Chapter 3

Repetition Without Repetition: A Comparison of the Laetoli G1, Ileret, Namibian Holocene and Modern Human Footprints Using Pedobarographic Statistical Parametric Mapping

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Abstract It is traditionally held that early hominins of the genus *Australopithecus* had a foot transitional in function between that of the other great apes and our own but that the appearance of genus *Homo* was marked by evolution of an essentially biomechanically modern foot, as well as modern body proportions. Here, we report the application of whole foot, pixel-wise topological statistical analysis, to compare four populations of footprints from across evolutionary time: *Australopithecus* at Laetoli (3.66 Ma, Tanzania), early African *Homo* from Ileret (1.5 Ma, Kenya) and recent modern (presumptively habitually barefoot) pastoralist *Homo sapiens* from Namibia (Holocene), with footprints from modern Western humans. Contrary to some previous analyses, we find that only limited areas of the footprints show any statistically significant difference in footprint depth (used here as an analogy for plantar pressure). A need for this comparison was highlighted by recent studies using the same statistical approach, to examine variability in the distribution of foot pressure in modern Western humans. This study revealed very high intra-variability (mean square error) step-to-step in over 500 steps. This result exemplifies the fundamental movement characteristic of dynamic biological systems, whereby regardless of the repetition in motor patterns for stepping, and even when constrained by experimental conditions, each step is unique or non-repetitive; hence, repetition without repetition. Thus, the small sample sizes predominant in the fossil and ichnofossil record do not reveal the fundamental neurobiological driver of locomotion (variability), essentially limiting our ability to make reliable interpretations which might be extrapolated to interpret hominin foot function at a population level. However, our need for conservatism in our conclusions does not equate with a conclusion that there has been functional stasis in the evolution of the hominin foot.

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Introduction

The origins and evolution of human striding bipedalism have long been a focus of human palaeontology and evolutionary biomechanics. However, the fossil evidence for the evolution of the postcranial skeleton has not been an unambiguous source of information. Claims that morphological features taken as human adaptations for terrestrial bipedalism reduce effectiveness in arboreal climbing are challenged by the combination of both capabilities in several indigenous modern human populations (Venkataraman et al. 2013a, b). This is a clear demonstration of neurobiological degeneracy (Seifert et al. 2016) and the high variability necessary for dynamic systems (Davids et al. 2003). These two theories underpinning biomechanical movement and locomotor adaptation are reviewed in the references provided but are not discussed in great detail here due to the nature of this publication. Briefly, however, both concepts can be illustrated by the everyday phrase, “there are many ways to skin a cat”. Thus, the long femoral necks and small femoral heads together with flaring iliac crests found in many australopiths (McHenry 1975) (but due to high biological variability, emphatically not all), versus large femoral heads and short femoral necks with sigmoid, non-flaring iliac crests in ourselves, must be interpreted as reflecting naturally high variation in biological forms. Undoubtedly, the mechanics of hip adduction and abduction must have been different in some australopiths; however, variation in morphology may act to achieve the same biomechanical effect on joint systems in different ways. Take, for example, clear evidence of facultative upright bipedal behaviour in *Gorilla gorilla* (see, e.g. Watson et al. 2009). Gorilla morphology isn’t designed specifically for upright bipedalism, but natural biological variation permits it. Very few papers in primatology, hominin palaeontology and human and non-human ape ichnopalaeontology address variation in bone morphology and footprint topology within the context of the locomotor system. Small fossil samples are often described as key for understanding human locomotor evolution or morphofunctional behaviour. Such relationships are often claimed from the evidence of a single individual without including either morphological variation or facultative capabilities. It is more reasonable to recognize that high natural intra-individual facultative variation elicits high inter-individual morphofunctional variation at a population level and vice versa. Both are a consequence of complex neurobiological evolution in biological systems. A noteworthy exception to a general lack of investigation of variability, however, is Dunn et al. (2014) on the *Gorilla* talus.

Leading cognitive and ecological motor skills specialists address biomechanical variation anchored by the theoretical paradigms of dynamical systems (Thelen 1995, 2005; Davids et al. 2003; Bartlett et al. 2007) and neurobiological degeneracy (Edelman and Gally 2001; Seifert et al. 2016). These paradigms have been increasingly influential in biomechanics, especially sports science. However, hominin

palaeontology has not yet taken these advances on board, while further being hampered by small sample size, which make it difficult to incorporate an understanding of the impact on variability in biological systems on evolutionary interpretations. For example, the biomechanical complexity involved in taking a step begins at the hip joint, a simple, single ball joint articulation, while the knee joint comprises the biarticular joint between femur and tibia and a third, sliding joint between the tibia and fibula. Thus, the knee joint is kinematically complex, with sliding (essentially planar), as well as rotatory motion. However, the structure predominantly concerned in transferring forces to the substrate (whether ground, branches or any other surface) is the foot. Here we face 26 bones (excluding sesamoids) which form 33 joints and are controlled by over 100 muscles, tendons and ligaments. Thus, given variation in the complexity of biomechanical forms, and a shortage of fossils, it is no wonder that functional interpretations of the evolution of the foot have been and still are interpreted in different and contradicting ways.

For example, the OH-8 *Homo habilis* foot has been described as (non-human) ape-like in some joints but not others (e.g. Kidd et al. 1996; and see Harcourt-Smith and Aiello 2004) but elsewhere more or less entirely humanlike in function (e.g. Day and Napier 1964). What humanlike in function implies for gait is obvious (habitually upright, striding steps), but what is the significance for gait of describing a foot as a mosaic of non-human ape-like and humanlike joints, when there are 33 joints to consider? In engineering parlance, such a complex system is described both as functionally redundant (there are many neuromechanical pathways to achieve a consistent motor pattern) and that its determinacy is low (it will be difficult to predict how the system will act in different iterations of the same task). Perhaps the most accessible review of these concepts as applied to biological systems can be found in Alexander (2003).

Since foot structure is so complex, and redundancy therefore so high, our confidence in eliciting functional information at a population level about species gait from comparisons of individual foot bones (e.g. Jungers et al. 2009; Ward et al. 2011) must be fairly low. There is some potential however to interpret biomechanical variability retrospectively from topological features of fossil footprint trails.¹ The basis of this potential is that a natural relationship between forces exerted on the ground by the foot, to balance, propel and control walking, and the consequent deformation of the ground could logically exist, given that

$$p = \frac{F}{A}$$

¹A *caveat* is required for the present paper: given our brief discussion here on variability and sample size, interpretations of the variability presented herein are made purely for the trackmaker as they took the 11 steps in this sample and cannot be extrapolated to predictions regarding a population locomotor mode. Furthermore, this is not an assessment of functional variability as would be required for inferring stability and balance behaviour: that would require thousands of steps. For an excellent tutorial on functional variability, equations and analysis techniques, see Bruijn et al. 2013.

where pressure (p) equals the amount of force (F) (the scalar of which is measured in Pascals (Pa)), acting per unit area (A) (Giancoli 2004). However, substrates, no matter their composition, will always reach a point at which maximum body weight is fully supported, and thus, the substrate stops deforming even though pressure is still being applied. Substrate composition at and below ground surface, substrate moisture content, even the electrical charge at the surface of substrate particles and a host of other factors can, however, be expected to interact with deforming forces delivered by the plantar surface of the foot. Thus, the shape of a footprint does not mirror the foot that made it due to substrate effects. We explored some of these interactions in Bates et al. (2013) (and see Supplementary Material) and concluded that the relationship of foot pressure and print depth varies with substrate compliance: substrate moisture and presence and depth of subsurface compaction levels, but also the mechanical requirements at toe off, influencing print topology.

A crucial recent discovery that of StW 573 *Australopithecus prometheus*, 3.67 Ma, which is over 90% complete (see e.g. Clarke 2019; Crompton et al. 2018) crucially, closely similar in date to the Laetoli footprint trails. The best known and most complete early human ancestor was *Australopithecus afarensis*, represented by the diminutive AL-288-1 Lucy skeleton, 3.4 Ma. Thus, despite her relatively late date, most locomotor interpretations of the Laetoli footprint trails have been based on the AL-288-1 Lucy skeleton (e.g. Crompton et al. 1998, 2012).

