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Letters to the Editor

Planimetric models to evaluate the pennate muscle force length characteristics

Van der Linden et al. (Van der Linden BJJ, Koopman HFJM, Huijing PA. Grootenboer, H.J., Revised planimetric model of unipennate skeletal muscle: a mechanical approach. Clinical Biomechanics 1998;13:256–260) used equilibrium of the point connecting tendon and aponeurosis to construct a model of a unipennate muscle. This results in an unrealistic high muscle force. Combining this muscle force with their proposed relation between fibre shortening and muscle shortening results in an improper power balance.

After reading the paper of van der Linden et al. [1] about modelling unipennate muscles I would like to make some remarks about it. I have six points that will be discussed.

Remark 1. *Van der Linden et al.* [1] *state that in Otten's approach* [2] *the force in the aponeurosis cannot be determined. I agree. This means that elastic effects of the aponeurosis cannot be incorporated in Otten's model. Though it is not explicitly stated in the text, I assume that Eq.* (7) *of van der Linde et al., which models elastic effects of the aponeurosis, has been applied to their model. This flaws the comparison between the two models, because now two things are compared: the effect of incorporating elastic effects of the aponeurosis* and *different ways of calculating muscle force. Van der Linden et al. state that their model predicts the length-force relation better than Otten's model because they used a different equation to calculate muscle force. However, this is a premature statement, because elastic effects are also a factor.*

Remark 2. *In a force equilibrium analysis it is common to point out the borders of the free body diagram. Apparently Fig.* 3 *of van der Linden et al. is an attempt to do so. However, the volume related force is an internal force in this free body diagram and should not be incorporated.*

Remark 3. *Van der Linden et al. state that the rule that work delivered by the muscle fibres should equal work delivered by the muscle is not compatible with the rule that the muscle area should remain constant during shortening. However, Otten* [2] *explicitly states on page 105 of his paper that "all types of muscles can be described with the constant volume rule and the work of fibres equals work of muscle rule or work balance rule, because both rules dictate the same geometric changes of a muscle. However, this is true only under the condition that the tendinous sheets do not stretch." The reason van der Linden et al. disagree is that according to them the volume related force is also able to do work. An important assumption in the model of van der Linden et al. is that muscle area remains constant. In a 3-D approach this is equivalent to preserving muscle volume. Internal muscular pressure fulfils this function. Work done by the pressure is calculated using the following equation*:

$$W_v = \int p \cdot \mathrm{d}V,$$

where W_v *is the work done by the pressure, p the internal muscular pressure*, *and* dV *the infinitesimal change of volume. From this it is clear that the volume related force can only do work if it is accompanied by a change in muscle volume. Since they explicitly state that muscle area remains constant, the volume related force cannot do work.*

Remark 4. *Van der Linden et al. use force equilibrium perpendicular on the aponeurosis at the point where the tendon and the aponeurosis are connected to calculate muscle force. This is done by the following equation*:

$$F_\mathrm{m} = \frac{1}{2} \cdot F_\mathrm{f} \cdot \frac{\sin(\alpha+\beta)}{\sin(\beta)},$$

where F_m *is the muscle force*, F_f *the fibre force*, α *angle between fibres and tendon, and* β *angle between aponeurosis and tendon. The volume related force does not appear in this equation nor in the derivation of this equation. A simple example where* α *is assumed* 30° *and* β *is assumed* 15° *shows that using this equation muscle force can by far exceed fibre force. In this example*:

$$F_\mathrm{m} = 1.4 \cdot F_\mathrm{f}.$$

Assuming constant muscle area dictates fibre length changes to be smaller than muscle length changes as can be deduced from equation (A3) *of van der Linden et al. In my example fibre length* L_f *is taken* 5 cm. *With the previous mentioned angles muscle length* L_m *can then be calculated to be 14 cm. An infinitesimal length change of the muscle is calculated by Eq.* (A3) *of van der Linden et al. which yields*:

$$\mathrm{d}L_\mathrm{m} = 1.4 \cdot \mathrm{d}L_\mathrm{f}.$$

Since the volume related force is not involved in these equations and, according to Remark 3, *cannot do work, an* *infinitesimal amount of work done by the muscle can be expressed in work done by the fibres*:

$$\mathrm{d}W_{\mathrm{m}} = F_{\mathrm{m}} \cdot \mathrm{d}L_{\mathrm{m}} = 1.4 \cdot F_{\mathrm{f}} \cdot 1.4 \cdot \mathrm{d}L_{\mathrm{f}} = 1.96 \cdot \mathrm{d}F_{\mathrm{f}} \cdot \mathrm{d}L_{\mathrm{f}} = 1.96 \cdot \mathrm{d}W_{\mathrm{f}},$$

where W_{f} equals work done by the fibres. Work done by the muscle far exceeds work done by the fibres. The source for this excessive work is unknown, so what we are dealing with is a perpetuum mobile. If I could equip myself with muscles like these I would certainly join the Olympics and win every game.

