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Osteogenic relationship between the lateral plantar process and the peroneal tubercle in the human calcaneus

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Abstract

The osteogenic relationship between the lateral plantar process and the peroneal tubercle has been an uncertainty for researchers over several decades. While some argue there to be no developmental relationship between these two calcaneal structures, others have suggested that there is an inverse relationship, the lateral plantar process forming from a part of the peroneal tubercle. However, no previous studies have offered quantitative measurements to test these hypotheses. In this study, we measured the size of the peroneal tubercle, retrotrochlear eminence, and the size and area of the lateral plantar process in 73 subjects using magnetic resonance imaging (MRI). Navicular height was measured using weight-bearing radiographs as a measurement of longitudinal arch in 35 of these subjects. Age, body mass, and body mass index (BMI) were also recorded for all subjects. We determined that there was a significant positive correlation between the lateral plantar process and size of the peroneal tubercle, body mass, and BMI. Thus, assertions that there is an inverse relationship between the size of the lateral plantar process and the peroneal tubercle are here unfounded. We also determined there to be a positive correlation between the peroneal tubercle and both the size of the retrotrochlear eminence and the height of the navicular. In conclusion, we relate these novel findings to hominin fossil calcanei and discuss the evolutionary and biomechanical implications.

Key words: *Australopithecus afarensis*; *Australopithecus sediba*; calcaneus; lateral plantar process; peroneal tubercle; retrotrochlear eminence.

Introduction

The calcaneus is the largest bone in the foot and has evolved specific anatomies thought to be functionally related to habitual bipedalism. Over the past century, many scholars have commented on the variability of several structures that make up the human calcaneus. Of particular interest in this study are three anatomies: the lateral plantar process (also known as the processus lateralis or the external plantar tubercle), the peroneal tubercle (also known as the peroneal trochlea or the processus trochlearis), and the bony ridge which connects the two protuberances known as the retrotrochlear eminence (see Fig. 1a,b for an anatomical representation).

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The lateral plantar process is a bony protuberance that has been hypothesized to increase the surface area of the heel to aid in force dissipation during heel-striking bipedalism (Latimer & Lovejoy, 1989). It is a uniquely human structure (Weidenreich, 1923). Both the relative position and the size of the lateral plantar process have featured prominently in debates about early hominin foot evolution and bipedal adaptations (Latimer et al. 1982; Stern & Susman, 1983; Susman et al. 1984; Latimer & Lovejoy, 1989; Zipfel et al. 2011; DeSilva et al. 2013). Moreover, the anteroposterior location of the lateral plantar process has been suggested to be variable in modern humans (Laidlaw, 1905; Edwards, 1928; Elftman & Manter, 1935).

The peroneal tubercle is a protuberance located on the lateral side of the calcaneus. The peroneus longus and peroneus brevis tendons pass on either side of the peroneal tubercle, and fibers of the peroneal retinaculum insert into this structure (Kelikian & Sarrafian, 2011). Hyer et al. (2005) suggests its function is to act as a pulley, or fulcrum, for the peroneus longus tendon, directing the tendon towards the cuboid. In humans, this structure is not weight-bearing and