Since discovery of this partial (circa 30% complete) skeleton, her combination of humanlike knees with reconstructed limb proportions that were thought to indicate long arms and short legs, and her clear digital curvature, has fostered a long-term dispute on her locomotor behaviour. Some (e.g. Stern and Susman 1983, 1991; Stern et al. 1984) assert that these traits would have compromised her terrestrial bipedalism, so that she would have walked with a bent hip and knee (BHBK) posture and even a somewhat shuffling gait. Opposing are those who argue that she was an effective terrestrial biped and that the arboreal features are simply retained anachronisms (Latimer et al. 1987; Latimer and Lovejoy 1989; Latimer 1991).

Computer simulation and experimental studies have since shown that even her proportions as first reconstructed with effective fully upright bipedalism (e.g. Crompton et al. 1998; Kramer 1999; Kramer and Eck 2000) and that a BHBK gait in humans causes an unsustainable rise in core body temperature within 5 min of walking (Carey and Crompton 2005). Given the general similarity of muscular physiology in placental mammals, and all other things being equal, forwards dynamic modelling has, similarly, predicted BHBK gait to near double the metabolic costs of transport in *Au. afarensis* (Sellers et al. 2005; Nagano et al. 2005). More recently, other partial skeletons of this species, most notably KSD/VP 1-1 from Woranso-Mille (Lovejoy et al. 2016), but also other isolated bones or partial material from Afar (including material referred to AL-333, see, e.g. McHenry 1986), have shown that Lucy's small stature and long forelimbs are the exception rather than the rule. In fact, analysis of the StW 573 longbones now suggests that AL-288-1 probably did not have

particularly short legs in relation to arm length (Heaton et al. 2019). *Au. afarensis* now appears to be a very variable species both in stature and postcranial morphology, and this is further attested to by KSD/VP 1-1 being assigned to this species by Lovejoy et al. (2016).

To gain further enlightenment on the mode of locomotion in *Au. afarensis*, several groups have analysed the penecontemporaneous Laetoli footprint trails, holding that on the basis of the above-cited equation, footprint depth and topographical features must at the very least reflect foot-ground interactions. Early attempts focussed on features of single footprints chosen from the clearer G1 trail, and some declared that the footprints are essentially modern in character (Day and Wickens 1980; White 1980). Others argued that features such as a relatively abducted hallux with limited hallux print depth support a BHBK model for gait (Stern and Susman 1983). However, White and Suwa (1987) regard these features as taphonomic artifacts. This more than 30-year-old debate continues today.

Although it is now broadly accepted that selection of single prints for study is inappropriate, Meldrum and colleagues, as late as 2011, claim that a line in one footprint shows a chimpanzee-like mid-tarsal break, so claiming that *Au. afarensis* lacked a medial longitudinal arch (Meldrum et al. 2011). An opposing argument based on discussions with the chief taphonomist of the Laetoli footprint trails (pers. comm. Craig Feibel to RHC) suggests that this topographical feature is simply a product of natural sedimentological fracture in the substrate over time although this would require micro-sedimentological analysis to confirm. Statistical and biomechanical approaches to the Laetoli footprint trails have predicted the stride length, foot shape, body proportions and speed of the trackmaker (Alexander 1984; Reynolds 1987; Raichlen et al. 2010), and spatio-temporal characteristics of the same trail have been used as an analogy to predict speed of walking and energetic costs in *Au. afarensis* (to date, primarily AL-288-1) (Kramer and Eck 2000; Sellers et al. 2005).

Hatala et al. (2016) compared just 5 of the 11 taphonomically usable footprints from Laetoli G1 using an inappropriate regionalized (and hence anatomically biased, see, e.g. Pataky et al. 2011) topological analysis, to prints made by modern humans and bipedally walking chimpanzees. The authors concluded that topological features from the Laetoli G1 prints are evidence for a functionally unique locomotor mode. Specifically, the authors claim to be able to identify kinematic distinctions in foot and lower limb function and that the trackmaker probably walked with a more flexed knee posture, describing it as a form of bipedalism that was well developed but not equivalent (Hatala et al. 2016) to that of modern humans. Raichlen et al. (2010) found that a simple whole foot statistical comparison of heel and toe depths in the 11 usable prints indicated a fully upright posture. Crompton et al. (2012) used a rigorous combination of topographical whole foot statistical analysis and computer modelling to compare the mean tendency of the 11 usable G1 prints, predicting foot pressure in upright and BHBK gait. The authors conclude, similarly to Raichlen and colleagues, that they cannot have been made by an individual walking BHBK and were more likely left by an upright striding biped. Raichlen and Gordon's (2017) preliminary statistical comparison of heel and toe depth confirms these findings for the more extensive Laetoli S series, which were made by individuals of greatly varying stature.

Recently, Bennett et al. (2016) made a broader comparison of the Laetoli G1 trail both to prints from Ileret, made presumptively by early African *Homo erectus* and to Holocene pastoralist footprints from Namibia. On the basis of footprint depth, substrate conditions at the time of footprint formation of the Namibian trails, which cross from drier sandy bank sediments, through muds, and back to drier bank deposits in an ancient streambed, bridged those at Laetoli (relatively shallow and only slightly moist) and Ileret (deep and wet muds). The Namibian trackways, made in the Holocene age, were made by presumptively habitually barefoot individuals, and given the alteration that footwear induces in human plantar pressure, they are an invaluable control. Using third-party open-source code to derive mean and median tendencies of the tracks, they conclude that there is functional stasis between the 3.66 Ma (Crompton et al. 2012) Laetoli G1 trails and the circa 1.5 Ma (Bennett et al. 2009) Ileret trails. Inasmuch as this implies a fully upright gait at the time of footprint formation at Laetoli G1, this study is in accord with both that of Raichlen et al. (2010) and Crompton et al. (2012). Each of these studies used at least twice as many G1 footprints as did Hatala et al. (2016), raising the possibility that sample size, and further possible loss of variability between footprints due to their subjective selection of only five footprints, could account for their very different interpretations.

Because of this contradiction, an extended statistical analysis of variability in footprint topology using pedobarographic statistical parametric analysis (pSPM) of the Laetoli G1, Ileret and Namibian fossil footprint trails in comparison with experimental modern human plantar pressure records is presented here.

Methods

We employ the robust method of statistical parametric mapping (SPM), a topographical statistical approach first developed by Friston et al. (1995) for functional brain imaging and extensively validated by that group (open source). The algorithms have been further developed for foot pressure studies and incorporated into our open-source software pedobarographic statistical parametric mapping (pSPM), which has been further and extensively validated (e.g. Pataky 2010; Pataky and Goulermas 2008; Pataky et al. 2008, 2011). In its analogous extension to footprint depth, statistical comparison of the samples also uses pixel-level pairwise t-tests (Pataky and Goulermas 2008; Pataky et al. 2008) but here after normalization by plantar surface maximum depths. Methods follow Crompton et al. (2012) and Bates et al. (2013) except that we now employ automated registration where possible and use an enhanced method for isolating and normalizing prints. These changes and a full description of the method are presented in Supplementary Material (Fig. 3.4, data processing prior to registration. Figures 3.5, 3.6, 3.7 and 3.8 diagrammatically illustrate, registration and re-registration), together with all data processing and methodological sensitivity checks.

Results and Interpretations

Figure 3.1 presents the mean footprints and the results of topological statistical comparisons of 11 prints from the G1 trail at Laetoli (Leakey and Hay 1979; Leakey and Harris 1987), with 9 prints from the upper surface at Ileret (FwJj14E; Kenya) (Bennett et al. 2009), a 32 print sample from the Holocene trail at Walvis Bay, Namibia (Kinahan 1996; Morse et al. 2013), and a modern Western (thus habitually shoe wearing) dataset collected on a treadmill ($N = 100$ pressure records registered to create one mean print each from 10 individuals).