Remark 5. *Although I do not agree with van der Linden's approach, I would like to explore the nature of the volume related force. In their Fig.* 3 *van der Linden et al. draw this force directed through both aponeurosis ends. I assume this is done to avoid a net couple on the muscle. However, as pointed out in Remark* 2 *the volume related force is not an external force when considering whole muscle equilibrium. The direction of this force is therefore not constrained by equilibrium demands of the whole muscle. The direction should be calculated by using the* 2 *equilibrium equations for the endpoint of the aponeurosis.*

$$F_v \cdot \cos(\delta) + \frac{1}{2} \cdot F_{\mathrm{f}} \cdot \cos(\alpha) - F_{\mathrm{a}} \cdot \cos(\beta) = 0,$$

$$F_v \cdot \sin(\delta) - \frac{1}{2} \cdot F_{\mathrm{f}} \cdot \sin(\alpha) - F_{\mathrm{a}} \cdot \sin(\beta) = 0.$$

The unknown variables are F_v and δ so these equations can be solved.

Remark 6. *Discussing other models van der Linden et al. state that models of Otten* [2] *and van Leeuwen* [3] *do not adequately predict the length-force relation of a muscle. Otten indeed predicts length-force curves, but van Leeuwen does not. This author "only" predicts muscle geometry and pressure distribution within a muscle. Apart from this van der Linden et al. state that these models derive geometry from local equilibrium equations and therefore* (?) *fail to adequately predict length-force curves. This statement lacks argumentation. I would even like to reverse it. Since the approach of van Leeuwen* [3,4] *ensures mechanical equilibrium at every single point in the muscle and of the muscle as a whole, this is the only way to do muscle modelling right. If length-force curves were predicted by a model based on the work of van Leeuwen I would expect a perfect fit on experimental data.*

Conclusion

Summarising, the model of van der Linden et al. does not obey basic mechanical laws. The fact that its normalised length-force curve fits the presented data well is in my opinion a coincidence.

I am looking forward to the author's response.

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Recently a paper by Van der Linden et al. on a planimetric model of a unipennate skeletal muscle appeared in *Clinical Biomechanics* [1]. The model is parallelogram-shaped and has straight aponeuroses and straight muscle fibres (see Fig. 1 of this letter). The total tensile force of all fibres is represented by equivalent tensile forces in the peripheral fibres only. The authors introduced a volume-related force to keep the volume of their model constant. They claim to have deduced, from mechanical equilibrium of the whole muscle, relationships between fibre and muscle force and also between fibre length change and muscle length change. These relationships are different from relationships derived by Otten [2] based on equilibrium of the aponeurosis only.

The paper surprised me by its unusual force analysis of the planimetric muscle model and by several disputable passages.

As is usual in simple muscle models, the planimetric model has straight elements only, which are connected by hinges. However, this approximation has an important consequence: the straight elements of the model (aponeuroses and muscle fibres) can withstand significant bending moments and can exert significant trans-

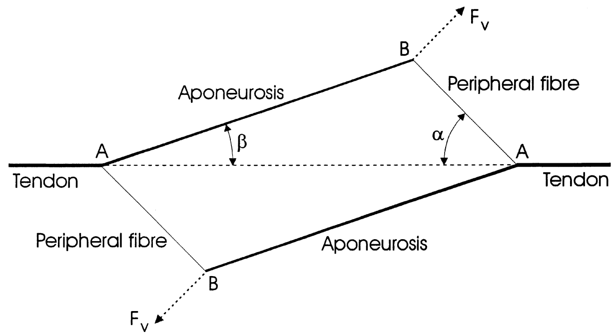

Fig. 1. A planimetric unipennate muscle model with straight muscle fibres and aponeuroses. Of all fibres, only the peripheral ones are shown. F_v is the volume-related force as proposed by Van der Linden et al. [1]. The positions of points A and B, the direction of F_v and the angles α and β agree with Figs. 3 and 4 from [1].

verse forces at their extremities, unlike their natural counterparts.