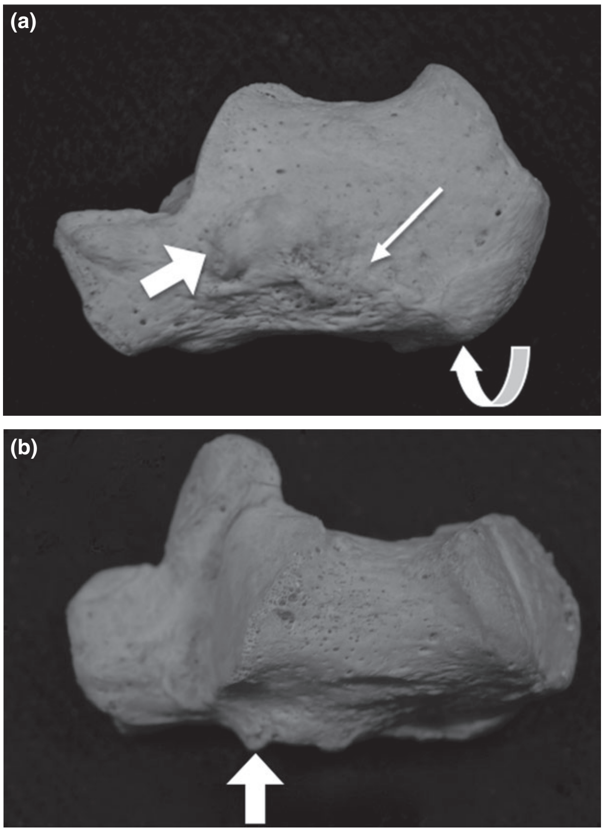

Fig. 1 (a) Photograph of a modern human calcaneus in lateral view with locations of the peroneal tubercle (straight arrow), retrotrochlear eminence (thin arrow), and lateral plantar process (curved arrow). (b) Photograph of a modern human calcaneus in axial view with location identified of the peroneal tubercle (straight arrow).

is relatively smaller than that seen in the apes, whose large peroneal tubercles are indicative both of an increased role of the peroneal musculature during arboreality (Stern & Susman, 1983) and an inverted foot structure, which causes the peroneal tubercle to support weight during the stance phase of gait (Lewis, 1983; Deloison, 1985).

Humans have a relatively large lateral plantar process and a small peroneal tubercle, whereas non-human anthropoids (monkeys and apes) have an indistinct (or absent) lateral plantar process and a rather large peroneal tubercle. For this reason, Weidenreich (1940) hypothesized that these structures share a developmental origin and that the large human lateral plantar process arose from the peroneal tubercle such that there exists an inverse relationship between these two bony structures (Weidenreich, 1923, 1940; Lewis, 1983; Susman et al. 1984). However, others have countered that there is no developmental association between the lateral plantar process and the peroneal tubercle (Meyer & O'Rahilly, 1976; Latimer & Lovejoy, 1989). Latimer & Lovejoy (1989:376) in particular argued that it is "developmentally implausible" for the lateral plantar process to be derived from the peroneal tubercle since the two structures arise from separate ossification sites. Instead, Latimer & Lovejoy (1989) hypothesize that a homologous region to the human lateral plantar process exists in the calcaneus of non-human anthropoids and can be best seen as an 'anterior projection' of the growth plate along the lateral aspect of a subadult ape calcaneus. Early in hominin evolution, this region of the calcaneal growth plate presumably migrated plantarly, forming the human lateral plantar process. In support of this hypothesis, Latimer & Lovejoy (1989) note that the structure connecting the lateral plantar process and the peroneal tubercle (the retrotrochlear eminence) is horizontally positioned in non-human apes, but is oblique in humans: indicative of this plantar migration of the lateral plantar process.

These disagreements in the developmental origin of the lateral plantar process cannot be dismissed as semantics. If the lateral plantar process is developmentally derived from the peroneal tubercle, then the enlarged peroneal tubercle and the somewhat small lateral plantar process in the early hominin *Australopithecus afarensis* would render their calcanei quite ape-like and therefore primitive in their bipedal mechanics (e.g. Stern & Susman, 1983). However, if the lateral plantar process has no developmental association with the peroneal tubercle, then the plantar position of the lateral plantar process in *Au. afarensis* (rather than the size) would be the critical anatomy and would align these bones with humans, suggesting that a major anatomical shift to upright walking had occurred by 3.2 million years ago (Ma). Furthermore, the primitive, *dorsal* position of the lateral plantar process in *Australopithecus sediba* (Zipfel et al. 2011) would be both functionally and perhaps phylogenetically surprising, given the species' 1.977 Ma date.

These previous studies which examined the relationship between the lateral plantar process and the peroneal tubercle did not provide quantitative evidence to support their claims, and instead relied on qualitative observations of dry-bone calcanei. In this study, we evaluate the hypothesis of a developmental relationship using magnetic resonance imaging (MRI) to quantify the size of the peroneal tubercle, retrotrochlear eminence, and lateral plantar process and relate these values to biometric information of modern human subjects. We test the hypothesis that an inverse relationship exists between the lateral plantar process and the peroneal tubercle as proposed by Weidenreich (1940) nearly 75 years ago.

