LETTERS

Foot strike patterns and collision forces in habitually barefoot versus shod runners

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Humans have engaged in endurance running for millions of years[1], but the modern running shoe was not invented until the 1970s. For most of human evolutionary history, runners were either barefoot or wore minimal footwear such as sandals or moccasins with smaller heels and little cushioning relative to modern running shoes. We wondered how runners coped with the impact caused by the foot colliding with the ground before the invention of the modern shoe. Here we show that habitually barefoot endurance runners often land on the fore-foot (fore-foot strike) before bringing down the heel, but they sometimes land with a flat foot (mid-foot strike) or, less often, on the heel (rear-foot strike). In contrast, habitually shod runners mostly rear-foot strike, facilitated by the elevated and cushioned heel of the modern running shoe. Kinematic and kinetic analyses show that even on hard surfaces, barefoot runners who fore-foot strike generate smaller collision forces than shod rear-foot strikers. This difference results primarily from a more plantarflexed foot at landing and more ankle compliance during impact, decreasing the effective mass of the body that collides with the ground. Fore-foot- and mid-foot-strike gaits were probably more common when humans ran barefoot or in minimal shoes, and may protect the feet and lower limbs from some of the impact-related injuries now experienced by a high percentage of runners.

Running can be most injurious at the moment the foot collides with the ground. This collision can occur in three ways: a rear-foot strike (RFS), in which the heel lands first; a mid-foot strike (MFS), in which the heel and ball of the foot land simultaneously; and a fore-foot strike (FFS), in which the ball of the foot lands before the heel comes down. Sprinters often FFS, but 75–80% of contemporary shod endurance runners RFS[2,3]. RFS runners must repeatedly cope with the impact transient of the vertical ground reaction force, an abrupt collision force of approximately 1.5–3 times body weight, within the first 50 ms of stance (Fig. 1a). The time integral of this force, the impulse, is equal to the change in the body's momentum during this period as parts of the body's mass decelerate suddenly while others decelerate gradually[4]. This pattern of deceleration is equivalent to some proportion of the body's mass (M_{eff}, the effective mass) stopping abruptly along with the point of impact on the foot[5]. The relation between the impulse, the body's momentum and M_{eff} is expressed as

$$\int_{0^-}^{T} F_z(t) = M_{body}(\Delta v_{com} + gT) = M_{eff}(-v_{foot} + gT) \qquad (1)$$

where $F_z(t)$ is the time-varying vertical ground reaction force, 0^- is the instant of time before impact, T is the duration of the impact transient, M_{body} is the body mass, v_{com} is the vertical speed of the centre of mass, v_{foot} is the vertical speed of the foot just before impact and g is the acceleration due to gravity at the Earth's surface.

Impact transients associated with RFS running are sudden forces with high rates and magnitudes of loading that travel rapidly up the body and thus may contribute to the high incidence of running-related injuries, especially tibial stress fractures and plantar fasciitis[6–8]. Modern running shoes are designed to make RFS running comfortable and less injurious by using elastic materials in a large heel to absorb some of the transient force and spread the impulse over more time[9] (Fig. 1b). The human heel pad also cushions impact transients, but to a lesser extent[5,10,11], raising the question of how runners struck the ground before the invention of modern running shoes. Previous studies have found that habitually shod runners tend to adopt a flatter foot placement when barefoot than when shod, thus reducing stresses on the foot[12–15], but there have been no detailed studies of foot kinematics and impact transients in long-term habitually barefoot runners.

We compared foot strike kinematics on tracks at preferred endurance running speeds (4–6 m s^{-1}) among five groups controlled for age and habitual footwear usage (Methods and Supplementary Data 2). Adults were sampled from three groups of individuals who run a minimum of 20 km per week: (1) habitually shod athletes from the USA; (2) athletes from the Rift Valley Province of Kenya (famed for endurance running[16]), most of whom grew up barefoot but now wear cushioned shoes when running; and (3) US runners who grew up shod but now habitually run barefoot or in minimal footwear. We also compared adolescents from two schools in the Rift Valley Province: one group (4) who have never worn shoes; and another group (5) who have been habitually shod most of their lives. Speed, age and distance run per week were not correlated significantly with strike type or foot and ankle angles within or among groups. However, because the preferred speed was approximately 1 m s^{-1} slower in indoor trials than in outdoor trials, we made statistical comparisons of kinematic and kinetic data only between groups 1 and 3 (Table 1).