Habitually shod Western modern and presumably habitually unshod Holocene modern human footprints (Fig. 3.1a) show no areas of significant difference. The Ileret dataset differs significantly from that for modern Western humans ($p = 0.000$), (Fig. 3.1b) showing a deeper medial arch. The Laetoli mean shows significantly deeper medial arch and anterior heel impressions than the modern Western human mean (Fig. 3.1c) and significantly shallower hallucal impressions. The Ileret footprints are significantly different from the Holocene modern human mean (Fig. 3.1d), having a shallower medial arch and deeper distal toes, albeit under a small area in the midfoot ($p = 0.044$) and restricted to print edges. The latter could be the result of imperfect registration due to minor overall shape differences in the two populations or the subject dragging the foot from where it would have been sunken into the soft sediment. Most notably, the Holocene modern humans from Namibia and Laetoli means differ significantly (Fig. 3.1e) in only a very small area under the hallux.

Fig. 3.1 Statistical whole foot comparison of four footprint populations. The first and second footprint images in each comparison (a–f) are the mean image from the two species being compared. The third footprint image is the comparison of the two population means. The fourth footprint image is the inference plot determining the pixel-level locations of statistically significant differences between the two populations being compared; (a) habitually shod anatomically modern *H. s. sapiens* vs. habitually unshod *H. s. sapiens*; (b) habitually shod *H. s. sapiens* vs. early African *Homo erectus* footprints from Ileret; (c) habitually shod *H. s. sapiens* vs. Laetoli footprints; (d) presumptively habitually unshod (Namibia) *H. s. sapiens* vs. Ileret *Homo erectus* footprints; (e) habitually unshod *H. s. sapiens* vs. Laetoli footprints; (f) Ileret *Homo erectus* vs. Laetoli footprints. Inference plots represent the probability values for areas with statistically significant differences in footprint depth and are represented in the far-right column of each comparison. This column is blank in (a) designating no statistically significant differences in topology in this comparison

Finally, statistically significant differences between the Ileret and Laetoli means (Fig. 3.1f) exist in deeper impressions under small areas of MTH1, the hallux and the posterior medial heel.

Visual inspection of the experimental footprints provided in the contribution by Hatala et al. (2016) reveals that similarities in the forefoot and hallux depths of their modern human and selected Laetoli footprints more than exist with their selected chimpanzee footprint. The statistically significant deeper medial midfoot impression in Laetoli ($p = 0.000$) than in Western modern humans (Fig. 3.1c), also reported by Hatala et al. (2016), could be attributed to the effect of habitual shoe wearing in Western modern humans, creating a higher medial arch in this group (Stolwijk et al. 2013). We have shown through experimental studies of the relationship of footprint depth to footprint morphology (Bates et al. 2013) that there is a clear tendency for deeper prints to have relatively deeper forefoot impressions. It is therefore likely that the statistically significant differences between Laetoli and Ileret (Fig. 3.1f), and Ileret and Holocene modern human footprints (Fig. 3.1d) sampled here, are attributable to the greater overall footprint depth at Ileret. (The Laetoli sample showed a mean of 31 mm, range 26–37 mm; for Ileret the mean maximum plantar depth was 49 mm, the range 24–94 mm; see Supplementary Material in additional footprint discussion.) Here, moisture content was likely higher, based on sidewall suction against the foot producing long narrow tracks; by this interpretation, the moisture content likely weakened the sediment in which the tracks were made (Craig 1997; Bennett et al. 2016). Similarly, the relatively greater number of deep prints from Holocene modern humans (from a wetter substrate, mean maximum plantar depth was 45 mm and range 23–77 mm) compared to Laetoli could readily account for deeper hallux impressions in Holocene human footprints. Crompton et al. (2012) used computer modelling to simulate contact pressures under the foot in upright and flexed knee walking. They showed that bent knee or flexed knee walking produced higher forefoot than hindfoot pressures because of the anterior shift of the centre of mass (CoM). Their analysis of a larger dataset including all of those prints analysed by Hatala et al. (2016) revealed consistently deeper hindfoot than forefoot impressions, indicating full extension at the knee during upright walking (Ferris et al. 1998; see Crompton et al. 2003, 2008 on the relationship between the heel-strike transient and extended knee postures in orangutans). While any comparison of human and *Au. afarensis* postcrania strongly suggests that the locomotor systems of the Laetoli trackmaker and modern humans form biomechanically distinct kinematic chains, this does not necessarily imply dramatically different external ability and function (Bock 1965, 1994; Laland et al. 2015; Seifert et al. 2016). This interpretation follows the expectations from effects due to high functional redundancy (Latash et al. 2002) and high degrees of freedom in the foot (e.g. Wolf et al. 2008), both natural and essential components to be considered in analyses of fossil footprint trails and explaining the difference between prints and between populations via high variability.

Figure 3.2 represents all prints in the Laetoli G1 sample used in this analysis alongside 11 consecutive p-images collected during treadmill walking from a healthy human at 1.1 m/s (McClymont et al. 2016). This figure is not a statistical

Fig. 3.2 A visual representation of the variability in relative foot print depth (a) and plantar pressure (b); (a) footprint of whole foot pixel-level statistical topographical depth map of the Laetoli footprints used in this analysis, showing variable distribution of maximum depth step-to-step. Greatest depth is evident in combinations of heel, lateral midfoot and the lateral MTH5-2 step-to-step; (b) 11 consecutive registered whole foot pixel-level statistical pressure images collected from a treadmill walking trial at 1.1 m/s in *H. s. sapiens*. Areas in yellow are areas of highest variability (mean square error (MSE)) step-to-step. Greatest pressure is consistently evident in combinations of heel and lateral MTH4-1

comparison of relative depths (Laetoli) and plantar pressures (modern human) as the two samples were collected under completely different conditions. It is simply presented to visually demonstrate the variability in each step or fluctuations in foot-ground interactions during just 11 steps. While there are undeniable differences in foot shape and topography, they share similar variation in topology step-to-step. The Laetoli prints (Fig. 3.2a) are consistently deeper under the heel and lateral forefoot with steps 10 and 11 showing deeper depth under the whole forefoot than in previous steps. The human prints (Fig. 3.2b) despite being more consistent step-to-step due to the normalizing effects of the treadmill (Kang and Dingwell 2008) also show consistently high variability in pressure under the heel and MTH4, 3 and 1. We should note that the human subject does not represent the most variable subject from our Western human sample but instead the average. Again, this figure is not intended as a statistical comparison of relative depths and variability in pressure between the two subjects or across deep time. It is simply presented to visually illustrate the step-to-step variability of foot-ground interactions during locomotion despite two very different substrates and in a relatively tiny interpretive sample of only 11 footprints out of the thousands the individual took the day they were made. Tudor-Locke et al. (2017) showed that the average 20-year-old American male walks between 2247 and 12,334 and females 1755 and 9824 steps per day. This underlines the requirement of steps necessary to interpret the natural and characteristic patterns of variability that contribute to morphofunctional interpretations of the individual making fossil footprint trails.

The variation in relative depth in the sequence of 11 footprints reflects similar and thus normal biomechanical variation in stride dynamics in both the G1 trackmaker (Fig. 3.2a) following Alexander's (2003) work (and see Wainwright 1991; Wainwright et al. 2002) and reflecting Bernstein's (1967) classic description of human movement as 'repetition without repetition'. That is, each movement task (e.g. step) is driven by a unique set of neural and motor patterns, temporarily assembled to produce a task outcome (Latash et al. 2002) based on the unique mechanics of each step and the substrate upon and environment in which it is taken. Thus, while each step is programmed by the suit of bipedal evolutionary traits, each

step is unique. Thus, not only have we shown that there is intra-species variation in foot pressure within the great apes, sufficient for both Asian and African apes (orangutan and bonobo) to overlap in midfoot pressure patterns with habitually shoe-wearing humans (Bates et al. 2013), but our interpretations here are founded on intra-individual variation step-to-step, as predicted by Bernstein (1967) and Latash et al. (2002).

