Investigating the running abilities of *Tyrannosaurus rex* using stress-constrained multibody dynamic analysis (#16524)

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Investigating the running abilities of *Tyrannosaurus rex* using stress-constrained multibody dynamic analysis

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The running ability of *Tyrannosaurus rex* ~~has been intensively debated due to its relevance~~ to interpretations of feeding behaviour and the biomechanics of scaling in giant predatory dinosaurs. Different studies using differing methodologies have produced a very wide range of top speed estimates and there is therefore a need to develop techniques that can improve these predictions. Here we present a new approach that combines two separate biomechanical techniques (multibody dynamic analysis and skeletal stress analysis) to demonstrate that true running gaits would probably lead to unacceptably high skeletal loads in *T. rex*. Combining these two approaches reduces the high-level of uncertainty in previous predictions associated with unknown soft tissue parameters in dinosaurs, and demonstrates that the relatively long and gracile limbs of *T. rex* - long argued to indicate competent running ability - would actually have mechanically limited this species to walking gaits. Being limited to walking speeds contradicts arguments of high-speed pursuit predation for the largest bipedal dinosaurs like *T. rex*, and demonstrates the power of multiphysics approaches for locomotor reconstructions of extinct animals.

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Summary

The running ability of *Tyrannosaurus rex* has been intensively debated due to its relevance to interpretations of feeding behaviour and the biomechanics of scaling in giant predatory dinosaurs. Different studies using differing methodologies have produced a very wide range of top speed estimates and there is therefore a need to develop techniques that can improve these predictions. Here we present a new approach that combines two separate biomechanical techniques (multibody dynamic analysis and skeletal stress analysis) to demonstrate that true running gaits would probably lead to unacceptably high skeletal loads in *T. rex*. Combining these two approaches reduces the high-level of uncertainty in previous predictions associated with unknown soft tissue parameters in dinosaurs, and demonstrates that the relatively long and gracile limbs of *T. rex* - long argued to indicate competent running ability - would actually have mechanically limited this species to walking gaits. Being limited to walking speeds contradicts arguments of high-speed pursuit predation for the largest bipedal dinosaurs like *T. rex*, and demonstrates the power of multiphysics approaches for locomotor reconstructions of extinct animals.

Introduction

Tyrannosaurus rex is one of the largest bipedal animals to have ever evolved and as such it represents a useful model organism for understanding morpho-functional adaptations and constraints at multi-tonne body sizes (1). The running ability of *T. rex* and other similarly giant dinosaurs has been intensely debated in the literature (2-6) and features prominently in reconstructions of the lifestyles and carnivorous behaviours of large theropod dinosaurs (2-4, 7-10). However, despite a century of research since Osborn's (11) work on tyrannosaur limb anatomy there remains no consensus on the most accurate maximum speeds for *T. rex*, or indeed whether or not its gigantic body size prohibited running completely.

Some qualitative anatomical studies (2-4), some employing a degree of quantitative biomechanical methods (3) have proposed very fast running speeds (up to 20ms-1) and an overall high degree of athleticism for large theropods like *T. rex*. These studies cite the long and gracile limbs of *T. rex* as a key adaptive feature indicative of high relative (12) and absolute speeds (2-4), along with possession of large tail-based hip extensor musculature (13). In contrast, more direct and quantitative biomechanical approaches have favoured intermediate (6, 14) or much slower speeds for *T. rex*, with the latter including within their predictive range an inability to reach true running gaits (5, 15, 16). Biomechanical approaches emphasize the well-known scaling principles (17, 18) that animals of larger body mass have more restricted locomotor performance because muscle mass scales isometrically, but muscle force, relative speed of contraction and power scale with negative allometry (19-22).

Biomechanical models inherently incorporate anatomical characters (e.g. limb proportions) on which more traditional qualitative assessments are based, but also require quantitative definitions for soft tissue parameters associated with mass distribution and muscle properties which are not preserved in dinosaur fossils. Typically minimum and maximum bounds are placed on such parameters based on data from living animals (5, 15, 23) and/or additional computer models (24-27). However, this yields very broad ranges for soft tissue parameters in dinosaurs which translates directly into imprecise values for performance estimates like running speed (25). Thus while biomechanical approaches are more explicit and direct by their inclusion of all major anatomical and physiological factors determining running ability, their utility within palaeontology in general has been severely restricted by high levels of uncertainty associated with soft tissues. Consequently estimates for *T. rex* running speed from biomechanical models range from 5 to 15m/s (5, 6, 15, 16).

