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Year: 2022

Version: Published version

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Please cite the original version:

Kunimasa, Y., Sano, K., Oda, T., Nicol, C., Komi, Paavo V., & Ishikawa, M. (2022). Muscle-tendon architecture in Kenyans and Japanese : Potential role of genetic endowment in the success of elite Kenyan endurance runners. *Acta Physiologica*, 235(2), Article e13821.
<https://doi.org/10.1111/apha.13821>

Muscle-tendon architecture in Kenyans and Japanese: Potential role of genetic endowment in the success of elite Kenyan endurance runners

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Funding information

Japan Society for the Promotion of Science, Grant/Award Number: 15KK0261, 23700756 and 26702026

Abstract

Aim: The specificity of muscle-tendon and foot architecture of elite Kenyan middle- and long-distance runners has been found to contribute to their superior running performance. To investigate the respective influence of genetic endowment and training on these characteristics, we compared leg and foot segmental lengths as well as muscle-tendon architecture of Kenyans and Japanese males (i) from infancy to adulthood and (ii) non-athletes versus elite runners.

Methods: The 676 participants were divided according to their nationality (Kenyans and Japanese), age (nine different age groups for non-athletes) and performance level in middle- and long-distance races (non-athlete, non-elite and elite adult runners). Shank and Achilles tendon (AT) lengths, medial gastrocnemius (MG) fascicle length, pennation angle and muscle thickness, AT moment arm (MA_{AT}), and foot lever ratio were measured.

Results: Above 8 years old, Kenyans had a longer shank and AT, shorter fascicle, greater pennation angle, thinner MG muscle as well as longer MA_{AT} , with lower foot lever ratio than age-matched Japanese. Among adults of different performance levels and independently of the performance level, Kenyans had longer shank, AT and MA_{AT} , thinner MG muscle thickness, and lower foot lever ratio than Japanese. The decrease in MG fascicle length and increase pennation angle observed for the adult Japanese with the increase in performance level resulted in a lack of difference between elite Kenyans and Japanese.

Conclusion: The specificity of muscle-tendon and foot architecture of elite Kenyan runners could result from genetic endowment and contribute to the dominance of Kenyans in middle- and long-distance races.

KEYWORDS

endurance running, ethnicity, foot structure, gear ratio, growth, ultrasonography

[†]Deceased.

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1 | INTRODUCTION

Given the undeniable success of Kenyan runners in world middle- and long-distance events for over half a century, their study is considered likely to shed light on the factors contributing to such running performances. Their dominance has been attributed to a combination of factors such as genetic inheritance, training, environment, lifestyle, and social factors.^{1–4} In particular, the question arises as to the relative share of athlete selection and training versus the influence of their genetic endowment.

Firstly, Bengt Saltin's group revealed key physiological aspects of Kenyan runners that could contribute to their superior endurance running performance.^{5,6} In their reports, while the elite Kenyan and Scandinavian runners were in the same range of maximal oxygen uptake, the Kenyans were metabolically more economical, especially at race-pace running velocities.⁵ To date, these physiological advantages of Kenyan endurance runners have been confirmed by comparison to other ethnic groups of elite and non-elite runners, such as Japanese⁷ and Caucasians.⁸

Among other factors, clear evidence has been provided that elite Kenyan runners have long legs and thin/light calf muscles that may provide biomechanical and metabolic advantages.^{9–12} In addition, as suggested by Saltin et al.,^{5,6} the architecture and function of the triceps surae muscle-tendon complex may also be of interest. Supporting this hypothesis, our own research group repeatedly found that elite Kenyan runners are characterized by a longer gastrocnemius Achilles tendon (AT), shorter fascicles in the medial gastrocnemius (MG) muscle and longer AT moment arm (MA_{AT}), as well as a lower foot lever ratio (forefoot length divided by MA_{AT}) than Japanese non-elite runners^{13,14} and healthy Caucasian adults.¹⁵ Furthermore, these specific muscle-tendon architecture showed the strong correlation to their records of running performance.^{13,14} The long AT and MA_{AT} of elite Kenyan runners resulted in reduced AT strain, MG muscle activity and fascicle shortening during the contact phase of running, compared to the Japanese runners.¹⁴ Thus, the neuromuscular interaction using the inherent anatomical advantages for Kenyan distance runners may be a unique alternative to the classical stretch-shortening cycle concept¹⁴ for enhancing the running economy. However, it still remains to be seen whether these differences are the effects of their genetic endowment, lifestyle, or training.

Firstly, the influence of genetic endowment is suggested by the fact that not only Kenyan elite runners, but also boys, have a thinner leg thickness than Caucasian (Danish) elite runners and boys.⁹ It may contribute to their better running economy.² In Kenyan and Danish boys with similar endurance training responses, running economy was also found to be better in the Kenyans.^{9,11,16}

Secondly, regarding the influence of lifestyle, the comparison of Kenyan village and city boys showed that village boys had a higher maximum oxygen consumption, but similar running economy and response to endurance training as city boys.^{9,11,16} These studies therefore suggest that Kenyan children already have the right genes to shape their bodies, contributing to their good running economy. However, these suggestions are based on comparisons of Kenyan and Caucasian data. Regarding the comparison of elite runners, although muscle-tendon unit characteristics of elite Kenyans have been compared with those of Japanese runners, their performance levels are not completely consistent.^{13,14} It remains to be seen whether the specificities of the muscle-tendon unit of Kenyan elite runners compared to Japanese elite runners^{13,14} are influenced by genetic endowment rather than training adaptation.

Therefore, to investigate the respective influence of the genetic endowment and training effect on the muscle-tendon characteristics of Kenyans, the present study compared a large sample of Kenyan and Japanese males, (i) non-athletes of different age groups and (ii) adult runners of different running performance levels. It was hypothesized that genetic endowment was more influential than the performance level, so that: Kenyans were expected to have a longer AT, shorter fascicles in the MG and longer MA_{AT} , as well as a lower foot lever ratio than Japanese from infancy to adulthood (hypothesis 1); At the adult age, these differences between Kenyans and Japanese were expected to remain, irrespective of the performance level (hypothesis 2).

2 | RESULTS

2.1 | Inter-group differences in anthropometry and performance level

Group means and statistical comparisons of anthropometry of Kenyan and Japanese children and non-athlete adults (from 4–5 to 20–30 years old) are shown in [Table 1](#). For body mass, a main significant effect of nationality with small effect size ($p = 0.032$, $\eta^2 = 0.01$) and a nationality \times age interaction with small effect size ($p = 0.008$, $\eta^2 = 0.04$) were also found: Kenyans were lighter than Japanese at 14–15 years old ([Table 1](#)).

