angle convention is shown; dorsiflexion relative to the ground plane is negative. (C) A Hadza man using a midfoot strike. Knee angle and ankle angle conventions are shown.

(∼26°) and distance from the trackway: a subject running 100 cm in front of the scale bar should appear to be moving ∼13% faster than she actually was. Therefore, speeds calculated from digital video were decreased by 13.4% for subsequent analysis and comparisons with other studies.

2.3. Ankle, knee, and foot angles

Ankle, knee, and plantar foot angles at foot strike were calculated using Kinovea, following angle conventions used by Lieberman and colleagues[6] (Fig. 1). Foot strike was defined as the first video frame in which the foot is in contact with the ground. The locations of anatomical landmarks were estimated; markers were not placed on the foot or leg. Ankle angle was defined as the angle connecting the head of fifth metatarsal, the lateral malleolus, and the knee. A negative ankle angle corresponds to dorsiflexion, while a positive angle indicates plantarflexion. Knee angle was defined as the angle connecting the lateral malleolus, the center of the knee, and major axis of thigh. The plantar foot angle was measured as the angle between the ground plane and the line connecting the posterior calcaneal tuber and distal fifth metatarsal. The lack of anatomical markers limited the resolution with which angles could be determined. Additionally, for plantar angles ±1° at foot strike, the angle between the plantar surface and ground plane was somewhat obscured by the shadow of the foot on the ground. As a result, for many MFS, where plantar angles were ±1°, plantar angles were recorded as 0° as it was not possible to reliably distinguish the angle between the plantar surface and the ground plane with greater precision.

2.4. Foot strike categorization and statistical analyses

All foot strikes were classified as RFS, MFS, or FFS following criteria reported by Altman and Davis.[19] Strike type was defined by the plantar angle and by the portion of the foot contacting the ground at foot strike. Strikes with a negative plantar angle less than −5°, in which the heel contacted the ground first, were classified as RFS. Strikes with a plantar angle between −5° and +1°, in which the middle portion of the foot contacted the ground first, were classified as MFS. We did not record any FFS, defined as a positive plantar angle greater than 1° and the front portion (i.e., the distal portion of the metatarsals) striking the ground first. To assess reliability of foot strike determination, two authors (HP and KS) assessed strike type for all trials independently. Their categorization agreed in all but one trial (65/66 trials, or 98.5% agreement).

Foot strike behavior (RFS, MFS, or FFS) was examined in relation to age class (adult or juvenile), sex, footwear (barefoot or shod), and trial type (respirometry *vs.* short-bout). Because subjects varied in the number of trials collected, foot strike was compared among individuals rather than among trials. For comparisons among age-class and sex, subjects were counted only once in each comparison (e.g., each adult male was counted once in the comparison of adult men and women). For comparisons across footwear and trial type, subjects that completed both conditions were counted once in each condition (e.g., a subject who completed 2 respirometry trials and 2 short-bout trials would be counted once in each condition). To account for the multiple comparisons among adults (sex, footwear, and trial type) and the inclusion of some subjects in both conditions, we used Bonferroni correction to adjust our significance criterion from $p = 0.05$ to $p = 0.01$ for analyses of adults. Comparisons of foot strike usage for each condition were done using chi-squared tests in Excel® (Microsoft, Redmond, WA, USA). Mulitvariate comparisons were performed in JMP® 10.0.0 (SAS, New York, NY, USA) using nominal logistic regression.

3. Results

3.1. Foot strike

A total of 66 running trials were recorded. Across all trials, 30 (45.4%) were RFS and 36 (54.6%) were MFS; no FFS was recorded. When data from adults and juveniles were combined, 60% (24/40) of subjects used RFS and 40% (16/40) used MFS. A substantial difference in foot strike behavior was evident across age-classes. Adults used MFS more often (53.8%, 14/26 subjects) than did juveniles (14.3%, 2/14), $p = 0.015$. Due to this difference adults were analyzed separately for subsequent analyses.