One solution is to find information in the preserved skeletal morphology that can be used to reduce the predictive dependence of biomechanical models on soft tissue. It has recently been suggested that bone loading can be used to improve the locomotor reconstruction of fossil vertebrates by excluding gaits that lead to overly high skeletal loads (28). It is highly likely that the skeletons of cursorial vertebrates are optimised for locomotor performance such that the peak locomotor stresses are 25 to 50% of their failure strength, indicating a safety factor of between two and four (18). There are notable exceptions where long bones are considerably stronger than required (29) but in general this trade-off between body mass and load bearing ability appears to be a widespread anatomical adaptation that is found in invertebrates as well as vertebrates (30). To calculate the loads sustained in vivo during high speed locomotion requires the integration of a large number of different force components from soft tissues, joints, substrate interactions and body segment accelerations. Virtual robotic approaches such as multibody dynamics (MBDA) allow calculation of the complete loading environment which can then be used to estimate bone loading through beam mechanics (e.g. (28)) or other simulation approaches like finite element analysis (FEA) (31). Herein we demonstrate the predictive power of this approach in palaeontology by integrating MBDA, machine learning algorithms and stress analysis to reconstruct maximum locomotor speed in *T. rex*. In this new approach machine learning algorithms are used to generate the muscle activation patterns that simultaneously produce maximum the locomotor speed of MBDA model of *T. rex* whilst maintaining defined skeletal safety factors.

Materials and Methods

MBDA musculoskeletal model of *T. rex*. MBDA approaches to locomotor reconstruction require a linked segment model of the animal to be built based on its skeletal morphology and inferred myology (Figure 1). The model used here was based on a 3D laser scan of BHI 3033 (32) and consisted of 15 independent segments: a single aggregated trunk segment, along with left and right thigh, shank, metatarsal and pes segments in the hind limb as well as arm, forearm and manus segments in the forelimb. All segments were linked by hinge joints that permitted only pure flexion-extension. Joint positions and ranges of motion were estimated directly from the skeleton. The origins, insertions and paths of 58 hindlimb muscles (29 per limb) were mapped onto the skeletal model based on comparative analysis of hindlimb muscles in related extant species presented in previous studies (24). In this simulations a highly simplified forelimb musculature was used since the limb was not judged to have an important locomotor role. Muscle mass properties were estimated following the simplified pattern where each muscle action is considered to have a specific fraction of the total body mass as calculated from a range of vertebrates (27). The total muscle mass was set at the highest plausible value of 50% (6) since the current simulation methodology (see below) is only minimally sensitive to the actual muscle proportion as long as there is sufficient muscle to power the movement. Muscle fibre lengths and tendon lengths were set as a proportion of the change in each muscle-tendon unit length across the range of joint permitted since this minimises the effects of errors in moment arms and lines of action (27, 28). Body mass was estimated from the minimum convex hull of the individual segments using a regression curve calculated from our combined comparative dataset (29, 33-35), and resulted in a total body mass of 7206.7kg, which is towards the lower-end of recent estimates from volumetric models (32, 36). Further information about this calculation and the full calibration dataset is included in the supplementary information. Limb segment masses were calculated using mass fractions based on running bird data (23). Inertial properties were calculated directly from the convex hulls and scaled to match the predicted masses. Contact with the substrate was modelled using contact spheres attached to the digits as in previous studies (e.g. (6, 27, 28)). These contacts act like stiff, damped springs under compression, but allow the foot to be lifted with no resistance when needed. However they do not attempt to model the complex, non-linear interactions that actually occur between the foot and the ground.

Multiphysics simulation. Bone stress analysis was performed by treating the limb long bones as irregular beams and calculating the mid-shaft loading. The load was calculated directly from the multibody simulator by splitting each of the leg segments into two separate bodies that were linked by a fixed joint. The simulator was then able to calculate both the linear forces and rotational torques acting around this non-mobile joint using the full dynamic model and therefore including inertial forces as well as muscle forces and joint reaction forces. A full finite element analysis would have been preferable but this is currently too computationally expensive in this context and previous work has shown that the error in long bone loading is likely to be approximately 10% (37). Bone stress was calculated following Alexander as the sum of the compressive/tensile stress and the normal bending stress (38, 39).