Strike patterns vary within subjects and groups, but these trials (Table 1 and Supplementary Data 6) confirm reports[2,3,9] that habitually shod runners who grew up wearing shoes (groups 1 and 5) mostly RFS when shod; these runners also predominantly RFS when barefoot on the same hard surfaces, but adopt flatter foot placements by dorsiflexing approximately 7–10° less (analysis of variance, $P < 0.05$). In contrast, runners who grew up barefoot or switched to barefoot running (groups 2 and 4) most often used FFS landings followed by heel contact (toe–heel–toe running) in both barefoot and shod conditions. MFS landings were sometimes used in barefoot conditions (group 4)

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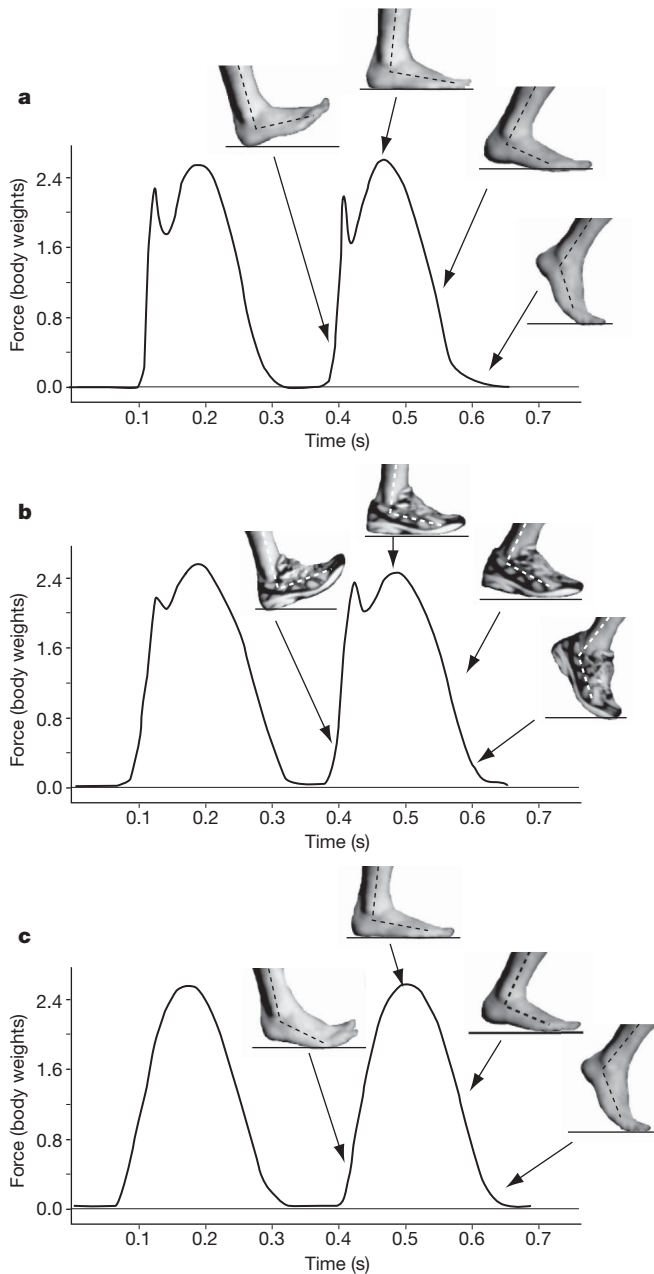*These authors contributed equally to this work.

a

b

c

Figure 1 | Vertical ground reaction forces and foot kinematics for three foot strikes at 3.5 m s⁻¹ in the same runner. a, RFS during barefoot heel–toe running; **b**, RFS during shod heel–toe running; **c**, FFS during barefoot toe–heel–toe running. Both RFS gaits generate an impact transient, but shoes slow the transient's rate of loading and lower its magnitude. FFS generates no impact transient even in the barefoot condition.