Material and methods

Subject selection

The study was approved by the Partners Healthcare Inc. Institutional Review Board and was Health Insurance Portability and Accountability Act compliant. A retrospective search was performed for ankle MRI imaging obtained at Massachusetts General Hospital from January to August 2012, regardless of clinical indication. Exclusion criteria included subjects who did not have an identifiable peroneal tubercle or a lateral plantar process; had a suboptimal MRI exam; or presented evidence of prior surgery and/or tumors in any structure of the foot/ankle. Females < 12 years old and males < 14 years old were also excluded because ossification of the posterior epiphysis to the main body of the calcaneus had not yet commenced (Scheuer & Black, 2000).

Seventy-three ankle MRI were chosen that met the above criteria. Age and body mass at time of scan were recorded. Of the 73 subjects, 35 also had a lateral weight-bearing plain film radiograph of their foot, which was used to quantify arch height. The 73 subjects included 27 males and 46 females, age range 12–84 (42.8 ± 15.9 years). Only 2.7% (2/73) of subjects were females below 18 years of age and 4.1% (3/73) of subjects were males all with commenced ossification of the posterior calcaneus to the calcaneal body. MRI data on the peroneal tendons and peroneal tubercle size from 50 subjects were previously reported (Taneja et al. 2013).

Imaging

All MRI exams were performed following a departmental protocol on 1.0-T, 1.5-T or 3.0-T scanners, in supine position and neutral flexion of the ankle, using a phased array coil. The majority of the exams used the following pulse sequence parameters: sagittal spin-echo (SE) T1-weighted [TR/TE, 550/11; NEX, 1; matrix, 384 × 320; slice thickness, 3 mm; field of view (FOV), 15 cm], sagittal fat-suppressed proton-density (PD)-weighted (TR/TE, 5366/37; NEX, 1; matrix, 384 × 320; slice thickness, 3 mm; FOV, 15 cm), axial fast spin-echo (FSE) PD-weighted (TR/TE, 3366/24; NEX, 2; matrix, 384 × 320; slice thickness, 3 mm; FOV, 13 cm), axial fat-suppressed PD-weighted (TR/TE, 4716/39; NEX, 2; matrix, 384 × 320; slice thickness, 3 mm; FOV, 13 cm), and coronal fat suppressed FSE PD-weighted (TR/TE, 2816/37; NEX, 2; matrix, 512 × 384; slice thickness, 4 mm; FOV, 14 cm). Intravenous contrast-enhanced pulse sequences were performed in some subjects when further visualization of the soft-tissue structures of the foot/ankle were clinically warranted but were not used for analysis and were not of any relevance for this study of bony anatomy.

Standard weight-bearing foot radiographs in lateral view were assessed when available. As none of the authors of this paper was present during the acquisition of these radiographs, it is not known whether these radiographs were taken in the more realistic angle and base of gait position or in the standard view with the feet together and positioned forward. However, we are unconcerned about this impacting the results of our study, given evidence that either position produces similar, reproducible measurements (Bryant, 2001).

Anatomical measurements

All measurements were performed in a Picture Archiving and Communication System (PACS) viewer (OsiriX software, version 5.6; Pixmeo SARL, Bernex, Switzerland). The size of the peroneal tubercle and retrotrochlear eminence were measured by tracing a line from their apex perpendicular to a baseline along the external surface of the lateral calcaneal cortex on axial PD-weighted or T1 images (Fig. 2). Both the maximum mediolateral width and area of the lateral plantar process were measured on the coronal