(1)

$$\sigma_{compressive} = \frac{F}{A}$$

Where:

$\sigma_{compressive}$ is the normal stress in the beam due to compression (N.m^{-2}).
F is the longitudinal force (N).
A is the cross-sectional area of bone (m^2).

(2)

$$\sigma_{bending} = \frac{M_x I_y + M_y I_{xy}}{I_x I_y - {I_{xy}}^2} y - \frac{M_y I_x + M_x I_{xy}}{I_x I_y - {I_{xy}}^2} x$$

Where:

$\sigma_{bending}$ is the normal stress in the beam due to bending (N.m^{-2}).
x is the perpendicular distance to the centroidal y-axis (m).
y the perpendicular distance to the centroidal x-axis.
M_x is the bending moment about the x-axis (N.m).
M_y is the bending moment about the y-axis (N.m).
I_x is the second moment of area about x-axis (m^4).
I_y is the second moment of area about y-axis (m^4).
I_{xy} is the product moment of area (m^4).

This ignores the effects of shear but previous work has identified bending and compression as the main loading modes (40). This calculation requires an estimate of the cross-sectional geometry of the limb bones and ideally this would have been obtained directly from a CT scan of the specimen. However since this was not available it was estimated using published cross sectional parameters of tyrannosaurs (14, 41, 42) (femur mean 38%, tibia mean 35%, fibula mean 96%, metatarsus mean 60%) and the external outline measured from the reconstruction. The complete simulation was implemented in our open source GaitSym system downloadable from www.animalsimulation.org and available as supplementary information.

To calculate the dynamic loads this simulation needs to be able to walk and run bipedally. This was achieved using our standard gait morphing methodology (43) to generate the necessary control parameters to maximise forward velocity. This is computationally extremely expensive because of the large number of muscles that are in the model and because of the available degrees of freedom within the model. To reduce the computational difficulty the model was restricted to the parasagittal plane which we have previously found to greatly simplify the control process whilst being unlikely to greatly affect the limb loading (44). Even so, finding a stable solution required a great deal of computer time and generating a stable gait took approximately 5,000 core hours before the gait morphing process. The additional constraint of keeping the bone stress below a particular value was implemented by using the peak stress as a hard fail criteria in the simulator. The stress value was measured across the three major hind limb segments and low-pass filtered at 5 Hz before testing to account for the lack of soft-tissue cushioning in the model and to reflect the level of filtering typically employed in neotological gait analysis (45). The simulation was run at a range of different maximum peak stress values using gait morphing to fully investigate the effects of changing this limit on the maximum running speed obtainable. In total over 200 individual optimisation runs were performed to ensure that the search space was adequately covered and that a reasonable estimate of the best performance had been obtained. The full specification of the model is available as a human-readable XML file in the supplementary information. The skeletal element outlines and hulls are downloadable from www.animalsimulation.org and as supplementary information.

Results

Figure 2 shows the results of repeated gait morphing whilst optimising for distance travelled in a fixed amount of time using a range of peak stress limits. Figure 2A shows the maximum velocities achieved, which peaks at a speed of 7.7 ms-1 for the high stress limit conditions (>200 MPa). Lowering the peak stress limit has little effect on this maximum speed until it is reduced below 150 MPa when the maximum speed drops rapidly. This clearly shows that limiting the stress at high values has no effect on running speed and therefore the simulation is not stress limited in these conditions. At lower stress limits, the stress limit controls the maximum speed indicating that the simulation is stress limited at physiologically realistic peak stresses. Figure 2B shows the Froude Number calculated from the horizontal velocity and standing hip height. Froude Number in this context is a measure of speed that controls for body size and is therefore useful for cross species comparisons in running velocity (46). From this we can see that the Froude number at 100 MPa is 1.0 which typically is the upper limit for walking gaits. Figure 2C shows the stride lengths adopted by the model. These are broadly in line with Froude number based predictions (47) and show a steady decrease with speed as expected. Figure 2D shows that the gait cycle time is relatively constant in the simulations.