a

b

Figure 2 | Variation in impact transients. a, b, Magnitude (**a**) and rate of loading (**b**) of impact transient in units of body weight for habitually shod runners who RFS (group 1; open boxes) and habitually barefoot runners who FFS when barefoot (group 3; shaded boxes). The rate of loading is calculated from 200 N to 90% of the impact transient (when present) or to $6.2 \pm 3.7\%$ (s.d.) of stance phase (when impact transient absent). The impact force is 0.58 ± 0.21 bodyweights (s.d.) in barefoot runners who FFS, which is three times lower than in RFS runners either barefoot (1.89 ± 0.72 body weights (s.d.)) or in shoes (1.74 ± 0.45 body weights (s.d.)). The average rate of impact loading for barefoot runners who FFS is 64.6 ± 70.1 body weights per second (s.d.), which is similar to that for shod RFS runners (69.7 ± 28.7 body weights per second (s.d.)) and seven times lower than that for shod runners who RFS when barefoot (463.1 ± 141.0 body weights per second (s.d.)). The nature of the measurement (force versus time) is shown schematically by the grey and red lines. Boxes, mean $\pm$ s.d.; whiskers, mean $\pm$ 2 s.d.

and shod conditions (group 2), but RFS landings were infrequent during barefoot running in both groups. A major factor contributing to the predominance of RFS landings in shod runners is the cushioned sole of most modern running shoes, which is thickest below the heel, orienting the sole of the foot so as to have about 5° less dorsiflexion than does the sole of the shoe, and allowing a runner to RFS comfortably (Fig. 1). Thus, RFS runners who dorsiflex the ankle at impact have shoe soles that are more dorsiflexed relative to the ground, and FFS runners who plantarflex the ankle at impact have shoe soles that are flatter (less plantarflexed) relative to the ground, even when knee and ankle angles are not different (Table 1). These data indicate that habitually unshod runners RFS less frequently, and that shoes with elevated, cushioned heels facilitate RFS running (Supplementary Data 3).

Kinematic differences among foot strikes generate markedly different collision forces at the ground, which we compared in habitually
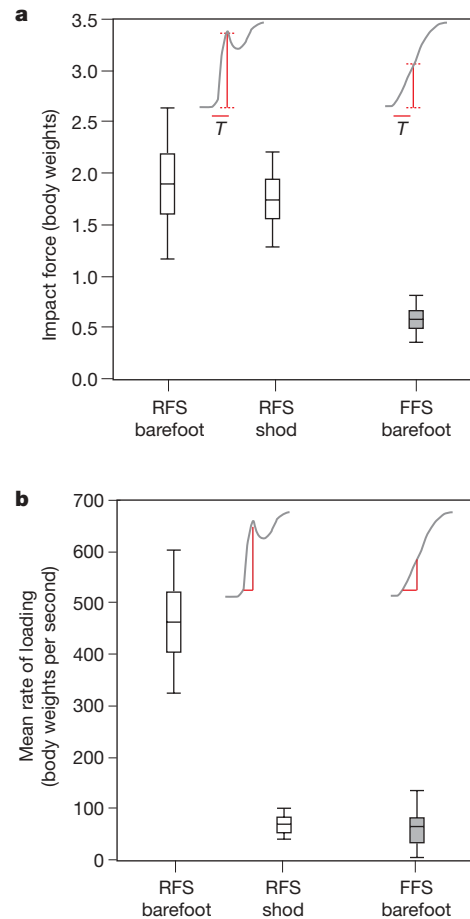
shod and barefoot adult runners from the USA during RFS and FFS running (Methods and Supplementary Data 2). Whereas RFS landings cause large impact transients in shod runners and even larger transients in unshod runners (Fig. 1a, b), FFS impacts during toe–heel–toe gaits typically generate ground reaction forces lacking a distinct transient (Fig. 1c), even on a stiff steel force plate[4,17–19]. At similar speeds, magnitudes of peak vertical force during the impact period ($6.2 \pm 3.7\%$ (all uncertainties are s.d. unless otherwise indicated) of stance for RFS runners) are approximately three times lower in habitual barefoot runners who FFS than in habitually shod runners who RFS either barefoot or in shoes (Fig. 2a). Also, over the same percentage of stance the average rate of loading in FFS runners when barefoot is seven times lower than in habitually shod runners who RFS when barefoot, and is similar to the rate of loading of shod RFS runners (Fig. 2b). Further, in the majority of barefoot FFS runners, rates of loading were approximately half those of shod RFS runners.