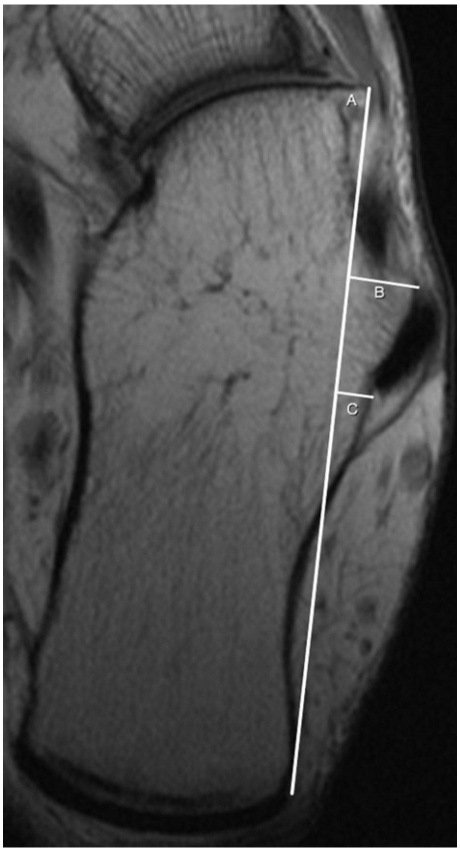

Fig. 2 Female, 49 years old, 32.2 kg m^{-2} BMI. Axial PD-weighted MRI image of the left foot at the calcaneus level. Line A represents baseline; line B, peroneal tubercle (7.0 mm); line C, retrotrochlear eminence (3.6 mm).

slice where the lateral plantar process apex appeared most prominent. Mediolateral width and area were measured in reference to an oblique line along the lateral cortical edge of the calcaneus (Fig. 3). Arch height was quantified by measuring the navicular height on the medial side of weight-bearing radiographs. This measurement was obtained by creating a horizontal baseline from the most plantar aspect of the first metatarsal head to the most plantar surface of the posterior calcaneus. A perpendicular line was then drawn from the most plantar surface of the navicular tuberosity to the reference baseline to yield a quantification of arch height.

Statistical analysis

All statistics were calculated using JMP (version 5.0.1; SAS Institute, Cary, NC) and MedCalc software (version 12.3.0.0, MedCalc, Ostend, Belgium). Variables were tested for normality of distribution using the Shapiro–Wilk test. Variables that were not normally distributed were log-transformed. Linear regression analysis was performed. Intra-class correlation coefficient (ICC) was performed to determine absolute intra-observer agreement by C.M.G. and absolute inter-observer agreement between C.M.G. and J.M.D. in 20 randomly selected subjects regarding lateral plantar process size and area. ICC ranges from 0 (no agreement) to 1 (perfect agreement). Data are presented as mean ± standard deviation.

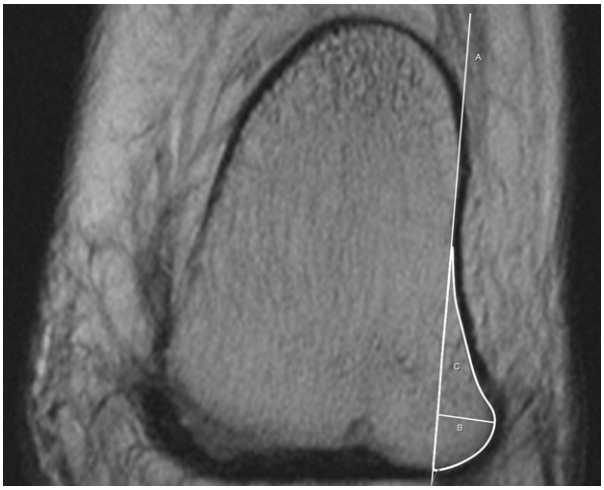

Fig. 3 Female, 49 years old, 32.2 kg m^{-2} BMI. Coronal PD-weighted MRI image of the left calcaneus. Line A represents baseline; line B, maximal mediolateral width of the lateral plantar process (5.8 mm); all of the area within 'B' and 'C' corresponds to the lateral plantar process area (0.6 cm^2).

Results

Subject characteristics and measurements are shown in Table 1.

Lateral plantar process

There was a positive correlation between lateral plantar process mediolateral width and log peroneal tubercle ($r = 0.25$, $P = 0.03$). The lateral plantar process positively correlated with log body mass ($r = 0.41$, $P = 0.0003$) (Fig. 4). There was a positive correlation with log body mass index (BMI) ($r = 0.38$, $P = 0.002$). No significant association was found with navicular height, retrotrochlear eminence, or age ($P > 0.1$). ICC was almost perfect for intra-observer agreement (0.9286, 95%CI: 0.8195–0.9718) and almost perfect for inter-observer agreement (0.9049, 95%CI: 0.7588–0.9624).

Table 1 Subject characteristics and measurements. Data are mean ± standard deviation. Ranges are in parentheses.

