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The extensibility of the plantar fascia influences the windlass mechanism during human running

Lauren Welte, Luke A. Kelly, Sarah E. Kessler, Daniel E. Lieberman, Susan E. D'Andrea, Glen A. Lichtwark and Michael J. Rainbow

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Review timeline

Original submission:	11 May 2020
1st revised submission:	2 September 2020
2nd revised submission:	4 December 2020
Final acceptance:	11 December 2020

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

Review History

RSPB-2020-1078.R0 (Original submission)

Review form: Reviewer 1

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Excellent

Quality of the paper: Is the overall quality of the paper suitable?
Excellent

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
This manuscript discusses the complex interaction between two fundamental mechanisms in the human foot and is highly relevant. I very much appreciate how the authors have managed to describe this complexity in a very clear and elegant way. I have some comments (see below), which are usually minor, but I believe more clarity is needed on foot strike types. In most cases I hope my comments can be solved with additional clarification.

L32 "the action of the toes": can you be more specific?

L46 "require contradictory behaviour", why would the windlass mechanism not work with a somewhat (not too) elastic fascia? The authors touch upon this (L64-67) and hypothesize (L 86-88) that the windlass effect is "inhibited" by plantar fascia strain. I would expect it to be influenced by fascia strain, but not inhibited (unless the fascia was _very_ compliant, but then it would not work very well as an energy-storing spring either).

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L169-179: The study authors make a number of reasonable assumptions to establish in which mode the plantar fascia is used, and then used vector coding to analyse these modes throughout stance phase. I find this in principle (as in Fig. 3) an elegant way to display which mode is used, or which combination of modes. However, the actual data are presented less clear and require to-and-fro checking of the colours in Figure 3; I’m also not sure how easily the plots (e.g. Fig. 4) would be read by colour blind people. I’m wondering whether the angular values (rather than their colour codes) could be plotted instead. I do realise this might lead to functionally irrelevant jumps around 0/360 degrees.

L230: Just a thought… I’m not sure I would call this a “catch” mechanism, there is no physical catch but in a way the dynamics make it behave as a catch mechanism. This reminds me of a similar “virtual catch” mechanism in jumping bushbabies (Aerts, 1998, Phil Trans R Soc B). I like the term “catch-like mechanism” later used in the Discussion (L264).

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Major revision is needed (please make suggestions in comments)

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Overall review
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The data in this paper are unique, using 3D skeletal imaging, and the question of how the windlass functions during locomotion, walking or running, is important to the field. However, I found this paper to be lacking a credible hypothesis and presenting far too many speculative claims presented as results. There are also technical issues with the data analysis or its presentation. Finally, there are numerous issues with a lack of details in the paper, which need to be addressed in proofing the paper.

Despite my apparent antagonism to the paper, I think it could be an important contribution with a broad impact on human locomotion biomechanics if the authors can respond to my criticisms.

Major points
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1. Problems with the hypothesis/hypotheses:
First, I was quite confused about which are the hypotheses being testing in the paper. Two sentences try to define hypotheses at the end of the introduction. But the results refer to hypotheses that do not correspond well with the statements in the introduction. There are additional statements that claim to be hypotheses but were never presented earlier in the text. So, I found the presentation of the logic of the paper quite confusing.

I find the hypothesis of apparent conflict in the function of the plantar fascia to be not very meaningful. I highlight my criticism using specific locations of the text:

a. For example, lines 29-30 in the abstract state, "How can the same tissue act like both a rubber band and a rope...?" That statement is a little baffling. Assuming that a "rope" is used to indicate inextensibility, the answer is either that it cannot or that it depends on the load. The PF is passive tissue but has complex interactions with intrinsic muscles in the foot. If the passive nature dominates, like all materials, it will be stretch under load. If the stretch remains constant at times, it is because the load remains constant. In that sense, the hypothesis is trivial. To be more quantitative, the analogy is inaccurate because everything is a rubber band. Depending upon the loading context, the rubber band may or may not experience large stretch or strain (both are different quantities). So, there is no real dichotomy.

b. Similarly, lines 64-64 state claims about the PF strain without consideration of how the loads may be transmitted. The statement in those lines is qualitatively true, but the details are important. How much strain is too much? Without that caveat, the importance of the point is not evident. To me, answering the question, "how much is too much" seems to be a central one. The hypothesis, as stated, could be interpreted arbitrarily in the absence of greater precision in saying it.

c. Lines 86-88 are probably the main statement of the hypothesis of this paper. This hypothesis is inevitably truecorrect. All elastic bodies stretch under load. Just because the PF stretches, one cannot conclude that its windlass effect is inhibited. To make such a claim, there should be a priori rationale provided for the amount of strain that would be significant. Without this estimate, the hypothesis has been set up to be inevitably correct, or inevitably false, depending on where the threshold is set.

2. Problems with the results (e.g. L229-232, L242-243, L244 onwards):

One of the main claims in this paper is that there may be evidence for a catch mechanism that holds elastic strain energy in the plantar fascia. I find that claim to be unsupported and probably incorrect. Consider, for example, lines 229-232. This speculative claim is unfounded. In order to make this assessment, the total external load on the foot and its transmission through these various elastic elements need to be known. Moreover, we do not know how, if any, the rest of the midfoot arch is being actively modulated. Without that information, this conclusion is premature and probably false. It is more likely that the combination of changing overall external loads on the foot, changing distribution of the load between the PF and midfoot arch, and active modulation of rest of the midfoot stiffness may explain the nearly constant length of the plantar fascia.

However, it is a striking observation that the PF length is that constant (at least in 1 trial that is shown in figure 5a). I urge the authors to refrain from diluting it by making unsupported claims about hypothetical catch mechanisms. I would go so far as to argue that this piece of data, the prolonged pure windlass phase is the main result of this paper if the authors can present data from all the trials to support the near constancy of the length. I am cautious because looking at the individual PF elongation traces, claiming it to be isometric is an overstatement. In time, the PF length is continually changing for any single trial. Of course, when it reaches a maximum and reverses, there will be a locally flat region in the curve, which may be interpreted as nearly isometric. But there is no evidence of an isometric region. The authors should show the MTPJ versus PF data for the supposed isometric region for all individual trials, should remove any claims of a catch mechanism, and discuss the result in terms of whether it occurs close to its length reversal. If so, the questions that need addressing are how synchronized is the reversal with the MTPJ angle, how the synchronization is maintained, and what makes the peak as flat as it is.

The only reasonable null hypothesis that I can think of for the paper is that there should never be a pure windlass phase because the plantar fascia are passive tissues, and windlass engagement would most likely increase the tension borne by the PF and thus their strain. That null hypothesis is mostly true, as seen from the sample trace in figure 5a, but the period of stance when the MTPJ angle is changing substantially with little PF length change is striking. To convince the reader that this is a general trend, can the authors please show that region for every trial as a separate figure? How reliable is the occurrence of that region?

Please allow me to elaborate further on why I think the catch mechanism is unlikely and why the load from the ground is important in this context. If the load is directed such that the bending moment about the midfoot is small, a large load could result in large joint contact forces within the foot but only a slight load that needs to be managed by the plantar fascia. So, the very minimum required to proceed with the claims presented by the authors is the bending moment data about midfoot landmarks, and compare that against the bending moment due to tension in the plantar fascia. Because the PF are passive, an initial assumption could be that PF stress is proportional to strain, and thus the tension in the PF is proportional to its length change. However, even this assumption is only partly true because of the branched structure of the PF, and the muscles that attach to it all along the length.

The claims are overly reliant on the single trace in figure 5a, instead of the temporal dynamics of the PF length and also including all the data. For example, consider the speculation in L242-234 about the PF "absorbing the load". I find this speculation to be one step too far because of the lack of load data on the PF. The load can be distributed between elements and energy can be absorbed if the load does work on the PF. But there is no way to make such an inference based on the data on hand. The trial sample in figure 5a shows that the reverse windlass is not as prolonged or "pure" as the forward windlass. So, this interpretation may simply be an artifact of the vector coding method and the many assumptions that went into it (see my major criticism of the technique later). For example, the equipartition of the space, treating it as if a vector space, or having sharp boundaries between regions are all problematic assumptions of the vector coding technique that could lead to such an over-interpretation of the data.

3. Problems in the discussion, related to those above in the results (L259-261, L291-292):

Hinging the paper on the role of the reverse windlass mechanism early in stance and its role in load management is flawed. I argue that this result has not been shown because of the direction of the load and its effective bending moment on the midfoot. I would argue that the tension needed in the PF to manage that moment is small because the initial bending moment is small. This is because the ground reaction force vector is more posteriorly directed earlier in stance, thus drastically reducing the moment on the midfoot. Similarly late in stance because of the foot posture and the ground reaction force vector's direction. The second result presented in lines 261-262 is fine, but not the claim of a catch mechanism that follows.

I find the discussion based on the supposed isometric nature of the PF also problematic. As I argued later, the isometric nature is not borne out in the time traces of the PF, although the length-rate reaches zero when the length reaches a local maximum. The authors may be able to show that this maximum is synchronized to coincide with peak velocity of MTPJ dorsiflexion, which may underlie the apparent pure windlass phase. But the authors have not yet demonstrated this to be the case. If they do, it begs to be explained.

4. Technical problems with the vector coding method:

I found the "phase space" plot of figure 5a far more informative and accurate representation of the data over the vector coding method that is fraught with problematic assumptions. Are the vectors on this classification diagram quantitative or are they merely qualitative? Does the length of the vector have quantitative meaning? In other words, are the MTPJ rotation and plantar fascia strain treated as independent coordinates of some vector? But describing that as a "vector space" is a provably false assumption because there is a clear dependence of their interaction on other unplotted coordinates. Maybe the authors want to think of it as a low-dimensional projection of some phase space. It makes for a simplified diagram to present what happens, but I find the simplifications to be oversimplified to the extent that it casts doubt on the results. Instead, the phase-space trajectories of figure 5a, with qualitative indicators of pure and mixed phases, is far more valuable.

While the classification scheme is a good attempt, I find its interpretation fraught with risks. The authors should devote considerable attention to the inaccuracies introduced by the classification scheme. Yet another significantly problematic assumption is that the space (which is not a vector space) is somehow equally partitioned by the chosen variables and normalization. That is a big assumption underlying this method and its implications to any of the presented results are unclear. I found it disappointing that such strong and unique data were negatively impacted by the assumptions underlying this rather arbitrary choice of data presentation. The phase space makes far fewer assumptions and is thus more compelling.

Minor issue with the description of the vector coding plots: nowhere is it mentioned what the variables being plotted are.

Minor points
============

L35: What is the logical basis to expect that the PF compromises arch function in the first place? I found this statement as cryptic in the abstract as in the discussion.

L54: To support their claim that the PF are important for elastic strain energy storage, the authors say, "that the arch of the foot is more compliant without the plantar fascia." But more compliant implies more energy storage. So, this point goes against the statement that the PF is important for elastic energy storage. The elastic energy stored in an elastic structure is proportional to its stiffness, but to the square of the displacement. So, when the load experienced is similar, lesser stiffness of the foot will lead to more elastic energy storage.

L80-81: "Using a unique paradigm": Unnecessarily hyped-up language.

L111 and L137: "inertial anatomical coordinate system:" What is inertial about the coordinate systems? Why are these coordinate axes referred to as "inertial"? Are they centered at the center of mass of each bone and oriented along the principal axes of the moment of inertia tensor? Later descriptions show that not to be the case. For example, the axes are oriented to reflect specific choices of kinematic descriptions.

L127-128: "bone occlusion": Which degrees of freedom were lost?

L129: "sesamoid-phalangeal ligament apparatus is quite stiff [20].": The reference cited here is an entire book. I searched the book and cannot find quantitative support for this claim. The stiffness of the ligament should be juxtaposed with the loads it experiences. Can the authors be more specific about the role of this citation and how they support this assumption?

L140: "YZX Tait-Bryan angle sequence": In that case, the Z-axis cannot truly represent adduction because it is a floating axis.

L164-165: "filter effectively preserves the high-frequency content": How is this shown? Was a systematic study of cutoff frequencies conducted to show that there is little power at higher frequencies?

L183: "reasonable assumption": Whether the assumption is reasonable is for the reader to assess. Please add quantitative support for this claim or remove "reasonable" and let the reader be the judge.

L211-212: claim that the pattern was similar in RFS and FFS runners: You only have three RFS traces, and they often fall outside the 1SD region. How can this claim be made?

Figure 5b: What are the gray regions? I cannot find a description or explanation for them.

Table 2: Why don't the percentages come anywhere near 100%? I understand slight deviations because you are reporting the mean, but it does not even come close.

L218: "in direct contradiction to our hypothesis": Which hypothesis is contradicted? I still don't see that there are any well-defined hypotheses in the paper, and when stated as a hypothesis, it is not clear what measurement, if any, could support or falsify it. Not every paper need be hypothesis-based. I think this paper is a case of making a careful examination of the plantar fascia using novel measurement methods and reporting the patterns that are seen. The paper seemed forced into a "hypothesis-driven" bin.

L219: "13±2%": Why round the percentages but not the angles?

L298: Reference [27]: This reference does not apply to the foot and is mostly about invertebrates.

Decision letter (RSPB-2020-1078.R0)

01-Jul-2020

Dear Miss Welte:

I am writing to inform you that your manuscript RSPB-2020-1078 entitled "Ropes and rubber bands: the dynamic function of the plantar fascia during human running" has, in its current form, been rejected for publication in Proceedings B.

This action has been taken on the advice of referees, who have recommended that substantial revisions are necessary. With this in mind we would be happy to consider a resubmission, provided the comments of the referees are fully addressed. However please note that this is not a provisional acceptance.

The resubmission will be treated as a new manuscript. However, we will approach the same reviewers if they are available and it is deemed appropriate to do so by the Editor. Please note that resubmissions must be submitted within six months of the date of this email. In exceptional circumstances, extensions may be possible if agreed with the Editorial Office. Manuscripts submitted after this date will be automatically rejected.

Please find below the comments made by the referees, not including confidential reports to the Editor, which I hope you will find useful. If you do choose to resubmit your manuscript, please upload the following:

1) A ‘response to referees’ document including details of how you have responded to the comments, and the adjustments you have made.
2) A clean copy of the manuscript and one with 'tracked changes' indicating your 'response to referees' comments document.
3) Line numbers in your main document.

To upload a resubmitted manuscript, log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions," click on "Create a Resubmission." Please be sure to indicate in your cover letter that it is a resubmission, and supply the previous reference number.

Please note that this decision may (or may not) have taken into account confidential comments.

In your revision process, please take a second look at how open your science is; our policy is that *ALL* (maximally inclusive) data involved with the study should be made openly accessible, fully enabling re-use, replication and transparency-- see:
https://royalsociety.org/journals/ethics-policies/data-sharing-mining/
Insufficient sharing of data can delay or even cause rejection of a paper.
Full data and code/scripts to enable reuse/replication/repurposing are what this policy intends.

Sincerely,
Dr John Hutchinson, Editor
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member: 1
Comments to Author:
Thank you for the opportunity to read this study. Herein the authors attempt to elucidate the complex dynamics of the human midfoot and its passive tissues during running. The authors attempt to tackle this difficult task using cutting edge x-ray motion analysis and some basic mathematical reconstructive modelling of soft tissue length change in-vivo. This a very topical subject and one that is likely to interest a diverse body of workers across the biological sciences. However, like Reviewer 2, I found the link or translation between the "rubber band and rope" analogy (upon which the study is marketed) and the actual data presented to be counterproductive. Any benefit this adds as an explanatory analogy for the generalist reader is outweighed, in my opinion, by the slight misconception it carries in terms of what specifically is being tested and the level of insight this work delivers in terms of understanding the foot as a functional organ. Specifically, it carries an implication that the study is providing insight at the most fundamental or higher-order level in terms of defining the foot as a functional organ (e.g. the way Ker did in terms of the arch functioning as a spring), when in fact this study is working one or two levels below that by quantifying aspects of fundamental behaviours that we know exist. I'm less familiar with the literature on running, but we know from walking that there is variation across healthy humans in tuning of the arch, and indeed that some healthy humans vary their tuning enormously step-to-step. So we shouldn't be surprised that tuning (sometimes "rubber band" sometimes "rope") goes or what's its basic causes are. The fact this study is working at slightly more detailed/less over-arching level than this is not problem for me at all: what this study is attempting to do with its data is potentially very significant and in principle is topical enough for Proceedings B, an opinion shared by both reviewers. But I do agree with Reviewer 2's criticisms about the clarity of the hypotheses/questions being tested. Reviewer 2 also has a number of major, and I think important, criticisms of the data and how it is being interpreted. My recommendation is therefore that the authors be given the opportunity to resubmit a revised version of the paper to Proceedings B that addresses all the comments from the two expert reviewers. If the technical issues raised by Reviewer 2 can be addressed without the loss of interesting new conclusions about the mechanics of the arch and its passive tissues then I think this study will make a very valuable contribution to the literature.