Modelling the foot and leg as an L-shaped double pendulum that collides with the ground (Fig. 3a) identifies two biomechanical factors,

namely the initial point of contact and ankle stiffness, that decrease M_{eff} and, hence, the magnitude of the impact transient (equation (1) and Supplementary Data 4). A RFS impact typically occurs just below the ankle, under the centre of mass of the foot plus leg, and with variable plantarflexion (Fig. 3b). Therefore, the ankle converts little translational energy into rotational energy and most of the translational kinetic energy is lost in the collision, leading to an increase in M_{eff} (ref. 20). In contrast, a FFS impact occurs towards the front of the foot (Fig. 3a), and the ankle dorsiflexes as the heel drops under control of the triceps surae muscles and the Achilles tendon (Fig. 3b). The ground reaction force in a FFS therefore torques the foot around the ankle, which reduces M_{eff} by converting part of the lower limb's translational kinetic energy into rotational kinetic energy, especially in FFS landings with low ankle stiffness (Fig. 3a). We note that MFS landings with intermediate contact points are predicted to generate intermediate M_{eff} values.

The conservation of angular impulse momentum during a rigid plastic collision can be used to predict M_{eff} as a function of the location of the centre of pressure at impact for ankles with zero and infinite joint stiffnesses (Supplementary Data 4). Figure 3 shows model values of M_{eff} for an average foot and shank comprising 1.4% and 4.5% M_{body}, respectively, where the shank is 1.53 times longer than the foot[21]. M_{eff} can be calculated, using experimental data from equation (1), as

$$M_{eff} = \frac{\int_{0^-}^{T} F_z(t)\, dt}{-v_{foot} + gT} \quad (2)$$

Using equation (2) with kinematic and kinetic data from groups 1 and 3 (Methods), we find that M_{eff} averages 4.49 ± 2.24 kg for RFS runners in the barefoot condition and 1.37 ± 0.42 kg for habitual barefoot runners who FFS (Fig. 3a). Normalized to M_{body}, the average M_{eff} is $6.8 \pm 3.0\%$ for barefoot RFS runners and $1.7 \pm 0.4\%$ for barefoot FFS runners. For all RFS landings, these values are not significantly different from the predicted M_{eff} values for a rigid ankle (5.5–5.9% M_{body}) or a compliant ankle (3.4–5.9% M_{body}), indicating that ankle compliance has little effect and that there is some contribution from mass above the knee, which is very extended in these runners (Fig. 3b). For FFS landings, M_{eff} values are smaller than the predicted values for a rigid ankle (2.7–4.1% M_{body}) and are insignificantly greater than those predicted for a compliant ankle (0.45–1.1% M_{body}), suggesting low levels of ankle stiffness. These results therefore support the prediction that FFS running generates collisions with a much lower M_{eff} than does RFS running. Furthermore, MFS running is predicted to generate intermediate M_{eff} values with a strong dependence on the centre of pressure at impact and on ankle stiffness.

How runners strike the ground also affects vertical leg compliance, defined as the drop in the body's centre of mass relative to the vertical force during the period of impact. Vertical compliance is greater in FFS running than in RFS running, leading to a lower rate of loading (Fig. 3c). More compliance during the impact period in FFS runners is partly explained by a 74% greater drop in the centre of mass (t-test, $P < 0.009$), resulting, in part, from ankle dorsiflexion and knee flexion (Fig. 3b). In addition, like shod runners, barefoot runners adjust leg stiffness depending on surface hardness[22]. As a result, we found no significant differences in rates or magnitudes of impact loading in barefoot runners on hard surfaces relative to cushioned surfaces (Supplementary Data 5).