Variable	Subjects (n = 73)
Age, years	42.8 ± 15.9 (12–84)
Body mass, kg	77.1 ± 22.8 (43.6–140.6)
Height, m	1.7 ± 0.1 (1.5–1.9)
BMI, kg m^{-2}	26.8 ± 7.9 (15.3–54.5)
Peroneal tubercle, mm	3.1 ± 1.7 (1.0–9.9)
Retrotrochlear eminence, mm	3.7 ± 1.4 (1.2–7.1)
Lateral plantar process, mm	3.0 ± 1.3 (0.1–6.2)
Lateral plantar process area, cm^2	0.2 ± 0.1 (0.03–0.6)
Navicular height, cm*	3.0 ± 0.7 (0.9–4.2)

*Data available for 35 subjects.

Lateral plantar process area

There was a trend towards a positive association between log lateral plantar process area and log peroneal tubercle ($r = 0.22$, $P = 0.07$) and the height of the subjects ($r = 0.25$, $P = 0.04$). The log lateral plantar process area positively correlated with log body mass ($r = 0.47$, $P \leq 0.0001$) (Fig. 4), and with log BMI ($r = 0.41$, $P = 0.001$). No significant association was found with navicular height, retrotrochlear eminence, or age ($P > 0.1$). ICC was almost perfect for intra-observer agreement (0.9341, 95%CI: 0.8333–0.9739) and almost perfect for inter-observer agreement (0.9523, 95% CI: 0.8647–0.9819).

Peroneal tubercle

There was a positive correlation between log peroneal tubercle and the retrotrochlear eminence ($r = 0.36$, $P = 0.002$). Navicular height positively correlated with log peroneal tubercle ($r = 0.40$, $P = 0.02$). The peroneal tubercle positively correlated with height ($r = 0.30$, $P = 0.02$). There were no significant associations between the peroneal tubercle and age, body mass or BMI ($P > 0.1$).

Discussion

In this study we present the first quantitative examination of the lateral plantar process and the peroneal tubercle in modern human calcanei. Rather than finding an inverse relationship between the lateral plantar process and the peroneal tubercle, we found that the sizes of these structures are positively correlated. These data therefore challenge suggestions that the lateral plantar process is developmentally derived from the peroneal tubercle. Our data further reveal that the size of the lateral plantar process is correlated with body mass. Furthermore, we determined that there was a positive association between the size of the peroneal tubercle and the retrotrochlear eminence, even though the relative size of the retrotrochlear eminence has been thought to have uninformative variability in comparison with surrounding structures (Laidlaw, 1904; Weidenreich, 1940).

As seen in Table 1, mean peroneal tubercle size was 3.1 mm, the same as that reported by Hyer et al. (2005) in a sample of 58 dry-bone calcanei. Many have previously reported that abnormally enlarged peroneal tubercles are correlated with an increased instance of peroneal tendon abnormalities and peroneus longus tenosynovitis due to increased tension on the tendons (Burman, 1953, 1956; Bisceglia et al. 1983; Ford, 1995; Boles et al. 1997; Hyer et al. 2005; Sugimoto et al. 2009). As a result of hypertrophied peroneal tubercles, which have been documented in