Comparison of the anthropometric data of the three adult groups (non-athletes, non-elite runners, and elite runners) revealed no significant nationality \times performance level interaction for age, height and body mass. There was a significant main effect of performance level, with a small effect size for age ($p = 0.011$, $\eta^2 = 0.04$) and a large effect size for body mass ($p < 0.001$, $\eta^2 = 0.29$):

TABLE 1 Anthropometric parameters and sample size for Kenyan and Japanese non-runners

	Age (years)		Height (cm)		Body mass (kg)		Sample size (n)	
	Kenyans	Japanese	Kenyans	Japanese	Kenyans	Japanese	Kenyans	Japanese
4–5 years	4.6 ± 0.5	4.6 ± 0.5	106.4 ± 5.5	105.5 ± 5.5	18.1 ± 2.4	16.8 ± 1.6	16	30
6–7 years	6.5 ± 0.5	6.4 ± 0.5	121.2 ± 5.2	119.2 ± 4.3	24.3 ± 6.9	21.8 ± 2.4	20	20
8–9 years	8.5 ± 0.5	8.3 ± 0.5	123.8 ± 5.5	125.7 ± 4.9	24.0 ± 2.7	25.1 ± 4.0	19	30
10–11 years	10.5 ± 0.5	10.5 ± 0.5	136.3 ± 7.3	138.4 ± 5.1	31.0 ± 5.7	33.3 ± 4.8	22	28
12–13 years	12.5 ± 0.5	12.5 ± 0.5	147.5 ± 8.2	149.7 ± 5.1	38.5 ± 8.4	40.6 ± 5.4	33	33
14–15 years	14.5 ± 0.5	14.5 ± 0.5	161.3 ± 10.1	162.0 ± 5.6	46.4 ± 5.7	52.8 ± 8.3†	21	48
16–17 years	16.7 ± 0.5	16.7 ± 0.5	168.6 ± 5.4	170.4 ± 4.7	59.4 ± 5.9	57.5 ± 6.4	23	51
18–19 years	18.6 ± 0.5	18.5 ± 0.5	167.3 ± 5.3	169.8 ± 4.3	56.8 ± 6.3	59.9 ± 6.8	22	50
20–30 years	24.0 ± 4.5	22.6 ± 2.8	171.8 ± 7.5	172.1 ± 4.8	64.3 ± 8.1	65.9 ± 7.2	33	65

Note: Group mean ± SD values. Bold values in case of statistical significant difference between Kenyans and Japanese.

†Significant difference between Kenyans and Japanese ($p < 0.01$).

Non-athlete adults were younger than non-elite runners and heavier than non-elite and elite runners (Table 2).

Comparison between non-elite and elite runners based on the International Amateur Athletic Federation (IAAF) scores¹⁷ revealed a main significant effect of the performance level with a large effect size ($p < 0.001$, $\eta^2 = 0.69$), but no nationality × performance level interaction. The average level of running performance was 1204 ± 40 points for elite Kenyans and 1176 ± 21 points for elite Japanese (e.g., 2:05:29–2:09:53 versus 2:08:03–2:10:23 in marathon), as well as 1046 ± 85 points for non-elite Kenyans and 1063 ± 45 points for non-elite Japanese (e.g., 2:11:44–2:21:46 versus 2:13:03–2:18:19 in marathon).

2.2 | Effects of nationality and age on muscle-tendon architecture in non-athletes

p -values and effect size (η^2) of main effects of nationality (Kenyan, Japanese) and age (9 age groups from 4–5 to 20–30 years old) as well as nationality × age interaction are shown in Table 3 for all shank, tendon, muscle and foot structure parameters. A significant main effect of age was

found, with mostly large effect size, for each of the measured parameters. We thus concentrated on the main effect of nationality and on the nationality × age interaction.

For the shank length and the absolute and relative AT lengths, significant main effect of nationality and interactions were found (Table 3). The interactions revealed that, compared with Japanese, Kenyans presented longer values for each of these parameters in all ages (Figure 1A,C,E), larger increases in shank and AT lengths in infancy and adolescence with no significant change in relative AT length.

A main effect of nationality was also found for the absolute and relative MG fascicle lengths (Figure 2A,C), pennation angle, and muscle thickness (Figure 3A,C): Kenyans had shorter absolute and relative MG fascicle lengths (Figure 2A,C), greater pennation angle (Figure 3A), but smaller MG muscle thickness (Figure 3C) than Japanese. The significant interactions found for absolute MG fascicle length (Figure 2A) and MG muscle thickness (Figure 3C) revealed a lesser increase of both of these parameters for Kenyans than for Japanese from 8–9 to 20–30 years old. In particular, Kenyans increased in MG muscle thickness only from 14–15 to 16–17 years old whereas Japanese increased from 10–11 to 16–17 years old

TABLE 2 Anthropometric parameters and sample size for the three Kenyan and Japanese adult groups

	Age (years)		Height (cm)		Body mass (kg)		Sample size (n)	
	Kenyans	Japanese	Kenyans	Japanese	Kenyans	Japanese	Kenyans	Japanese
Non-athletes (20–30 years)	24.0 ± 4.5	22.6 ± 2.8	171.8 ± 7.5	172.1 ± 4.8	64.3 ± 8.1	65.9 ± 7.2	33	65
Non-elite runners	25.2 ± 4.8*	24.8 ± 4.6*	171.3 ± 7.0	171.1 ± 4.5	57.5 ± 5.5	56.5 ± 4.3‡	36	49
Elite runners	24.1 ± 4.1	26.7 ± 4.6	172.2 ± 7.5	171.3 ± 3.8	57.0 ± 5.4	56.0 ± 4.4‡	17	10

Note: Group mean ± SD values. Bold values in case of statistical significant difference.

* and ‡: $p < 0.05$ and $p < 0.001$, respectively, compared to non-athletes. [Correction added on April 29, 2022 after first online publication. The values in the footnote of Table 2 have been changed from ' $p < 0.001$ and $p < 0.05$ ' to ' $p < 0.05$ and $p < 0.001$ ']

TABLE 3 Influence of nationality and age on all parameters among non-runners

Parameters	$P_{\text{Nationality}} (\eta^2)$	$P_{\text{Age}} (\eta^2)$	$P_{\text{Nationality} \times \text{Age}} (\eta^2)$
Shank length	<0.001 (0.36, large)	<0.001 (0.89, large)	0.001 (0.05, small)
Absolute Achilles tendon (AT) length	<0.001 (0.53, large)	<0.001 (0.79, large)	0.018 (0.03, small)
Relative AT length	<0.001 (0.31, large)	<0.001 (0.05, small)	<0.001 (0.05, small)
Absolute MG fascicle length	<0.001 (0.26, large)	<0.001 (0.43, large)	<0.001 (0.06, small)
Relative MG fascicle length	<0.001 (0.43, large)	<0.001 (0.23, large)	0.065
MG pennation angle	<0.001 (0.05, small)	<0.001 (0.28, large)	0.473
MG muscle thickness	<0.001 (0.27, large)	<0.001 (0.68, large)	<0.001 (0.09, moderate)
Forefoot length	0.111	<0.001 (0.75, large)	0.396
Moment arm	<0.001 (0.13, moderate)	<0.001 (0.68, large)	0.001 (0.05, small)
Foot lever ratio	<0.001 (0.10, moderate)	<0.001 (0.22, large)	0.110

Note: p -value (effect size when p -value is significant).

(Figure 3C). In both Kenyans and Japanese, we found that MG muscle thickness could be explained by MG fascicle length by about 70% (Figure 4A) and by MG pennation angle by about 33% (Figure 4B).

A main effect of nationality was found for MA_{AT} and foot lever ratio (Figure 5C,E), but not for forefoot length (Figure 5A): Kenyans showed longer MA_{AT} (Figure 5C) and lower foot lever ratio than Japanese (Figure 5E). A significant interaction was only found for MA_{AT} that revealed a larger increase for Kenyans than for Japanese from 8–9 to 20–30 years old ($p < 0.05$), the significant increase occurring for each group between 8–9 to 12–13 years old (Figure 5C).