Differences between RFS and FFS running make sense from an evolutionary perspective. If endurance running was an important behaviour before the invention of modern shoes, then natural selection is expected to have operated to lower the risk of injury and discomfort when barefoot or in minimal footwear. Most shod runners today land on their heels almost exclusively. In contrast, runners who cannot or prefer not to use cushioned shoes with elevated heels often avoid RFS landings and thus experience lower impact transients than do most shod runners today, even on very stiff surfaces (Fig. 2). Early
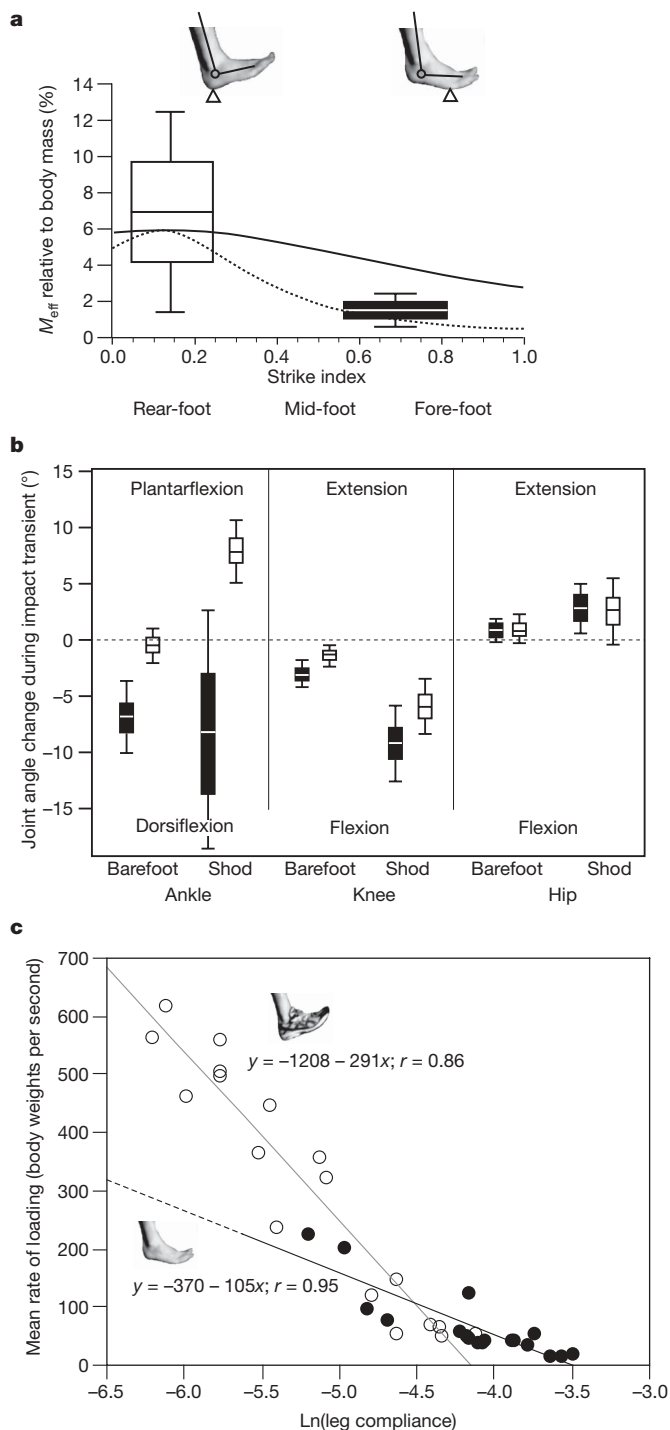
Figure 3 | Differences during impact between shod RFS runners (group 1) and barefoot FFS runners (group 3) at approximately 4 m s⁻¹.
a, Predicted (lines) and measured (boxes) effective mass, M_{eff}, relative to body mass, versus foot length at impact (strike index) for FFS and RFS runners in the barefoot condition (Methods). The solid and dotted lines show predicted M_{eff} values for infinitely stiff and infinitely compliant ankles, respectively, at different centres of pressure. **b**, During the impact period, FFS runners (filled boxes) dorsiflex the ankle rather than plantarflexing it, and have more ankle and knee flexion than do RFS runners (open boxes). Boxes, mean ± s.d.; whiskers, mean ± 2 s.d. **c**, Overall dimensionless leg compliance (natural logarithm) during the impact-transient period (ratio of vertical hip drop relative to leg length at 90% of impact transient peak, normalized by body weight) relative to the rate of impact loading (body weights per second) for RFS runners (open circles) and FFS runners (filled circles) (shod and unshod conditions). Compliance is greater and is correlated with lower rates of loading in FFS impacts than in RFS impacts (plotted lines determined by least-squares regression; r, Pearson's correlation coefficient).