Among adults, more men used MFS (86.7%, 13/15) than women (9.1%, 1/11), $p < 0.001$. In contrast, there was no significant difference between adults in respirometry trials (54.5% MFS, 6/11) versus short-bout trials (61.9% MFS, 13/21), $p = 0.469$, nor between adults wearing sandals (66.7% MFS, 6/9) versus running barefoot (52.4% MFS, 11/21), $p = 0.687$. Four adults (3 males, 1 female) completed trials in four conditions (barefoot and shod; respirometry and short-bout); none of these four changed their foot strike behavior across conditions.

Median speed for all adult trials was 3.4 m/s. Below this speed more adults used RFS (57.9% RFS, 11/19), while above the median speed more subjects used MFS (71.4% MFS, 10/14), but this trend did not achieve significance ($p = 0.095$). Further examination suggests that this trend derives from differences among men and women in their chosen running speed rather than an effect of speed *per se*. Running speeds (mean ± SD) for women and men were 2.98 ± 0.44 and 3.74 ± 0.59 m/s, respectively, and the difference was significant ($p = 0.001$, t test). As noted above, all but one woman used RFS while all but two men used MFS. Further, of the six adults with trials at both slow (<3.4 m/s) and fast (>3.4 m/s) speeds, none changed their foot strike usage at faster speeds. In fact, in all subjects with multiple recorded trials, none changed foot strike usage between trials. Thus, women were more likely to use RFS and to use a slower running speed than men. There is no evidence that subjects changed from RFS to MFS as speed increased.

Results from bivariate comparisons were consistent with those of a multivariate nominal logistic regression. When speed, sex, and footwear (shod, barefoot) were used as independent variables predicting foot strike, only sex was a significant factor ($p = 0.001$). When adult and juvenile trials

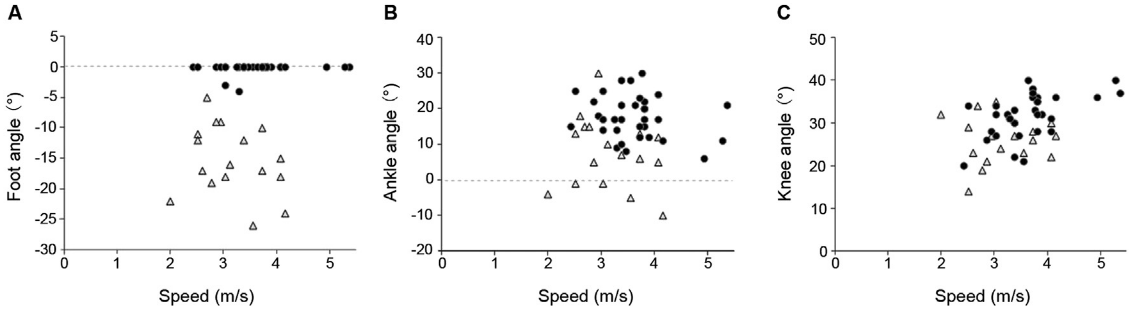

Fig. 2. Foot, ankle, and knee angles at foot strike for Hadza adults. Each point is one trial; some subjects are represented in multiple trials. Gray triangles: rearfoot strike trials; black circles: midfoot strike trials. See Fig. 1 for angle conventions.

were pooled, both sex ($p = 0.001$) and age-class ($p < 0.001$) were significant predictors of foot strike usage, while speed ($p = 0.157$) and footwear ($p = 0.101$) were not.

3.2. Joint angles

Foot, ankle, and knee angles at foot strike for Hadza adults are plotted against speed in Fig. 2. The effects of footwear, speed, and foot strike usage were entered into a multivariate nominal logistic regression to examine their effect on these angles. Not surprisingly, foot strike usage (RFS *vs.* MFS) was a significant predictor of foot angle at impact ($p < 0.001$), but speed ($p = 0.54$) and footwear (shod *vs.* unshod, $p = 0.37$) had no effect. Similarly, foot strike usage significantly predicted ankle angle at foot strike ($p < 0.001$), while neither speed ($p = 0.21$) nor footwear ($p = 0.74$) were significant factors. For knee angle, both foot strike ($p = 0.006$) and speed ($p = 0.011$) were significant factors, with more acute knee flexion at faster speeds, but footwear had no effect ($p = 0.54$). When juvenile trials are added to these comparisons, age-class does not significantly affect foot, ankle, or knee angles ($p > 0.05$ all comparisons).