Equilibrium in corner points and constancy of area are correct principles for a planimetric muscle model. The constant area corresponds with the practically constant volume of a muscle, which means that relaxation, contraction and length changes of a muscle do not practically change the volume. If the muscle fibres in a model are represented by contractile elements without thickness, then the model would collapse into a structure with zero area. The model needs some influence to maintain its area. A good way to preserve area constancy is to take account of the pressure inside the muscle. This is a realistic mechanism: just like in solids and fluids the pressure resists a volume (or here: area) change.

The volume-related force F_V in the paper is a way to preserve area constancy, but it is not realistic: there is no such external force acting on the corner points B (at the thin ends of the aponeuroses in their Fig. 3). Here the mechanical analysis of the model must be considered erroneous.

It is possible though to replace the influence of internal pressure by forces acting at the corner points, but it should be realised that these forces must have an identical resulting effect compared to the pressure. The best way to achieve this is to calculate the force on each side of the parallelogram (aponeurosis or peripheral fibre) as caused by the pressure, divide it equally over its corner points, and then add the two forces acting at each corner point. I performed the analysis and found forces that acted at the *four* corners of the parallelogram, not just at two of them. I also found that the forces at the points B have other directions than as were shown in Fig. 3 of the paper: they should be at right angles to the tendon direction. It should further be realised that the pressure-replacing forces are not external forces of the model and that they will not do work on the muscle as a whole: pressure forces in a constant volume cannot do any resulting work. Consequences of introducing wrong forces at the corner points are: (i) incorrect force analysis in points A in their Fig. 3 (thick ends of aponeuroses) and (ii) disturbed work balance.

In their Fig. 4 it is suggested that forces on points A are only exerted in the directions of the tendon, aponeurosis and peripheral fibre. Here it is essential to take account of pressure forces at right angles to the aponeurosis and other pressure forces at right angles to the fibre. It can easily be shown that the equilibrium equations then lead to their formulas (1), if corrected, and (2) as quoted from Otten [2]. Formula (1) of the paper has been inaccurately quoted from Otten [2]: the denominator should be $\cos(\beta)$ instead of $\sin(\beta)$. The incorrectness of formulas (3) and (4) in the paper, apart from resulting from an incorrect analysis, can also be illustrated by the following example.

Consider a square muscle with angles $\alpha = \beta = 45°$. The fibres are at right angles to the aponeuroses. Whatever tensile force they exert, they cannot further contract the muscle; so the muscle force F_m is zero for even the maximum possible fibre force F_f. (A possibly vanishing fibre force owing to short sarcomeres would not be relevant to this part of the muscle model analysis.) Substitution of the above α and β in their formula (4) yields $F_m = 1/2\sqrt{2}F_f$ in obvious disagreement with the correct $F_m = 0$. It can be shown that for the angles in their Fig. 1 the result of formula (3) is 75% too large and the result of formula (4) even a factor 6.

The authors claim incompatibility between (i) the area constancy, and (ii) the assumption of Otten [2] that fibre work equals muscle work. Their argument is based on an erroneous volume force, and is therefore untenable. There is no external volume force, so it cannot contribute to work. As long as no elastic, plastic, friction or viscous force can absorb work (as is true for the analysed simple model), all fibre work can only be transformed into muscle work: they are equal.

About the general approach, the authors suggest that models with local equilibrium are inferior to their own model with equilibrium for the whole muscle. In fact, equilibrium of small parts of a structure implies equilibrium of any combination of these parts. In the case of equilibrium of all parts (in casu aponeuroses and fibres), consequently the whole structure is also in equilibrium. The approach with local equilibrium all through the muscle is superior to the approach of the authors with equilibrium of only the whole muscle, since the latter approach allows for local unrealistic deviations of equilibrium. Bipennate and unipennate muscle models in [3] and [4], respectively, with curved fibres and aponeuroses in local equilibrium with the pressure all through the muscle are far more realistic than the models with straight and infinitely stiff muscle elements.

The authors suggested that the model in [3] predicts the force–length relationship of the muscle inadequately.

In fact no such relationship was predicted in [3], certainly not an inadequate one.

The expression for dl_m/dl_f (which means the ratio of muscle length change over fibre length change) in the Appendix of the paper can be reduced to the much simpler form $dl_m/dl_f = \cos(\beta)/\cos(\alpha + \beta)$. Combination with their formula (2) from Otten [2] shows that $F_f\, dl_f = F_m\, dl_m$, which elegantly confirms that fibre work equals muscle work.

In conclusion, I wonder what arguments the authors have to defend their approach (whole muscle equilibrium rather than local equilibrium), their analysis of the mechanics of the model (introduction of the volume-related force instead of pressure forces), their statements on muscle and fibre work and unsubstantial criticism on publication [3].