As mentioned earlier a very serious limitation in the analysis of fossil footprint data is sample size. Figure 3.3 (below) simulates the possible effects of Hatala et al.'s (2016) subjective selection of just 5 G1 footprints, by sampling the first, middle and last group of 5 prints from the 11 used here and available for ready analysis (Raichlen et al. 2010; Crompton et al. 2012). Indeed, as Hatala et al. (2016) observed, modern humans consistently have a deeper impression in the forefoot than that of the Laetoli hominin, irrespective of which sample is selected. However, the last final comparison in set (Fig. 3.2c) shows (considerably smaller) areas of the midfoot and anterior heel, where it is the Laetoli prints which are deeper. Thus, interpreting topological differences between the G1 prints is not immune to a subjective choice of prints, raising concerns about the conclusions of Hatala et al. (2016). On the assumption that footprints are correlated with foot pressure, even given the interactions with substrate characteristics alluded to above and which we dealt with in detail in Bates et al. (2013), our concerns are very deeply amplified by new data concerning the sample size required to reliably characterize human gait. Arts and Bus (2011) recommend only 12 steps per foot for clinical assessment of plantar pressure. Sample sizes of as little as 10, and at most 50, are commonly used to assess gait parameters including pressure and kinematics in clinical practice. The higher value of 50 slightly mitigates the effect of step-to-step variability that would otherwise perhaps lead to false interpretations, due to the high variability step-to-step (McClymont et al. 2016). Owings and Grabiner (2003) however have demonstrated that sample sizes of over 100 steps are needed to reliably characterize an individual's kinematics, to within 95% confidence. Equally, McClymont (2017) showed through a Monte Carlo subsampling analysis of random samples of >2000 footprints per subject that the individual trial N typically collected in plantar pressure studies in the literature ($N = 10\text{--}50$ p -images) produces MSE ranges that are more than 50% higher than from when sampled from a larger total individual N of >500. At $N = <10$ records this increases to more than 75%, indicating a high probability that such a small individual trial N would not reflect either the range of variation or the habitual mean pressure that would be represented by a larger dataset of consecutive foot print records. Acquiring a sample of more than 500 is clearly unfeasible for footprints and even for foot pressure in the infirm. However, samples of 100–138 would deliver around 95% confidence and might be achievable in the future at Laetoli S. But even assuming a close link between pressure and footprint depth, a sample of five, as used by Hatala et al. (2016), offers well under 25% confidence of assessing pressure characteristics, i.e. a probability of unreliable assessments. Indeed, our own sample of 11 would allow no better than 50% reliability; however, we are accounting for the effects of variability in our interpretations and not making confident claims for a new

locomotor mode, from what we know to be a biomechanically unsatisfactory sample size.

Discussion

Based on only very minimal statistically significant differences (just a few pixels) between Laetoli and unshod (Holocene) modern humans (Fig. 3.1e), and the commonality of stride-to-stride and step-to-step fluctuations illustrated in the Laetoli G-1 trail and the modern human example (Fig. 3.3a, b), we cannot find any evidence that the Laetoli trackmaker utilized a flexed knee posture at the time of formation of the prints examined, supporting previous results (Sellers et al. 2005; Raichlen et al. 2010; Crompton et al. 2012). The extended evolutionary synthesis (EES) (Laland et al. 2015), and the unifying theory of dynamical biological systems (Davids et al. 2003) and neurobiological degeneracy (Seifert et al. 2016), all predict high variability in adaptive biological systems, permitting rapid evolutionary change (Laland et al. 2015) and stable, functional movement (Bernstein 1967; Seifert et al. 2016). The high redundancy present in the anatomically complex structure of the foot is likely to be employed to control step-to-step dynamic variability in walking (Dingwell et al. 2010), and activation patterns are substantially subject to stochastic processes, reflecting neurobiological degeneracy (Seifert et al. 2016). We (Pataky et al. 2013) also found in a large sample of foot pressure records ($N = 5243$) that autocorrelation in maximal plantar pressure between steps is very weak, such that statistical power calculations found that a null hypothesis that local plantar pressure values are uncorrelated in short gait bouts is likely true with an average probability of 78.9%. This is both consistent with dynamical systems theory and very worrying for the analysis of short/discontinuous trails such as those at Ileret and similarly for the Hatala et al. G1 sample of five. While we have not attempted to quantify dynamic behaviour here, when pressure is taken as analogous to, but not equivalent to, depth in the Laetoli footprints, we can infer a flexible, upright hominin gait variably resisting perturbations to stabilize the CoM across the hot, damp ash (Dingwell et al. 2010). Recent evidence from a variety of substrates found that forefoot depth increased with moisture content in a modern human sample (Bates et al. 2013), leading to a requirement for increased forefoot forces to clear the foot from the substrate. We conclude that the differences in relative forefoot depths are a product of substrate, specifically of high moisture content in the modern human experimental sample, Ileret, and part of the Walvis Bay trail, versus relatively low moisture content (Craig 1997) at Laetoli.

Further visual inspection of the experimental footprints provided in the contribution by Hatala et al. (2016) reveals similarities in the forefoot and hallux depths of modern human and Laetoli footprints, more so than with the selected chimpanzee

Fig. 3.3 Subtraction of the *H. s. sapiens* mean p-images from the dataset collected in soft sandy sediments from Bates et al. (2013) and 3 alternative set means of 5 registered prints from the 11-print dataset of the Laetoli G1 trail; (a) the first set of five Laetoli footprints registered and the mean image compared with *H. s. sapiens* mean p-images following registration; (b) the second set of five Laetoli footprints registered and the mean image compared with *H. s. sapiens* mean p-images following registration; (c) the third set of five Laetoli footprints registered and the mean image, compared with *H. s. sapiens* mean p-images following registration

footprint. The relatively deeper experimental toe depths observed in the human and chimpanzee prints are likely due to the substrate effects described extensively by Bates et al. (2013), while the human and Laetoli hallucal impression indicating toe off is also clear. While not directly measuring dynamic behaviour, the unique case of fossil footprint trails is a reflection of dynamic behaviour that occurred at one time.

The reliability of assessment, putting aside substrate characteristics, is a major issue in interpreting gait from footprints: very loosely, Raichlen et al. (2010) and

Crompton et al. (2012) have at best a 50% chance that their conclusions that the G1 trackmaker walked upright are correct, and similarly Bennett et al. (2016) have at best a 50% chance that their conclusion of functional stasis between Laetoli and Ileret is correct. Hatala et al. (2016) have at best a one-in-four chance of having drawn a correct conclusion in claiming that the five prints chosen shown that the G1 trackmaker walked with a more flexed posture than ourselves. But, should Masao et al. (2016) discover more extensive footprints at Laetoli S, we may well get 50 continuous steps and up to near 90% reliability (again always given a good relationship of footprint depth with foot pressure), which would make the analysis of gait from footprint depth much more meaningful and promising.

The reconstruction of gait from the postcrania of early hominins however will require a different and more indirect strategy, as even in single bones, and not taking into account the functional redundancy of distal segments, we can expect high intra- and inter-taxon variability of trait morphology, some of which variation will not be functional (Bock and von Wahlert 1965), since motor control patterns adapt locomotor behaviour step-to-step based on each interaction between the body and the environment (Bernstein 1967; Riley and Turvey 2002). This is a primary tenet of dynamical systems theory, which has now matured into the concept of neurobiological degeneracy (see, e.g. Seifert et al. 2016), on which current biomechanical studies of gait variability are now almost always based. The prediction of overall gait patterns in early hominins such as *Au. afarensis* from morphology of proximal bony elements such as long-bone shaft and femoral neck cross-sectional geometry, as attempted by Ruff et al. (2016), is hazardous enough unless dynamic modelling is used to assess summed forces applied to the foot.

Conclusion

Based on the lack of statistically significant differences between Laetoli and unshod modern humans from Namibian footprint trails (Fig. 3.1e), and considering the commonality of stride-to-stride and step-to-step fluctuations in both trails (Fig. 3.1a, b), we find no evidence from this analysis that indicates the Laetoli trackmaker utilized a flexed knee posture beyond the range of variation in modern humans today (given the sediment characteristics and small sample of footprints). This supports previous findings for footprint analyses (Sellers et al. 2005; Raichlen et al. 2010; Crompton et al. 2012) and is consonant with studies showing that *Au. afarensis* was biomechanically capable of, and therefore likely to have performed, erect bipedality. It is possible that some or most australopith populations engaged in substantial arboreality, as suggested for AL-288-1 Lucy (Ruff et al. 2016), based on cross-sectional geometry of her long bones and femoral neck. It does not however follow that selection for arboreal activity reduced effectiveness in terrestrial bipedalism in australopiths. We have shown that footprints in the habitually unshod Holocene Namibian population and in the maker of Laetoli G1 could be very similar.