Table 1 | Foot strike type and joint angles of habitual barefoot and shod runners from Kenya and the USA

Group	N (male/female)	Age (age shod) (yr)	Strike-type mode (%)*				Joint angle at foot strike			Speed (m s⁻¹)
			Condition	RFS	MFS	FFS	Plantar foot†	Ankle†	Knee	
(1) Habitually shod adults, USA‡	8 (6/2)	19.1 ± 0.4 (<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
(2) Recently shod adults, Kenya	14 (13/1)	23.1 ± 3.5 (12.4 ± 5.6)	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
(3) Habitually barefoot adults, USA§	8 (7/1)	38.3 ± 8.9 (<2)	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
(4) Barefoot adolescents, Kenya	16 (8/8)	13.5 ± 1.4 (never)	Barefoot	12	22	66	1.13 ± 6.8°	14.6 ± 8.3°	22.8 ± 5.4°	5.5 ± 0.5
			Shod‖	—	—	—	—	—	—	—
(5) Shod adolescents, Kenya	17 (10/7)	15.0 ± 0.8 (<5)	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

Data shown as mean ± s.d.
* RFS equivalent to heel-toe running; FFS equivalent to toe–heel–toe running.
† Angle of the sole of the foot or shoe (column 8), or of the ankle (column 9), relative to ground. Negative values indicate dorsiflexion relative to standing position; positive values indicate plantarflexion relative to standing position.
‡ Joint angles calculated from RFS only.
§ Joint angles calculated from FFS only.
‖ No shod condition reported because subjects had never worn shoes.

bipedal hominins such as *Australopithecus afarensis* had enlarged calcaneal tubers and probably walked with a RFS[23]. However, they lacked some derived features of the modern human foot, such as a strong longitudinal arch[1,24] that functionally improves the mass–spring mechanics of running by storing and releasing elastic energy[25]. We do not know whether early hominins ran with a RFS, a MFS or a FFS gait. However, the evolution of a strong longitudinal arch in genus *Homo* would increase performance more for non-RFS landings because the arch stretches passively during the entire first half of stance in FFS and MFS gaits. In contrast, the arch can stretch passively only later in stance during RFS running, when both the fore-foot and the rear-foot are on the ground. This difference may account for the lower cost of barefoot running relative to shod running[15,26].

Evidence that barefoot and minimally shod runners avoid RFS strikes with high-impact collisions may have public health implications. The average runner strikes the ground 600 times per kilometre, making runners prone to repetitive stress injuries[6–8]. The incidence of such injuries has remained considerable for 30 years despite technological advancements that provide more cushioning and motion control in shoes designed for heel–toe running[27–29]. Although cushioned, high-heeled running shoes are comfortable, they limit proprioception and make it easier for runners to land on their heels. Furthermore, many running shoes have arch supports and stiffened soles that may lead to weaker foot muscles, reducing arch strength. This weakness contributes to excessive pronation and places greater demands on the plantar fascia, which may cause plantar fasciitis. Although there are anecdotal reports of reduced injuries in barefoot populations[30], controlled prospective studies are needed to test the hypothesis that individuals who do not predominantly RFS either barefoot or in minimal footwear, as the foot apparently evolved to do, have reduced injury rates.

METHODS SUMMARY

We studied five subject groups (Table 1 and Supplementary Data 1), both barefoot and in running shoes. Habitually shod and barefoot US subjects ran over a force plate embedded 80% of the way along a 20–25-m-long indoor track. We quantified joint angles using a three-dimensional infrared kinematic system (Qualisys) at 240 Hz and a 500-Hz video camera (Fastec InLine 500M). African subjects were recorded on a 20–25-m outdoor track of hard dirt using a 500-Hz video camera. All subjects ran at preferred speeds with several habituation trials before each condition, and were recorded for five to seven trials per condition. We taped kinematic markers on joints and segments in all subjects. Video frames were analysed using IMAGEJ (http://rsb.info.nih.gov/nih-image/) to measure the angle of the plantar surface of the foot relative to earth horizontal (plantar foot angle), as well as ankle, knee and hip angles (Methods). We recorded the vertical ground reaction force (F_z) in US subjects at 4,800 Hz using AMTI force plates (BP400600 Biomechanics Force Platform), and normalized the results to body weight. The impact-transient magnitude and percentage of stance were measured at peak, and the rate of loading was quantified between 200 N and 90% of peak (following ref. 18). When there was no distinct impact transient, the same