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Reply by authors

In the paper by van der Linden et al. [1] a planimetric model of unipennate muscle is presented as an alternative to an earlier planimetric model derived by Otten [2]. The main difference between these models is that the force $\boldsymbol{F}_p$ in the model of Otten (Fig. 1c), is repositioned from the central area of the aponeurosis to the corner point of the muscle and expressed as a volume related force $\boldsymbol{F}_v$ (Fig. 1b). $\boldsymbol{F}_v$ represents the effect of the internal pressure in the muscle, with the function to keep the muscle volume (or area in the 2-D case) constant. $\boldsymbol{F}_v$ should be treated as a (somewhat artificial) external modeling force. While $\boldsymbol{F}_p$ can be related directly to the internal muscle pressure, this is not possible for $\boldsymbol{F}_v$.

The repositioning of the volume related force has large consequences for the equations that describe the system: sine functions suddenly change in cosine functions, the structural elements of the system (aponeuroses and fibers) are loaded differently. The alternative planimetric model fitted our purposes better:

(1) It is able to describe the force-length characteristic of homogeneous unipennate muscle as a function of the fiber force-length characteristic. This can also be achieved with the model of Otten. (2) We can immediately implement without further assumptions an elastic aponeurosis, as the elements of the muscle (fibers and aponeuroses) are loaded in axial direction only. In the original model of Otten the aponeurosis is not loaded uniformly, one has to make additional assumptions regarding the bending stiffness and stiffness against shear loads (these have to be infinite). (3) The model is consistent, i.e. without further assumptions every part of the model is in mechanical equilibrium. The original model of Otten is in mechanical equilibrium with a somewhat eccentrically placed pressure force $\boldsymbol{F}_p$. This might result from a non-uniform pressure distribution along the aponeurosis. However, in Otten's model no structures are present that would justify this non-uniform distribution.

A planimetric model is attractive because it is very simple and can be computed analytically, at least when a rigid aponeurosis is assumed. The demand of constant muscle area is implemented directly in the equations.

From the letters of Spoor as well as Faber, we conclude that both authors may not fully understand the assumptions and purposes of the alternative model and their resulting consequences. If this would be the result of an unclear formulation in the original paper, we apologize for this and hope that the present paper will shed some light in the darkness. In trying to evaluate the alternative model, both authors basically make the same mistake: They mix up properties of the original and alternative models (i.e., assume properties that are not present in the alternative model, such as assuming some pressure or ignoring the volume force). Evidently, they end up with incorrect results, since this mixed model is not consistent. They incorrectly conclude that the alternative model is also not correct. We will clarify this by deriving a generalized planimetric model. Incorporating appropriate assumptions, this generalized model

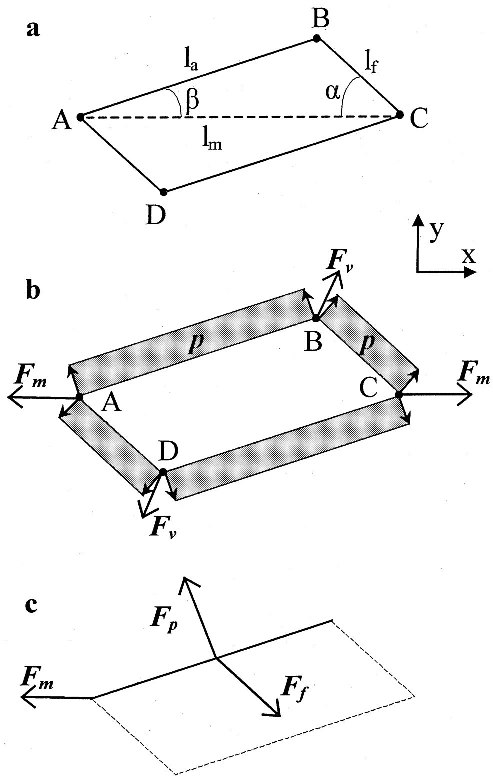

Fig. 1. Planimetric model of unipennate muscle with fiber angle α and aponeurosis angle β: (a) Dimensions of the model; (b) Forces acting on the generalized model: muscle force $\boldsymbol{F}_\mathrm{m}$, volume force $\boldsymbol{F}_\mathrm{v}$ and force distribution $\boldsymbol{p}$; (c) Original model of Otten (adapted from [2]).