The primary theoretical argument underpinning our conclusions is that this is possible due to high degrees of variability expected in all aspects of morphology and locomotor behaviour across all biological species, and quantifiable by functional variability during movement (Bruijn et al. 2013). However, as is typical of paleontology, we are restricted by small sample sizes, and hence unable to capture the full biomechanical variation in movement which would have been present in the trackmaker at the time footprints were made. Thus, without the inclusion of, or reference to, the known variability in fossil populations, and the functional variability in locomotion in analogous, extant non-human ape populations, interpretations should only be made for the trackmaker and not used to predict species level behavior, or to suggest unique locomotor modes at the species level. Variability in morphology and behavior, and ontogenetic plasticity, although challenging for our understanding of human and non-human ape fossils, should equally be seen as key to our success in dealing with environmental change and expanding into a very wide range of new environments. Plasticity, in a real sense, is key to evolutionary biological success of all species.

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Supplementary Material

Detailed Materials and Methods

Ileret prints used in this analysis are from the upper footprint surface at FwJj14E (4° 18' 44" N; 36° 16' 16" E) and include five prints from the longest trail (FUT1-1, FUT1-3, FUT1-5, FUT1-6, FUT1-7), two prints from a shorter trail, (FUT3-1, FUT3-2) and four individual prints (FUI1, FUI2, FUI6, FUI7). They were imprinted in fine-grained tuffaceous silt and fine sand deposited as overbank flood deposits and assigned to *Homo erectus* on the basis of biometric inferences of body mass and stature (Bennett et al. 2009). The Laetoli prints (Leakey and Harris 1987) (Trail G1) used here are scans of first-generation casts of the Laetoli G1 prints at the National Museum of Kenya, laser-scanned using a Konica Minolta VI900 with a vertical resolution of 90 µm. Access to Day's photogrammetric data provided a vital check

on print morphology. Prints G1/28 and G1/30 were omitted due to excessive erosion and vegetation damaged and also G1/38 as the posterior heel imprint is missing through faulting (Crompton et al. 2012). On the edge of the Namib Sand Sea (Walvis Bay, Namibia), unshod footprints from the Holocene (11,500 ka) (Kinahan 1996; Morse et al. 2013) occur on silt surfaces, deposited as overbank flood deposits from the Kuiseb River and exposed between sand dunes (23° 00' 25" S; 14° 29' 26" E). These prints were excavated in 2010 and scanned using a Konica Minolta VI900 (Morse et al. 2013). The print makers are assumed to have been habitually unshod due to their African context and date, as well as the presence of skin (callus) texture visible in the footprints (Kinahan 1996; Morse et al. 2013). If footwear was worn on occasions, it is unlikely to have been laterally constrictive. Optical laser scans of 100 prints from 10 living, Western individuals, made in a laboratory tray filled with fine, moist sand, were recorded using an LDI PS-400, and the 10 subject means combined into an overall modern human mean (Crompton et al. 2012). Photographs and stereopairs of individual Laetoli prints are available in the Laetoli monograph (Leakey and Harris 1987), scans of both the Laetoli and Ileret prints have been previously published (Bennett et al. 2009; Crompton et al. 2012), and the prints from Namibia have also been well documented (Kinahan 1996; Morse et al. 2013). Consequently the replication of individual print images here would be redundant. Many are freely available online via Bennett's Bournemouth University website.

All footprint scans were rectified to the orthogonal plane and cropped so that only the plantar surface of each footprint was retained (Fig. 3.4). After removal of any additional surrounding sediment, the data was imported as XYZ point clouds into Matlab and processed using Liverpool's in-house software pedobarographic statistical parametric mapping (pSPM) (Pataky and Goulermas 2008; Pataky et al. 2008). This software was designed to compute measures of central tendency across multiple foot pressure images (Friston et al. 1995; Pataky and Goulermas 2008); however, by substituting pressure for depth, it has here been applied to footprint trails (Crompton et al. 2012). This substitution does not imply that we believe the relationship between foot pressure and footprint depth to be linear, permitting a direct and simple (yet biomechanically incorrect) interpretation of gait from footprint depth. Nevertheless, a natural relationship must exist given $p = \frac{F}{A}$, where pressure (p) is the amount of force (F) acting per unit area (A). Following this nomological premise, we trust this analogue to more robustly underpin interpretation from statistical comparisons and inferences on multiple records.

The pSPM software co-registers the entire plantar surface of a sample of footprints such that each pixel (footprint depth) corresponds to the equal anatomical location in all co-registered images. To achieve standardized comparisons, all point clouds were down-sampled into images of 1 mm² pixel dimensions. To enable standardized comparison of footprints of different absolute depths, each image was normalized by its own maximum depth such that pixel values ranged 0–1, with 0 corresponding to shallowest depth and 1 the point of maximum depth of the footprint as in our previous study (Bates et al. 2013). Registration of images within pSPM can be undertaken using a number of automated algorithms or through

Fig. 3.4 Diagrammatic explanation of the data processing carried out prior to registration and topological statistical analysis; (a) surfaced laser scan of modern human footprint; (b) ten points were selected on the under-formed surface surrounding the print (i.e. outside any displacement rims, fractured areas, etc.). A plane was subsequently fitted through these points, and (c) the rotation required to align this plane with the horizontal was applied to the footprint, thereby aligning print depth with the vertical axis; (d–e) the same horizontal plane was then lowered until it reached the highest topological point (i.e. shallowest depth) on the plantar surface of the footprint. All pixels above this plane were then cropped out leaving only the plantar surface (occasionally small surrounding areas of sediment were manually removed). Depth normalization was then carried out using the range of depths present across the plantar surface, culminated with a scaled depth range of 0–1, with the shallowest point (within the midfoot in e) having a value of 0 and the deepest point (in the hallux in e) having a value of 1

manual manipulation that involves the rotation and scaling of individual images to a common template image (Pataky et al. 2008). A previous study tested the accuracy and repeatability of manual registration and showed that it produces comparable and in some cases better results than various registration algorithms (Pataky et al. 2008). Where a higher level of divergence in topology occurs, such as with inter-species

comparisons, manual registration has been found to give better results (Crompton et al. 2012).

In this analysis topological variation required that the 9 Ileret prints were manually registered to each other, as were the 11 prints used from the G1 trail (Crompton et al. 2012). The Walvis Bay and modern human footprints were internally registered using an automated algorithm that minimized the root mean square error of pixels globally across pressure images (Pataky and Goulermas 2008). Registrations between populations of prints, facilitating cross-site (i.e. cross-species) comparisons were all performed manually. Here, all manual registrations were repeated three times to observe any impact of operator subjectivity on subsequent statistical tests.

Once registered, measures of central tendency can then be calculated to create statistical parametric maps (SPMs) and compared pixel by pixel using pairwise t-tests. Statistical comparison between print populations (i.e. different trails) is possible since probability values are available for every pixel in the SPM. Pixel-wise two-sample t-tests can be used to create a statistical image known as an “SPM {t}” (Pataky and Goulermas 2008; Pataky et al. 2008; Crompton et al. 2012) that provides a statistical comparison between two print populations. The large pixel numbers pose a potential problem since large t values (e.g. $t > 3$) are likely to occur simply by chance, and in a footprint or plantar pressure (which are the product of interaction between two continuous media) neighbouring pixels are clearly not independent.

However, neighbouring pixels tend to behave in a similar way due to the smooth outline, or boarder, of a print, and their t values form a generally smooth SPM, which can be shown to be topologically characteristic of a thresholded SPM (e.g. cluster size, number of clusters, etc.). Specifically, random field theory (RFT) is used to determine the t-threshold at which $\alpha = 5\%$ of the pixels would be expected to reach, simply by chance, based on the smoothness and on the foot shape which is parameterized by pixel connectivity with the plantar surface. Shape information is necessary because a square field, for example, would be expected to produce fewer suprathreshold clusters than would a long, narrow rectangular field of the same area and same smoothness. The SPM is then thresholded based on this critical t value, and one is left with some suprathreshold clusters of pixels that have survived the threshold. RFT then uses analytical probability density functions to compute the likelihood that clusters of the given size could have been produced by chance (Friston et al. 1995; Pataky and Goulermas 2008).