4. Discussion

4.1. Comparisons with other studies

Foot strike usage among Hadza adults was intermediate between that reported among the Kalenjin and Daasanach populations (Table 1), and similar in some ways to the pattern reported for Tarahumara adults. When Hadza juveniles, adult men, and adult women are examined separately, some similarities with other populations emerge. Hadza men rarely use RFS (13.3% of subjects), similar to foot strike patterns of barefoot Kalenjin adolescents and Kalenjin adults who grew up barefoot, and to minimally-shod Tarahumara.[6,8,13] In contrast, Hadza women and juveniles often used RFS (90.9% and 85.7% of subjects, respectively), similar to Daasanach adults, habitually shod Kalenjin adolescents, and Tarahumara wearing conventional running shoes. The high rate of RFS among Hadza women and juveniles was also similar to that reported for habitually shod adults.[7] Unlike Kalenjin adults that grew up barefoot, habitually barefoot Kalenjin adolescents, and habitually barefoot U.S. adults, Hadza runners never used FFS in trials recorded for this study.

Due to the mix of MFS and RFS among the Hadza, mean plantar foot strike angle among adults was intermediate between habitually shod U.S. adults and Kalenjins. U.S. adults ran with a high frequency of RFS, thus leading to the large dorsiflexion upon plantar foot strike, causing smaller (negative) foot angles. Kalenjins had a high frequency of FFS, thus showing the large plantarflexion upon foot strike and larger angles. Ankle angles among Hadza adults were similar to those of habitually barefoot U.S. adults, barefoot Kalenjin adolescents, and Kalenjin adults who grew up barefoot. Knee angles at foot strike were consistently greater (i.e., more flexed) among Hadza adults than for Kalenjin or U.S. groups.

Table 1
Foot strike, limb angles at foot strike, and speed for Hadza, Kalenjin, Daasanach, and U.S. populations.

Group (habitual footwear)	*n* (male/female)	Strike-type mode (%)				Angle at foot strike (mean ± SD)			Speed (m/s)
		Condition	Rearfoot	Midfoot	Forefoot	Plantar foot	Ankle	Knee	
Hadza adults (minimally shod)	26 (15/11)	Barefoot	48	52	0	−5.0 ± 7.3	14.7 ± 7.9	29.9 ± 6.5	3.4 ± 0.7
		Shod	33	67	0	−5.8 ± 9.0	13.7 ± 10.5	29.6 ± 4.9	3.7 ± 0.7
Hadza juveniles (minimally shod)	14 (9/5)	Barefoot	86	14	0	−15.5 ± 9.0	7.9 ± 10.9	29.7 ± 6.7	3.2 ± 0.5
Kalenjin adults (recently shod)	14 (13/1)	Barefoot	9	0	91	3.7 ± 9.8	18.6 ± 7.7	21.2 ± 4.4	5.9 ± 0.6
		Shod	29	18	54	−1.8 ± 7.4	15.0 ± 6.7	22.2 ± 4.3	5.7 ± 0.6
Kalenjin adolescents (barefoot)	16 (8/8)	Barefoot	12	22	66	1.13 ± 6.8	14.6 ± 8.3	22.8 ± 5.4	5.5 ± 0.5
Kalenjin adolescents (shod)	17 (10/7)	Barefoot	62	19	19	−10.1 ± 9.7	4.1 ± 10.9	18.9 ± 6.5	5.1 ± 0.5
		Shod	97	3	0	−19.8 ± 10.3	−2.7 ± 9.0	18.4 ± 6.6	4.9 ± 0.5
Daasanach adults (barefoot)	38 (19/19)	Barefoot	72	24	4	–	–	–	3.3 ± 0.4
U.S. adults (shod)	8 (6/2)	Barefoot	83	17	0	−16.4 ± 4.4	0.2 ± 3.0	12.1 ± 7.9	4.0 ± 0.3
		Shod	100	0	0	−28.3 ± 6.2	−9.3 ± 6.5	9.1 ± 6.4	4.2 ± 0.3
U.S. adults (barefoot)	8 (7/1)	Barefoot	25	0	75	8.4 ± 4.4	17.6 ± 5.8	17.3 ± 2.5	3.9 ± 0.4
		Shod	50	13	37	−2.2 ± 14.0	8.1 ± 15.9	16.6 ± 2.4	4.0 ± 0.3