2.3 | Effects of nationality and performance level on muscle-tendon architecture in adults

p -values and effect size (η^2) of main effects of nationality (Kenyan, Japanese) and performance level (non-athletes, non-elite and elite runners) as well as nationality \times performance level interaction are shown in Table 4 for all shank, tendon, muscle and foot structure parameters. No significant interaction was found for the shank length, absolute and relative AT lengths of Kenyan and Japanese adult runners. However, a significant main effect of nationality was found for each of these parameters: Adult Kenyans were characterized by longer shank, absolute and relative AT values than Japanese (Figure 1B,D,F).

A significant interaction was found for both the absolute and relative MG fascicle lengths. As shown on Figure 2 (B,D), no significant difference was found for the Kenyans whereas non-athletic Japanese had longer absolute and relative MG fascicles than non-elite ($p = 0.006$ and $p = 0.002$, respectively) and elite ($p = 0.022$ and $p = 0.012$, respectively) runners. The decrease in fascicle

length observed for Japanese with the increase in performance level resulted in a lack of difference between elite Kenyans and Japanese in the absolute MG fascicle length (Figure 2B). A significant difference between Kenyans and Japanese was always found otherwise ($p < 0.01$).

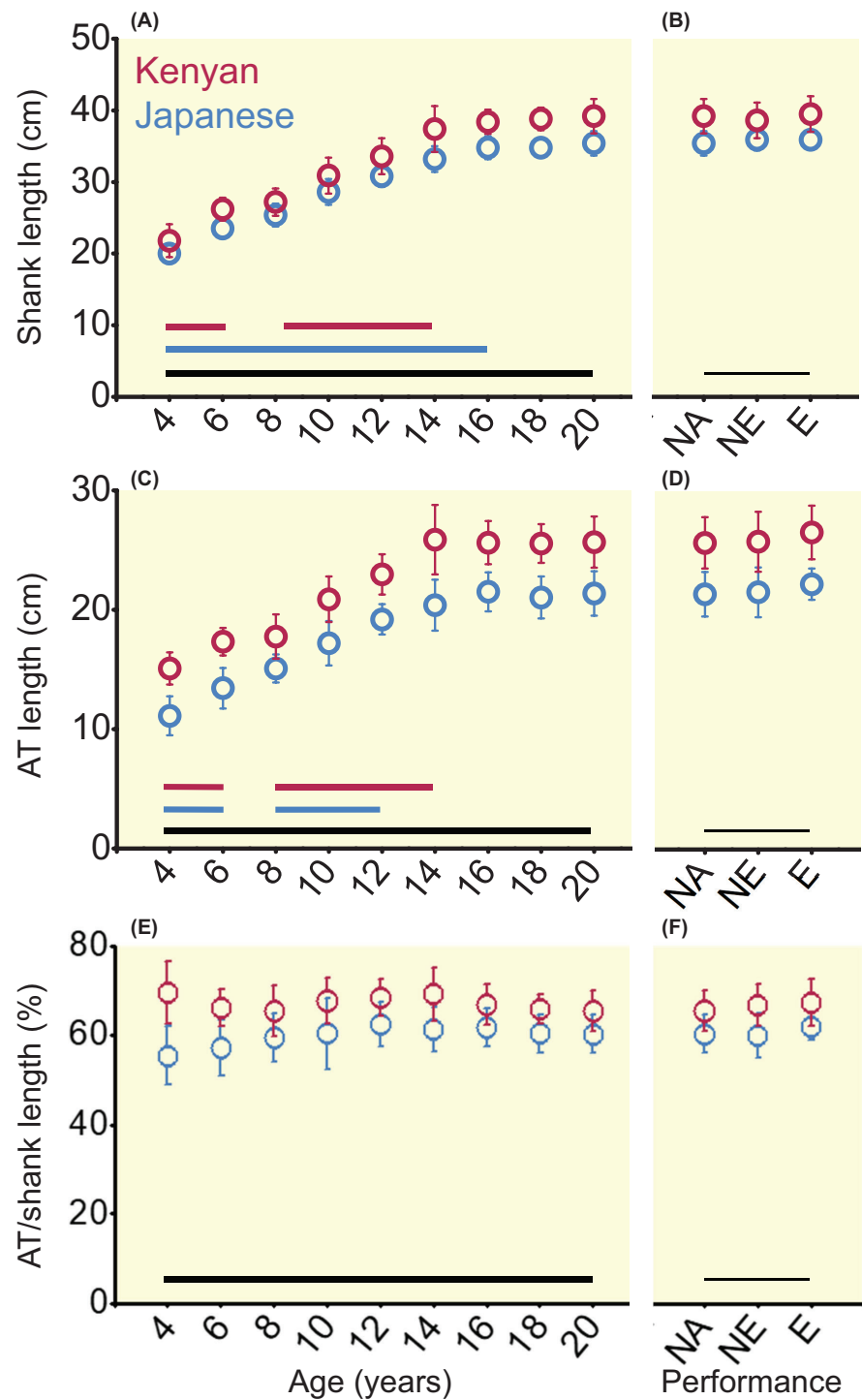
An interaction was also found for the MG pennation angle. As shown in Figure 3 (B), non-athletic Japanese had smaller pennation angle than non-elite ($p = 0.031$) and elite ($p = 0.011$) runners whereas, among Kenyans, non-elite runners had greater MG pennation angle than non-athletes ($p = 0.005$) and elite runners ($p = 0.017$). The increase in MG pennation angle observed for Japanese with the increase in performance level resulted in a lack of difference between Kenyan and Japanese elite runners (Figure 3B). A significant difference between Kenyans and Japanese was found otherwise ($p < 0.01$). Regarding the MG muscle thickness (Figure 3D), only main significant effects of nationality and performance level were found: Independently of their nationality, non-elite runners had thicker MG muscle than non-athletes ($p = 0.023$). All Kenyans had thinner MG muscle than their Japanese counterparts.

No significant interaction was found for the forefoot length, AT moment arm (MA_{AT}) and lever ratio (forefoot length/ MA_{AT}) (Figure 5B,D,F). Only a main significant effect of nationality was found for MA_{AT} and lever ratio: Kenyans were characterized by longer MA_{AT} and lower foot lever ratio than Japanese (Figure 5D,F).

3 | DISCUSSION

We hypothesized that Kenyan and Japanese structural differences in their leg and foot segmental lengths as well as muscle-tendon architecture (i) would exist from early childhood (hypothesis 1) and (ii) would differ between Kenyan and Japanese adults regardless their performance

FIGURE 1 Effect of nationality, age and performance level on shank and Achilles tendon (AT) lengths. The left-hand side of each graph shows the effect of nationality and age on shank length (A), absolute (C) and relative (E) AT lengths. The right-hand side of each graph shows the effects of nationality and performance level on each of these parameters (B, D and F) for non-athletes (NA), non-elite (NE), and elite (E) runners. Results are presented as mean \pm SD. The two-way ANOVA analysis revealed a significant nationality \times age interaction, with significant *post-hoc* differences between subsequent age groups indicated by thick lines: black for different nationalities ($p < 0.01$), red for Kenyans ($p < 0.01$), and blue for Japanese ($p < 0.05$). The thin black line shows the main effect of nationality between the adult groups



level (non-athlete, non-elite and elite runners), but not between Kenyan adults (hypothesis 2). Confirming hypothesis 1, the present study demonstrated that, above 8 years old, Kenyans had longer shank and AT, shorter fascicle, greater pennation angle, thinner MG muscle as well as longer MA_{AT} , with lower foot-lever ratio than Japanese. Hypothesis 2 was also partly supported: as expected, the three adult groups of Kenyans did not differ in their structural characteristics, and significant differences

were found between Kenyan and Japanese non-athletes and non-elite runners. However, differing from our expectations, Kenyan and Japanese elite-runners did not differ in their absolute MG fascicle length and pennation angle, although significant differences were found in other parameters.