Reviewer(s)' Comments to Author:

Referee: 1

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2. Problems with the results (e.g. L229-232, L242-243, L244 onwards):

One of the main claims in this paper is that there may be evidence for a catch mechanism that holds elastic strain energy in the plantar fascia. I find that claim to be unsupported and probably incorrect. Consider, for example, lines 229-232. This speculative claim is unfounded. In order to make this assessment, the total external load on the foot and its transmission through these various elastic elements need to be known. Moreover, we do not know how, if any, the rest of the midfoot arch is being actively modulated. Without that information, this conclusion is premature and probably false. It is more likely that the combination of changing overall external loads on the foot, changing distribution of the load between the PF and midfoot arch, and active modulation of rest of the midfoot stiffness may explain the nearly constant length of the plantar fascia.

However, it is a striking observation that the PF length is that constant (at least in 1 trial that is shown in figure 5a). I urge the authors to refrain from diluting it by making unsupported claims about hypothetical catch mechanisms. I would go so far as to argue that this piece of data, the prolonged pure windlass phase is the main result of this paper if the authors can present data from all the trials to support the near constancy of the length. I am cautious because looking at the individual PF elongation traces, claiming it to be isometric is an overstatement. In time, the PF length is continually changing for any single trial. Of course, when it reaches a maximum and reverses, there will be a locally flat region in the curve, which may be interpreted as nearly isometric. But there is no evidence of an isometric region. The authors should show the MTPJ versus PF data for the supposed isometric region for all individual trials, should remove any claims of a catch mechanism, and discuss the result in terms of whether it occurs close to its length reversal. If so, the questions that need addressing are how synchronized is the reversal with the MTPJ angle, how the synchronization is maintained, and what makes the peak as flat as it is.

The only reasonable null hypothesis that I can think of for the paper is that there should never be a pure windlass phase because the plantar fascia are passive tissues, and windlass engagement would most likely increase the tension borne by the PF and thus their strain. That null hypothesis is mostly true, as seen from the sample trace in figure 5a, but the period of stance when the MTPJ angle is changing substantially with little PF length change is striking. To convince the reader that this is a general trend, can the authors please show that region for every trial as a separate figure? How reliable is the occurrence of that region?

Please allow me to elaborate further on why I think the catch mechanism is unlikely and why the load from the ground is important in this context. If the load is directed such that the bending moment about the midfoot is small, a large load could result in large joint contact forces within the foot but only a slight load that needs to be managed by the plantar fascia. So, the very minimum required to proceed with the claims presented by the authors is the bending moment data about midfoot landmarks, and compare that against the bending moment due to tension in the plantar fascia. Because the PF are passive, an initial assumption could be that PF stress is proportional to strain, and thus the tension in the PF is proportional to its length change. However, even this assumption is only partly true because of the branched structure of the PF, and the muscles that attach to it all along the length.

The claims are overly reliant on the single trace in figure 5a, instead of the temporal dynamics of the PF length and also including all the data. For example, consider the speculation in L242-234 about the PF "absorbing the load". I find this speculation to be one step too far because of the lack of load data on the PF. The load can be distributed between elements and energy can be absorbed if the load does work on the PF. But there is no way to make such an inference based on the data on hand. The trial sample in figure 5a shows that the reverse windlass is not as prolonged or "pure" as the forward windlass. So, this interpretation may simply be an artifact of the vector coding method and the many assumptions that went into it (see my major criticism of the technique later). For example, the equipartition of the space, treating it as if a vector space, or having sharp boundaries between regions are all problematic assumptions of the vector coding technique that could lead to such an over-interpretation of the data.

3. Problems in the discussion, related to those above in the results (L259-261, L291-292):

Hinging the paper on the role of the reverse windlass mechanism early in stance and its role in load management is flawed. I argue that this result has not been shown because of the direction of the load and its effective bending moment on the midfoot. I would argue that the tension needed in the PF to manage that moment is small because the initial bending moment is small. This is because the ground reaction force vector is more posteriorly directed earlier in stance, thus drastically reducing the moment on the midfoot. Similarly late in stance because of the foot posture and the ground reaction force vector's direction. The second result presented in lines 261-262 is fine, but not the claim of a catch mechanism that follows.

I find the discussion based on the supposed isometric nature of the PF also problematic. As I argued later, the isometric nature is not borne out in the time traces of the PF, although the length-rate reaches zero when the length reaches a local maximum. The authors may be able to show that this maximum is synchronized to coincide with peak velocity of MTPJ dorsiflexion, which may underlie the apparent pure windlass phase. But the authors have not yet demonstrated this to be the case. If they do, it begs to be explained.

4. Technical problems with the vector coding method:

I found the "phase space" plot of figure 5a far more informative and accurate representation of the data over the vector coding method that is fraught with problematic assumptions. Are the vectors on this classification diagram quantitative or are they merely qualitative? Does the length of the vector have quantitative meaning? In other words, are the MTPJ rotation and plantar fascia strain treated as independent coordinates of some vector? But describing that as a "vector space" is a provably false assumption because there is a clear dependence of their interaction on other unplotted coordinates. Maybe the authors want to think of it as a low-dimensional projection of some phase space. It makes for a simplified diagram to present what happens, but I find the simplifications to be oversimplified to the extent that it casts doubt on the results. Instead, the phase-space trajectories of figure 5a, with qualitative indicators of pure and mixed phases, is far more valuable.

While the classification scheme is a good attempt, I find its interpretation fraught with risks. The authors should devote considerable attention to the inaccuracies introduced by the classification scheme. Yet another significantly problematic assumption is that the space (which is not a vector space) is somehow equally partitioned by the chosen variables and normalization. That is a big assumption underlying this method and its implications to any of the presented results are unclear. I found it disappointing that such strong and unique data were negatively impacted by the assumptions underlying this rather arbitrary choice of data presentation. The phase space makes far fewer assumptions and is thus more compelling.

Minor issue with the description of the vector coding plots: nowhere is it mentioned what the variables being plotted are.

Minor points
============

L35: What is the logical basis to expect that the PF compromises arch function in the first place? I found this statement as cryptic in the abstract as in the discussion.

L54: To support their claim that the PF are important for elastic strain energy storage, the authors say, "that the arch of the foot is more compliant without the plantar fascia." But more compliant implies more energy storage. So, this point goes against the statement that the PF is important for elastic energy storage. The elastic energy stored in an elastic structure is proportional to its stiffness, but to the square of the displacement. So, when the load experienced is similar, lesser stiffness of the foot will lead to more elastic energy storage.

L80-81: "Using a unique paradigm": Unnecessarily hyped-up language.

L111 and L137: "inertial anatomical coordinate system:" What is inertial about the coordinate systems? Why are these coordinate axes referred to as "inertial"? Are they centered at the center of mass of each bone and oriented along the principal axes of the moment of inertia tensor? Later descriptions show that not to be the case. For example, the axes are oriented to reflect specific choices of kinematic descriptions.

L127-128: "bone occlusion": Which degrees of freedom were lost?

L129: "sesamoid-phalangeal ligament apparatus is quite stiff [20].": The reference cited here is an entire book. I searched the book and cannot find quantitative support for this claim. The stiffness of the ligament should be juxtaposed with the loads it experiences. Can the authors be more specific about the role of this citation and how they support this assumption?

L140: "YZX Tait-Bryan angle sequence": In that case, the Z-axis cannot truly represent adduction because it is a floating axis.

L164-165: "filter effectively preserves the high-frequency content": How is this shown? Was a systematic study of cutoff frequencies conducted to show that there is little power at higher frequencies?

L183: "reasonable assumption": Whether the assumption is reasonable is for the reader to assess. Please add quantitative support for this claim or remove "reasonable" and let the reader be the judge.

L211-212: claim that the pattern was similar in RFS and FFS runners: You only have three RFS traces, and they often fall outside the 1SD region. How can this claim be made?

Figure 5b: What are the gray regions? I cannot find a description or explanation for them.

Table 2: Why don't the percentages come anywhere near 100%? I understand slight deviations because you are reporting the mean, but it does not even come close.

L218: "in direct contradiction to our hypothesis": Which hypothesis is contradicted? I still don't see that there are any well-defined hypotheses in the paper, and when stated as a hypothesis, it is not clear what measurement, if any, could support or falsify it. Not every paper need be hypothesis-based. I think this paper is a case of making a careful examination of the plantar fascia using novel measurement methods and reporting the patterns that are seen. The paper seemed forced into a "hypothesis-driven" bin.

L219: "13±2%": Why round the percentages but not the angles?

L298: Reference [27]: This reference does not apply to the foot and is mostly about invertebrates.

Author's Response to Decision Letter for (RSPB-2020-1078.R0)

See Appendix A.

RSPB-2020-2095.R0

Review form: Reviewer 1 (Kristiaan D'Aout)

Recommendation
Accept as is

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Excellent

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
I thank the authors for their clear reply to my queries in a separate letter, as well as for the additions and clarifications made in the manuscript. I am satisfied that all issues are either resolved or acknowledged better in the revised version of the manuscript. I have no further issues.

Review form: Reviewer 2

Recommendation
Major revision is needed (please make suggestions in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Acceptable

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

> **Is it accessible?**
> N/A
>
> **Is it clear?**
> N/A
>
> **Is it adequate?**
> N/A

Do you have any ethical concerns with this paper?
No

Comments to the Author
I attach PDF comments in case the text comes out poorly formatted.

Major comments
==========

The authors have revised many parts of the text in response to the previous round of reviews. They have responded constructively to the problems identified with the lack of plausible hypothesis, but have still carried over several problematic portions from the previous version. As a result, I still find this paper somewhat lacking, despite the novelty of the dataset.

Problems with the hypothesis

The previous problematic hypothesis on rope versus rubber bands was removed but the paper is still lacking a well-defined hypothesis that is not a straw man. I find the data reported in the manuscript to be quite important for the community, whether it is hypothesis-based or not. So, I am tried to find specific locations in the text that are problematic and make suggestions that may help frame the objective of the paper.

L78--79: What is stated as testing a prediction, "...we test in vivo if the elastic behaviour of the plantar fascia compromises its function as a windlass in running", is really not a well-defined prediction. What is meant by "compromise"? What "function" is being compromised? There are no functional efficacy measures to know the answers to these questions. Thus, I still find the text lacking in a hypothesis.

L81--82: "We classify the coupling of MTPJ dorsiflexion and plantar fascia elongation to test if the foot can exhibit a pure windlass mechanism."

Like my criticism in the previous review, this is a straw man. The answer will be, "depends". How about stating the objective of the paper as not testing a hypothesis but making measurements to quantify the deviations from pure forward-windlass function? The functional consequences of this departure are not answered by this work but the measurements set the stage for such future studies.

L85--88: "We hypothesize that due to the elasticity of the plantar fascia, we will only see periods of stance where the forward-windlass is inhibited by the elongation or enhanced by the shortening of the plantar fascia, and that we will not see a pure forward-windlass mechanism."

This is still not a hypothesis. Given the nature of elasticity, there are only three possibilities. The hypothesis, as stated by the authors, seems to be that two out of three possibilities may occur. Why would they expect that a pure forward-windlass cannot occur? Given the lack of load measurements (here and in past work), there is no basis to expect that. Alternatively, perhaps the authors have a mathematical model upon which this hypothesis is being founded. But no such reference is provided. So I still find that the authors are forcing a hypothesis where there may be none. If the authors do have a plausible hypothesis and alternative hypotheses in mind, it does not come through in the paper.

L63--65: "For the windlass to change the shape of the arch effectively, the plantar fascia must undergo minimal strain ..."

What is meant by "minimal" and by "effectively"? I point to figure 1, where the arch changes shape in all three of the cartoons.

I think this is the point in the paper where a clear objective can be defined. Under the classical windlass picture of an inextensible PF, the expectation is that the arch height is a function solely of toe dorsiflexion. However, we know that the plantar fascia is extensible and likely to be stretched by the tension acting upon it. The possibility of stretch raises the need to quantify the windlass mechanism and how it differs in response from the assumption of an inextensible PF. The issue is the partitioning of elastic strain energy between the plantar fascia and rest of the foot's structures when the toe is dorsiflexed. Stated in those terms, one can compare apples with apples but direct measurement of elastic strain energy associated with the PF and all of the midfoot is impractical. Given that limitation, the authors have arrived at a proxy for the elastic strain energy partitioning, which is the relationship between toe dorsiflexion, PF extension, and midfoot deformation.

Methodological issues

1. Coordinate system choice: The authors have used a YZX Tait-Bryan angle sequence (L147). I find this choice hard to justify. I raised this objection previously, which was set aside by the authors as unimportant. As the authors know well, the middle floating axis defies simple anatomical explanation. The phalanx motion with respect to the metatarsal is mostly in plantar/dorsiflexion (X) and ad/abduction (Z). There may be some degree of ev/inversion, but that is generally much smaller than the other changes. Given these, the choice of the angle sequence should have been ZYX or XYZ, so that the reported angles can be anatomically

interpreted. This may seem like a minor point, but I contend that it is important for future researchers to be able to interpret these data. Please use a convention that is consistent with the broader usage among anatomists and podiatrists, to promote repeatability of the science.

L144-147: "The inertial axes computed from the surface meshes defined the anatomical co-ordinate systems for the tibia, calcaneus, first metatarsal and first proximal phalanx [18]. The coordinate systems were oriented so that the x-axis represented dorsiflexion, the y-axis represented inversion and the z-axis represented adduction, with reference to the right foot."

I find this description confusing. The coordinate system is inertial because the axes are oriented along the principal axes of the moment of inertia tensor. But the description here states that the axes were oriented to fit joint degrees of freedom. Which system was used? I cannot see how both are the same.

2. Vector coding: I am disappointed that the authors have mostly ignored the criticisms on the vector coding approach when revising the manuscript. They acknowledged in their rebuttal that the space of MTPJ angle versus PF elongation is not a vector space. But then they go on to interpret the vector coding results as if it were a vector space.

In their rebuttal, the authors included one useful piece of information, which is to examine the extent of MTPJ rotation or PF extension during the different phases as identified by the coding approach. Reassuringly, it is consistent with what one would define intuitively. But that does not make the process of coding somehow a generic method that will always lead to valid interpretations. I am quite concerned that this paper will be used as justification for the misapplication of the technique in future papers by the community. So it is essential that the authors refrain from relying on the vector coding as the primary tool. Instead, they should discuss why it is a subjective tool that shows reasonable correspondence with the data presented in Table 1 (as they do in their rebuttal). Also needed is a discussion of why the choices made in defining the sections are somewhat arbitrary and thus the technique is not necessarily generalizable to all settings.

Here are specific areas of the text where I found problematic interpretations based on the vector coding approach, with no discussion of the issues with the method.

L193--194: "Vector coding evaluates the dominance of one variable over another"

This statement exemplifies the deep problems with vector coding. How can an angle change be compared to a length change? Is 1 degree more or less than 1 cm? I raised the issue during the previous review and also raise it in the caption for figure 2 in this version. The authors have ignored my major criticism from the previous round of reviews, which is not acceptable.

Figure 2 caption: "In the example time point Pi and the adjacent time points, the subject's plantar fascia elongation is more substantial between time points than the MTPJ dorsiflexion."

This comparison between angle and length is not meaningful. One quantity is an angle and another is a length change. Even if both of them were somehow normalized in order to make them both dimensionless, they are physically different variables and their comparison is based upon tacit assumptions that have not been identified. This was the same issue raised in the first round of reviews and the authors have not responded to those criticisms.