The difference in knee angle is more substantial when differences in running speed are considered; Hadza speeds were lower, on average, than those of the Kalenjin or U.S. groups reported by Lieberman and colleagues,[6] yet knee flexion generally increased with speed in our sample.

Direct comparison of joint angles among studies is hampered by the different methods used to measure them. Unlike Lieberman and colleagues,[6] we did not place visual markers on anatomical landmarks. Instead, the knee angle in our study was calculated using the major axes of the thigh and shank, which may have resulted in systematic differences in knee angle calculation relative to the analysis of Lieberman and colleagues. The image resolution and lack of visual markers probably also decreased the precision of our angle measurements, an effect that was most evident in our inability to distinguish plantar angles $\pm 1°$ for MFS trials (Fig. 2). Thus, while we took care to calculate angles in a manner that would maximize comparability to other studies (Fig. 1), it is possible that some differences between studies arise from methodological differences.

4.2. Factors influencing foot strike type

Foot strike behavior among traditional Hadza hunter-gatherers was mixed, with consistent differences between men and women and between juveniles and adults. Women and juveniles used RFS more often than MFS, while men used MFS almost exclusively. There was no difference between shod versus barefoot conditions, nor among respirometry trials (which lasted for several minutes) and short-bout trials (which lasted a few seconds). The lack of difference between short-bout and respirometry trials lends confidence that the duration of the trial did not affect foot strike choice. Further, there is no evidence that Hadza adults switched from RFS to MFS as speed increased.

While the Hadza used MFS rather than FFS, comparisons with other populations suggest that Hadza men are similar to experienced barefoot runners such as the Kalenjin in avoiding RFS. In addition, Hadza men achieve MFS patterns using generally comparable joint kinematics to other groups that habitually MFS. Hadza women and juveniles are similar to shod U.S. runners and inexperienced runners such as the Daasanach in preferring RFS, and use comparable joint kinematics to achieve these foot strikes. This pattern of foot strike usage suggests running experience may be important in developing foot strike preferences. As children learn to walk and their gait matures, RFS develops as a normal part of the walking gait cycle;[20] thus RFS is the behavior learned first. As the musculoskeletal system and motor control develop further during adolescence, experience running barefoot or minimally shod may lead to a preference for MFS or FFS during running, perhaps in response to the high impact forces[21] experienced when running with RFS. Individuals who rarely run might not have the same accumulated experience of high impact forces due to RFS, and thus never switch from RFS to MFS or FFS for running.

Our data are cross-sectional and do not provide the ontogenetic data or other measures of personal history and experience that longitudinal studies might afford. Nonetheless, the pattern of foot strike use among the Hadza are consistent with the hypothesis that running experience and skill play a role in shaping foot strike behavior. Hadza adolescents used RFS almost exclusively. Indeed, the only two adolescents that used MFS were also the oldest (13- and 14-year-old boys). Hadza women apparently maintain this preference for RFS into adulthood, while Hadza men come to prefer MFS. We suggest that the change in foot strike behavior by Hadza men may develop as they learn to hunt and track wild game. While Hadza men do not typically engage in endurance running, it is likely that they run more often as they learn to hunt than their female counterparts do in learning to gather plant foods. Indeed, our measurements of travel speeds used while out of camp on forays, taken using wearable GPS devices,[16] indicate that men use running speeds approximately twice as often as women (Fig. 3). Perhaps men's running experience, and the greater impact force experienced during RFS, lead Hadza men to prefer running with MFS as their foraging efforts and experience grow.