Figure 3 shows the actual peak stresses calculated in the limb during the complete gait cycle as well as showing the periods of foot contact. Relatively high stresses are seen in all the long bones but it is clearly the stress in the mid-tarsus that is highest at high speeds (Fig 3M-O). As expected the highest stresses occur during stance phase and the relative symmetry of the maximum and minimum stresses seen at any time show that this stress is primarily due to bending and not to compressive loading on the limb. The foot contact timings confirm the predictions from the Froude numbers that the higher speeds have a clear aerial phase and represent running (i.e. duty factors <0.5) whereas the slower speeds have no aerial phase and represent a grounded gait (i.e. duty factors >0.5). The 400 & 800 MPa limit cases are almost identical and the peak stress does not reach 400 MPa again showing that stress is not a limiting factor in these cases.

There are two definitions of walking and running that are commonly used when considering bipedal gait. The traditional definition relies on duty factors: walking is has a duty factor of >0.5 and therefore has a period of dual support, whereas running has a duty factor of <0.5 and there has an aerial phase (48). However it is also possible to define bipedal gait based on the energy transformations that are seen between kinetic and potential energy (49). This allows the definition of hybrid gaits such as grounded running which are commonly seen in birds (50). We can perform a similar analysis to the gaits generated by our *T. rex* simulation to further investigate the gaits generated. Figure 4 shows the horizontal speed of the centre of mass of the simulation and also the vertical height of the centre of mass. At the lowest speed there is a 22% phase difference between these two measured using autocorrelation which drops to <15% at higher speeds. This would indicate moderate energy exchange at low speeds as might be expected. However Figure 5 shows the actual horizontal kinetic energy of the simulations and the gravitational potential energy and it can be clearly seen that because of the difference in magnitude of the values there is actually very little scope for energy recovery. When constrained by leg stress, the simulation appears to minimises the vertical movement of the centre of mass so that very little gravitational potential energy is ever stored. Our simulation is therefore not taking advantage of pendular energy saving mechanisms which might reflect a preference for grounded running, or it might alternatively be that the model optimisation is for maximum speed and not for minimum energy cost and this has led grounded running to minimise the leg stress as opposed to pendular walking to minimise energy cost.

In the supplementary information there are two movie files illustrating the output of the simulator for the fast grounded gait at 100 MPa limit (S2), and the fast run at 400 MPa limit (S3). The full model specification for the models that generated these movies are also available in the SI. (S3, S4).

Discussion

The velocity changes in Figure 1 clearly show the marked difference in peak load when comparing walking with running gaits. Extensive work on safety factors in cursorial vertebrates suggests that bone would have a typical maximum stress of not more than 100 MPa (18). In our simulations, fast walking leads to stresses that match this prediction well (Figures 2 & 3). However all simulations with true running gaits show a large jump in maximum peak stresses that clearly exceeds the maximum allowable value. Body accelerations are higher in running and the force during the contact phase must also be higher because the duty factor is lower. In contrast, accelerations in walking are lower and the increased duty factor reduces forces, and slow walking allows a substantial double support phase so the load on the legs can be divided between both limbs. These factors acting together produce the sharp increase noted in peak load and, based on the typical stress limits in living animals (18), the skeleton is not strong enough to cope with this load level. Therefore, even if safety factors below the lower limit seen in living animals are allowed, our analysis demonstrates that *T. rex* was not mechanically capable of true running gaits (Figures 2 & 3). Previous estimates quantitative estimates of absolute maximal speeds for *T. rex* from 5-15m/s (5, 6, 15, 16) identified soft tissue unknowns as a major source of uncertainty but by including hard tissue mechanical information we can show that the highest values, whilst possible if we allow generous estimates for soft tissue, are impossible given skeletal strength. Bone strength is based directly on the skeletal dimensions and in our analysis of *T. rex* the forces generated by the muscles are not limiting the top speed. When extremely high stresses are permitted in the model (>150MPa, and especially 400-800MPa) then predicted speeds are consistent with mean estimates from previous models in which only muscular constraint on maximal performance are considered results (6). In addition our analysis of energy transformations (Figures 4 & 5) further reinforces the suggestion that the simulation is finding solutions that minimise the skeletal load and that low impact, bird-style grounded running (50) may be an appropriate gait for bipedal dinosaurs.