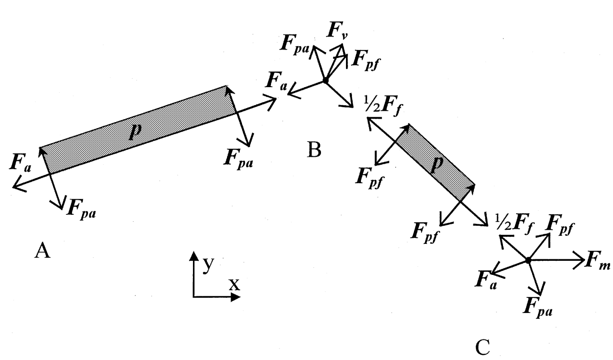

Fig. 2. Forces acting on aponeurosis and fiber. Balance equations are derived from equilibrium of internal and external forces in the muscle's corner points and equilibrium of aponeurosis and fiber.

will yield either the alternative model or the (slightly modified) model of Otten.

Spoor and Faber make another mistake in the way they apply the work balance: For the alternative model, the work balance is different from the work balance in the model of Otten. The work balance for the generalized model is derived to explain this.

As this will take care of most complaints of Spoor and Faber, the remaining remarks will be discussed in a separate section. In a final section some general properties of both models are discussed with some concluding remarks.

Generalized planimetric model

Consider a planimetric model consisting of four structural elements: Two aponeuroses and two fibers (Fig. 1a). The elements are connected with friction-free hinges at the muscle's corner points *A*, *B*, *C* and *D*. Line *A–C* with length l_m is the muscle line of pull. The aponeurosis has length l_a and angle β with the muscle line of pull; the fiber has length l_f and angle α.

The structure is loaded with external forces as shown in Fig. 1b. The muscle force $\boldsymbol{F}_\mathrm{m}$ acts at points *A* and *C*. To prevent the structure from collapsing, a volume force $\boldsymbol{F}_\mathrm{v}$ applies in points *B* and *D* and the elements are loaded with a uniform force distribution $\boldsymbol{p}$.

Balance of the complete structure requires each element in balance. The equations are derived with Fig. 2, where additional internal forces are shown: The fiber force $\boldsymbol{F}_\mathrm{f}$, aponeurosis force $\boldsymbol{F}_\mathrm{a}$, and balancing forces $\boldsymbol{F}_\mathrm{pf}$ and $\boldsymbol{F}_\mathrm{pa}$. These latter forces are needed to balance the force distribution $\boldsymbol{p}$ for fiber and aponeurosis, respectively. It is immediately seen that $F_\mathrm{pf} = 1/2\ p\ l_\mathrm{f}$ and $F_\mathrm{pa} = 1/2\ p\ l_\mathrm{a}$.

Evaluation of the balance equations yields, with F_{vx} and F_{vy} the components of $\boldsymbol{F}_\mathrm{v}$:

$$
\begin{aligned}
&F_{vx} + 1/2\ F_\mathrm{f} \cos\alpha - F_\mathrm{a} \cos\beta = 0,\\
&F_{vy} + 1/2 p\, l_\mathrm{m} - 1/2 F_\mathrm{f} \sin\alpha - F_\mathrm{a} \sin\beta = 0,\\
&1/2 p(l_\mathrm{a} \sin\beta + l_\mathrm{f} \sin\alpha) - 1/2 F_\mathrm{f} \cos\alpha\\
&\quad - F_\mathrm{a} \cos\beta + F_\mathrm{m} = 0,\\
&1/2 p(l_\mathrm{a} \cos\beta - l_\mathrm{f} \cos\beta) - 1/2\ F_\mathrm{f} \sin\alpha\\
&\quad + F_\mathrm{a} \sin\beta = 0.
\end{aligned}
\tag{1}
$$

For the total model (Fig. 1b) the moments of force have to be balanced:

$$
\oint \boldsymbol{r}(s) \times \boldsymbol{p}(s)\, \mathrm{d}s + 2\boldsymbol{r}_B \times \boldsymbol{F}_\mathrm{v} = \boldsymbol{0}, \tag{2}
$$

where s is co-ordinate along the contour of the model and $\boldsymbol{r}$ and $\boldsymbol{r}_B$ are appropriate moment arms relative to the center of the muscle for $\boldsymbol{p}$ and $\boldsymbol{F}_\mathrm{v}$, respectively. As the integral is always zero, Eq. (2) yields a condition for the direction of $\boldsymbol{F}_\mathrm{v}$, which has to be along the line *B–D*. It can be shown that Eq. (2) is dependent of Eq. (1), so Eq. (2) can be omitted when describing the system. This dependency reflects the observation that the complete system is in mechanical equilibrium when each part of it is in equilibrium, i.e., the system is consistent.