L195--196: "The angle of this vector indicates the dominant variable."

This really shows the problematic nature of the vector coding approach. By choosing to normalize the elongation and MTPJ angle by different baseline values, I can make this angle anything I want to it to be. Not only is the name "vector coding" deceptive, because this is not a vector space, the interpretations based on the method could also be problematic.

L201--202: "The unit circle was divided into 8 equal segments, centred around the axes."

Please read my reviews from the previous time for why an equipartition of the space is incorrect. Also see my comments in other areas of this text.

Just because the extremes --- 0, 90, 180, and 270 --- appear to correlate with intuitive definitions, the intermediate values cannot be linearly interpolated. The authors have chosen to ignore my comments on this from the past review round, which is quite disappointing.

L203--204: "The time spent in the primary phases (windlass, contribution to arch-spring) and the interaction phases were calculated as a percentage of stance."

This fractional time is founded upon the notion that the angle-length space is linear and equally scaled. Given the problematic line of reasoning adopted in constructing the "vector code", the "time spent" measures are equally problematic. I urge the authors to not push this method and to not ignore the reviews with detailed arguments for why it is incorrect. I am concerned that the method's usage in this paper will set the precedent for further false inferences to be made in the literature.

L269: "Discussion"

The vector coding diagram seems unnecessary to draw the inferences presented in the discussion. If the PF elongation (DL) versus MTPJ dorsiflexion (q) data are displayed as a curve of % stance versus instantaneous heading of the plot of the DL vs q curve, the regions of pure windlass action should be quite apparent. Although I believe that the authors saw these trends in their data, the vector coding scheme has thrown the inferences into question. Can the authors instead plot the heading as a function of percent stance for all subjects so that we can see when the stated inferences are applicable and when it may be an artifact of the mean response.

Detailed comments
===========

L70--72: "During both walking and running gaits, there is evidence of the forward-windlass mechanism [4,7,8,14] and that the plantar fascia strains during mid- to late- stance, simultaneously to the expected timing of the windlass."

Expected in what sense? Also, what is meant by "timing of the windlass"? It is a mechanism that is continuously varying in its involvement and not a discrete event.

L75--78: "While current approaches such as motion capture [7–10], ultrasound [7,9,10], or single plane fluoroscopy [12,13] have provided insight into plantar fascia and foot function, they do not capture the complex, three- dimensional motions of the structures within the foot during locomotion."

The analyses and viewpoints presented in this paper are two-dimensional, within the sagittal plane. So I don't see the basis for claiming that the lack of 3D measurement is somehow the problem. What novel information from 3D X-ray imaging is needed to address your questions that cannot be provided by a sagittal plane X-ray view? This case needs to be made more clearly.

L150--151: "The time of minimum arch angular velocity was selected as the point where the arch angle started to decrease."

Do you mean the point in time when the velocity changed sign and became negative? The minimum of velocity is when the angular acceleration is zero. When the arch angle starts to decrease, it was presumable increasing until that point. This means that the velocity, which is the first derivative, would be zero. So I do not see how the minimum of arch angular velocity relates to "the point where the arch angle started to decrease."

L168: "converged to optimal solutions"

Which optimization routine was used? How was convergence verified?

L174--175: "potential trade-offs of the plantar fascia's role in the arch-spring and windlass mechanisms"

The fallacious dichotomy from the previous submission appears to have been carried forward into the revised manuscript. As argued previously, the plantar fascia will always stretch under load. How much it will stretch depends on the load. In case the authors are making a functional argument about PF function, I argue that they are lacking hypotheses and evidence to show how the extensibility of the plantar fascia affects locomotor function.

L178: "when the arch flattens"

Given the quantitative details of the methods, it is not clear how the authors define arch height. Terms like the arch flattening or rising only make sense when the height is specified with respect to some baseline. The kinematics are defined in terms of the rotation of the first metatarsal with respect to the calcaneus. So, complex motion of the calcaneus that involves a combination of translation and rotation could manifest as arch deformation according to the kinematic variable used by the authors, without any apparent change in the externally perceived arch height.

L187--188: "therefore, fibre elongation is analogous to strain"

This statement is confusing. Strain is a dimensionless quantity that tracks deformation or elongation relative to a reference length. So strain and elongation cannot be analogous. Further, why is the assumption of a non-slack PF related to the normalization of elongation to a strain variable?

L212--213: "In theory, the change in arch length, Δl, and MTPJ dorsiflexion, θ, should be coupled."

Depends on the theory. There are many elastic bodies involved here, including the PF, the midfoot region, and the subtalar area. The degree of coupling between Delta L and theta depends on whether some of these elastic regions deform more than the others. So, there is no single "in theory" that I can see. Can the authors be more precise about the premise under which the coupling is expected?

L230: "a temporally consistent pattern during the running gait cycle"

What does the word "consistent" mean in this context? In table 1, for example, the authors state that because of too much inter-subject variability in the timing of the transitions between the different behaviors, they only report the time spent in each region of the coding diagram. That indicates a lack of temporally consistent patterns.

L231--235: "Consistent with our hypothesis, we found an inhibited forward-windlass just prior to the pure forward-windlass, where the plantar fascia elongated while the toes dorsiflexed and the arch rose slightly. However, in direct contradiction to our hypothesis, the plantar fascia spent a substantial period (11 ± 1% of stance) in the pure forward-windlass phase, approximately at heel rise (see Supplemental Video)"

The strength of the claim is far more than can be supported by the data. I don't know if these are because the authors only look at the mean response or because of the problems with the vector coding approach. Please allow me to explain further.

The authors claim that "consistent with our hypothesis, we found an inhibited forward-windlass." Even if one were to use the problematic vector coding scheme, the results are not consistent with the hypothesis that the windlass is inhibited by PF elongation. For example, in subjects 1, 3, 6, and others, the inhibited windlass is far smaller in duration than the mean. Even the sequencing of the different phases is quite variable, with some subject data showing multiple visits to the same phase. Whether that is capturing real phenomena or is simply an artifact of the coding system is unclear.

I urge the authors to follow my earlier recommendation to avoid the language of a hypothesis-based narrative, and instead focus on the objective of providing the first-ever measurement of PF function during windlass engagement and arch deformation. Then, the language of the paper can be more consistent with what the evidence shows.

L271: "in a consistent sequence"

This is not true. There is substantial variability, even when using the problematic coding scheme.

L277: "maximally strained"

That is a strong claim. Maximal with respect to what measure? Is the claim that there is some limiting maximal value of strain that is reached by the PF in every trial? I saw no evidence of that.

L281--284: "Our data show that in early stance, the plantar fascia does not elongate substantially until arch flattening has already slowed; instead, the plantar fascia facilitates the reverse-windlass motion of the foot, likely so that arch tissues proximal to the plantar fascia manage more of the load than the plantar fascia."

I see a means to strengthen this argument. There was an underlying assumption that the PF were not slack to begin with. Even if they are not completely slack and are bearing low tension, the nonlinear nature of the load-displacement curve of the PF would imply that it cannot bear much load initially. So the expectation under the slack or light tension scenario is a compliant PF that would easily stretch. That is the opposite of what you see, demonstrating the importance of the pure reverse windlass phase.

Decision letter (RSPB-2020-2095.R0)

28-Oct-2020

Dear Miss Welte:

Your manuscript has now been peer reviewed and the reviews have been assessed by an Associate Editor. The reviewers' comments (not including confidential comments to the Editor) and the comments from the Associate Editor are included at the end of this email for your reference. As you will see, the reviewers and the Editors have raised some concerns with your manuscript and we would like to invite you to revise your manuscript to address them.

We do not allow multiple rounds of revision so we urge you to make every effort to fully address all of the comments at this stage. If deemed necessary by the Associate Editor, your manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers are not available we may invite new reviewers. Please note that we cannot guarantee eventual acceptance of your manuscript at this stage.

This MS came close to outright rejection because one reviewer did not feel sufficiently taken seriously in revisions. To avoid rejection if you resubmit, that reviewer needs to be better satisfied. We cannot allow further rounds of substantial revision; the manuscript must be brought to the level of "accept with minor revisions" at resubmission + re-review or it will be rejected. However, the Associate Editor and I will be weighing revisions vs. fairness of peer review so that one reviewer does not bias the chance the paper has at being acceptable.

To submit your revision please log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions", click on "Create a Revision". Your manuscript number has been appended to denote a revision.

When submitting your revision please upload a file under "Response to Referees" in the "File Upload" section. This should document, point by point, how you have responded to the reviewers' and Editors' comments, and the adjustments you have made to the manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Your main manuscript should be submitted as a text file (doc, txt, rtf or tex), not a PDF. Your figures should be submitted as separate files and not included within the main manuscript file.

When revising your manuscript you should also ensure that it adheres to our editorial policies (https://royalsociety.org/journals/ethics-policies/). You should pay particular attention to the following:

Research ethics:
If your study contains research on humans please ensure that you detail in the methods section whether you obtained ethical approval from your local research ethics committee and gained informed consent to participate from each of the participants.

Use of animals and field studies:
If your study uses animals please include details in the methods section of any approval and licences given to carry out the study and include full details of how animal welfare standards were ensured. Field studies should be conducted in accordance with local legislation; please include details of the appropriate permission and licences that you obtained to carry out the field work.

Data accessibility and data citation:
It is a condition of publication that you make available the data and research materials supporting the results in the article (https://royalsociety.org/journals/authors/author-guidelines/#data). Datasets should be deposited in an appropriate publicly available repository and details of the associated accession number, link or DOI to the datasets must be included in the Data Accessibility section of the article (https://royalsociety.org/journals/ethics-policies/data-sharing-mining/). Reference(s) to datasets should also be included in the reference list of the article with DOIs (where available).

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should also be fully cited and listed in the references.

If you wish to submit your data to Dryad (http://datadryad.org/) and have not already done so you can submit your data via this link http://datadryad.org/submit?journalID=RSPB&manu=(Document not available), which will take you to your unique entry in the Dryad repository.

If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link.

For more information please see our open data policy http://royalsocietypublishing.org/data-sharing.

Electronic supplementary material:
All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI. Please try to submit all supplementary material as a single file.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

Please submit a copy of your revised paper within three weeks. If we do not hear from you within this time your manuscript will be rejected. If you are unable to meet this deadline please let us know as soon as possible, as we may be able to grant a short extension.

Thank you for submitting your manuscript to Proceedings B; we look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Best wishes,
Dr John Hutchinson, Editor
mailto: proceedingsb@royalsociety.org

Associate Editor Board Member: 1
Comments to Author:
Once again, I enjoyed reading this study, and I thank the authors for submitting a revised version. In particular I found the revised figures, and the inclusion of more data, very helpful when attempting to follow the interpretations of plantar fascia behaviour vs time. I'm also glad the authors have revised the paper overall along the lines suggested, in terms of dropping the rope vs rubber band paradigm. That said, I am in agreement with the reviewer that suggests revision is still needed: the paper still requires some further revision both in terms of the writing/interpretation and the approach used to analyse the data. I would urge the authors to seriously consider the comments from the reviewer and address them robustly and directly.

Reviewer(s)' Comments to Author:
Referee: 2
Comments to the Author(s).

Major comments
==========

The authors have revised many parts of the text in response to the previous round of reviews. They have responded constructively to the problems identified with the lack of plausible hypothesis, but have still carried over several problematic portions from the previous version. As a result, I still find this paper somewhat lacking, despite the novelty of the dataset.

Problems with the hypothesis

The previous problematic hypothesis on rope versus rubber bands was removed but the paper is still lacking a well-defined hypothesis that is not a straw man. I find the data reported in the manuscript to be quite important for the community, whether it is hypothesis-based or not. So, I am tried to find specific locations in the text that are problematic and make suggestions that may help frame the objective of the paper.

L78--79: What is stated as testing a prediction, "...we test in vivo if the elastic behaviour of the plantar fascia compromises its function as a windlass in running", is really not a well-defined prediction. What is meant by "compromise"? What "function" is being compromised? There are no functional efficacy measures to know the answers to these questions. Thus, I still find the text lacking in a hypothesis.

L81--82: "We classify the coupling of MTPJ dorsiflexion and plantar fascia elongation to test if the foot can exhibit a pure windlass mechanism."

Like my criticism in the previous review, this is a straw man. The answer will be, "depends". How about stating the objective of the paper as not testing a hypothesis but making measurements to quantify the deviations from pure forward-windlass function? The functional consequences of this departure are not answered by this work but the measurements set the stage for such future studies.

L85--88: "We hypothesize that due to the elasticity of the plantar fascia, we will only see periods of stance where the forward-windlass is inhibited by the elongation or enhanced by the shortening of the plantar fascia, and that we will not see a pure forward-windlass mechanism."

This is still not a hypothesis. Given the nature of elasticity, there are only three possibilities. The hypothesis, as stated by the authors, seems to be that two out of three possibilities may occur. Why would they expect that a pure forward-windlass cannot occur? Given the lack of load measurements (here and in past work), there is no basis to expect that. Alternatively, perhaps the authors have a mathematical model upon which this hypothesis is being founded. But no such reference is provided. So I still find that the authors are forcing a hypothesis where there may be none. If the authors do have a plausible hypothesis and alternative hypotheses in mind, it does not come through in the paper.

L63--65: "For the windlass to change the shape of the arch effectively, the plantar fascia must undergo minimal strain ..."

What is meant by "minimal" and by "effectively"? I point to figure 1, where the arch changes shape in all three of the cartoons.

I think this is the point in the paper where a clear objective can be defined. Under the classical windlass picture of an inextensible PF, the expectation is that the arch height is a function solely of toe dorsiflexion. However, we know that the plantar fascia is extensible and likely to be stretched by the tension acting upon it. The possibility of stretch raises the need to quantify the windlass mechanism and how it differs in response from the assumption of an inextensible PF. The issue is the partitioning of elastic strain energy between the plantar fascia and rest of the foot's structures when the toe is dorsiflexed. Stated in those terms, one can compare apples with apples but direct measurement of elastic strain energy associated with the PF and all of the midfoot is impractical. Given that limitation, the authors have arrived at a proxy for the elastic strain energy partitioning, which is the relationship between toe dorsiflexion, PF extension, and midfoot deformation.

Methodological issues
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1. Coordinate system choice: The authors have used a YZX Tait-Bryan angle sequence (L147). I find this choice hard to justify. I raised this objection previously, which was set aside by the authors as unimportant. As the authors know well, the middle floating axis defies simple anatomical explanation. The phalanx motion with respect to the metatarsal is mostly in plantar/dorsiflexion (X) and ad/abduction (Z). There may be some degree of ev/inversion, but that is generally much smaller than the other changes. Given these, the choice of the angle sequence should have been ZYX or XYZ, so that the reported angles can be anatomically interpreted. This may seem like a minor point, but I contend that it is important for future researchers to be able to interpret these data. Please use a convention that is consistent with the broader usage among anatomists and podiatrists, to promote repeatability of the science.

L144-147: "The inertial axes computed from the surface meshes defined the anatomical co-ordinate systems for the tibia, calcaneus, first metatarsal and first proximal phalanx [18]. The coordinate systems were oriented so that the x-axis represented dorsiflexion, the y-axis represented inversion and the z-axis represented adduction, with reference to the right foot."

I find this description confusing. The coordinate system is inertial because the axes are oriented along the principal axes of the moment of inertia tensor. But the description here states that the axes were oriented to fit joint degrees of freedom. Which system was used? I cannot see how both are the same.

2. Vector coding: I am disappointed that the authors have mostly ignored the criticisms on the vector coding approach when revising the manuscript. They acknowledged in their rebuttal that the space of MTPJ angle versus PF elongation is not a vector space. But then they go on to interpret the vector coding results as if it were a vector space.

In their rebuttal, the authors included one useful piece of information, which is to examine the extent of MTPJ rotation or PF extension during the different phases as identified by the coding approach. Reassuringly, it is consistent with what one would define intuitively. But that does not make the process of coding somehow a generic method that will always lead to valid interpretations. I am quite concerned that this paper will be used as justification for the misapplication of the technique in future papers by the community. So it is essential that the authors refrain from relying on the vector coding as the primary tool. Instead, they should discuss why it is a subjective tool that shows reasonable correspondence with the data presented in Table 1 (as they do in their rebuttal). Also needed is a discussion of why the choices made in defining the sections are somewhat arbitrary and thus the technique is not necessarily generalizable to all settings.