parameters were measured at the same percentage of stance plus/minus 1 s.d. as determined for each condition in trials with an impact transient. The effective mass (M_{eff}) in RFS runners was calculated using the integral of F_z (equation (2)) between the time when F_z exceeded 4 s.d. above baseline noise and the time when the transient peak was reached as measured in RFS runners; the impulse over the same percentage of stance (6.2 ± 3.7%) was used to calculated M_{eff} in FFS runners. Vertical foot and leg speed were calculated using a central difference method and the three-dimensional kinematic data.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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METHODS

Subjects. We used five groups of subjects (outlined in Table 1 and Supplemental Table 1), including the following three groups of adults. Group 1 comprised amateur and collegiate athletes from the Harvard University community, recruited by word of mouth, all of whom were habitually shod since early childhood. Group 2 comprised Kalenjin athletes from the Rift Valley Province of Kenya, all training for competition, and recruited by word of mouth in the town of Kapsabet and at Chepkoilel Stadium, Eldoret. All adult Kenyan subjects were habitually shod, but 75% did not start wearing shoes and training in running shoes until late adolescence. Group 3 comprised self-identified habitual barefoot runners from the USA, recruited through the internet, who run either barefoot and/or in minimal footwear such as Vibram FiveFingers shoes, defined as lacking arch support and cushioning. In addition, two groups of adolescent subjects (aged 11–16 yr) were sampled from two schools in the Kalenjin-speaking region of Kenya. Group 4 comprised habitually unshod runners ($N = 16$; eight male, eight female) recruited from a rural primary school in the South Nandi District of Kenya in which none of children have ever worn shoes (verified by observation and interviews with teachers at the school). Group 5 comprised habitually shod runners ($N = 16$; nine male, seven female) recruited from an urban primary school in Eldoret in which all of the children have been habitually shod since early childhood.

For all adults, criteria for inclusion in the study included a minimum of 20 km per week of distance running and no history of significant injury during the previous six months. Habitual barefoot runners were included if they had run either barefoot or in minimal footwear for more than six months and if more than 66% of their running was either barefoot or in minimal footwear. To compare habitual barefoot FFS (toe–heel–toe) runners and habitually shod RFS (heel–toe) runners, we analysed kinematic and kinetic data from subsamples of six RFS runners from group 1 and six FFS runners from group 3 in greater depth (Supplementary Data Table 1).

All information on subject running history was self-reported (with the assistance of teachers for the Kenyan adolescents). All subjects participated on a voluntary basis and gave their informed consent according to the protocols approved by the Harvard Institutional Review Board and, for Kenyan subjects, the Moi University Medical School. Subjects were not informed about the hypotheses tested before recording began.

Treatments. All subjects were recorded on flat tracks approximately 20–25-m long. Subjects in groups 1–3 and 5 were recorded barefoot and in running shoes. A neutral running shoe (ASICS GEL-CUMULUS 10) was provided for groups 1 and 3, but groups 2 and 5 ran in their own shoes. Subjects in group 4 were recorded only in the barefoot condition because they had never worn shoes. For groups 1 and 3, two force plates (see below) were embedded at ground level 80% of the way along the track, with a combined force-plate length of 1.2 m. Force plates were covered with grip tape (3M Safety-Walk Medium Duty Resilient Tread 7741), and runners were asked to practice running before recording began so that they did not have to modify their stride to strike the plates. Kenyan runners in groups 2, 4 and 5 were recorded on flat, outdoor dirt tracks (with no force plates) that were 20–25-m long and cleaned to remove any pebbles or debris. In all groups, subjects were asked to run at a preferred speed and were given several habituation trials before each data collection phase, and were recorded in five to seven trials per condition, with at least one minute's rest between trials to avoid fatigue.