Figure 3.1 presents the mean footprints and the results of statistical comparisons of 9 prints from the upper surface at Ileret (FwJj14E; Kenya) (Bennett et al. 2009), with 11 prints from the G1 Trail at Laetoli (Leakey and Hay 1979; Leakey and Harris 1987), a 32-print sample from the Holocene trail at Walvis Bay, Namibia (Morse et al. 2013), and the modern Western, habitually shoe-wearing dataset ($N = 100$ footprints from 10 individuals). The first two images in each set are the site means, the third is their subtraction to show where they differ, while the fourth identifies those areas where the difference is statistically different using pixel-level pairwise t-tests

(Pataky and Goulermas 2008; Pataky et al. 2008) after normalization by plantar surface maximum depths and their probability level. These tests were carried out using the same methods used in previous studies (Crompton et al. 2012; Bates et al. 2013).

Additional Footprint Discussion

Comparison of footprint topology between sites with different substrates and geological properties is potentially difficult since the biomechanical signature of a trackmaker is mediated through the geotechnical properties of the substrate, and the substrate may also influence taphonomic modification (Craig 1997; Ditchfield

Fig. 3.5 An example of within-subject registration using ten prints from the modern, Western human dataset; (a) the ten prints are preprocessed as explained in Fig. 3.4. An initial registration is then performed that individually (i.e. one at a time) aligns the last nine prints with the first print in the dataset (not depicted above); (b) subsequently a second registration is performed in which all ten prints are individually (i.e. one at a time) aligned with their mean image; (c) the mean image itself. For the modern Western human and Namibian prints, this was carried out using automated algorithms

Fig. 3.6 Depiction of the same registration process shown in Fig. 3.5 for the Laetoli prints, in which registration was carried out manually (operator rotation and scaling of images) rather than using automated algorithms. The same manual registration was necessary on the Ileret prints

and Harrison 2011). In this analysis, at a macroscale we compared print populations from three natural environments, two from silt-rich flood/overbank deposits (Walvis Bay, Namibia and Ileret) (Crompton et al. 2012; Morse et al. 2013) and one from volcanic ash deposited via air-fall at Laetoli (Leakey and Harris 1987), with a sample of modern prints collected from fine sand in the laboratory. At the microscale, variation also exists within each depositional environment, dependent on local variations in grain size, moisture content, vertical stratigraphy and, significantly (especially the case at Laetoli), the degree of turbation by animal trampling (Morse et al. 2013). Substrate affects are particularly obvious in the Ileret prints, whereby withdrawal of the heel from soft, wet substrates causes side wall suction, naturally decreasing the macro-shape, specifically the width of the print (Craig 1997; Bennett et al. 2009; Morse et al. 2013). The enhanced longitudinal asymmetry – deeper forefoot (MTH1-3) than the heel – is also a feature of a softer substrate and is a visible feature in the mean Ileret print.

Technically, the substrate first holds the weight of the individual during the first phase of stance, only to fail further during the second phase associated with higher plantar pressures during toe off. The lack of clarity of toe impressions is a feature of deeper prints where foot withdrawal often modifies the impressions left by phalanges (Crompton et al. 2012). This is particularly evident at Ileret where toe drag is clear, associated with higher forces required to pull the toes out of deeper substrate. The medial longitudinal arch is also modified in softer substrates by the proximal movement of sediment under rotation of the ball of the foot, potentially producing a tendency towards a flatter arch in deeper prints.

Fig. 3.7 Non-linear registration of (a) modern human; (b) Ileret; (c) Laetoli; (d) Holocene human means registered to the Namibian mean

Fig. 3.8 Stage after registration to the reference mean, here Namibia, when individual prints are re-registered to the non-linear mean templates and the means regenerated

However, the methodology used in this analysis helps mitigate these influences. Principally, we are able to compare whole footprint populations on the basis of measures of central tendency rather than by comparing individual prints, which may

show strong individual substrate influences (Leakey and Harris 1987; Bennett et al. 2016; Morse et al. 2013). For cross-site comparisons it subsequently becomes important that the range of sedimentological properties exhibit overlap (i.e. in terms of their geomechanical strength), thereby isolating biological (anatomy and gait) similarities and differences that impact on footprint form. It is important to note that these sedimentological conditions may not directly or obviously translate into sediment characteristics that are easily measurable in the geological record, such as average grain size, sorting or composition. Broadly similar geomechanical properties (e.g. bearing capacity, Poisson ratio, etc.) may be produced by different combinations of physical sediment characteristics (Craig 1997). There is no doubt that further experimental work is needed to explore the influence of sedimentology on footprint form (and the range of variables that define a sediment's rheology). However, we suggest that in the absence of this experimental work, and a detailed mechanistic understanding, it is perhaps most appropriate to ensure comparisons are made on prints of overlapping depths since depth does appear to correlate with substrate strength (Bates et al. 2013; Morse et al. 2013).

References

- Alexander, R. M. N. (1984). Stride length and speed for adults, children, and fossil hominids. *American Journal of Physical Anthropology*, 63, 2–27.
- Alexander, R. M. N. (2003). *Principles of animal locomotion*. Princeton: Princeton University Press.
- Arts, M., & Bus, S. (2011). Twelve steps per foot are recommended for valid and reliable in-shoe plantar pressure data in neuropathic diabetic patients wearing custom made footwear. *Clinical biomechanics*, 26, 880–884.
- Bartlett, R., Wheat, J., & Robins, M. (2007). Is movement variability important for sports biomechanists? *Sports Biomechanics*, 6(2), 224–243.
- Bates, K.T., Savage, R., Pataky, T. C., Morse, S. A., Webster, E., Falkingham, P. L., Ren, L., Qian, Z., Collins, D., Bennett, M.R. McClymont, J., Crompton R.H. (2013). Does footprint depth correlate with foot motion and pressure? *Journal of the Royal Society Interface*, 10. <https://doi.org/10.1098/rsif.2013.0009>.
- Bennett, M. R., Harris, J. W. K., Richmond, B. G., Braun, D. R., Mbua, E., Kiura, P., Olago, D., Kibunjia, M., Omuombo, C., Behrensmeyer, A. K., Huddart, D., & Gonzalez, S. (2009). Early hominin foot morphology based on 1.5-million-year-old footprints from Ileret, Kenya. *Science*, 323(5918), 1197–1201. <https://doi.org/10.1126/science.1168132>.
- Bennett, M. R., Reynolds, S. C., Morse, S. A., & Budka, M. (2016). Footprints and human evolution: Homeostasis in foot function? *Palaeogeography, Palaeoclimatology, Palaeoecology*. <https://doi.org/10.1016/j.palaeo.2016.08.026>.
- Bernstein, N. (1967). *The co-ordination and regulation of movements*. Oxford: Pergamon.
- Bock, W. (1965). The role of adaptive mechanisms in the origin of higher levels of organisation. *Systematic Zoology*, 14(4), 272–287.
- Bock, W. (1994). Concepts and methods in ecomorphology. *Journal of Biosciences*, 19, 403–413.
- Bock, W., & von Wahlert, G. (1965). Adaptation and the form-function complex. *Evolution*, 19(3), 269.
- Bruijn, S. M., Meijer, O. G., Beek, P. J., & Van Dieën, J. H. (2013). Assessing the stability of human locomotion: A review of current measures. *Journal of the Royal Society Interface*, 10(83), 20120999.