As there are four equations to describe a system with six unknowns, we have to make additional assumptions to solve this. Two assumptions are possible and sensible: $\boldsymbol{p} = \boldsymbol{0}$ or $\boldsymbol{F}_\mathrm{v} = \boldsymbol{0}$.

1. $\boldsymbol{p} = \boldsymbol{0}$.

With four equations and five unknowns, we can express the variables as a function of one of the unknowns, say F_f. This system has a solution when $\sin\beta$ does not equal zero:

$$\begin{aligned}F_{vx} &= 1/2F_f\sin(\alpha-\beta)/\sin\beta,\\ F_{vy} &= F_f\sin\alpha,\\ F_a &= 1/2F_f\ \sin\alpha/\sin\beta,\\ F_m &= 1/2\ F_f\sin(\alpha+\beta)/\sin\beta.\end{aligned}\tag{3}$$

This solution is identical to the alternative model.

2. $\boldsymbol{F}_v=\mathbf{0}$ or $F_{vx}=F_{vy}=0$.

After analysis, this system appears to have three independent equations with four unknowns. It can be solved for F_f when $\cos\beta$ does not equal zero:

$$\begin{aligned}p\,l_a &= F_f\sin\alpha/\cos\beta,\\ F_a &= 1/2F_f\cos\alpha/\cos\beta,\\ F_m &= F_f\cos(\alpha+\beta)/\cos\beta.\end{aligned}\tag{4}$$

This is essentially the model of Otten with some adaptations: The aponeurosis force is defined and the solution is based on a consistent system. It appears that the figure that explains the model (Fig. 1c) is not complete, some internal forces are missing.

In this derivation the properties of the muscle (i.e., internal pressure, constant volume) are not used. The forces $\boldsymbol{p}$ and $\boldsymbol{F}_v$ are modeled as external loads that act on the elements of the structure to prevent it from collapsing.

Generalized work balance

The work balance is derived in a general way. Assume corner points A, B, C and D have displacements $\boldsymbol{\delta A}$, $\boldsymbol{\delta B}$, $\boldsymbol{\delta C}$ and $\boldsymbol{\delta D}$. Since $\Sigma\boldsymbol{F}_A=\Sigma\boldsymbol{F}_B=\Sigma\boldsymbol{F}_C=\Sigma\boldsymbol{F}_D=\mathbf{0}$ (Fig. 2), we can write a general work balance as the vector product equation $\Sigma\boldsymbol{F}_A\cdot\boldsymbol{\delta A}+\Sigma\boldsymbol{F}_B\cdot\boldsymbol{\delta B}+\Sigma\boldsymbol{F}_C\cdot\boldsymbol{\delta C}+\Sigma\boldsymbol{F}_D\cdot\boldsymbol{\delta D}=0$. As this equation is correct for any $\boldsymbol{\delta A}$, $\boldsymbol{\delta B}$, $\boldsymbol{\delta C}$ and $\boldsymbol{\delta D}$, we may choose these according to the properties of the planimetric model. A simple and direct choice is $\boldsymbol{\delta A}=\mathbf{0}$ and $\boldsymbol{\delta C}=\mathbf{d}\boldsymbol{l}_\mathbf{m}$, with the change of muscle length $\mathbf{d}\boldsymbol{l}_\mathbf{m}$ in the direction of $\boldsymbol{F}_{mC}$, the muscle force in point C. Symmetry requires that $\boldsymbol{\delta D}+\boldsymbol{\delta B}=\mathbf{d}\boldsymbol{l}_\mathbf{m}$. Finally, choose the size and the direction of $\boldsymbol{\delta B}$ such that the muscle area is constant and the aponeurosis work equals the amount of energy stored or released by the aponeurosis. By defining $\boldsymbol{\delta B}=\mathbf{d}\boldsymbol{l}_\mathbf{a}$, the vector representing the aponeurosis length change, and substitution of all forces in the corner points, this results in the work balance for the generalized planimetric model

$$\begin{aligned}&\boldsymbol{F}_{mC}\cdot\mathbf{d}\boldsymbol{l}_\mathbf{m}+\boldsymbol{F}_{fD}\cdot(\mathbf{d}\boldsymbol{l}_\mathbf{a}-\mathbf{d}\boldsymbol{l}_\mathbf{m})+2\boldsymbol{F}_{aB}\cdot\mathbf{d}\boldsymbol{l}_\mathbf{a}\\ &\quad+\boldsymbol{F}_{vB}\cdot(2\,\mathbf{d}\boldsymbol{l}_\mathbf{a}-\mathbf{d}\boldsymbol{l}_\mathbf{m})=0.\end{aligned}\tag{5}$$