Here are specific areas of the text where I found problematic interpretations based on the vector coding approach, with no discussion of the issues with the method.

L193--194: "Vector coding evaluates the dominance of one variable over another"

This statement exemplifies the deep problems with vector coding. How can an angle change be compared to a length change? Is 1 degree more or less than 1 cm? I raised the issue during the previous review and also raise it in the caption for figure 2 in this version. The authors have ignored my major criticism from the previous round of reviews, which is not acceptable.

Figure 2 caption: "In the example time point Pi and the adjacent time
points, the subject's plantar fascia elongation is more substantial between time points than the MTPJ dorsiflexion."

This comparison between angle and length is not meaningful. One quantity is an angle and another is a length change. Even if both of them were somehow normalized in order to make them both dimensionless, they are physically different variables and their comparison is based upon tacit assumptions that have not been identified. This was the same issue raised in the first round of reviews and the authors have not responded to those criticisms.

L195--196: "The angle of this vector indicates the dominant variable."

This really shows the problematic nature of the vector coding approach. By choosing to normalize the elongation and MTPJ angle by different baseline values, I can make this angle anything I want to it to be. Not only is the name "vector coding" deceptive, because this is not a vector space, the interpretations based on the method could also be problematic.

L201--202: "The unit circle was divided into 8 equal segments, centred around the axes."

Please read my reviews from the previous time for why an equipartition of the space is incorrect. Also see my comments in other areas of this text.

Just because the extremes --- 0, 90, 180, and 270 --- appear to correlate with intuitive definitions, the intermediate values cannot be linearly interpolated. The authors have chosen to ignore my comments on this from the past review round, which is quite disappointing.

L203--204: "The time spent in the primary phases (windlass, contribution to arch-spring) and the interaction phases were calculated as a percentage of stance."

This fractional time is founded upon the notion that the angle-length space is linear and equally scaled. Given the problematic line of reasoning adopted in constructing the "vector code", the "time spent" measures are equally problematic. I urge the authors to not push this method and to not ignore the reviews with detailed arguments for why it is incorrect. I am concerned that the method's usage in this paper will set the precedent for further false inferences to be made in the literature.

L269: "Discussion"

The vector coding diagram seems unnecessary to draw the inferences presented in the discussion. If the PF elongation (DL) versus MTPJ dorsiflexion (q) data are displayed as a curve of % stance versus instantaneous heading of the plot of the DL vs q curve, the regions of pure windlass action should be quite apparent. Although I believe that the authors saw these trends in their data, the vector coding scheme has thrown the inferences into question. Can the authors instead plot the heading as a function of percent stance for all subjects so that we can see when the stated inferences are applicable and when it may be an artifact of the mean response.

Detailed comments
===========

L70--72: "During both walking and running gaits, there is evidence of the forward-windlass mechanism [4,7,8,14] and that the plantar fascia strains during mid- to late- stance, simultaneously to the expected timing of the windlass."

Expected in what sense? Also, what is meant by "timing of the windlass"? It is a mechanism that is continuously varying in its involvement and not a discrete event.

L75--78: "While current approaches such as motion capture [7–10], ultrasound [7,9,10], or single plane fluoroscopy [12,13] have provided insight into plantar fascia and foot function, they do not capture the complex, three- dimensional motions of the structures within the foot during locomotion."

The analyses and viewpoints presented in this paper are two-dimensional, within the sagittal plane. So I don't see the basis for claiming that the lack of 3D measurement is somehow the problem. What novel information from 3D X-ray imaging is needed to address your questions that cannot be provided by a sagittal plane X-ray view? This case needs to be made more clearly.

L150--151: "The time of minimum arch angular velocity was selected as the point where the arch angle started to decrease."

Do you mean the point in time when the velocity changed sign and became negative? The minimum of velocity is when the angular acceleration is zero. When the arch angle starts to decrease, it was presumable increasing until that point. This means that the velocity, which is the first derivative, would be zero. So I do not see how the minimum of arch angular velocity relates to "the point where the arch angle started to decrease."

L168: "converged to optimal solutions"

Which optimization routine was used? How was convergence verified?

L174--175: "potential trade-offs of the plantar fascia’s role in the arch-spring and windlass mechanisms"

The fallacious dichotomy from the previous submission appears to have been carried forward into the revised manuscript. As argued previously, the plantar fascia will always stretch under load. How much it will stretch depends on the load. In case the authors are making a functional argument about PF function, I argue that they are lacking hypotheses and evidence to show how the extensibility of the plantar fascia affects locomotor function.

L178: "when the arch flattens"

Given the quantitative details of the methods, it is not clear how the authors define arch height. Terms like the arch flattening or rising only make sense when the height is specified with respect to some baseline. The kinematics are defined in terms of the rotation of the first metatarsal with respect to the calcaneus. So, complex motion of the calcaneus that involves a combination of translation and rotation could manifest as arch deformation according to the kinematic variable used by the authors, without any apparent change in the externally perceived arch height.

L187--188: "therefore, fibre elongation is analogous to strain"

This statement is confusing. Strain is a dimensionless quantity that tracks deformation or elongation relative to a reference length. So strain and elongation cannot be analogous. Further, why is the assumption of a non-slack PF related to the normalization of elongation to a strain variable?

L212--213: "In theory, the change in arch length, Δl, and MTPJ dorsiflexion, θ, should be coupled."

Depends on the theory. There are many elastic bodies involved here, including the PF, the midfoot region, and the subtalar area. The degree of coupling between Delta L and theta depends on whether some of these elastic regions deform more than the others. So, there is no single "in theory" that I can see. Can the authors be more precise about the premise under which the coupling is expected?

L230: "a temporally consistent pattern during the running gait cycle"

What does the word "consistent" mean in this context? In table 1, for example, the authors state that because of too much inter-subject variability in the timing of the transitions between the different behaviors, they only report the time spent in each region of the coding diagram. That indicates a lack of temporally consistent patterns.

L231--235: "Consistent with our hypothesis, we found an inhibited forward-windlass just prior to the pure forward-windlass, where the plantar fascia elongated while the toes dorsiflexed and the arch rose slightly. However, in direct contradiction to our hypothesis, the plantar fascia spent a substantial period (11 ± 1% of stance) in the pure forward-windlass phase, approximately at heel rise (see Supplemental Video)"

The strength of the claim is far more than can be supported by the data. I don't know if these are because the authors only look at the mean response or because of the problems with the vector coding approach. Please allow me to explain further.

The authors claim that "consistent with our hypothesis, we found an inhibited forward-windlass." Even if one were to use the problematic vector coding scheme, the results are not consistent with the hypothesis that the windlass is inhibited by PF elongation. For example, in subjects 1, 3, 6, and others, the inhibited windlass is far smaller in duration than the mean. Even the sequencing of the different phases is quite variable, with some subject data showing multiple visits to the same phase. Whether that is capturing real phenomena or is simply an artifact of the coding system is unclear.

I urge the authors to follow my earlier recommendation to avoid the language of a hypothesis-based narrative, and instead focus on the objective of providing the first-ever measurement of PF function during windlass engagement and arch deformation. Then, the language of the paper can be more consistent with what the evidence shows.

L271: "in a consistent sequence"

This is not true. There is substantial variability, even when using the problematic coding scheme.

L277: "maximally strained"

That is a strong claim. Maximal with respect to what measure? Is the claim that there is some limiting maximal value of strain that is reached by the PF in every trial? I saw no evidence of that.

L281--284: "Our data show that in early stance, the plantar fascia does not elongate substantially until arch flattening has already slowed; instead, the plantar fascia facilitates the reverse-windlass motion of the foot, likely so that arch tissues proximal to the plantar fascia manage more of the load than the plantar fascia."

I see a means to strengthen this argument. There was an underlying assumption that the PF were not slack to begin with. Even if they are not completely slack and are bearing low tension, the nonlinear nature of the load-displacement curve of the PF would imply that it cannot bear much load initially. So the expectation under the slack or light tension scenario is a compliant PF that would easily stretch. That is the opposite of what you see, demonstrating the importance of the pure reverse windlass phase.

Referee: 1
Comments to the Author(s).
I thank the authors for their clear reply to my queries in a separate letter, as well as for the additions and clarifications made in the manuscript. I am satisfied that all issues are either resolved or acknowledged better in the revised version of the manuscript. I have no further issues.

Author's Response to Decision Letter for (RSPB-2020-2095.R0)

See Appendix B.

Decision letter (RSPB-2020-2095.R1)

11-Dec-2020

Dear Miss Welte

I am pleased to inform you that your manuscript entitled "The extensibility of the plantar fascia influences the windlass mechanism during human running" has been accepted for publication in Proceedings B. Congratulations!! We appreciate your attentiveness in these revisions.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

If you have any queries regarding the production of your final article or the publication date please contact procb_proofs@royalsociety.org

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All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,
Dr John Hutchinson
Editor, Proceedings B

mailto: proceedingsb@royalsociety.org

Associate Editor:
Board Member
Comments to Author:
I would like to thank the authors for their hard work and persistence. Although the MS has lost some of the "curb appeal" it had from the marketing of the original submission, I think the quality of the data and insight provided into foot function remains novel and significant.

Appendix A

We would like to thank the reviewers and board member for their careful review of our work and thoughtful comments. Based on the feedback, we changed the title, simplified the hypothesis, and reworked the paper to acknowledge that the elastic plantar fascia's behaviour is not mutually exclusive as either a rope or a rubber band. By dropping the ropes and rubber bands analogy as suggested, we believe we have now highlighted the nuances of how the elasticity of the plantar fascia influences the behavior of the windlass mechanism. We also introduce a simple subject-specific model that can directly test how well the *in vivo* data matches the modelled ideal, inhibited, or enhanced windlass behavior. We have also softened many of our arguments, and clarified where our results may lead to future work.

Associate Editor
Board Member: 1
Comments to Author:
Thank you for the opportunity to read this study. Herein the authors attempt to elucidate the complex dynamics of the human midfoot and its passive tissues during running. The authors attempt to tackle this difficult task using cutting edge x-ray motion analysis and some basic mathematical reconstructive modelling of soft tissue length change in-vivo. This a very topical subject and one that is likely to interest a diverse body of workers across the biological sciences. However, like Reviewer 2, I found the link or translation between the "rubber band and rope" analogy (upon which the study is marketed) and the actual data presented to be counterproductive. Any benefit this adds as an explanatory analogy for the generalist reader is outweighed, in my opinion, by the slight misconception it carries in terms of what specifically is being tested and the level of insight this work delivers in terms of understanding the foot as a functional organ. Specifically, it carries an implication that the study is providing insight at the most fundamental or higher-order level in terms of defining the foot as a functional organ (e.g. the way Ker did in terms of the arch functioning as a spring), when in fact this study is working one or two levels below that by quantifying aspects of fundamental behaviours that we know exist. I'm less familiar with the literature on running, but we know from walking that there is variation across healthy humans in tuning of the arch, and indeed that some healthy humans vary their tuning enormously step-to-step. So we shouldn't be surprised that tuning (sometimes "rubber band" sometimes "rope") goes or what's its basic causes are. The fact this study is working at slightly more detailed/less over-arching level than this is not problem for me at all: what this study is attempting to do with its data is potentially very significant and in principle is topical enough for Proceedings B, an opinion shared by both reviewers. But I do agree with Reviewer 2's criticisms about the clarity of the hypotheses/questions being tested. Reviewer 2 also has a number of major, and I think important, criticisms of the data and how it is being interpreted. My recommendation is therefore that the authors be given the opportunity to resubmit a revised version of the paper to Proceedings B that addresses all the comments from the two expert reviewers. If the technical issues raised by Reviewer 2 can be addressed without the loss of interesting new conclusions about the mechanics of the arch and its passive tissues then I think this study will make a very valuable contribution to the literature.

Thank you for the encouraging feedback and guidance on improving our manuscript. We have removed the "rope and rubber band" analogy in favor of describing the influence of an elastic plantar fascia on the windlass mechanism. We have also addressed the additional comments brought forth by Reviewers 1 and 2, which we believe has led to an improved discussion on the nuances of the plantar fascia's behaviour.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)
This manuscript discusses the complex interaction between two fundamental mechanisms in the human foot and is highly relevant. I very much appreciate how the authors have managed to describe this complexity in a very clear and elegant way. I have some comments (see below), which are usually minor, but I believe more clarity is needed on foot strike types. In most cases I hope my comments can be solved with additional clarification.

Thank you for your positive review of our work and for the insightful comments. We have added additional details on the differences in strike patterns, and improved the clarity in the figures to assist the reader in understanding our approach. We formulated a simple model that we feel better explains the inhibited/enhanced effects on the arch.

L32 “the action of the toes”: can you be more specific?

We have replaced this with “toe plantarflexion” instead.

L33-34: We discovered that toe plantarflexion delays plantar fascia stretching at foot-strike

L46 “require contradictory behaviour”, why would the windlass mechanism not work with a somewhat (not too) elastic fascia? The authors touch upon this (L64-67) and hypothesize (L 86-88) that the windlass effect is “inhibited” by plantar fascia strain. I would expect it to be influenced by fascia strain, but not inhibited (unless the fascia was _very_ compliant, but then it would not work very well as an energy-storing spring either).

This is an excellent point, and one that was brought up by Reviewer 2 as well. We have added an additional simple model to describe what inhibition of the windlass mechanism on the arch would look like in each case and have updated Figure 1 to more accurately represent what we mean. In brief, for every degree of MTPJ dorsiflexion, we would expect a corresponding length change in the arch. If the arch is changing more than this ideal value, then the windlass effect is enhanced, whereas if the arch is shortening less that the ideal value, the windlass effect is reduced.

We have also changed the word contradictory to different, and modified the explanation of inhibited/enhanced windlass

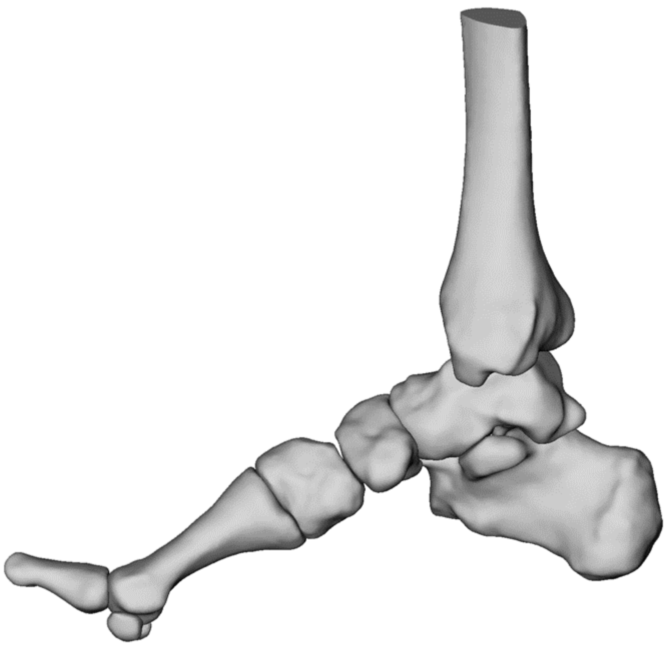
L47-49: As originally described, the arch-spring and windlass mechanisms require different plantar fascia behaviour, and their timing and interplay during running is unclear.

L63-69: For the windlass to change the shape of the arch effectively, the plantar fascia must undergo minimal strain; otherwise, the effect of the windlass on arch shape could be enhanced or reduced

(Figure 1). Since both the windlass and a shortening plantar fascia act to raise the arch, we termed this an enhanced forward-windlass action. Alternatively, if the plantar fascia elongates while the windlass attempts to raise the arch, the arch raising effect could be inhibited. Analogously, pulling a weight (the calcaneus) with an elongating elastic band is much less effective than pulling it with a steel rope.

L59: sesamoid bones are only present in the 1st ray (and I believe occasionally in the 2nd ray). I don't think they are essential for the windlass mechanism.