- Carey, T. S., & Crompton, R. H. (2005). The metabolic costs of 'bent-hip, bent knee' walking in humans. *Journal of Human Evolution*, 48, 25–44.
- Clarke, R. J. (2019). Excavation, reconstruction and taphonomy of the StW 573 *Australopithecus prometheus* skeleton from Sterkfontein Caves, South Africa. *Journal of Human Evolution*, 127, 41.
- Craig, R. (1997). *Soil mechanics*. London: Chapman & Hall.
- Crompton, R. H., Li, Y., Wang, W., Günther, M. M., & Savage, R. (1998). The mechanical effectiveness of erect and 'bent-hip, bent-knee' bipedal walking in *Australopithecus afarensis*. *Journal of Human Evolution*, 35, 55–74.
- Crompton, R. H., Thorpe, S. K. S., Wang, W., Li, Y., Payne, R., Savage, R., Carey, T., Aerts, P., Van Elsacker, L., Hofstetter, A., Günther, M., & Richardson, R. (2003). The biomechanical evolution of erect bipedality. *Courier Forschungs-Institut Senckenberg*, 243, 115–126.
- Crompton, R. H., Vereecke, E. E., & Thorpe, S. (2008). Locomotion and posture from the common hominoid ancestor to fully modern hominins, with special reference to the last common panin/hominin ancestor. *Journal of Anatomy*, 212(4), 501–543.
- Crompton, R. H., Pataky, T. C., Savage, R., D'Aout, K., Bennett, M. R., Day, M. H., Bates, K., Morse, S., & Sellers, W. I. (2012). Human-like external function of the foot, and fully upright gait, confirmed in the 3.66-million-year-old Laetoli hominin footprints by topographic statistics, experimental footprint-formation and computer simulation. *Journal of the Royal Society Interface*, 9, 707–719.
- Crompton, R. H., McClymont, J., Thorpe, S., Sellers, S., Heaton, S., Pickering, T. R., Pataky, T., Stratford, D., Carlson, K., Jashashvili, T., Beaudet, A., Bruxelles, L., Goh, C., Kuman, K., & Clarke, R. (2018). Functional anatomy, biomechanical performance capabilities and potential Niche of StW 573: An *Australopithecus* Skeleton (circa 3.67 Ma) From Sterkfontein Member 2, 3 and its significance for The Last Common Ancestor of the African Apes and for Hominin Origins. *BioRxiv*. <https://doi.org/10.1101/481556>.
- Davids, K., Glazier, P., Araujo, D., & Bartlett, R. (2003). Movement systems as dynamical systems. *Sports Medicine*, 33(4), 245–260.
- Day, M. H., & Napier, J. R. (1964). Fossil foot bones. *Nature*, 201, 969–970.
- Day, M. H., & Wickens, E. H. (1980). Laetoli Pliocene hominid footprints and bipedalism. *Nature*, 286, 385–387.
- Dingwell, J., John, J., & Cusumano, J. (2010). Do humans optimally exploit redundancy to control step variability in walking? *PLoS Computational Biology*, 6(7). <https://doi.org/10.1371/journal.pcbi.1000856>.
- Ditchfield, P., & Harrison, T. (2011). Sedimentology, lithostratigraphy and depositional history of the Laetoli area. In T. Harrison (Ed.), *Paleontology and geology of Laetoli: Human evolution in context* (Geology, geochronology, paleoecology and paleoenvironment, vertebrate paleobiology and paleoanthropology) (Vol. 1, pp. 47–76). Dordrecht: Springer.
- Dunn, R. H., Tocheri, M. W., Orr, C. M., & Jungers, W. L. (2014). Ecological divergence and talar morphology in gorillas. *American Journal of Physical Anthropology*, 153(4), 526–541.
- Edelman, G. M., & Gally, J. A. (2001). Degeneracy and complexity in biological systems. *Proceedings of the National Academy of Sciences*, 98(24), 13763–13768.
- Ferris, D., Louie, M., & Farley, C. (1998). Running in the real world: Adjusting leg stiffness for different surfaces. *Proceedings of the Royal Society of London Series B: Biological Sciences*, 265(1400), 989–994.
- Friston, K. J., Holmes, A. P., Worsley, K. J., Poline, J. P., Frith, C. D., & Frackowiak, R. S. (1995). Statistical parametric maps in functional imaging: A general linear approach. *Human Brain Mapping*, 3, 165–189.
- Giancoli, D. (2004). *Physics: Principles with applications*. Upper Saddle River: Pearson Education.
- Harcourt-Smith, W. E. H., & Aiello, L. C. (2004). Fossils, feet and the evolution of human bipedal locomotion. *Journal of Anatomy*, 204, 403–416.
- Hatala, K., Demes, B., & Richmond, B. (2016). Laetoli footprints reveal bipedal gait biomechanics different from those of modern humans and chimpanzees. *Proceedings of the Royal Society Series B*, 283(1836), 20160235.

- Heaton, J. L., Pickering, T. R., Beaudet, A., Clarke, R. J., Bruxelles, L., Carlson, K. J., Crompton, R., Stratford, D. T., Kuman, K., McClymont, J., & Jashashvili, T. (2019). The long limb bones of the StW 573 *Australopithecus* skeleton from Sterkfontein Member 2: Descriptions and proportions. *Journal of Human Evolution*, 133, 167–197.
- Jungers, W. L., Harcourt-Smith, W. E. H., Wunderlich, R. E., Tocheri, M. W., Larson, S. G., Sutikna, T., Due, R. A., & Morwood, M. J. (2009). The foot of *Homo floresiensis*. *Nature*, 459, 81–84. <https://doi.org/10.1038/nature07989>.
- Kang, H. G., & Dingwell, J. B. (2008). Effects of walking speed, strength and range of motion on gait stability in healthy older adults. *Journal of Biomechanics*, 41(14), 2899–2905.
- Kidd, R. S., O'Higgins, P. O., & Oxnard, C. E. (1996). The OH8 foot: A reappraisal of the hindfoot utilizing a multivariate analysis. *Journal of Human Evolution*, 31, 269–291.
- Kinahan, J. (1996). Human and domestic animal tracks in an archaeological lagoon deposit on the coast of Namibia. *South African Archaeological Bulletin*, 51, 94–98.
- Kramer, P. A. (1999). Modeling the locomotor energetics of extinct hominids. *Journal of Experimental Biology*, 202, 2807–2818.
- Kramer, P. A., & Eck, G. G. (2000). Locomotor energetics and leg length in hominid bipedality. *Journal of Human Evolution*, 38, 651–666.
- Laland, K. N., Uller, T., Feldman, M. W., Sterelny, K., Müller, G. B., Moczek, A., Jablonka, E., & Odling-Smee, J. (2015). The extended evolutionary synthesis: Its structure, assumptions and predictions. *Proceedings of the Royal Society B: Biological Sciences*, 282(1813), 20151019.
- Latash, M., Scholz, J., & Schöner, G. (2002). Motor control strategies revealed in the structure of motor variability. *Exercise and Sports Science Review*, 30, 26–31.
- Latimer, B. (1991). Locomotor adaptations in *Australopithecus afarensis*: The issue of arboreality. In B. Senut & Y. Coppens (Eds.), *Origine(s) de la bipédie chez les Hominidés* (pp. 169–176). Paris: CNRS.
- Latimer, B., & Lovejoy, C. O. (1989). The calcaneus of *Australopithecus afarensis* and its implications for the evolution of bipedality. *American Journal of Physical Anthropology*, 78, 369–386.
- Latimer, B., Ohman, J. C., & Lovejoy, C. O. (1987). Talocrural joint in African hominoids: Implications for *Australopithecus afarensis*. *American Journal of Physical Anthropology*, 74, 155–175.
- Leakey, M., & Harris, J. (1987). *Laetoli: A Pliocene site in northern Tanzania*. Oxford: Clarendon Press.
- Leakey, M., & Hay, R. (1979). Pliocene footprints in the Laetoli beds at Laetoli, northern Tanzania. *Nature*, 278(5702), 317–323.
- Lovejoy, C. O., Latimer, B. M., Spurlock, L., & Haile-Selassie, Y. (2016). The pelvic girdle and limb bones of KSD/VP-1-1. Ethiopia. In Y. Haile-Selassie & D. F. Su (Eds.), *The postcranial anatomy of Australopithecus afarensis: 1051 New Insights from KSD-VP-1/1* (pp. 155–177). Dordrecht: Springer.
- Masao, F. T., Ichumbaki, E. B., Cherin, M., Barili, A., Boschian, G., Iurino, D. A., Menconero, S., Moggi-Cecchi, J., & Manzi, G. (2016). New footprints from Laetoli (Tanzania) provide evidence for marked body size variation in early hominins. *eLife*, 5, e19568. <https://doi.org/10.7554/eLife.19568>.
- McClymont, J. (2017). *Foot pressure variability and locomotor plasticity in hominins* (Doctoral dissertation, University of Liverpool).
- McClymont, J., Pataky, T. C., Crompton, R. H., Savage, R., & Bates, K. T. (2016). The nature of functional variability in plantar pressure during a range of controlled walking speeds. *Royal Society Open Science*, 3(8), 160369.
- McHenry, H. M. (1975). Biomechanical interpretation of the early hominid hip. *Journal of Human Evolution*, 4(5), 343–355.
- McHenry, H. M. (1986). Size variation in the postcranium of *Australopithecus afarensis* and extant species of Hominoidea. *Human Evolution*, 1(2), 149–155.