Elite Kenyan runners are characterized by (i) a small gastrocnemius muscle mass, which allows them to run with minimal energy used to swing the lower limbs,⁶

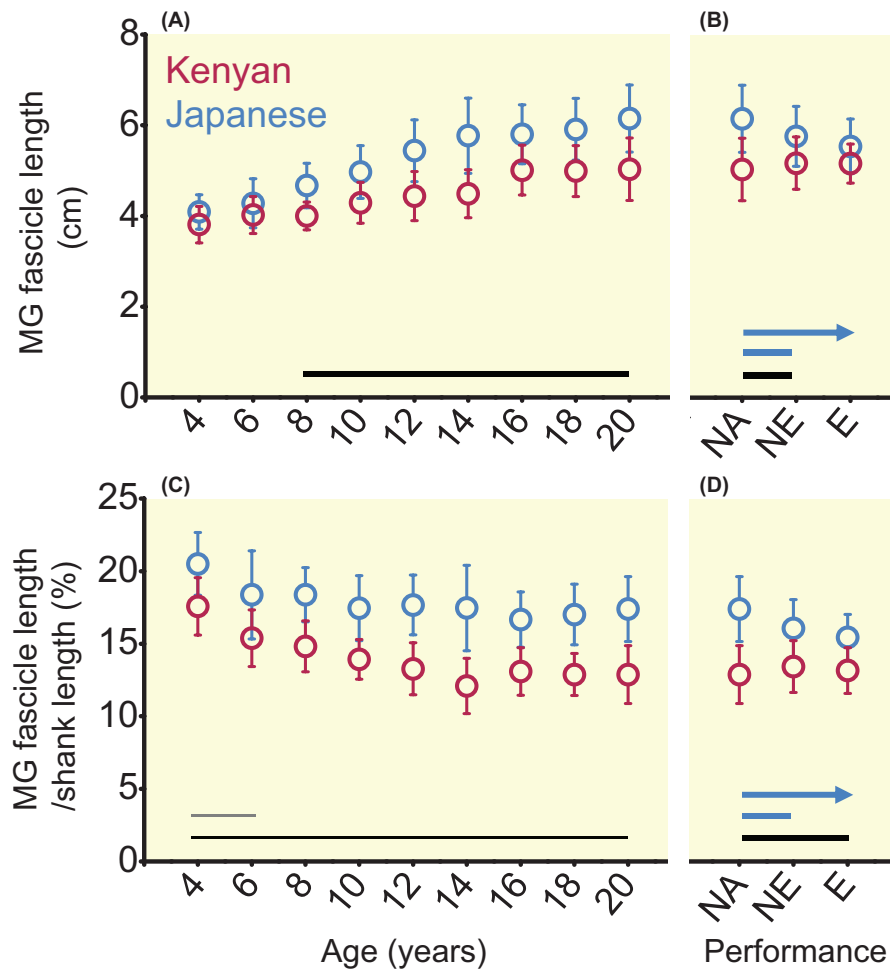


FIGURE 2 Effect of nationality, age, and performance level on absolute and relative medial gastrocnemius (MG) fascicle lengths. The left-hand side of the graphs shows the effects of nationality and age on absolute (A) and relative (C) MG fascicle lengths. The right-hand side of the graphs shows the effects of nationality and performance level on each of these parameters (B, D) for non-athletes (NA), non-elite (NE), and elite (E) runners. Results are presented as mean \pm SD. The two-way ANOVA analysis revealed significant nationality \times age and nationality \times performance level interactions, with significant *post-hoc* differences between subsequent groups indicated by thick lines: black for different nationalities ($p < 0.01$) and blue for Japanese ($p < 0.05$). The blue arrow indicates a significant difference between non-athletes (NA) and elite-runners (E) ($p < 0.05$). The thin lines show the main effect of nationality in black ($p < 0.01$) and of age in gray ($p < 0.001$)

(ii) short muscle fascicles with long AT that reduce the muscle fiber shortening during the contact phase and thus the energy expenditure of the muscles,^{14,18} and (iii) long MA_{AT} and low foot lever ratio to reduce plantar flexor muscle force to produce the same torque.^{13,14,19} How did elite Kenyan runners acquire these foot and muscle-tendon architecture that give them the advantage of efficient running and superior running performance? Resulting the comparison of the foot and muscle-tendon architecture since early childhood between two nationalities, most of the structural differences between Kenyans and Japanese were already present at the age of 4 years, with the difference in MA_{AT} , absolute length of MG fascicles and MG muscle thickness only existing after the age of 8 years, confirming hypothesis 1 of a major influence of genetic endowment. The longer shank and AT lengths of Kenyans are in perfect agreement with the

long legs and thin/light calf muscles reported in the literature to provide biomechanical and metabolic benefits since a young age.^{9–11} The demonstrated longer AT and MA_{AT} as well as the shorter absolute MG fascicle length and lower foot lever ratio in Kenyans, at least since the age of 8, provide further support for the influence of genetic endowment on the architectural characteristics of elite Kenyan runners.^{13,14} In addition, Kenyans were characterised by a greater influence of increasing MG fascicle length than pennation angle on MG muscle thickness compared to Japanese. These trends differ from the linear relationship reported between increasing MG fascicle pennation angle and MG muscle thickness in Caucasians from infancy to adulthood.^{20,21} This could partly explain the lower triceps surae muscle thickness reported for Kenyans (including elite runners) compared to Caucasians.^{9,11}