The force distribution $\boldsymbol{p}$ does not contribute to the work balance. This equation may be solved analytically when a rigid aponeurosis is assumed (i.e., when $\mathbf{d}\boldsymbol{l}_a$ is perpendicular to $\boldsymbol{F}_a$): The muscle work $\mathrm{d}W_m=\boldsymbol{F}_{mC}\cdot\mathbf{d}\boldsymbol{l}_m=F_m\cdot\mathbf{d}\boldsymbol{l}_m$, the fiber work $\mathrm{d}W_f=\boldsymbol{F}_{fD}(\mathbf{d}\boldsymbol{l}_\mathbf{a}-\mathbf{d}\boldsymbol{l}_\mathbf{m})=-F_f\,\mathbf{d}\boldsymbol{l}_\mathbf{f}$ and the aponeurosis work $\mathrm{d}W_a=2\boldsymbol{F}_{aB}\cdot\mathbf{d}\boldsymbol{l}_\mathbf{a}=0$. It can be proven that in this case the work by the volume force $\mathrm{d}W_v=\boldsymbol{F}_{vB}\cdot(2\,\mathbf{d}\boldsymbol{l}_\mathbf{a}-\mathbf{d}\boldsymbol{l}_\mathbf{m})=-\mathrm{d}W_f-\mathrm{d}W_m$ balances the equation. In the model of Otten, where the volume force equals zero, the work balance with a rigid aponeurosis reduces to $F_m\,\mathrm{d}l_m=F_f\,\mathrm{d}l_f$. However, in the alternative approach, the volume force $\boldsymbol{F}_v$ does contribute to the work balance.

This shows that the force distribution $\boldsymbol{p}$ is a pressure-replacing force: Both pressure and $\boldsymbol{p}$ do not contribute to the work balance in a constant volume. However, it should be noted that $\boldsymbol{p}$ does not represent the pressure exactly, since in the corner points $\boldsymbol{p}$ is not defined. Perhaps one should conclude that in planimetric models the pressure is not properly defined: Any pressure would result in the curvature of the elements, and corners could not exist. If one is interested in modeling the pressure properly, one should adopt an approach as proposed by van Leeuwen and Spoor [3].

In the alternative model, $\boldsymbol{F}_v$ should be considered as an external modeling force, representing the *effect* the pressure has in keeping the volume constant. When the pressure is related to the radius of curvature, it has to be very large in the corner points and very small along the aponeuroses and fibers. This more or less reflects the alternative model.

Detailed response

As most objections from Spoor as well as Faber are answered by the analysis above, we will focus on some issues that may still be unclear.

Reply to Spoor

Forces do act at each corner point in the alternative model, they are called $\boldsymbol{F}_m$ and $\boldsymbol{F}_v$. The volume force $\boldsymbol{F}_v$ is not a pressure-replacing force, balance requires that $\boldsymbol{F}_v$ does in general not act perpendicular to the muscle line of pull (Eq. 2).

Formula (1) in Ref. [1] is corrected in Eq. (4).

There is no reason why in the alternative model the condition $\alpha+\beta=90°$ should not result in a muscle force. In real life, we can imagine that under such conditions the pressure would increase with increasing fiber force, resulting in an increased muscle force. However, we could be convinced to the opposite with experimental evidence regarding this matter. We also do not see how results of a formula can be too large, larger than what?

The key of the objections of Spoor is reflected in his sentence “There is no external volume force, so it cannot contribute to work”. Of course, in reality, the volume force does not exist; we never suggested that it does. Likewise, a real muscle does not consist of straight elements connected by hinges, a real muscle does have a curved surface, and a real muscle is not two-dimensional. It is the nature of any model that it is a simplification of often very complex processes in order to understand and predict some selected functional aspects. With the planimetric model the force-length characteristics of unipennate muscle as well as the muscle's linearized geometry at different lengths are predicted. In the process of modeling (i.e., simplification), often assumptions are made that have no direct mathematical relation to physical quantities in order to achieve internal consistency of the model. However, often is shown that these assumptions can be related to the effects of physical quantities. This is also shown for the volume force.