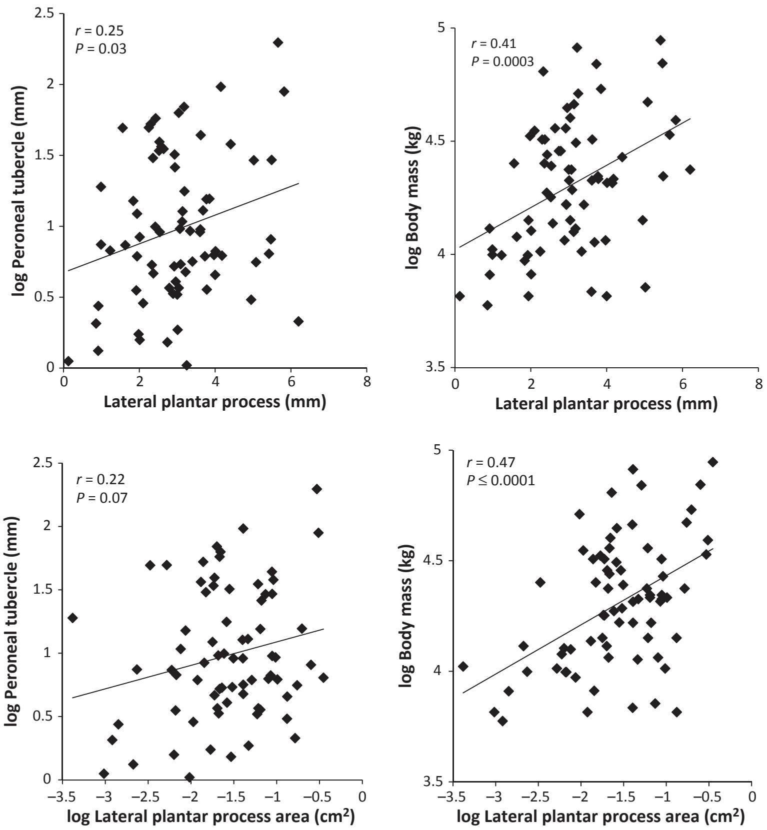

Fig. 4 Positive associations with the lateral plantar process mediolateral width and area with both the peroneal tubercle and body mass.

some cases to be in the same plane as the lateral malleolus, peroneal tubercle reductive surgery has occurred to relieve pain in the feet, when orthotics or other therapeutic methods did not reduce clinical discomfort (Berenter & Goldman, 1989).

The anatomical positioning of the lateral plantar process, although presumably a weight-bearing structure, was seen to be qualitatively variable in our study population of modern human calcanei. Overall, the lateral plantar process was anteroposteriorly variable to a degree of approximately 8 mm in our population (equivalent to two 4-mm coronal MRI slices) when viewed alongside sagittal images. Additionally, there was also a great degree of variation in the dorsoplantar positioning of the lateral plantar process, as represented in Fig. 5a,b in two individuals with similar BMI. How the anteroposterior or dorsoplantar positioning of the lateral plantar process impacts heel position during gait is currently unclear and is under study.

Calcanei (A.L. 333-8 and A.L. 333-55) from the 3.2 Ma *Au. afarensis* have enlarged peroneal tubercles (Latimer et al. 1982; Stern & Susman, 1983; Susman et al. 1984). These calcanei were later described to have lateral plantar processes in the modern human position (plantar), though relatively smaller than seen in most modern humans (Latimer & Lovejoy, 1989). In light of our data, the smaller lateral plantar processes of *Au. afarensis* may simply reflect smaller body size in this species than in most modern humans. Furthermore, our data provide evidence for a positive correlation between the lateral plantar process and the peroneal tubercle, supporting Latimer & Lovejoy (1989), who suggested that these structures are developmentally disjointed. The inverse correlation predicted by many scholars (Weidenreich, 1923, 1940; Lewis, 1983; Stern & Susman, 1983; Susman et al. 1984; Deloison, 1985, 1991; Stern, 2000; Sarmiento, 2012) to exist between the lateral plantar process and the peroneal tubercle was not found in this study. Therefore, we suggest that a critical evolutionary difference between the calcaneus of a human and that of an ape is not the relative sizes of the lateral plantar process and the peroneal tubercle, but the relative *position* of the lateral plantar process (as argued by Latimer & Lovejoy, 1989). One quite important consequence of this interpretation of calcaneal evolution is the strikingly primitive, ape-like, morphology of the calcaneal tuber in *Au. sediba* (Zipfel et al. 2011; DeSilva et al. 2013), a species that otherwise has quite *Homo*-like anatomies (Berger et al. 2010; Kibii et al. 2011; Kivell et al. 2011). This mosaic would imply considerable homoplasy in postcranial anatomies during hominin evolution (Wood & Harrison, 2011).

What remains unclear is why *Australopithecus* had a significantly larger peroneal tubercle than modern humans have. Stern & Susman (1983) maintained that the enlarged peroneal tubercles in *Au. afarensis* were skeletal indicators of large peroneus longus and peroneus brevis musculature