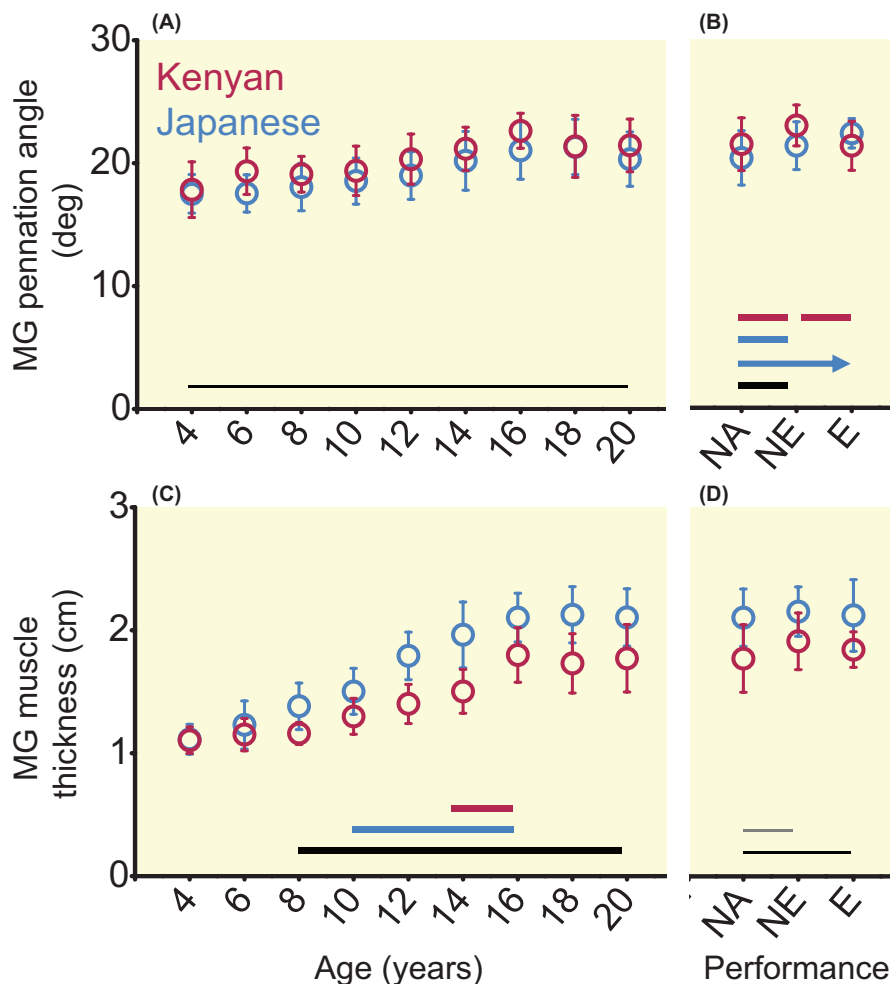


FIGURE 3 Effect of nationality, age and performance level on medial gastrocnemius (MG) pennation angle and muscle thickness. The left-hand side of the graphs shows the effects of nationality and age on MG pennation angle (A) and MG muscle thickness (C). The right-hand side of the graphs shows the effects of nationality and performance level on each of these parameters (B, D) for non-athletes (NA), non-elite (NE), and elite (E) runners. Results are presented as mean \pm SD. The two-way ANOVA analysis revealed significant nationality \times age and nationality \times performance level interactions, with significant *post-hoc* differences between subsequent groups indicated by thick lines: black for different nationalities ($p < 0.01$), red for Kenyans ($p < 0.05$) and blue for Japanese ($p < 0.05$). The blue arrow indicates a significant difference between non-athletes (NA) and elite-runners (E) ($p < 0.05$). The thin lines show the main effect of nationality in black ($p < 0.001$) and of performance level in gray ($p < 0.05$)

Hypothesis 2 was supported for all parameters, except the absolute MG muscle fascicle length and pennation angle that did not differ between elite Kenyan and Japanese runners. In this study, we improved the number of participants and the range of running performance level from the previous studies.^{13,14} In the results, as previously reported for middle and long-distance runners,^{13,14} Kenyan elite runners showed longer length values of shank, AT and MA_{AT} , as well as thinner MG muscle and lower foot lever ratio than Japanese non-elite runners. However, the lack of difference in the absolute MG fascicle length and pennation angle between elite Kenyan and Japanese runners is particularly interesting as it results from the contrast between the stability of absolute and relative fascicle length values in the three Kenyan groups

and the significant decreases observed in the Japanese, from non-athletes to elite runners. Furthermore, the decrease in fascicle length observed among Japanese was associated with an increase in pennation angle. Such trends were not observed in Kenyans. In our previous study,¹⁴ we compared muscle-tendon architecture in Kenyan and Japanese runners at different running performance levels (IAAF score: 1126.9 ± 105.2 versus 909.4 ± 130.8 points) and showed that Kenyan had significantly shorter fascicles and greater pennation angle of the MG than Japanese. In the present study, however, we recruited both elite Kenyan and elite Japanese runners, with matched group mean performance levels (1204 ± 40 versus 1176 ± 21 points). This comparison revealed that the muscle architecture characteristics (short fascicle length and large

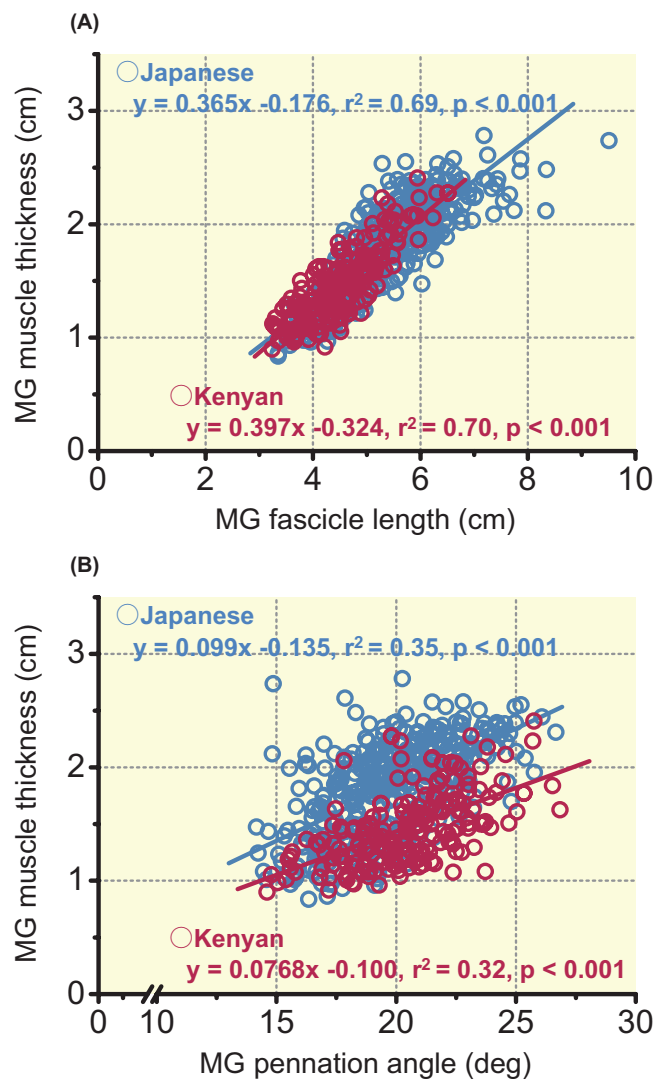


FIGURE 4 Linear regressions between medial gastrocnemius (MG) fascicle characteristics and muscle thickness for Kenyans and Japanese. (A) between MG fascicle length and MG muscle thickness, and (B) between MG pennation angle and MG muscle thickness for Kenyans (red) and Japanese (blue)

pennation angle) of the elite Japanese runners was very close to those of the Kenyans. As suggested by Abe et al,²² who found different muscle characteristics in endurance runners compared to sprinters, both genetic endowments and training adaptation may be involved. Supporting the latter hypothesis, Murach et al²³ reported decreased fascicle length and increased pennation angle with no change in muscle thickness of the lateral gastrocnemius after 12 weeks of endurance run training. These observations suggest that the specific muscle architecture of the elite Japanese runners could result from specific training and/or athletic selection based on genetic endowments, whereas elite Kenyan runners' features would be already common among non-athlete Kenyan adults. Therefore, the performance enhancements of non-elite Kenyan runners

may depend on the developments of trainable physiological factors^{1,24} and on the success of economical running movements utilizing inherent anatomical benefits.¹⁴

Some methodological limitations need to be addressed. First, as the present study had a cross-sectional design, no cause-effect relationship can yet be drawn between the structural characteristics and the nationality, age and running performance level of the middle and long-distance runners. In addition, the growth and maturity status were not fully matched between Kenyan and Japanese children. We tried to match height and body mass at each age group, but did not succeed in for the age of 14–15 years: Kenyans had a lower body mass than the selected Japanese of the same age. The generalization of muscle-tendon architecture in this population is of course unknown without further study. It cannot be sure that the study cohort is representative of Kenyan children and non-athletic adults and *vice versa* in Japanese non-athletes. Whilst some selection bias cannot be excluded, all participants were identified without prior knowledge of the physical activity levels and running performance level and blind to the aims and objectives of the study. Finally, the AT length was measured with tape along the line close to skin. This may have been underestimated²⁵ or overestimated because the actual curvature, twist, or straight of the AT was not considered in this study.