It is true that the sesamoid bones are primarily in the first ray, however the windlass effect is most pronounced in the first ray of the foot (Hicks 1954), likely due to the sesamoids increasing the effective moment arm by ~50%. We have attached an example image to indicate the substantial size of the sesamoids. Because this slip of the plantar fascia is embedded in the sesamoids, and we included them in our model, we chose to keep this in the introduction.



L110: the acronym DRR is only used twice in the paper. I suggest (in general) spelling out rather than using an acronym if the term is only used scarcely, as this will make the paper easier to read.

We have removed all instances of the acronym DRR from the paper & figure captions.

L114: participants ran barefoot. What was their foot strike type – were they heel-striking, forefoot striking with no heel contact, or almost flat "midfoot striking" with delayed heel contact? (see also next comment)
I would expect different behaviours of the plantar fascia under different conditions (e.g. the Ker et al study, supporting both the heel and metatarsal heads, would be equivalent to heel striking but not to forefoot striking).

Figures 4 and 5 are not very clear, if anything it seems just about a forefoot strike. The text typically refers to “ground contact” or “initial contact” without specifying which part of the foot contacts the ground first. I think the manuscript needs to be very clear on foot strike type (I’m sure the authors will agree on its functional importance in running) and elaborate on the interpretation of the results.
It is only in the Discussion (L313 etc.) that it is mentioned there are 3 rearfoot strikers and 9 forefoot strikers in the study. Who are they on the plots? Do they stand out (e.g. subjects 1 and 7 seem to be quite different from the other at heel strike and 9 is around 40% stance)? Please be more explicit.

More detail has been added to the manuscript regarding the different strike types. We did not find any patterns between strike types, and unfortunately, we do not have the statistical power to test for differences. In figure 4, the three rear-foot strikers are spread across the sample (i.e. one is at -1SD, one is at the mean, and one is at +1SD). Therefore, we did not feel it appropriate to discuss the strike patterns in great depth. We have added some additional discussion however.

We have added more detail in the gait events section to highlight how we defined the strike patterns and that initial contact is a catch-all for the first part of the body to contact the ground.

We have also added labels to figure 5b to clarify, and grouped the strike patterns together.

L117-118 (Methods (c)) : Participants in all collections were instructed to run barefoot at a self-selected speed and strike pattern along a raised walkway.

L 136-139: Gait events were defined using kinematic trajectories of specified inferior points on each bone surface. The strike pattern was classified as either fore-foot strike (FFS) or rear-foot strike (RFS) from the x-ray images. Initial contact was defined as the instant that either the sesamoids (for FFS) or calcaneus (for RFS) contacted the ground.

L 341-349 (Discussion): Early stance pre-loading of the plantar fascia has been shown in running, and is significantly higher in rear-foot strike participants [8,9]. While we unfortunately do not have the statistical power to make inferences between strike patterns, and our distribution of rear-foot strikers and fore-foot strikers was skewed (3:9), the plantar fascia of the rear-foot strikers was not consistently more strained at heel strike. Further, most participants had some form of plantar fascia shortening at initial contact, which has only been shown for RFS patterns [8]. We did not see any consistent differences in the vector coding analysis, however there may be a later transition from arch-flattening to arch rise for the RFS runners, consistent with Bruening et al. [14].

L133 “heel and forefoot contact”: please clarify whether you mean initial foot contact (which is either by the heel or by the forefoot), or two separate instances within a single stance (i.e. a heel-strike followed by the forefoot making ground contact). If the latter, please justify why the maximum negative vertical velocity would necessarily correspond to ground contact. (If the former, I can imagine this will be the case in practice albeit not necessarily in theory).

We mean the initial foot contact (either heel or forefoot) and have clarified the description of the gait events to describe the strike patterns. We also verified this kinematic approach with one subject with force plate data and found that it appropriately indicated initial contact.

L 136-139: Gait events were defined using kinematic trajectories of specified inferior points on each bone surface. The strike pattern was classified as either fore-foot strike (FFS) or rear-foot strike (RFS) from the x-ray images. Initial contact was defined as the instant that either the sesamoids (for FFS) or calcaneus (for RFS) contacted the ground.

L169-179: The study authors make a number of reasonable assumptions to establish in which mode the plantar fascia is used, and then used vector coding to analyse these modes throughout stance phase. I find this in principle (as in Fig. 3) an elegant way to display which mode is used, or which combination of modes. However, the actual data are presented less clear and require to-and-fro checking of the colours in Figure 3; I'm also not sure how easily the plots (e.g. Fig. 4) would be read by colour blind people. I'm wondering whether the angular values (rather than their colour codes) could be plotted instead. I do realise this might lead to functionally irrelevant jumps around 0/360 degrees.

Thank you for your positive comments on the vector coding approach. We have clarified these figures to limit the to-and-fro checking by adding all the phases to Figure 5a. We tried plotting the angles, but found that it was more difficult to then make the jump from the number to the phase without the addition of colour. We have modified our colour palate to be more colour-blind friendly, and verified it using an online colour-blind assessment tool. We have also updated the caption to clarify that 5a/c can be used as a legend for 5b.

Caption for Figure 5: "…The consistent sequence of phases of the contributions of the plantar fascia to the windlass and the arch-spring mechanisms during the stance phase of running for each participant. The colour is consistent between (a-c)."

L230: Just a thought… I'm not sure I would call this a "catch" mechanism, there is no physical catch but in a way the dynamics make it behave as a catch mechanism. This reminds me of a similar "virtual catch" mechanism in jumping bushbabies (Aerts, 1998, Phil Trans R Soc B). I like the term "catch-like mechanism" later used in the Discussion (L264).

Thank you for the reference. We have removed the description of the behavior as a catch (in concert with Reviewer 2's comments) and have described the behavior more explicitly.

L320-329 (discussion): The quasi-isometric length during the pure forward-windlass phase suggests that tension in the plantar fascia is relatively constant, while the ankle has already started to plantarflex and generate power. The mechanism that mediates this prolonged quasi-isometric behaviour cannot be deduced without measures of forces acting on the foot. However, it seems likely that after this period, the rapid shortening of the plantar fascia would contribute to arch power generation as the arch is rising rapidly and generating positive power during this phase of gait [14]. We speculate that through a fine-tuned balance of the extrinsic and intrinsic muscle forces as the toes move into dorsiflexion, the plantar fascia's strain energy is maintained from approximately 60-80% of stance, such that it can then contribute to arch power in late stance (80-100%).

L286:The recent paper by some of the same authors in J Biomech (Kessler et al, 2020) on foot (quasi) stiffness might be relevant here.

We have updated this section and included the reference to Kessler et al, as well as the newly published study by Farris et al. (2020).

L314-316: While this study lacks kinetic data to measure dynamic stiffness of the arch, previous studies have shown that the windlass mechanism does not stiffen the foot [27–29], and that the arch is more compliant in late stance than in the first half of stance [14].

L341: I understand it was not easily feasible to measure running speed (and potentially the speed was not very constant given the small runway length?), but contact times along with leg length should be able to give a reasonable estimate for speed. I feel that even an estimate is worth reporting for future reference, because speed has an influence on strike type, because ground reaction forces change with speed, etc.

We unfortunately do not have a measurement of leg length as we only have the kinematic motion of the lower half of the shank and foot.

We agree however that some estimate is a good idea. Using the relationship in de Ruiter et al., we estimated the Froude numbers from contact time. We then estimate leg length using published anthropometric ratios of buttocks height relative to stature (Winter 2009-Anthropometry). This allowed us to estimate that our participants ran between 3.0 and 3.8 m/s.

L359-364: Additionally, we are unable to measure running speed accurately during the trials as we only have distal tibia and foot kinematic data. We likely have differences in running speed among subjects, supported by the range of contact times from 0.22s to 0.37s, which could represent variations of Froude numbers from 0.3 to 1.6 [31]. We estimated the participants' leg lengths using the proportion of 48.5% of their stature and found a group mean estimate of speed of 3.4 m/s (range: 3.0-3.8 m/s) [32].

Referee: 2

Comments to the Author(s)
Summary of the paper
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This paper presents data on plantar fascia (PF) strain and its association with toe dorsiflexion to investigate how the foot's so-called windlass mechanism interacts with the elasticity of the PF.

Overall review
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The data in this paper are unique, using 3D skeletal imaging, and the question of how the windlass functions during locomotion, walking or running, is important to the field. However, I found this paper to be lacking a credible hypothesis and presenting far too many speculative claims presented as results. There are also technical issues with the data analysis or its presentation. Finally, there are numerous issues with a lack of details in the paper, which need to be addressed in proofing the paper.

Despite my apparent antagonism to the paper, I think it could be an important contribution with a broad impact on human locomotion biomechanics if the authors can respond to my criticisms.

Thank you to Reviewer 2 for thoroughly assessing our paper and for the critical feedback and thoughtful advice. We have simplified the hypothesis as you suggested and removed the ropes and rubber bands analogy in favor of a more nuanced discussion. We feel that the addition of a simple model to assess the quantitative effect of an inhibited or enhanced windlass effect on arch shape adds new depth to the paper. We also revised and softened our explanations of the effect of the reverse-windlass mechanism and the catch-like mechanism to better communicate our ideas and place them in context.

Major points
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1. Problems with the hypothesis/hypotheses:
First, I was quite confused about which are the hypotheses being testing in the paper. Two sentences try to define hypotheses at the end of the introduction. But the results refer to hypotheses that do not correspond well with the statements in the introduction. There are additional statements that claim to be hypotheses but were never presented earlier in the text. So, I found the presentation of the logic of the paper quite confusing.

I find the hypothesis of apparent conflict in the function of the plantar fascia to be not very meaningful. I highlight my criticism using specific locations of the text:

a. For example, lines 29-30 in the abstract state, "How can the same tissue act like both a rubber band and a rope...?" That statement is a little baffling. Assuming that a "rope" is used to indicate inextensibility, the answer is either that it cannot or that it depends on the load. The PF is passive tissue but has complex interactions with intrinsic muscles in the foot. If the passive nature dominates, like all materials, it will be stretch under load. If the stretch remains constant at times, it is because the load remains constant. In that sense, the hypothesis is trivial. To be more quantitative, the analogy is inaccurate because everything is a rubber band. Depending upon the loading context, the rubber band may or may not experience large stretch or strain (both are different quantities). So, there is no real dichotomy.

Thank you for this point. It has helped us clarify that there is not necessarily a dichotomy between these behaviours, but instead, the likely possibility that the windlass effect is constantly influenced by the elastic nature of the plantar fascia. Changes have been made throughout the paper to reflect this, and we have completely removed the ropes and rubber bands analogy. We have also updated Figure 1 and simplified our hypothesis. (Changes in the text are highlighted below)

b. Similarly, lines 64-64 state claims about the PF strain without consideration of how the loads may be transmitted. The statement in those lines is qualitatively true, but the details are important. How much strain is too much? Without that caveat, the importance of the point is not evident. To me, answering the question, "how much is too much" seems to be a central one. The hypothesis, as stated, could be interpreted arbitrarily in the absence of greater precision in saying it.

c. Lines 86-88 are probably the main statement of the hypothesis of this paper. This hypothesis is inevitably truecorrect. All elastic bodies stretch under load. Just because the PF stretches, one cannot conclude that its windlass effect is inhibited. To make such a claim, there should be a priori rationale provided for the amount of strain that would be significant. Without this estimate, the hypothesis has been set up to be inevitably correct, or inevitably false, depending on where the threshold is set.

These are great points. We have added a simple analysis based on the original description of the windlass. In brief, for every degree of MTPJ dorsiflexion, we would expect a corresponding length change in the arch. If the arch is changing more than this quasi-isometric value, then the windlass effect is enhanced, whereas if the arch is shortening less than the quasi-isometric value, the windlass effect is reduced.

The results of this analysis are shown in Figure 6.

L82-88 (Introduction): We use a simple model (depicted two-dimensionally in Figure 1) to show whether the forward-windlass's effect on the arch can be inhibited by a simultaneous lengthening of the plantar fascia, or enhanced by the simultaneous shortening of the plantar fascia. We hypothesize that due to the elasticity of the plantar fascia, we will only see periods of stance where the forward-windlass is inhibited by the elongation or enhanced by the shortening of the plantar fascia, and that we will not see a pure forward-windlass mechanism.

L211-225 (Methods): To test whether the straining or shortening plantar fascia could respectively inhibit or enhance the windlass, we tested a simple model. In theory, the change in arch length, Δl, and MTPJ dorsiflexion, θ, should be coupled. For $\theta = 1°$ of MTP dorsiflexion, there is an $s = r\theta$ change in arc length (s) (Figure 1), which, in the ideal forward-windlass case, should be identical with the change in arch length (Δl). The radius of the metatarsal head (r) was measured as the radius of a least-squares sphere fit to the bone mesh vertices. The expected arch length change (Δl) per 1° of MTPJ dorsiflexion for an ideal windlass was then calculated for each subject. The arch length was measured as the 3D distance between an inferior point on both the calcaneus and the metatarsal, and the change in arch length was measured between every 1% of stance. The change in arch length was divided by the change in MTPJ dorsiflexion and subtracted from the model's ideal windlass ratio. If positive, this indicates that the arch is shortening more than predicted by the ideal windlass (enhanced windlass); if negative, it is less than predicted by the ideal windlass (inhibited windlass); or if close to 0, it is equivalent to an ideal windlass. The mean arch length change per °MTPJ dorsiflexion is computed in the inhibited, pure, and enhanced forward-windlass phases as classified by the vector coding analysis.

L235-237 (Results): (with reference to pure windlass) The ratio of arch length change to MTPJ dorsiflexion was remarkably similar to that predicted by the radius of the metatarsal head, as originally described by Hicks (Figure 5) [4].

L239-243 (Results): (inhibited windlass) Our ideal windlass model indicated that arch rising can be inhibited during this phase, as the arch length change was 0.15mm/1°MTPJ dorsiflexion less than the expected length change for the ideal windlass. Therefore, when the plantar fascia strains concurrently to the forward- windlass mechanism, the windlass's ability to shorten the arch is inhibited.

L247-249: (enhanced windlass) Additionally, the rising effect of the arch was shown to be enhanced by the increase in arch length change of 0.12 mm/1°MTPJ dorsiflexion over the expected ideal windlass arch length change (Figure 5).

2. Problems with the results (e.g. L229-232, L242-243, L244 onwards):

One of the main claims in this paper is that there may be evidence for a catch mechanism that holds elastic strain energy in the plantar fascia. I find that claim to be unsupported and probably incorrect. Consider, for example, lines 229-232. This speculative claim is unfounded. In order to make this assessment, the total external load on the foot and its transmission through these various elastic elements need to be known. Moreover, we do not know how, if any, the rest of the midfoot arch is being actively modulated. Without that information, this conclusion is premature and probably false. It is more likely that the combination of changing overall external loads on the foot, changing distribution of the load between the PF and midfoot arch, and active modulation of rest of the midfoot stiffness may explain the nearly constant length of the plantar fascia.

Thank you for your description of the limitations of the catch mechanism. We have removed the description as a catch mechanism and have opted for a more descriptive approach as we do not have measures of external load on the foot. Please see point P2 below for further details.

However, it is a striking observation that the PF length is that constant (at least in 1 trial that is shown in figure 5a). I urge the authors to refrain from diluting it by making unsupported claims about hypothetical catch mechanisms. I would go so far as to argue that this piece of data, the prolonged pure windlass phase is the main result of this paper if the authors can present data from all the trials to support the near constancy of the length. I am cautious because looking at the individual PF elongation traces, claiming it to be isometric is an overstatement. In time, the PF length is continually changing for any single trial. Of course, when it reaches a maximum and reverses, there will be a locally flat region in the curve, which may be interpreted as nearly isometric. But there is no evidence of an isometric region. The authors should show the MTPJ versus PF data for the supposed isometric region for all individual trials, should remove any claims of a catch mechanism, and discuss the result in terms of whether it occurs close to its length reversal. If so, the questions that need addressing are how synchronized is the reversal with the MTPJ angle, how the synchronization is maintained, and what makes the peak as flat as it is.

The only reasonable null hypothesis that I can think of for the paper is that there should never be a pure windlass phase because the plantar fascia are passive tissues, and windlass engagement would most likely increase the tension borne by the PF and thus their strain. That null hypothesis is mostly true, as seen from the sample trace in figure 5a, but the period of stance when the MTPJ angle is changing substantially with little PF length change is striking. To convince the reader that this is a general trend, can the authors please show that region for every trial as a separate figure? How reliable is the occurrence of that region?