We did not suggest that the model of van Leeuwen and Spoor [3] is inferior to the planimetric model, it is a different model with quite different purposes and with totally different assumptions. We did, and still do, suggest, however, that this type of model may not be very suitable to calculate the force-length relation of muscle. The reason for this is that we suspect that the demand of constant muscle area is not easily implemented and would require large computational efforts (in planimetric models, the demand of constant muscle area is directly incorporated in the equations). The demand of constant muscle area is not easily implemented because local equilibrium equations are applied, and constant muscle area applies to the whole muscle.

We would have welcomed a reply in which was shown that we are incorrect in this point. Spoor only points out his belief that this type of model is "far more realistic". This may be true when the pressure and shape of the muscle are considered, but not for the functional output of the muscle, which is the muscle force as a function of length. The force-length characteristic is in fact never computed with the model of van Leeuwen and Spoor [3].

The planimetric model is based on the balance of all elements incorporated, as in the model of van Leeuwen Spoor. However, the planimetric model has the additional advantage that equilibrium of the whole structure can be used. This allows for the implementation of properties that apply to the whole structure, such as the demand of constant area.

The equation $F_\mathrm{m}\,\mathrm{d}l_\mathrm{m} = F_\mathrm{f}\,\mathrm{d}l_\mathrm{f}$ is correct in the model of Otten with a rigid aponeurosis. It is however not the work balance in the alternative model (Eq. 5), where fiber work does not equal muscle work.

Reply to Faber

As pointed out correctly by Dr. Faber, the original paper [1] is not complete in its discussion of the elastic aponeurosis. In the data presented, both models incorporated an elastic aponeurosis. With a rigid aponeurosis we observed a comparable shift of force-length characteristic between the models, however, these data were not presented. In the alternative model we could implement the elastic aponeurosis without further assumptions. For the model of Otten, we assumed the aponeurosis being rigid against bending moments and shear forces but elastic in its longitudinal direction. The aponeurosis force was chosen to be consistent with the other equations of the model of Otten, in effect equal to the aponeurosis force in Eq. (4).

Obviously, the volume force is an external force since no force within the structure balances it. The volume force does appear in the work balance, so the alternative model does not represent a perpetuum mobile and Faber will probably not win the Olympics.

If Faber had solved the equations shown in Remark 5, he would have noticed that these imply that the volume force must be directed through both aponeurosis ends.

Remark 6 is discussed in the reply to Spoor. We would, however, not expect a perfect fit on experimental data with the model of van Leeuwen Spoor, since that model is based on different assumptions. For example, that model describes the pressure distribution in the deformed muscle tissue, but the stresses related to this deformation are assumed zero. Even if these stresses are taken into account (i.e. a finite element approach), still other assumptions are made, and the muscle properties have to be described by an increasing number of not well-known parameters.

Discussion

Instead of rejecting one model in favor of the other, it is more fruitful to view the different models as alternatives to describe the same system. One should be aware of the different assumptions incorporated in each model, and choose the model that fits the purpose of study best. In addition, one could choose the simplest possible model, as this requires the least number of (possibly unknown) parameters.

To describe the force-length characteristics of unipennate muscle and its linearized geometry as a function of length, our alternative planimetric model seems a good option. If the internal pressure is deemed important, the planimetric model of Otten is more appropriate, at the cost of the assumption that the structural elements (aponeurosis and fibers) are rigid. As this leads to a contradiction for the fibers, one has to accept fiber behavior that is flexible in longitudinal direction but rigid against bending and shear.

If the morphology of the muscle is studied in more detail or the pressure should be defined properly, the model of van Leeuwen Spoor or a finite element model can be chosen. This is at the cost of increasing complexity. Finally, to study the interaction between fibers, a finite element model seems to be the only reasonable option (e.g., [4]).

We would like to make a final remark about the nature of the discussion on planimetric models. Spoor and Faber especially commented on the assumptions of the alternative model. As modeling assumptions are in the end a matter of acceptance (or not), we had no other option than to clarify the model with a rather technical reply. We feel it is better to discuss the properties of models based on experimental evidence. We showed that the predictions of the alternative model compare well with experimental data [1]. Both Spoor and Faber seem to prefer another model but fail to make this comparison.

Experimental validation and comparison of the alternative model and the model of Otten is possible on a number of points, besides the predicted force-length relation. For example, the alternative model predicts that a muscle force exists when the angle $\alpha + \beta$ equals 90°, the model of Otten predicts that this force equals zero. The alternative model predicts that the muscle force is larger than the fiber force, the model of Otten predicts the opposite. If one of the approaches should be rejected, then this should be done exclusively on the basis of experimental evidence that invalidates this kind of predictions.

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