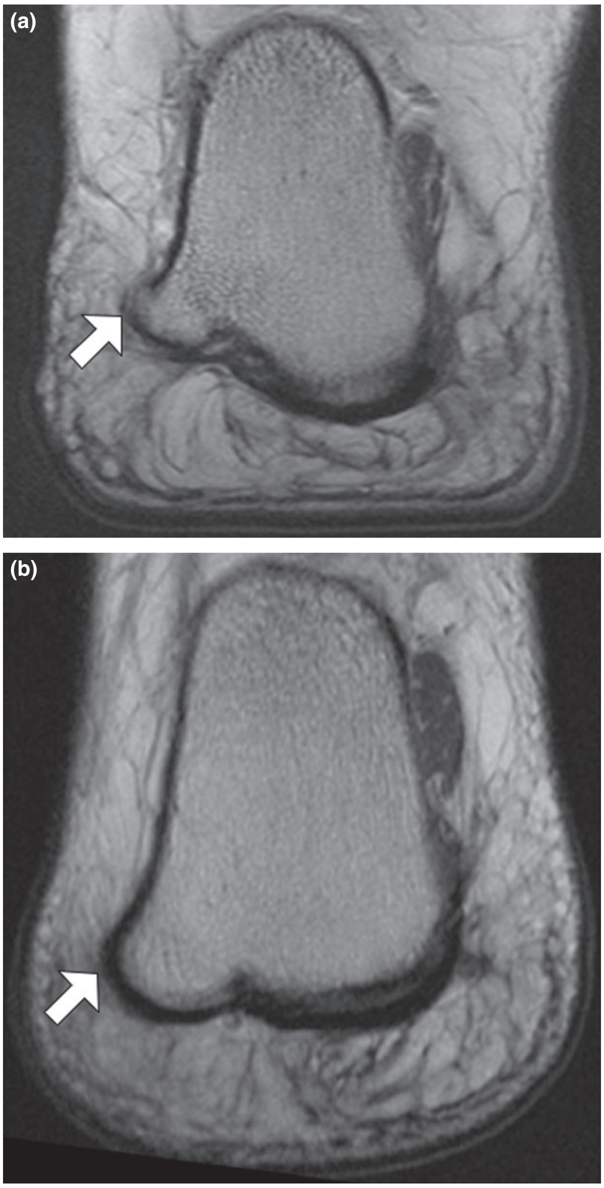

Fig. 5 (a) Female, 44 years old, 27.4 kg m^{-2} BMI. Coronal PD-weighted MRI image of the right calcaneus with a more superior-oriented lateral plantar process (white arrow). (b) Male, 18 years old, 28.1 kg m^{-2} BMI. Coronal PD-weighted MRI image of the left calcaneus with a more plantar-oriented lateral plantar process (white arrow). Image has been vertically mirrored for comparison.

which were critical for foot posture and weight transfer during tree-climbing. Latimer & Lovejoy (1989) countered that the peroneals were enlarged in *Australopithecus* to assist with foot plantar flexion during bipedalism in the absence of a strong Achilles tendon, which may have evolved later. Both of these hypotheses are reasonable and our data do not support one or the other. Additional fossil calcanei from Pleistocene *Homo* will help test these hypotheses by determining when the peroneal tubercle began to reduce in size.

Hyer et al. (2005) suggested that an increase in peroneal tubercle size is not just congenital but also may be an acquired bony abnormality as a result of having flat feet. However, in measuring navicular height as representative of the longitudinal arch in 35 of the 73 subjects, we determined that there was a *positive* correlation between navicular height (arch height) and peroneal tubercle size. Therefore, modern individuals with higher arches are more likely, in our study, to have larger peroneal tubercles. On the other hand, it is also true that chimpanzees have relatively larger peroneal tubercles than modern humans, but also have a flat foot. It is therefore likely that there are different driving mechanisms between enlarged peroneal tubercles in chimpanzee and in humans, making it difficult to interpret the functional significance of the peroneal tubercle in early human ancestors.

In conclusion, we have presented the first quantification of a positive relationship between the lateral plantar process and the peroneal tubercle and body mass using modern MRI imaging techniques. We have also determined that there is a positive correlation between navicular height and the size of the peroneal tubercle. A limitation of this retrospective study is that we did not have clinical data on gait kinematics of our subjects. Despite this limitation, the large cohort of patients used and the precise digital measurements collected increased the strength of our findings. We hope that future anatomical work on the calcaneus will report quantitative results and also employ more modern quantification techniques to test our findings and to better understand the evolutionary and functional significance of anatomies present in early hominin fossils.

Conflict of interest

No conflicts of interests.

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