Thank you for your comments about the isometric plantar fascia and the reliability of the pure windlass region. We have opted to describe the plantar fascia's length changes as quasi-isometric instead. Further, we have now included all the traces in supplementary material S1. We find it is difficult to present all the traces on the same figure due to variations in strain and MTPJ dorsiflexion magnitude. Indeed, there is variation between subjects in the length of the phases and this is a topic for further investigation, but the general shape is the same. Please see point P1 below for further discussion.

Please allow me to elaborate further on why I think the catch mechanism is unlikely and why the load from the ground is important in this context. If the load is directed such that the bending moment about the midfoot is small, a large load could result in large joint contact forces within the foot but only a slight load that needs to be managed by the plantar fascia. So, the very minimum required to proceed with the claims presented by the authors is the bending moment data about midfoot landmarks, and compare that against the bending moment due to tension in the plantar fascia. Because the PF are passive, an initial assumption could be that PF stress is proportional to strain, and thus the tension in the PF is proportional to its length change. However, even this assumption is only partly true because of the branched structure of the PF, and the muscles that attach to it all along the length.

You are correct that the bending moment may be small and the load may primarily be borne through the bones, leading to high joint contact forces in the foot. However, the results from Erdemir et al. (JB&JS, 2004) suggest that the load in the plantar fascia is highly correlated to the load in the Achilles tendon, and that it is substantial in the late stance phase of walking. Thus, we have assumed that tension in the plantar fascia is proportional to its strain, but have softened our comment as to the magnitude of direct contributions to the arch. Please see point P2 below for further discussion of the catch mechanism.

The claims are overly reliant on the single trace in figure 5a, instead of the temporal dynamics of the PF length and also including all the data. For example, consider the speculation in L242-234 about the PF "absorbing the load". I find this speculation to be one step too far because of the lack of load data on the PF. The load can be distributed between elements and energy can be absorbed if the load does work on the PF. But there is no way to make such an inference based on the data on hand. The trial sample in figure 5a shows that the reverse windlass is not as prolonged or "pure" as the forward windlass. So, this interpretation may simply be an artifact of the vector coding method and the many assumptions that went into it (see my major criticism of the technique later). For example, the equipartition of the space, treating it as if a vector space, or having sharp boundaries between regions are all problematic assumptions of the vector coding technique that could lead to such an over-interpretation of the data.

P1: Isometric plantar fascia:

We have modified our phrasing to “quasi-isometric”, similar to the muscle literature, as you are correct that it is not exactly the same length. However, the magnitudes of plantar fascia strain during the quasi-isometric phase are quite small (in the range of 0.0005% strain between time points), with -0.1% plantar fascia strain during that entire pure forward-windlass phase.

The pure forward-windlass phase is prolonged for many subjects, as opposed to a quick local minimum during the reversing from lengthening to shortening. There are some subjects that have a much shorter pure forward-windlass phase, but they have consistent arch velocity, plantar fascia elongation and arch deformation characteristics as the subjects with a longer pure forward-windlass phase. We have included all traces in the supplementary material.

P2: Catch mechanism:

Thank you for your description about the limitations of the catch mechanism. We agree that this may not be the most apt description for this mechanism and have opted to describe it qualitatively instead and clearly indicate the speculative components of this paragraph in the discussion. We have removed all mentions of the catch mechanism throughout the paper.

L320-329 (discussion): The quasi-isometric length during the pure forward-windlass phase suggests that tension in the plantar fascia is relatively constant, while the ankle has already started to plantarflex and generate power. The mechanism that mediates this prolonged quasi-isometric behaviour cannot be deduced without measures of forces acting on the foot. However, it seems likely that after this period, the rapid shortening of the plantar fascia would contribute to arch power generation as the arch is rising rapidly and generating positive power during this phase of gait [14]. We speculate that through a fine-tuned balance of the extrinsic and intrinsic muscle forces as the toes move into dorsiflexion, the plantar fascia’s strain energy is maintained from approximately 60-80% of stance, such that it can then contribute to arch power in late stance (80-100%).

3. Problems in the discussion, related to those above in the results (L259-261, L291-292):

Hinging the paper on the role of the reverse windlass mechanism early in stance and its role in load management is flawed. I argue that this result has not been shown because of the direction of the load and its effective bending moment on the midfoot. I would argue that the tension needed in the PF to manage that moment is small because the initial bending moment is small. This is because the ground reaction force vector is more posteriorly directed earlier in stance, thus drastically reducing the moment on the midfoot. Similarly late in stance because of the foot posture and the ground reaction force vector's direction. The second result presented in lines 261-262 is fine, but not the claim of a catch mechanism that follows.

I find the discussion based on the supposed isometric nature of the PF also problematic. As I argued later, the isometric nature is not borne out in the time traces of the PF, although the length-rate reaches zero when the length reaches a local maximum. The authors may be able to show that this maximum is synchronized to coincide with peak velocity of MTPJ dorsiflexion, which may underlie the apparent pure windlass phase. But the authors have not yet demonstrated this to be the case. If they do, it begs to be explained.

Maximum MTPJ dorsiflexion velocity is typically partway through the enhanced windlass phase, so unfortunately does not line up with maximum PF elongation.

Please see response in point P1 above for the comments about the isometric plantar fascia.

We have softened the statements in the discussion regarding the reverse-windlass managing load. We believe that the arch is managing some of the load despite the potentially small bending moment because there is measured arch deformation during this period (see Figure 3a for arch deformation & Table 1 for arch deformation during the reverse windlass phase). The arch may not be taking up a significant portion of the overall load – as you mentioned the joint contact forces manage some of that load – but we are measuring tissue elongations during this time that coincide with arch flattening (for ligaments that are contained within the arch - see Figure 7). Therefore, there must be some mitigation of the load, even if that amount is small. We have clarified that we are discussing the distribution of the load to arch ligaments in the discussion, as opposed to overall load management.

L273-275: First, at initial contact, the plantar fascia's pure reverse-windlass motion may allow arch-spanning tissues to mitigate more of the load of impact than the plantar fascia, eliminating the need for the plantar fascia to directly strain to slow arch deformation.

L282-284: […] instead, the plantar fascia facilitates the reverse-windlass motion of the foot, likely so that arch tissues proximal to the plantar fascia manage more of the load than the plantar fascia.

4. Technical problems with the vector coding method:

I found the "phase space" plot of figure 5a far more informative and accurate representation of the data over the vector coding method that is fraught with problematic assumptions. Are the vectors on this classification diagram quantitative or are they merely qualitative? Does the length of the vector have quantitative meaning? In other words, are the MTPJ rotation and plantar fascia strain treated as independent coordinates of some vector? But describing that as a "vector space" is a provably false assumption because there is a clear dependence of their interaction on other unplotted coordinates. Maybe the authors want to think of it as a low-dimensional projection of some phase space. It makes for a simplified diagram to present what happens, but I find the simplifications to be oversimplified to the extent that it casts doubt on the results. Instead, the phase-space trajectories of figure 5a, with qualitative indicators of pure and mixed phases, is far more valuable.

While the classification scheme is a good attempt, I find its interpretation fraught with risks. The authors should devote considerable attention to the inaccuracies introduced by the classification scheme. Yet another significantly problematic assumption is that the space (which is not a vector space) is somehow equally partitioned by the chosen variables and normalization. That is a big assumption underlying this method and its implications to any of the presented results are unclear. I found it disappointing that such strong and unique data were negatively impacted by the assumptions underlying this rather arbitrary choice of data presentation. The phase space makes far fewer assumptions and is thus more compelling.

Minor issue with the description of the vector coding plots: nowhere is it mentioned what the variables being plotted are.

Addressing the technical issues with the vector coding technique:

The pure and mixed phases on figure 5a are determined from the vector coding approach. We have not made a vector space, but represented instead the relationship between two variables from one time point to the next, similar to the approach taken in the coordination variability literature (with angle-angle or angle-angular velocity plots: ex: Tabayashi et al. 2018 –Journal of Foot and Ankle Research.). It is a quantitative assessment of how much one variable is changing with respect to another. To make Figure 5b, it would be equivalent to laying out the curve in Figure 5a in a straight line instead of a curve.

The plantar fascia elongation and MTPJ angle are normalized to the standard deviation of all values for all subjects. We verified that this appropriately classified the phases by looking at the quantity of MTPJ angle change in the pure plantar fascia elongation phases (< 0.5 ° over the entire phases) and the quantity of PF elongation in the pure forward- and reverse-windlass mechanisms (-0.1 % for both phases). Therefore, we feel that the phases have been appropriately classified. Table 1 is highlighted below for clarity.

Phase	MTPJ angle [°] (+) dorsi-flexion (-) plantar-flexion	Plantar fascia elongation [% of max length] (+) lengthening (-) shortening
reverse- windlass	-15.5 ± 2.3	-0.1 ± 0.1
plantar fascia elongation, MTPJ plantarflexion	-11.1 ± 1.9	0.9 ± 0.1
contribution to arch- spring strain energy absorption	0.4 ± 0.5	1.9 ± 0.3
forward- windlass (inhibited)	8.4 ± 1.4	0.9 ± 0.1
forward- windlass	15.9 ± 1.9	-0.1 ± 0.0
forward- windlass (enhanced)	19.9 ± 2.2	-1.9 ± 0.2
contribution to arch- spring strain energy return	0.1 ± 0.9	-3.0 ± 0.6
plantar fascia shortening, MTPJ plantarflexion	-9.4 ± 1.7	-1.6 ± 0.3

Minor points

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L35: What is the logical basis to expect that the PF compromises arch function in the first place? I found this statement as cryptic in the abstract as in the discussion.

We have rephrased this in the abstract.

L37-38: The elasticity of the plantar fascia then enables complementary behaviour of the windlass and arch-spring mechanisms to meet the demands of locomotion.

L54: To support their claim that the PF are important for elastic strain energy storage, the authors say, "that the arch of the foot is more compliant without the plantar fascia." But more compliant implies more energy storage. So, this point goes against the statement that the PF is important for elastic energy storage. The elastic energy stored in an elastic structure is proportional to its stiffness, but to the square of the displacement. So, when the load experienced is similar, lesser stiffness of the foot will lead to more elastic energy storage.

For an elastic material, the amount of energy is indeed proportional to the stiffness (i.e. $E = ½ k x^2$, where E is energy, k is stiffness and x is displacement). However, we are referring to the case where for the same applied force, the energy stored is higher for reduced stiffness. In this ideal case, $F = kx$ (where F is force), can be re-arranged and substituted into the elastic energy equation, giving : $E = ½ (F^2/k)$, showing that for the same force, the energy stored is inversely proportional to the stiffness of the elastic material. We have updated this line in the introduction for clarity.

Line 55-58: Furthermore, several studies have shown that the plantar fascia strains during stance [7–13], and that the arch of the foot stores less elastic energy without a plantar fascia [3], indicating that the plantar fascia contributes to the energy-saving arch- spring mechanism.

L80-81: "Using a unique paradigm": Unnecessarily hyped-up language.

We have removed this language.

L111 and L137: "inertial anatomical coordinate system:" What is inertial about the coordinate systems? Why are these coordinate axes referred to as "inertial"? Are they centered at the center of mass of each bone and oriented along the principal axes of the moment of inertia tensor? Later descriptions show that not to be the case. For example, the axes are oriented to reflect specific choices of kinematic descriptions.

We agree that this was unclear. We have added the details to the methods.

Line 110-115: Tessellated meshes representing the bone surfaces were also created from the CT scans. Inertial anatomical coordinate systems were generated from the bone meshes, with the origin located at the centroid and the x-y-z axes aligned along the principal axes of the moment of inertia tensor [18]. The axes were re-labelled such that the x-axis was lateral, the y-axis was anterior, and the z-axis was superior.

L127-128: "bone occlusion": Which degrees of freedom were lost?

The three rotational degrees of freedom were fixed with the proximal phalanx. The translational degrees-of-freedom were maintained.

L132-135: The rotation of the phalanx was used as a starting point, as the sesamoid-phalangeal ligament apparatus is quite stiff [20], and likely rotates similarly about the metatarsal head. The sesamoid unit was then purely translated to best fit the x-ray images.

L129: "sesamoid-phalangeal ligament apparatus is quite stiff [20].": The reference cited here is an entire book. I searched the book and cannot find quantitative support for this claim. The stiffness of the ligament should be juxtaposed with the loads it experiences. Can the authors be more specific about the role of this citation and how they support this assumption?

We updated the reference to be a book section to better describe the source.

20. Sarrafian S. 1993 Proximal Phalangeal Apparatus of the Big Toe. In *Anatomy of the Foot and Ankle*, pp. 211–214. J.B. Lippincott Company.

In this section, the author states "The two sesamoids, embedded in the thick fibrous plantar plate and united to the proximal phalanx of the big toe, form an anatomic and functional unit called by Gilette the sesamophalangeal apparatus […] The sesamophalangeal apparatus moves backward or forward relative to the fixed metatarsal head; […] the sesamoids always follow the proximal phalanx and are displaced with the latter, not the metatarsal head."

We visually assessed the position of the sesamoids in our tracking software, using the motion fixed with the phalanx and found that it was quite reasonable. We translated the bones slightly to better match the x-ray images, but when we assessed the amount of translation over the trials, it was on average less than 0.05 mm from the phalanx, as represented in the phalanx anatomical co-ordinate system.

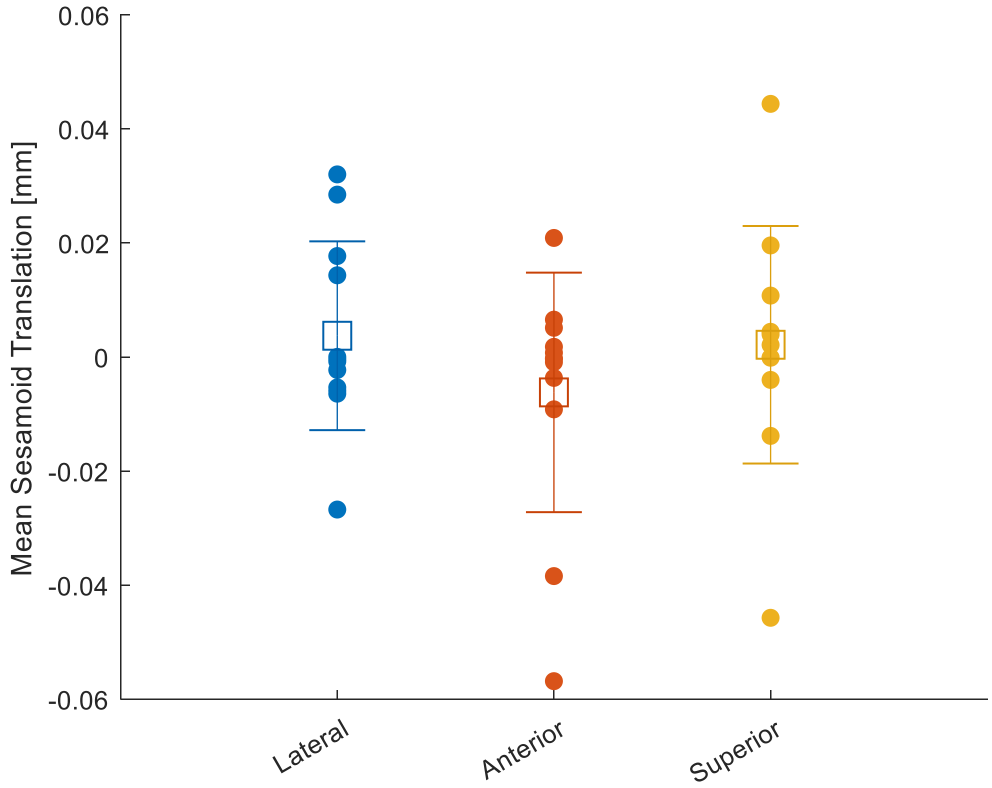

Figure: The mean (□) and ±1SD of the sesamoid translation from the phalanx, in the phalanx co-ordinate system, over all frames for each subject (●).