An alternative explanation for the observed differences in foot strike usage between Hadza men and women, and between Hadza children and adult men, is that adult men experience larger ground reaction forces due to their greater body mass and running speed, leading to proprioceptive responses in foot strike preference. Hadza men in this sample were 10.0% heavier than women ($p = 0.04$, t test) and 5.4% taller ($p = 0.01$, t test) and, as noted above, used faster running speeds than women. While we did not measure ground forces

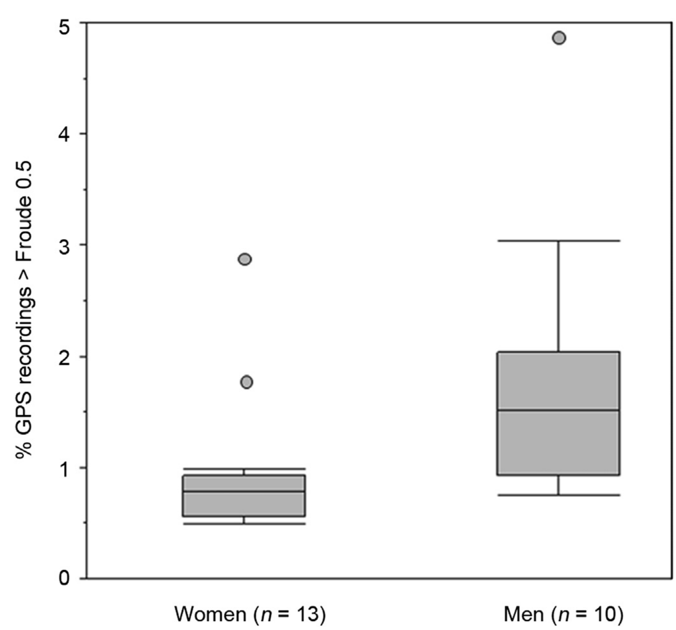

Fig. 3. Percentage of travel during forays (i.e., outside of their camps) in which travel speed exceeded froude = 0.5 for 13 adult Hadza women and 10 adult Hadza men. Travel was defined as a GPS epoch in which speed exceeded 0.5 m/s. Speed was calculated from GPS units worn during daylight hours. Froude = 0.5 was calculated from hip height for each subject using the formula: Froude = speed^2/(hip height × g). Epoch duration was variable, with a median of 10 s. See Pontzer and colleagues[16] for GPS methods and protocol.

in this study, the difference in mass and speed suggests men would have experienced correspondingly larger ground forces. Nonetheless, the observed variation in foot strike preference indicates that this mechanical hypothesis does not capture all of the inter-individual variance in behavior. The two men who employed RFS were among the largest (54.6 and 58.2 kg), and their mean running speed (3.55 m/s) was near the mean of the men's sample. Notably, there was no difference in hip height between men and women in the Hadza sample ($p = 0.44$, t test) indicating that sex differences in foot strike usage were not a result of differences in hind limb length.

Whatever the reason for their foot strike preference, it is notable that MFS is common among Hadza men even though they rarely run. This finding holds implications for the evolution of human running gait. In populations with even minimal experience running, we can expect that many individuals would prefer MFS (or perhaps FFS) rather than RFS on occasions when they do run. Some threshold level of exposure to running may be necessary to promote MFS or FFS, but extensive running experience is not needed. Thus MFS (and perhaps FFS) may have been common among hunter-gatherer groups in the past, even those that did not engage in endurance running or employ exhaustion hunting techniques regularly.

Including our data from this study, foot strike behavior during running has been described for only three habitually barefoot or minimally shod populations. The variability in foot strike preference both within and between these groups is notable, and suggests caution is warranted when drawing conclusions about "average" or "typical" gait in unshod populations. For example, it is possible that groups such as the Daasanach run with RFS due simply to a lack of endurance running experience. Documenting foot strike behavior and other aspects of walking and running gait in other barefoot and minimally shod populations will improve our understanding of cultural and ecological factors influencing locomotor behavior and anatomy in humans.

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