Kinematics. To record angles in lateral view of the ankle, knee, hip and plantar surface of the foot, a high-speed video camera (Fastec InLine 500M, Fastec Imaging) was placed approximately 0.5 m above ground level between 2.0 and 3.5 m lateral to the recording region and set to record at 500 Hz. Circular markers were taped on the posterior calcaneus (at the level of the Achilles tendon insertion), the head of metatarsal V, the lateral malleolus, the joint centre between the lateral femoral epicondyle and the lateral tibial plateau (posterior to Gerdy's tubercle), the midpoint of the thigh between the lateral femoral epicondyle

and the greater trochantor of the femur (in groups 2, 4 and 5); the greater trochantor of the femur (only in groups 1 and 3); and the lateral-most point on the anterior superior iliac spine (only in groups 1 and 3). We could not place hip and pelvis markers on adolescent Kenyan subjects (groups 4 and 5). IMAGEJ (http://rsb.info.nih.gov/nih-image/) was used to measure three angles in all subjects: (1) the plantar foot angle, that is, the angle between the earth horizontal and the plantar surface of the foot (calculated using the angle between the lines formed by the posterior calcaneus and metatarsal V head markers and the earth horizontal at impact, and corrected by the same angle during quiet stance); (2) the ankle angle, defined by the metatarsal V head, lateral malleolus and knee markers; (3) the knee angle, defined by the line connecting the lateral malleolus and the knee and the line connecting the knee and the thigh midpoint (or greater trochantor). Hip angle was also measured in groups 1 and 2 as the angle between the lateral femoral condyle, the greater trochantor and the anterior superior iliac spine. All angles were corrected against angles measured during a standing, quiet stance. Average measurement precision, determined by repeated measurements (more than five) on the same subjects was $\pm0.26°$.

Under ideal conditions, plantar foot angles greater than $0°$ indicate a FFS, angles less than $0°$ indicate a RFS (heel strike) and angles of $0°$ indicate a MFS. However, because of inversion of the foot at impact, lighting conditions and other sources of error, determination of foot strike type was also evaluated by visual examination of the high-speed video by three of us. We also note that ankle angles greater than $0°$ indicate plantarflexion and that angles less than $0°$ indicate dorsiflexion.

Additional kinematic data for groups 1 and 3 were recorded with a six-camera system (ProReflex MCU240, Qualysis) at 240 Hz. The system was calibrated using a wand with average residuals of <1 mm for all cameras. Four infrared reflective markers were mounted on two 2-cm-long balsawood posts, affixed to the heel with two layers of tape following methods described in ref. 18. The average of these four markers was used to determine the total and vertical speeds of the foot before impact.

Kinetics. Ground reaction forces (GRFs) were recorded in groups 1 and 3 at 4,800 Hz using force plates (BP400600 Biomechanics Force Platform, AMTI). All GRFs were normalized to body weight. Traces were not filtered. When a distinct impact transient was present, transient magnitude and the percentage of stance was measured at peak; the rate of loading was quantified between 200 N and 90% of the peak (following ref. 18); the instantaneous rate of loading was quantified over time intervals of 1.04 ms. When no distinct impact transient was present, the same parameters were measured using the average percentage of stance ±1 s.d. as determined for each condition in trials with an impact transient.

Estimation of effective mass. For groups 1 and 3, we used equation (2) to estimate the effective mass that generates the impulse at foot landing. The start of the impulse was identified as the instant at which the vertical GRF exceeded 4 s.d. of baseline noise above the baseline mean, and its end was chosen to be 90% of the impact transient peak (a 'real' time point among RFS runners, the average of which was used as the end of the transient in FFS runners who lacked a transient); this resulted in an impulse experienced, on average, through the first $6.2 \pm 3.7\%$ of stance. The integral of vertical GRF over the period of the impulse is the total impulse and was calculated using trapezoidal numerical integration within the MATLAB 7.7 environment using the TRAPZ function (Mathworks). Three-dimensional kinematic data of the foot (see above) were low-pass-filtered using a fourth-order Butterworth filter with a 25-Hz cut-off frequency. The vertical speed at the moment of impact was found by differentiating the smoothed vertical coordinate (smoothed with a piecewise-cubic Hermite interpolating polynomial) of the foot using numerical central difference. To minimize the effects of measurement noise, especially because we used differentiated data, we used the average of the three samples measured immediately before impact in calculating the impact speed. M_{eff} was then estimated as the ratio of the vertical GRF impulse (found by numerical integration) and the vertical impact speed (found by numerical differentiation).