L140: "YZX Tait-Bryan angle sequence": In that case, the Z-axis cannot truly represent adduction because it is a floating axis.

We interpret the angles as per the Grood and Suntay (Journal of Biomechanical Engineering, 1983). The first rotation is about the proximal X axis (dorsiflexion about the proximal body's axis) and the second rotation is about the floating axis (Z) which is the mutual perpendicular of the proximal X (dorsiflexion) and the distal Y (inversion). The resultant Z axis rotation would still be anatomically relevant and very similar to adduction, but may not exactly the same as if we used an alternative angle sequence. We use adduction only in part of a supplemental figure, and have therefore opted to keep this convention.

L164-165: "filter effectively preserves the high-frequency content": How is this shown? Was a systematic study of cutoff frequencies conducted to show that there is little power at higher frequencies?

The design of the adaptive low pass Butterworth filter (Erer et al., J Biomech, 2007) takes the frequency content of the signal into account by computing the first and second derivatives of the signal. Based on the behaviour of the signal at each time point, it assigns a specific frequency within the range specified. In our case, we filtered each time point somewhere between 14 and 40 Hz. The higher the frequency content of the signal (i.e. at impact), the higher the cut-off frequency.

L151-154: All angles were filtered with an adaptive low pass Butterworth filter with a cut-off frequency between 14 and 40 Hz, depending on the signal content at each time point [21].

L183: "reasonable assumption": Whether the assumption is reasonable is for the reader to assess. Please add quantitative support for this claim or remove "reasonable" and let the reader be the judge.

We have removed “reasonable” from the sentence.

Line 188-190: While strain energy cannot be directly quantified using this approach, we proceed with the assumption that elongating fibres are absorbing strain energy, while shortening fibres are releasing strain energy.

L211-212: claim that the pattern was similar in RFS and FFS runners: You only have three RFS traces, and they often fall outside the 1SD region. How can this claim be made?

By this, we meant that they were no obvious differences between RFS and FFS runners. The RFS runners were often on the extremes of the 1SD region, but not necessarily on the same side. We have added an observation to the discussion about the timing of maximum arch deformation between strike patterns, and clarified our discussion, as was also suggested by Reviewer 1.

L336-338: Our plantar fascia elongation values are consistent with existing data, however we did not observe consistent differences in running strike patterns, and we measured a later time of peak strain.

Figure 5b: What are the gray regions? I cannot find a description or explanation for them.
We apologize for this oversight. The gray regions have been changed to black, and it is now indicated in the caption that they are frames for which the calcaneus was out of frame, and therefore the plantar fascia length could not be measured.

Figure 4b caption: (b) The consistent sequence of phases of the contributions of the plantar fascia to the windlass and the arch-spring mechanisms during the stance phase of running for each participant. The colour is consistent between (a-c). The black regions indicate frames where the subject’s calcaneus was out of the frame of view, and therefore the plantar fascia elongation could not be measured.

Table 2: Why don't the percentages come anywhere near 100%? I understand slight deviations because you are reporting the mean, but it does not even come close.

The subjects had variations in the number of frames that could be classified due to bones going out of the field of view in the x-ray. Therefore, some subjects only have 90-95% of stance phase, and others have 100%.

L218: "in direct contradiction to our hypothesis": Which hypothesis is contradicted? I still don't see that there are any well-defined hypotheses in the paper, and when stated as a hypothesis, it is not clear what measurement, if any, could support or falsify it. Not every paper need be hypothesis-based. I think this paper is a case of making a careful examination of the plantar fascia using novel measurement methods and reporting the patterns that are seen. The paper seemed forced into a "hypothesis-driven" bin.

Thank you for this insight. We have simplified our hypothesis as you have suggested, in that we did not expect to see an ideal windlass, and instead expected to see an inhibited or enhanced windlass.

L85-88: We hypothesize that due to the elasticity of the plantar fascia, we will only see periods of stance where the forward-windlass is inhibited by the elongation or enhanced by the shortening of the plantar fascia, and that we will not see a pure forward-windlass mechanism.

L219: "13±2%": Why round the percentages but not the angles?

The angles have been rounded to match the percentages throughout the results.

L298: Reference [27]: This reference does not apply to the foot and is mostly about invertebrates.

We have removed this reference.

Appendix B

Associate Editor Board Member: 1
Comments to Author:
Once again, I enjoyed reading this study, and I thank the authors for submitting a revised version. In particular I found the revised figures, and the inclusion of more data, very helpful when attempting to follow the interpretations of plantar fascia behaviour vs time. I'm also glad the authors have revised the paper overall along the lines suggested, in terms of dropping the rope vs rubber band paradigm. That said, I am in agreement with the reviewer that suggests revision is still needed: the paper still requires some further revision both in terms of the writing/interpretation and the approach used to analyse the data. I would urge the authors to seriously consider the comments from the reviewer and address them robustly and directly.

Thank you for your positive comments on our revision and the opportunity to address the comments from the reviewer. As a result of their suggestions, we have removed the vector coding analysis and changed our approach to analysing the data. We have also more clearly stated the underlying assumptions of our analysis and assessed the sensitivity of our results. Finally, we have modified our paper to be primarily descriptive instead of hypothesis-based.

Reviewer(s)' Comments to Author:
Referee: 2
Comments to the Author(s).

Major comments
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The authors have revised many parts of the text in response to the previous round of reviews. They have responded constructively to the problems identified with the lack of plausible hypothesis, but have still carried over several problematic portions from the previous version. As a result, I still find this paper somewhat lacking, despite the novelty of the dataset.

We first and foremost apologize for not making adequate changes to address your comments. We misunderstood some of the issues in the first round of review and did not intend to dismiss the comments. We would like to thank you for your dedication to pointing out problematic areas and suggesting implementable improvements. As a result, we have removed the problematic vector coding analysis, and simplified our description of the phases. The revisions have resulted in a more descriptive paper as you had suggested, which we hope better conveys our work.

Problems with the hypothesis

The previous problematic hypothesis on rope versus rubber bands was removed but the paper is still lacking a well-defined hypothesis that is not a straw man. I find the data reported in the manuscript to be quite important for the community, whether it is hypothesis-based or not. So, I am tried to find specific locations in the text that are problematic and make suggestions that may help frame the objective of the paper.

Thank you for taking the time to make specific suggestions. We found your approach clear and helpful for making changes to the manuscript.

L78--79: What is stated as testing a prediction, "...we test in vivo if the elastic behaviour of the plantar fascia compromises its function as a windlass in running", is really not a well-defined prediction. What is meant by "compromise"? What "function" is being compromised? There are no functional efficacy measures to know the answers to these questions. Thus, I still find the text lacking in a hypothesis.

We agree and have modified this statement to reflect the study as a description of the influence of the plantar fascia's extensibility on the windlass mechanism. We have modified our wording such that we acknowledge that we cannot ascribe the arch deformation that occurs to either mechanism without measures of force.

Line 77-81 : Using three-dimensional biplanar videoradiography, we modelled plantar fascia elongation using subject-specific bone motion in addition to MTPJ dorsiflexion as a proxy for an engaged windlass mechanism. We investigate the timing of the extensibility of the plantar fascia and discuss how deviations from a pure windlass mechanism may affect arch function in running.

L81--82: "We classify the coupling of MTPJ dorsiflexion and plantar fascia elongation to test if the foot can exhibit a pure windlass mechanism."

Like my criticism in the previous review, this is a straw man. The answer will be, "depends". How about stating the objective of the paper as not testing a hypothesis but making measurements to quantify the deviations from pure forward-windlass function? The functional consequences of this departure are not answered by this work but the measurements set the stage for such future studies.

Thank you for this comment. We have adopted a more descriptive framework instead of the hypothesis-testing approach we had previously. You are correct that we cannot prove the implications of deviations from the pure windlass mechanism; only discuss the potential functional consequences. We have removed this line from the manuscript.

L85--88: "We hypothesize that due to the elasticity of the plantar fascia, we will only see periods of stance where the forward-windlass is inhibited by the elongation or enhanced by the shortening of the plantar fascia, and that we will not see a pure forward-windlass mechanism."

This is still not a hypothesis. Given the nature of elasticity, there are only three possibilities. The hypothesis, as stated by the authors, seems to be that two out of three possibilities may occur. Why would they expect that a pure forward-windlass cannot occur? Given the lack of load measurements (here and in past work), there is no basis to expect that. Alternatively, perhaps the authors have a mathematical model upon which this hypothesis is being founded. But no such reference is provided. So I still find that the authors are forcing a hypothesis where there may be none. If the authors do have a plausible hypothesis and alternative hypotheses in mind, it does not come through in the paper.

We have adopted the descriptive framework and removed the hypothesis as you suggested. This sentence has been removed from the manuscript.

L63--65: "For the windlass to change the shape of the arch effectively, the plantar fascia must undergo minimal strain ..."

What is meant by "minimal" and by "effectively"? I point to figure 1, where the arch changes shape in all three of the cartoons.

Thank you for this point. It highlights that we can only describe the windlass mechanism's effect on the arch, and not necessarily whether it is effective. We have made the appropriate changes in the text.

Line 63-66: However, the extensibility of the plantar fascia could influence the arch shape changing effect of the windlass mechanism. If the plantar fascia elongates or shortens simultaneously to the windlass mechanism, it could respectively reduce or increase the magnitude of arch deformation with respect to the pure windlass mechanism.

I think this is the point in the paper where a clear objective can be defined. Under the classical windlass picture of an inextensible PF, the expectation is that the arch height is a function solely of toe dorsiflexion. However, we know that the plantar fascia is extensible and likely to be stretched by the tension acting upon it. The possibility of stretch raises the need to quantify the windlass mechanism and how it differs in response from the assumption of an inextensible PF. The issue is the partitioning of elastic strain energy between the plantar fascia and rest of the foot's structures when the toe is dorsiflexed. Stated in those terms, one can compare apples with apples but direct measurement of elastic strain energy associated with the PF and all of the midfoot is impractical. Given that limitation, the authors have arrived at a proxy for the elastic strain energy partitioning, which is the relationship between toe dorsiflexion, PF extension, and midfoot deformation.

We have revised the focus at the end of the introduction to more clearly describe our analysis.

Line 77-81: Using three-dimensional biplanar videoradiography, we modelled plantar fascia elongation using subject-specific bone motion in addition to MTPJ dorsiflexion as a proxy for an engaged windlass mechanism. We investigate the timing of the extensibility of the plantar fascia and discuss how deviations from a pure windlass mechanism may affect arch function in running.

We have also added detail in the discussion.

Line 368-370 (discussion) : Future work is required to understand […] whether the plantar fascia and windlass mechanism are responsible for the variations in arch deformation seen here.

Methodological issues
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1. Coordinate system choice: The authors have used a YZX Tait-Bryan angle sequence (L147). I find this choice hard to justify. I raised this objection previously, which was set aside by the authors as unimportant. As the authors know well, the middle floating axis defies simple anatomical explanation. The phalanx motion with respect to the metatarsal is mostly in plantar/dorsiflexion (X) and ad/abduction (Z). There may be some degree of ev/inversion, but that is generally much smaller than the other changes. Given these, the choice of the angle sequence should have been ZYX or XYZ, so that the reported angles can be anatomically interpreted. This may seem like a minor point, but I contend that it is important for future researchers to be able to interpret these data. Please use a convention that is consistent with the broader usage among anatomists and podiatrists, to promote repeatability of the science.

We apologize for not making the change in the previous round of review. We have modified all our sequences to be ZYX. Thus, MTPJ dorsiflexion is about the X axis of the first metatarsal; dorsiflexion of the arch is about the X axis of the calcaneus, while adduction is about the Z axis of the first metatarsal. Further, we have decided to include the arch angles in the paper and not supplementary material to make the arch angles more approachable to a broader audience. In addition, we have added depictions on Figure 2 to clarify the axes of rotation.

Line 140-142: A ZYX Tait-Bryan angle sequence determined the angles of the first metatarsal relative to the calcaneus (arch angles) and the phalanx relative to the metatarsal (MTPJ angle).

L144-147: "The inertial axes computed from the surface meshes defined the anatomical co-ordinate systems for the tibia, calcaneus, first metatarsal and first proximal phalanx [18]. The coordinate systems were oriented so that the x-axis represented dorsiflexion, the y-axis represented inversion and the z-axis represented adduction, with reference to the right foot."

I find this description confusing. The coordinate system is inertial because the axes are oriented along the principal axes of the moment of inertia tensor. But the description here states that the axes were oriented to fit joint degrees of freedom. Which system was used? I cannot see how both are the same.

The axes are inertial as you described, but the direction of the first inertial axis would not necessarily be in the x direction. We have modified the description to more clearly describe this.

We have also added the axes on the foot bones on Figure 2 to make the axes of rotation clearer.

Line 137-140: The inertial axes computed from the surface meshes defined the anatomical co-ordinate systems for the tibia, calcaneus, first metatarsal and first proximal phalanx [18]. The coordinate system axes were re-labelled such that the x-, y- and z-axes more closely represented dorsiflexion, inversion, and adduction respectively, with reference to the right foot

2. Vector coding: I am disappointed that the authors have mostly ignored the criticisms on the vector coding approach when revising the manuscript. They acknowledged in their rebuttal that the space of MTPJ angle versus PF elongation is not a vector space. But then they go on to interpret the vector coding results as if it were a vector space.

In their rebuttal, the authors included one useful piece of information, which is to examine the extent of MTPJ rotation or PF extension during the different phases as identified by the coding approach. Reassuringly, it is consistent with what one would define intuitively. But that does not make the process of coding somehow a generic method that will always lead to valid interpretations. I am quite concerned that this paper will be used as justification for the misapplication of the technique in future papers by the community. So it is essential that the authors refrain from relying on the vector coding as the primary tool. Instead, they should discuss why it is a subjective tool that shows reasonable correspondence with the data presented in Table 1 (as they do in their rebuttal). Also needed is a discussion of why the choices made in defining the sections are somewhat arbitrary and thus the technique is not necessarily generalizable to all settings.

We apologize for not fully addressing your criticisms. Thank you for further describing them as it helped us better understand the issues, and subsequently improve our manuscript. We have removed the vector coding approach and opted for a more descriptive approach with a clearer indication of how we coded different phases. In this modified analysis, MTPJ dorsiflexion and plantar fascia elongation are divided into phases based on a clear selection of thresholds on their individual time-series curves, and independent of how one variable changes with respect to the other (as was a primary issue with vector coding). We also emphasize that the new thresholding is a subjective tool (dependent on the selected threshold values) to quantify what we qualitatively observed from the time-series curves, as suggested. We believe this clarifies and solidifies the analysis because our focus was on describing the timing of plantar fascia elongation with respect to the windlass mechanism.

Line 171-186: We describe the effect of the plantar fascia's extensibility on the windlass mechanism by examining the coupling between MTPJ rotation and plantar fascia elongation during stance phase. We examined the time-series curves qualitatively, and then quantified our observations by selecting a threshold change in MTPJ rotation and plantar fascia elongation that we considered quasi-constant. We classified each 1% of stance into phases using our selected thresholds, which equate to less than 2% of the range of each variable. Specifically, if the MTPJ angle change was less than 0.5º, it was classified as quasi-constant. If the MTPJ angle change was larger than 0.5º and positive, the MTPJ was classified as dorsiflexing, while if it was larger than 0.5º and negative, the MTPJ was classified as plantarflexing. Similarly, if the plantar fascia underwent less than 0.0005 normalized elongation between each percentage of stance, it was classified as quasi-isometric. If it was larger than 0.0005 and positive, the plantar fascia was elongating; if it was larger than 0.0005 and negative, the plantar fascia was shortening. The thresholds were selected to visually correspond with the mean time-series curves and then applied to each participant's individual data. We conducted a sensitivity analysis on our classification paradigm, altering each threshold by ±40% and ±20% while keeping the other variable at the selected threshold.

Further, we have also added the limitations of choosing a threshold to the discussion.