- Meldrum, D. J., Lockley, M. G., Lucas, S. G., & Musiba, C. (2011). Ichnotaxonomy of the Laetoli trackways: The earliest hominin footprints. *Journal of African Earth Sciences*, 60(1–2), 1–12.
- Morse, S. A., Bennett, M. R., Liutkus-Pierce, C., Thackeray, F., McClymont, J., Savage, R., & Crompton, R. H. (2013). Holocene footprints in Namibia: The influence of substrate on footprint variability. *American Journal of Physical Anthropology*, 151(2), 265–279.
- Nagano, A., Umberger, B. R., Marzke, M. W., & Gerritsen, K. G. M. (2005). Neuromusculoskeletal computer modeling and simulation of upright, straight-legged, bipedal locomotion of *Australopithecus afarensis* (A.L. 288-1). *American Journal of Physical Anthropology*, 126, 2–13.
- Owings, T., & Grabiner, M. (2003). Measuring step kinematic variability on an instrumented treadmill: How many steps are enough? *Journal of Biomechanics*, 36, 1215–1218.
- Pataky, T. (2010). Generalized n-dimensional biomechanical field analysis using statistical parametric mapping. *Journal of Biomechanics*, 43(10), 1976–1982.
- Pataky, T., & Goulermas, J. (2008). Pedobarographic statistical parametric mapping (pSPM): A pixel-level approach to plantar pressures image analysis. *Journal of Biomechanics*, 41, 2136–2143.
- Pataky, T. C., Caravaggi, P., Savage, R., Parker, D., Goulermas, J. Y., Sellers, W. I., & Crompton, R. H. (2008). New insights into the plantar pressure correlates of walking speed using pedobarographic statistical parametric mapping (pSPM). *Journal of Biomechanics*, 41(9), 1987–1994.
- Pataky, T. C., Bosch, K., Mu, T., Keijsers, N. L., Segers, V., Rosenbaum, D., & Goulermas, J. Y. (2011). An anatomically unbiased foot template for inter-subject plantar pressure evaluation. *Gait & Posture*, 33(3), 418–422.
- Pataky, T. C., Savage, R., Bates, K. T., Sellers, W. I., & Crompton, R. H. (2013). Short-term step-to-step correlation in plantar pressure distributions during treadmill walking, and implications for footprint trail analysis. *Gait & Posture*, 38(4), 1054–1057.
- Raichlen, D. A., & Gordon, A. D. (2017). Interpretation of footprints from site S confirms human-like bipedal biomechanics in Laetoli hominins. *Journal of Human Evolution*, 107, 134–138.
- Raichlen, D. A., Gordon, A. D., Harcourt-Smith, W. E., Foster, A. D. H., Jr., & W.R. (2010). Laetoli footprints preserve earliest direct evidence of human-like bipedal biomechanics. *PLoS One*, 5(3), e9769.
- Reynolds, T. (1987). Stride length and its determinants in humans, early hominids, primates, and mammals. *American Journal of Physical Anthropology*, 72, 101–115.
- Riley, M., & Turvey, M. (2002). Variability and determinism in motor behavior. *Journal of Motor Behaviour*, 34, 99–125.
- Ruff, C. B., Burgess, M. L., Ketcham, R. A., & Kappelman, J. (2016). Limb bone structural proportions and locomotor behavior in A.L. 288-1 (“Lucy”). *PLoS ONE*, 11(11), e0166095. <https://doi.org/10.1371/journal.pone.0166095>.
- Seifert, L., Komar, J., Araújo, D., & Davids, K. (2016). Neurobiological degeneracy: A key property for functional adaptations of perception and action to constraints. *Neuroscience & Biobehavioral Reviews*, 69, 159–165. <https://doi.org/10.1016/j.neubiorev.2016.08.006>.
- Sellers, W. I., Cain, G., Wang, W. J., & Crompton, R. H. (2005). Stride lengths, speed and energy costs in walking of *Australopithecus afarensis*: Using evolutionary robotics to predict locomotion of early human ancestors. *Royal Society Interface*, 2, 431–442.
- Stern, J. T., & Susman, R. L. (1983). The locomotor anatomy of *Australopithecus afarensis*. *American Journal of Physical Anthropology*, 60, 279–317.
- Stern, J. T., & Susman, R. L. (1991). ‘Total morphological pattern’ versus the ‘magic trait’: Conflicting approaches to the study of early hominid bipedalism. In B. Senut & Y. Coppens (Eds.), *Origine(s) de la bipédie chez les Hominidés* (pp. 99–112). Paris: CNRS.
- Stern, J. T., Susman, R. L., & Jungers, W. (1984). Arboreality and bipedality in the Hadar hominids. *Folia Primatologica*, 43, 113–156.
- Stolwijk, N. M., Duysens, J., Louwerens, J. W. K., van de Ven, Y. H., & Keijsers, N. L. (2013). Flat feet, happy feet? Comparison of the dynamic plantar pressure distribution and static medial foot geometry between Malawian and Dutch adults. *PloS One*, 8(2), e57209.
- Thelen, E. (1995). Motor development: A new synthesis. *American Psychologist*, 50(2), 79.

- Thelen, E. (2005). Dynamic systems theory and the complexity of change. *Psychoanalytic Dialogues*, 15(2), 255–283.
- Tudor-Locke, C., Schuna, J. M., Jr., Han, H. O., Aguiar, E. J., Green, M. A., Busa, M. A., Larrivee, S., & Johnson, W. D. (2017). Step-based physical activity metrics and cardiometabolic risk: NHANES 2005–06. *Medicine and Science in Sports and Exercise*, 49(2), 283.
- Venkataraman, V. V., Kraft, T. S., & Dominy, N. J. (2013a). Tree climbing and human evolution. *Proceedings of the National Academy of Sciences*, 110, 1237–1242.
- Venkataraman, V. V., Kraft, T. S., & Dominy, N. J. (2013b). Phenotypic plasticity of climbing-related traits in the ankle joint of great apes and rainforest hunter-gatherers. *Human Biology*, 85, 309–328.
- Wainwright, P. C. (1991). Ecomorphology: Experimental functional anatomy for ecological problems. *American Zoologist*, 31(4), 680–693.
- Wainwright, P., Bellwood, D., & Westneat, M. (2002). Ecomorphology of locomotion in labrid fishes. *Environmental Biology of Fishes*, 65(1), 47–62.
- Ward, C. V., Kimbel, W. H., & Johanson, D. C. (2011). Complete fourth metatarsal and arches in the foot of *Australopithecus afarensis*. *Science*, 331, 750–753.
- Watson, J., Payne, R., Chamberlain, A., Jones, R., & Sellers, W. I. (2009). The kinematics of load carrying in humans and great apes: Implications for the evolution of human bipedalism. *Folia Primatologica*, 80(5), 309–328.
- White, T. D. (1980). Evolutionary implications of Pliocene hominid footprints. *Science*, 208, 175–176.
- White, T. D., & Suwa, G. (1987). Hominid footprints at Laetoli: Facts and interpretations. *American Journal of Physical Anthropology*, 72, 485–514.
- Wolf, P., Stacoff, A., Liu, A., Nester, C., Arndt, A., Lundberg, A., & Stuessi, E. (2008). Functional units of the human foot. *Gait & Posture*, 28(3), 434–441.

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