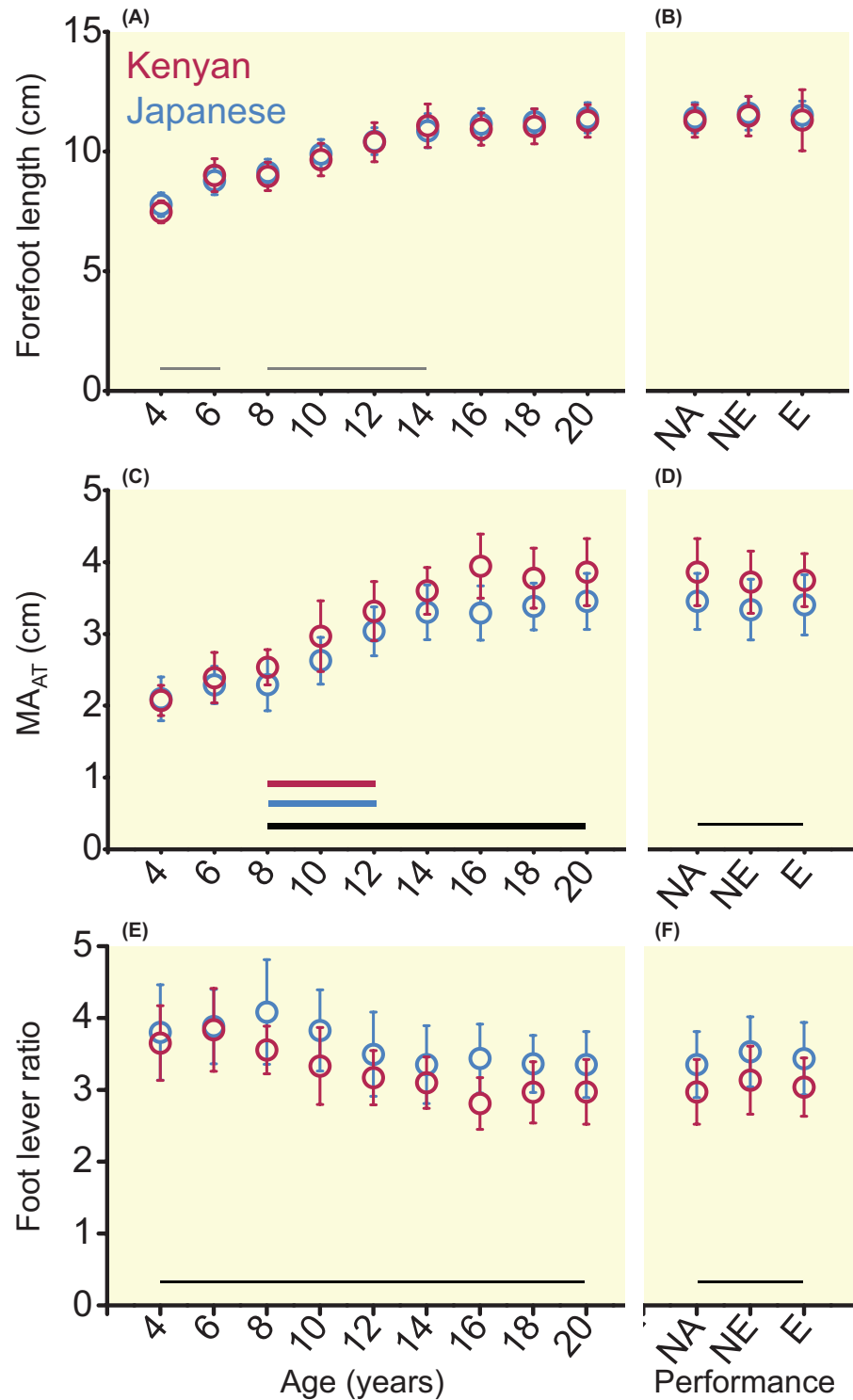
In conclusion, by conducting a study on a large number of Kenyans and Japanese of all ages, we have shown that not only Kenyan elite runners but also the general population since early childhood have structural advantages in their leg and foot segmental lengths as well as in their muscle-tendon architecture for middle and long distance running performance. These findings suggest that genetic endowment plays a major role in the dominance of Kenyans in middle- and long-distance races.

4 | MATERIALS AND METHODS

4.1 | Participants

A total of 676 healthy male participants including children, untrained adults and highly trained runners from Kenya ($n = 262$) and Japan ($n = 414$) volunteered for this study. Kenyans were recruited and tested in their home cities (Nairobi, Kitui, and Embu for non-athletes and Eldoret for elite runners). Non-athletic and elite Japanese runners were recruited from different Japanese cities (i.e. Osaka, Hyogo, Shiga, Okayama, Hiroshima, and Fukuoka), and the tests were conducted in Osaka. This 5-year global project involved mainly the same operators for the US measurements. Children and non-athlete adults were divided according to their nationality and age.

FIGURE 5 Effect of nationality, age, and performance level on foot architecture. The left-hand side of the graphs shows the effects of nationality and age on forefoot length (A), Achilles tendon moment arm (MA_{AT}) (C), and foot lever ratio (forefoot length/Achilles tendon moment arm) (E). The right-hand side of the graphs shows the effects of nationality and performance level on each of these parameters (B, D and F) for non-athletes (NA), non-elite (NE), and elite (E) runners. Results are presented as mean \pm SD. The two-way ANOVA analysis revealed a significant nationality \times age interaction, with significant post-hoc differences between subsequent age groups indicated by thick lines: black for different nationalities ($p < 0.05$), red for Kenyans ($p < 0.05$) and blue for Japanese ($p < 0.05$). The thin lines show the main effect of nationality in black ($p < 0.001$) and of age in gray ($p < 0.001$)



People aged 4–19 years were divided into groups of 2 years each and those aged 20 years and over into one group (Table 1). As shown in Table 2, the adult participants were divided based on their nationality (Kenyan versus Japanese) and running performance level (non-athletes, non-elite runners, and elite runners). The runners were classified based on their middle- and/or long-distance running performance using their best official records. To account for differences in race distance (e.g., 5000 m

and marathon), their best official records were converted based on the IAAF score table system.¹⁷ The IAAF scores of the elite runners were set above 1150 points (e.g., 2020 Tokyo Olympic entry mark was 2:11:30 for marathon and its corresponding IAAF points were 1136).