Line 347-370 (discussion): The thresholds in the analysis of windlass mechanism timing and plantar fascia elongation were selected subjectively based on visual assessment of the time-series curves. We modified each threshold by ±20% and ±40%, keeping the other at the selected value (0%), to determine the sensitivity of our results to the threshold values. The order of the phases changed minimally, while the time spent in each phase varied. As the thresholds were increased, as expected, all quasi-constant phases lengthened. Thus, when the plantar fascia elongation threshold increased, the pure forward-windlass phase lengthened, while the inhibited forward-windlass phase shortened because the plantar fascia elongation that was originally coded as elongation changed to a quasi-isometric phase. Furthermore, as the MTPJ angle threshold increased, the quasi-constant angle phase lengthened, reducing the MTPJ dorsiflexion phase. The overall time available for any forward-windlass phase was thus reduced, consequently shortening the inhibited and enhanced forward-windlass phases. When the threshold was decreased by 20%, an additional participant experienced the inhibited forward-windlass phase, while a different participant no longer had an inhibited forward-windlass phase when the threshold was increased by 40%. The plantar fascia elongation threshold played a bigger role at initial contact than the MTPJ threshold change. As the plantar fascia elongation threshold decreased, the pure reverse-windlass phase had plantar fascia shortening as well. This indicates that the foot may not always have a pure reverse-windlass mechanism; however, it does not change our interpretation of limited plantar fascia elongation at initial contact, in favour of the elongation of more proximal arch ligaments. Overall, these changes do not influence our interpretations as there is clear variability among subjects regardless, and we assess primarily the existence, order and potential significance of the phases. Future work is required to understand variation in the length of the phases, and whether the plantar fascia and windlass mechanism are responsible for the variations in arch deformation seen here.

Here are specific areas of the text where I found problematic interpretations based on the vector coding approach, with no discussion of the issues with the method.

Thank you for pointing out these specific problem areas. We have removed the vector coding and discussed the sensitivity and limitations of our revised approach, as indicated in the previous comment.

L193--194: "Vector coding evaluates the dominance of one variable over another"

This statement exemplifies the deep problems with vector coding. How can an angle change be compared to a length change? Is 1 degree more or less than 1 cm? I raised the issue during the previous review and also raise it in the caption for figure 2 in this version. The authors have ignored my major criticism from the previous round of reviews, which is not acceptable.

We apologize for neglecting this major criticism. We misunderstood what you meant by the magnitude/angle comparison and thought you were commenting on the vector itself as opposed to the relationship between the two variables. We have removed this in line with the removal of vector coding.

Figure 2 caption: "In the example time point Pi and the adjacent time points, the subject's plantar fascia elongation is more substantial between time points than the MTPJ dorsiflexion."

This comparison between angle and length is not meaningful. One quantity is an angle and another is a length change. Even if both of them were somehow normalized in order to make them both dimensionless, they are physically different variables and their comparison is based upon tacit assumptions that have not been identified. This was the same issue raised in the first round of reviews and the authors have not responded to those criticisms.

We apologize for not responding appropriately. We now understand that the assumptions that underlie the vector coding are not clear and would require further discussion. As a result, we have removed vector coding, and modified the analysis to have clearer assumptions, and have correspondingly removed this figure.

L195--196: "The angle of this vector indicates the dominant variable."

This really shows the problematic nature of the vector coding approach. By choosing to normalize the elongation and MTPJ angle by different baseline values, I can make this angle anything I want to it to be. Not only is the name "vector coding" deceptive, because this is not a vector space, the interpretations based on the method could also be problematic.

Thank you for this point. As described above, we have removed vector coding.

L201--202: "The unit circle was divided into 8 equal segments, centred around the axes."

Please read my reviews from the previous time for why an equipartition of the space is incorrect. Also see my comments in other areas of this text.

Just because the extremes --- 0, 90, 180, and 270 --- appear to correlate with intuitive definitions, the intermediate values cannot be linearly interpolated. The authors have chosen to ignore my comments on this from the past review round, which is quite disappointing.

As described above, we have removed vector coding.

L203--204: "The time spent in the primary phases (windlass, contribution to arch-spring) and the interaction phases were calculated as a percentage of stance."

This fractional time is founded upon the notion that the angle-length space is linear and equally scaled. Given the problematic line of reasoning adopted in constructing the "vector code", the "time spent" measures are equally problematic. I urge the authors to not push this method and to not ignore the reviews with detailed arguments for why it is incorrect. I am concerned that the method's usage in this paper will set the precedent for further false inferences to be made in the literature.

Thank you for making these important points. We realized that interpreting the time series curves, per your recommendation noted below, is much more intuitive than we first assumed, and we understand the issues with the vector coding metrics. We have removed Table 1 and the vector coding derived metrics completely.

L269: "Discussion"

The vector coding diagram seems unnecessary to draw the inferences presented in the discussion. If the PF elongation (DL) versus MTPJ dorsiflexion (q) data are displayed as a curve of % stance versus instantaneous heading of the plot of the DL vs q curve, the regions of pure windlass action should be quite apparent. Although I believe that the authors saw these trends in their data, the vector coding scheme has thrown the inferences into question. Can the authors instead plot the heading as a function of percent stance for all subjects so that we can see when the stated inferences are applicable and when it may be an artifact of the mean response.

We removed the vector coding and heading, instead opting to show the phases directly on the time-series curves such that the reader can see clearly how the phases are annotated. We also added a description of the sensitivity of our metrics to the discussion, because of the subjective nature of selecting a threshold value.

Line 347-370 (discussion): The thresholds in the analysis of windlass mechanism timing and plantar fascia elongation were selected subjectively based on visual assessment of the time-series curves. We modified each threshold by ±20% and ±40%, keeping the other at the selected value (0%), to determine the sensitivity of our results to the threshold values. The order of the phases changed minimally, while the time spent in each phase varied. As the thresholds were increased, as expected, all quasi-constant phases lengthened. Thus, when the plantar fascia elongation threshold increased, the pure forward-windlass phase lengthened, while the inhibited forward-windlass phase shortened because the plantar fascia elongation that was originally coded as elongation changed to a quasi-isometric phase. Furthermore, as the MTPJ angle threshold increased, the quasi-constant angle phase lengthened, reducing the MTPJ dorsiflexion phase. The overall time available for any forward-windlass phase was thus reduced, consequently shortening the inhibited and enhanced forward-windlass phases. When the threshold was decreased by 20%, an additional participant experienced the inhibited forward-windlass phase, while a different participant no longer had an inhibited forward-windlass phase when the threshold was increased by 40%. The plantar fascia elongation threshold played a bigger role at initial contact than the MTPJ threshold change. As the plantar fascia elongation threshold decreased, the pure reverse-windlass phase had plantar fascia shortening as well. This indicates that the foot may not always have a pure reverse-windlass mechanism; however, it does not change our interpretation of limited plantar fascia elongation at initial contact, in favour of the elongation of more proximal arch ligaments. Overall, these changes do not influence our interpretations as there is clear variability among subjects regardless, and we assess primarily the existence, order and potential significance of the phases. Future work is required to understand variation in the length of the phases, and whether the plantar fascia and windlass mechanism are responsible for the variations in arch deformation seen here.

Detailed comments
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L70--72: "During both walking and running gaits, there is evidence of the forward-windlass mechanism [4,7,8,14] and that the plantar fascia strains during mid- to late- stance, simultaneously to the expected timing of the windlass."

Expected in what sense? Also, what is meant by "timing of the windlass"? It is a mechanism that is continuously varying in its involvement and not a discrete event.

We have clarified this statement to indicate what is meant by the windlass mechanism.

Line 69-71: During both walking and running gaits, there is evidence that the plantar fascia strains during mid- to late- stance [7–13], simultaneously to MTPJ dorsiflexion and arch rise, and thus the forward-windlass mechanism [4,7,8,14].

L75--78: "While current approaches such as motion capture [7–10], ultrasound [7,9,10], or single plane fluoroscopy [12,13] have provided insight into plantar fascia and foot function, they do not capture the complex, three- dimensional motions of the structures within the foot during locomotion."

The analyses and viewpoints presented in this paper are two-dimensional, within the sagittal plane. So I don't see the basis for claiming that the lack of 3D measurement is somehow the problem. What novel information from 3D X-ray imaging is needed to address your questions that cannot be provided by a sagittal plane X-ray view? This case needs to be made more clearly.

Biplanar videoradiography enables us to capture the subject-specific bone motion in the foot in three-dimensions. The windlass mechanism is usually described based on a two-dimensional model (Figure 1), however our analysis extends it to three dimensions, therefore capturing arch adduction in addition to arch dorsiflexion. We have updated the text to reflect the advantage of three-dimensional biplanar videoradiography.

Line 74-79: While current approaches such as motion capture [7–10], ultrasound [7,9,10], or single plane fluoroscopy [12,13] have provided insight into plantar fascia and foot function, they do not capture the three-dimensional motions of individual bones within the foot during locomotion. Using three-dimensional biplanar videoradiography, we modelled plantar fascia elongation using subject-specific bone motion in addition to MTPJ dorsiflexion as a proxy for an engaged windlass mechanism.

L150--151: "The time of minimum arch angular velocity was selected as the point where the arch angle started to decrease."

Do you mean the point in time when the velocity changed sign and became negative? The minimum of velocity is when the angular acceleration is zero. When the arch angle starts to decrease, it was presumable increasing until that point. This means that the velocity, which is the first derivative, would be zero. So I do not see how the minimum of arch angular velocity relates to "the point where the arch angle started to decrease."

We apologize for the confusing statements. We have opted to remove the net 3D arch angle measurement, in favour of the more approachable arch dorsiflexion and adduction. This also removes the assumption of when the arch begins to recoil.

L168: "converged to optimal solutions"

Which optimization routine was used? How was convergence verified?

The sequential quadratic programming routine implemented within the MATLAB function ‘fmincon’ was used for the optimization. Convergence was output from the function and visually verified. All frames converged within a step tolerance of $1x10^{-6}$ mm.

Line 159- 166: Using generated distance fields for each bone, a custom optimization was implemented using the sequential quadratic programming routine with fmincon in MATLAB (R2019a, Mathworks, USA), with 100 points used for each fibre [24]. A convex hull was created around the sesamoids to model the inter- sesamoid ligaments and to prevent the fibre from falling between them. The optimization algorithm was given an initial guess using guiding points on the inferior side of sesamoid, which then converged to optimal solutions around the sesamoids. The optimal solution was also visually verified.

L174--175: "potential trade-offs of the plantar fascia’s role in the arch-spring and windlass mechanisms"

The fallacious dichotomy from the previous submission appears to have been carried forward into the revised manuscript. As argued previously, the plantar fascia will always stretch under load. How much it will stretch depends on the load. In case the authors are making a functional argument about PF function, I argue that they are lacking hypotheses and evidence to show how the extensibility of the plantar fascia affects locomotor function.

We apologize that this made it through the last round of review. We have modified this line to indicate our goal of understanding the role of the plantar fascia’s extensibility on the windlass mechanism.

Line 171-173: We describe the effect of the plantar fascia’s extensibility on the windlass mechanism by examining the coupling between MTPJ rotation and plantar fascia elongation during stance phase.

L178: "when the arch flattens"

Given the quantitative details of the methods, it is not clear how the authors define arch height. Terms like the arch flattening or rising only make sense when the height is specified with respect to some baseline. The kinematics are defined in terms of the rotation of the first metatarsal with respect to the calcaneus. So, complex motion of the calcaneus that involves a combination of translation and rotation could manifest as arch deformation according to the kinematic variable used by the authors, without any apparent change in the externally perceived arch height.

We used the term flattening and rising to provide a more intuitive understanding of the motion occurring in the arch. As suggested, it is more applicable to have a reference to the measured variables that describe the direction. Thus, we have added a line in the methods to be more specific about what we mean by arch flattening and arch rise.

Line 142-144 : To simplify our description of arch motion, we refer to arch flattening as a combination of arch dorsiflexion and abduction, and arch rise as the combination of arch plantarflexion and adduction.

L187--188: "therefore, fibre elongation is analogous to strain"

This statement is confusing. Strain is a dimensionless quantity that tracks deformation or elongation relative to a reference length. So strain and elongation cannot be analogous. Further, why is the assumption of a non-slack PF related to the normalization of elongation to a strain variable?

We have removed this line from the text.

L212--213: "In theory, the change in arch length, Δl, and MTPJ dorsiflexion, θ, should be coupled."

Depends on the theory. There are many elastic bodies involved here, including the PF, the midfoot region, and the subtalar area. The degree of coupling between Delta L and theta depends on whether some of these elastic regions deform more than the others. So, there is no single "in theory" that I can see. Can the authors be more precise about the premise under which the coupling is expected?

We have specified that we mean the original windlass mechanism theory. We have modified this sentence to better explain our rationale.

Line 198-200: The original description of the windlass mechanism states that the arc length change around the MTPJ (Δs) should be directly coupled with arch length change (Δl) [4] (Figure 1).

L230: "a temporally consistent pattern during the running gait cycle"

What does the word "consistent" mean in this context? In table 1, for example, the authors state that because of too much inter-subject variability in the timing of the transitions between the different behaviors, they only report the time spent in each region of the coding diagram. That indicates a lack of temporally consistent patterns.

We have clarified the results section to be primarily descriptive and highlight the variability among subjects. In the process, we have removed this line from the text.

L231--235: "Consistent with our hypothesis, we found an inhibited forward-windlass just prior to the pure forward-windlass, where the plantar fascia elongated while the toes dorsiflexed and the arch rose slightly. However, in direct contradiction to our hypothesis, the plantar fascia spent a substantial period (11 ± 1% of stance) in the pure forward-windlass phase, approximately at heel rise (see Supplemental Video)"

The strength of the claim is far more than can be supported by the data. I don't know if these are because the authors only look at the mean response or because of the problems with the vector coding approach. Please allow me to explain further.

The authors claim that "consistent with our hypothesis, we found an inhibited forward-windlass." Even if one were to use the problematic vector coding scheme, the results are not consistent with the hypothesis that the windlass is inhibited by PF elongation. For example, in subjects 1, 3, 6, and others, the inhibited windlass is far smaller in duration than the mean. Even the sequencing of the different phases is quite variable, with some subject data showing multiple visits to the same phase. Whether that is capturing real phenomena or is simply an artifact of the coding system is unclear.

I urge the authors to follow my earlier recommendation to avoid the language of a hypothesis-based narrative, and instead focus on the objective of providing the first-ever measurement of PF function during windlass engagement and arch deformation. Then, the language of the paper can be more consistent with what the evidence shows.

Thank you for this point. As mentioned in section 2, we have removed the vector coding analysis and simplified our description to coincide with time-series MTPJ dorsiflexion and plantar fascia elongation. Further, we highlight the variability in the data and have placed more emphasis on it in the results and discussion. We also recognize that we can not say that the interactions cause changes in arch deformation; instead, we highlight that they happen concurrently.

L271: "in a consistent sequence"

This is not true. There is substantial variability, even when using the problematic coding scheme.

We have removed this line from the manuscript.

L277: "maximally strained"

That is a strong claim. Maximal with respect to what measure? Is the claim that there is some limiting maximal value of strain that is reached by the PF in every trial? I saw no evidence of that.

We apologize for our lack of specificity. We meant the maximal value for a participant within the trial. We have removed this sentence as we re-wrote the results section.

L281--284: "Our data show that in early stance, the plantar fascia does not elongate substantially until arch flattening has already slowed; instead, the plantar fascia facilitates the reverse-windlass motion of the foot, likely so that arch tissues proximal to the plantar fascia manage more of the load than the plantar fascia."

I see a means to strengthen this argument. There was an underlying assumption that the PF were not slack to begin with. Even if they are not completely slack and are bearing low tension, the nonlinear nature of the load-displacement curve of the PF would imply that it cannot bear much load initially. So the expectation under the slack or light tension scenario is a compliant PF that would easily stretch. That is the opposite of what you see, demonstrating the importance of the pure reverse windlass phase.

Thank you. This is an excellent point and we have incorporated it into our discussion on slack length.

Line 391-393: If the plantar fascia was slack or bearing low tension at initial contact, we would expect it to strain substantially when the foot is loaded; however, we saw plantar fascia shortening or quasi-isometric behaviour.

Referee: 1

Comments to the Author(s).
I thank the authors for their clear reply to my queries in a separate letter, as well as for the additions and clarifications made in the manuscript. I am satisfied that all issues are either resolved or acknowledged better in the revised version of the manuscript. I have no further issues.

Thank you for taking the time to re-read and review our revised manuscript.