All adult participants gave written informed consent to take part in this study, which was performed in accordance with the guidelines of the Declaration of Helsinki and was approved by the local Ethics Committee of Osaka

TABLE 4 Influence of nationality and performance level on all parameters among adults

Parameters	$p_{\text{Nationality}} (\eta^2)$	$p_{\text{Performance level}} (\eta^2)$	$p_{\text{Nationality} \times \text{Performance level}} (\eta^2)$
Shank length	<0.001 (0.33, large)	0.636	0.237
Absolute Achilles tendon (AT) length	<0.001 (0.42, large)	0.196	0.991
Relative AT length	<0.001 (0.22, large)	0.256	0.570
Absolute MG fascicle length	<0.001 (0.16, large)	0.203	0.009 (0.05, moderate)
Relative MG fascicle length	<0.001 (0.30, large)	0.140	0.003 (0.06, moderate)
MG pennation angle	0.082	<0.001 (0.08, moderate)	0.015 (0.04, moderate)
MG muscle thickness	<0.001 (0.21, large)	0.028 (0.03, moderate)	0.438
Forefoot length	0.246	0.251	0.969
Moment arm	<0.001 (0.13, moderate)	0.136	0.941
Foot lever ratio	<0.001 (0.11, moderate)	0.059	0.994

Note: p -value (effect size when p -value is significant).

University of Health and Sport Sciences (approval number 16-1). Regarding the informed consent of the children, parents or teachers (primary schools, junior high school, and high school) gave written informed consent for the children's participation in the study.

4.2 | Shank and Achilles tendon length measurements

All parameters were measured bilaterally while standing at rest and averaged for both legs. *Shank length* was defined as the distance from the proximal head of the fibula to the tip of the lateral malleolus. The AT length from the point of its distal insertion on the calcaneus to the AT junction between medial and lateral gastrocnemii muscles was quantified using a portable ultrasonography (Noblus, Hitachi-Aloka Medical Ltd) and then was measured with tape along the line close to the skin.^{26,27}

4.3 | Structural measurements of medial gastrocnemius muscle

The MG fascicle length, pennation angle, and muscle thickness were measured from sagittal ultrasound images obtained with a 55 mm linear probe (13–5 MHz, model: L55, Hitachi-Aloka Medical Ltd) placed on the MG muscle belly, in the mid-sagittal plane. In the recorded scans, echoes reflected from muscle fascicles and aponeuroses tissue were identified. The fascicle in the center of the MG ultrasound image was chosen for analysis. The fascicle length was measured as the distance between the insertion of the fascicle into the superficial and deep aponeuroses²⁸ and these were digitized using analysis software (ImageJ, NIH). The muscle thickness was measured as

the largest perpendicular distance between deep and superficial aponeuroses. The pennation angle was measured from the fascicle insertion points in the superficial and deep aponeuroses and from a different point on the deep aponeurosis. Apart from the present study, the daily repeatability of the muscle architecture measurement ($n = 9$) was confirmed using an intraclass correlation coefficient ($ICC_{1,1}$). We confirmed good repeatability; $ICC_{1,1}$ was 0.980, 0.971 and 0.960 (MG fascicle length, pennation angle, and muscle thickness, respectively).

4.4 | Measurements of foot characteristics

Achilles tendon moment arm (MA_{AT}) was defined by a line projected orthogonally from the nearest point on the AT force application line to the ankle joint axis. In this study, the ankle joint axis was defined using the trans-malleolar axis²⁹ and the MA_{AT} was estimated geometrically using the Heron's formula.³⁰ First, ultrasound transverse images from each medial and lateral malleolar tip to the posterior aspect of the AT were taken by a portable ultrasonography (Noblus, Hitachi-Aloka Medical Ltd) with a 55 mm linear probe (13–5 MHz, model: L55, Hitachi-Aloka Medical Ltd). Then, image analysis software was used to calculate the distances from the center of the AT to the tips of the medial (L_{med}) and lateral malleoli (L_{lat}), respectively. Finally, the distance between the tips of the medial and lateral malleoli (L_{mal}) was measured on the skin using a Martin breadth caliper:

$$S = \frac{(L_{mal} + L_{med} + L_{lat})}{2}$$

$$MA_{AT} = \frac{2\sqrt{S(S - L_{mal})(S - L_{med})(S - L_{lat})}}{L_{mal}}$$

where S is half of the total length of L_{mal} , L_{med} and L_{lat} , and MA_{AT} is the length of the AT moment arm. Repeatability and reliability of this method have been previously checked in Japanese participants as follows: The repeatability of the MA_{AT} measurement at two given times of the day in 6 participants showed a high intraclass correlation coefficient ($ICC_{1,1}$) of 0.945. The reliability was confirmed by high intraclass correlation coefficient ($ICC_{3,2} = 0.822$) when comparing the MA_{AT} values of 12 participants obtained either with our method or when using Hashizume's method³¹ based on a three-dimensional approach with magnetic resonance imaging.

Foot lever ratio was defined as the ratio of the forefoot length divided by MA_{AT} , in which the forefoot length is the distance between the vertical projection of the lateral malleolus tip to the distal head of the fifth metatarsal.

4.5 | Statistics

Statistical analyses were performed using statistical software (SPSS Statistics 25, IBM Japan). Values in the text and tables are reported as mean \pm standard deviation (SD). To test the first hypothesis (hypothesis 1), a two-way (nationality and age) ANOVA analysis was conducted on the different age group data (from 4–5 to 20–30 years for both Kenyan and Japanese non-athletes). To test the second hypothesis (hypothesis 2), we conducted a two-way (nationality and performance level) ANOVA analysis based on data from non-athletes, non-elite and elite runners from Kenya and Japan. The non-athlete groups corresponded to the 20–30 years age group used when testing hypothesis 1. The IAAF scores of non-elite and elite runners from Kenya and Japan were compared using a two-way ANOVA (nationality and performance level) analysis. In case of significant interaction, additional one-way ANOVA with Bonferroni test was performed to determine whether significant differences existed between groups. The magnitude of these differences was examined using effect size η^2 and evaluated as small for $\eta^2 > 0.01$, moderate for $\eta^2 > 0.06$, and large for $\eta^2 > 0.14$.³² Linear regression analysis was used to assess the relationships between MG muscle thickness and MG fascicle length or pennation angle in Kenyan and Japanese non-athletes. The coefficient of determination (r^2) was used to quantify the variance explained by the given factors. A criterion alpha level of $p < 0.05$ was used to determine statistical significance for all data.

ACKNOWLEDGMENTS

The authors would like to acknowledge, Dr Keino K (the IAAF High Performance Training Centre, Kenya) Dr Kurihara T, and Dr Hashizume S (Ritsumeikan

University) as well as Mr Makino A and Hisano T for their assistance during the measurements and Mr Macchi R (Aix-Marseille Université) for his help in statistical analysis. This work was supported by Open Partnership Joint Projects of JSPS Bilateral Joint Research Projects (2015–2017) and by MEXT/JSPS KAKENHI Grant Number 23700756, 26702026, 15KK0261. [Correction added on April 29, 2022 after first online publication. The name 'Kurihara' has been corrected to 'Kurihara T.']

CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

I confirm that my article contains a data availability statement even if no data is available (list of sample statements) unless my article type does not require one.

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REFERENCES

1. Billat V, Lepretre P-M, Heugas A-M, Laurence M-H, Salim D, Koralsztein JP. Training and bioenergetic characteristics in elite male and female Kenyan runners. *Med Sci Sports Exerc.* 2003;35(2):297-304.
2. Larsen HB, Sheel AW. The Kenyan runners. *Scand J Med Sci Sports.* 2015;25:110-118.
3. Tucker R, Onyvera VO, Santos-Concejero J. Analysis of the Kenyan distance-running phenomenon. *Int J Sports Physiol Perform.* 2015;10(3):285-291.
4. Aibast H, Okutoyi P, Sigei T, et al. Foot structure and function in habitually barefoot and shod adolescents in Kenya. *Curr Sports Med Rep.* 2017;16(6):448-458.
5. Saltin B, Larsen H, Terrados N, et al. Aerobic exercise capacity at sea level and at altitude in Kenyan boys, junior and senior runners compared with Scandinavian runners. *Scand J Med Sci Sports.* 1995;5(4):209-221.
6. Saltin B, Kim CK, Terrados N, Larsen H, Svedenhag J, Rolf CJ. Morphology, enzyme activities and buffer capacity in leg muscles of Kenyan and Scandinavian runners. *Scand J Med Sci Sports.* 1995;5(4):222-230.
7. Yoshioka T, Nakagai K, Nakamura K, Mukai N, Nabekura Y. Physiological and morphological characteristics of a Kenyan world-class long-distance runner: a case study. *Jpn J Phys Educ Health Sport Sci.* 2012;57(1):237-248. <https://doi.org/10.5432/jjpehss.11072>
8. Weston AR, Mbambo Z, Myburgh KH. Running economy of African and Caucasian distance runners. *Med Sci Sports Exerc.* 2000;32(6):1130-1134.
9. Saltin B. The Kenya project - final report. *New Stud Athlet.* 2003;18(2):15-26.
10. Larsen HB. Kenyan dominance in distance running. *Comp Biochem Physiol A Mol Integr Physiol.* 2003;136(1):161-170.

11. Larsen HB, Christensen DL, Nolan T, Søndergaard H. Body dimensions, exercise capacity and physical activity level of adolescent Nandi boys in western Kenya. *Ann Hum Biol.* 2004;31(2):159-173.
12. Vernillo G, Schena F, Berardelli C, et al. Anthropometric characteristics of top-class Kenyan marathon runners. *J Sports Med Phys Fitness.* 2013;53(4):403-408.
13. Kunimasa Y, Sano K, Oda T, et al. Specific muscle-tendon architecture in elite Kenyan distance runners: Achilles tendon moment arm for Kenyan runners. *Scand J Med Sci Sports.* 2014;24(4):e269-e274. DOI: [10.1111/sms.12161](https://doi.org/10.1111/sms.12161)
14. Sano K, Nicol C, Akiyama M, et al. Can measures of muscle-tendon interaction improve our understanding of the superiority of Kenyan endurance runners? *Eur J Appl Physiol.* 2015;115(4):849-859.
15. Sano K, Ishikawa M, Nobue A, et al. Muscle-tendon interaction and EMG profiles of world class endurance runners during hopping. *Eur J Appl Physiol.* 2013;113(6):1395-1403.
16. Larsen HB, Nolan T, Borch C, Søndergaard H. Training response of adolescent Kenyan town and village boys to endurance running. *Scand J Med Sci Sports.* 2005;15(1):48-57.
17. Spiriev B IAAF scoring tables of athletics. 2011. https://test-swiss-athletics.ch/wp-content/uploads/IAAF_Scoring_Tables_Outdoor-1.pdf
18. Fletcher JR, Groves EM, Pfister TR, MacIntosh BR. Can muscle shortening alone, explain the energy cost of muscle contraction in vivo? *Eur J Appl Physiol.* 2013;113(9):2313-2322.
19. Kovács B, Kóbor I, Sebestyén Ö, Tihanyi J. Longer Achilles tendon moment arm results in better running economy. *Physiol Int.* 2021;107(4):527-541.
20. Binzoni T, Bianchi S, Hanquinet S, et al. Human gastrocnemius medialis pennation angle as a function of age: from newborn to the elderly. *J Physiol Anthropol.* 2001;20(5):293-298.
21. Radnor JM, Oliver JL, Waugh CM, Myer GD, Moore IS, Lloyd RS. The influence of growth and maturation on stretch-shortening cycle function in youth. *Sports Med.* 2018;48(1):57-71.
22. Abe T, Kumagai K, Brechue WF. Fascicle length of leg muscles is greater in sprinters than distance runners. *Med Sci Sports Exerc.* 2000;32(6):1125-1129.
23. Murach K, Greever C, Luden ND. Skeletal muscle architectural adaptations to marathon run training. *Appl Physiol Nutr Metab.* 2015;40(1):99-102.
24. Jones AM, Kirby BS, Clark IE, et al. Physiological demands of running at 2-hour marathon race pace. *J Appl Physiol.* 2021;130(2):369-379.
25. Obst SJ, Newsham-West R, Barrett RS. In vivo measurement of human achilles tendon morphology using freehand 3-D ultrasound. *Ultrasound Med Biol.* 2014;40(1):62-70.
26. Stenroth L, Peltonen J, Cronin NJ, Sipilä S, Finni T. Age-related differences in Achilles tendon properties and triceps surae muscle architecture in vivo. *J Appl Physiol.* 2012;113(10):1537-1544.
27. Oda H, Sano K, Kunimasa Y, Komi PV, Ishikawa M. Neuromechanical modulation of the Achilles tendon during bilateral hopping in patients with unilateral Achilles tendon rupture, over 1 year after surgical repair. *Sports Med.* 2017;47(6):1221-1230.
28. Narici MV, Binzoni T, Hiltbrand E, Fasel J, Terrier F, Cerretelli P. In vivo human gastrocnemius architecture with changing joint angle at rest and during graded isometric contraction. *J Physiol.* 1996;496(1):287-297.
29. Obst SJ, Barber L, Miller A, Barrett RS. Reliability of Achilles tendon moment arm measured in vivo using freehand three-dimensional ultrasound. *J Appl Biomech.* 2017;33(4):300-304.
30. Kunimasa Y, Sano K, Hisano T, et al. Musculoskeletal characteristics for East-African elite distance runners. *Osaka R J Phys Educ.* 2017;55. https://www.osaka-taiikugakkai.jp/journal/vol55/55_Kunimasa_01-09.pdf
31. Hashizume S, Iwanuma S, Akagi R, Kanehisa H, Kawakami Y, Yanai T. In vivo determination of the Achilles tendon moment arm in three-dimensions. *J Biomech.* 2012;45(2):409-413.
32. Cohen J. *Statistical power analysis for the behavioral sciences.* Hillsdale; 1988.

How to cite this article: Kunimasa Y, Sano K, Oda T, Nicol C, Komi PV, Ishikawa M. Muscle-tendon architecture in Kenyans and Japanese: Potential role of genetic endowment in the success of elite Kenyan endurance runners. *Acta Physiol.* 2022;235:e13821. doi:[10.1111/apha.13821](https://doi.org/10.1111/apha.13821)