As with all attempts at reconstructing the locomotor capabilities of fossil animals it is important to be somewhat cautious with our interpretations. These results improve on those obtained by previous biomechanical work by excluding some of the previously plausible values and thereby reducing the range of uncertainty but many of the previous caveats still apply. Our previous work on sensitivity analysis (25) tested the effects of body mass, centre of mass location and various measures of muscle physiology, but these complex models have a large number of additional parameters that could potentially affect the model predictions. Ideally a full Monte Carlo style sensitivity analysis would be performed to analyse the effects of all of these parameters (51) but unfortunately the computational requirement for such an analysis is enormous and currently not a practical undertaking. It would also be useful to ground truth our predictions based on experimental work with living animals. Direct bone strain measurement is a well-established technique that has been performed on a wide range of animals (e.g. (52-55) and multibody dynamic analysis derived strains have been validated against the literature in several cases (e.g. (31, 56)) but there is certainly a need to combine these approaches in the same experimental system and this would be a useful future approach. The models used in our simulations are currently the most anatomically complete reconstructions ever attempted. However they are still appreciable simplifications of the true complexity of the living organism. In particular extending the stress analysis to a full finite element model would be of considerable benefit especially if coupled with a more realistic muscle coverage achieved by subdividing anatomical muscles into multiple functional units and by including other non-bone tissues. These extra elements would potentially allow the model to exploit the possibilities of peak stress reduction using soft tissue tensile elements to produce tensegrity structures (57)~~)~~ which might turn out to have a substantial effect. Finally our simulations rely on machine learning to find muscle activation patterns that maximise the speed given a range of constraints. There are too many possibilities to perform and exhaustive search over all possibilities so we need to use a non-exhaustive approach. This is a very active area of current computational research and we would certainly expect that better solutions will be found using a combination of the improved algorithms and the greater computational power which will be available in future.

The finding that *T. rex* was restricted to walking gaits supports arguments for a less athletic lifestyle for the largest bipedal dinosaurs like *T. rex*. Tyrannosaurs underwent pronounced allometric changes during ontogeny (1) and previous studies have suggested the torso became longer and heavier whereas the limbs became proportionately shorter and lighter as *T. rex* grew (36). It would therefore be very valuable not only to investigate other species but also apply our multiphysics approach to different growth stages within species. Ontogenetic niche partitioning has been suggested for many dinosaurs (58, 59), and energetic considerations (60) and changes in skull anatomy (61) and bite performance (62) may indicate a shift towards increased consumption of larger prey and/or carrion as *T. rex* grew. Such a shift towards large prey specialism is not incompatible with our findings here regarding locomotor speed, as presumably large multi-ton herbivores similarly experienced the same general scaling-related restrictions on musculoskeletal performance as *T. rex* (5, 6, 15, 24-26). It is somewhat paradoxical that the relatively long and gracile limbs of *T. rex* - long argued to indicate competent running ability (2-4, 12) - would actually have mechanically limited it to walking gaits, and indeed maximised its walking speed. This observation illustrates the limitation of approaches that rely on solely analogy and the importance of a full biomechanical analysis when investigating animals with extreme morphologies such as *T. rex*. The new approach we introduce here clearly has the potential to contribute widely to our understanding of the evolution of animal locomotion, particularly major ecological shifts such as colonization of land or bipedal-quadrupedal transitions.

Conclusion

The results presented demonstrate that the range of speeds predicted by earlier biomechanical models for *T. rex* locomotion include speeds that would apply greater loads to the skeleton than it would have been able to withstand. These high load speeds can therefore be excluded from our predictions and this means that the possible range of maximum speeds has been greatly reduced and essentially limits adults of this species to walking gaits. This work demonstrates how including multiple physical modalities and multiple goals can improve our reconstructions of the locomotor biology of ancient organisms and lead to a better understanding of the mechanical constraints of large body size.

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Ethical Statement

The research presented does not include any experimental work with animals or humans.

Funding Statement

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Data Accessibility

The XML files defining the models are available in the Supplementary Information as well as movie files illustrating the simulation outputs. GaitSym is an open source simulation system available from http://www.animalsimulation.org, and the skeletal scans are also available from this source.

Competing Interests

We have no competing interests.’

Authors' Contributions

All authors contributed to the design of the study and simulation and writing the paper. The software was written and HPC computing was performed by WIS. The model was scanned by KB and PM and the myology was implemented by KB. SBP & WIS produced the final simplified the model for simulation, and CAB provided additional guidance on beam mechanics.

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Figure and table captions

Figure 1. Snapshot from GaitSym2016 showing the details of the model. Muscle paths are in red and joints are in blue. The axes arrows are 1 m long.

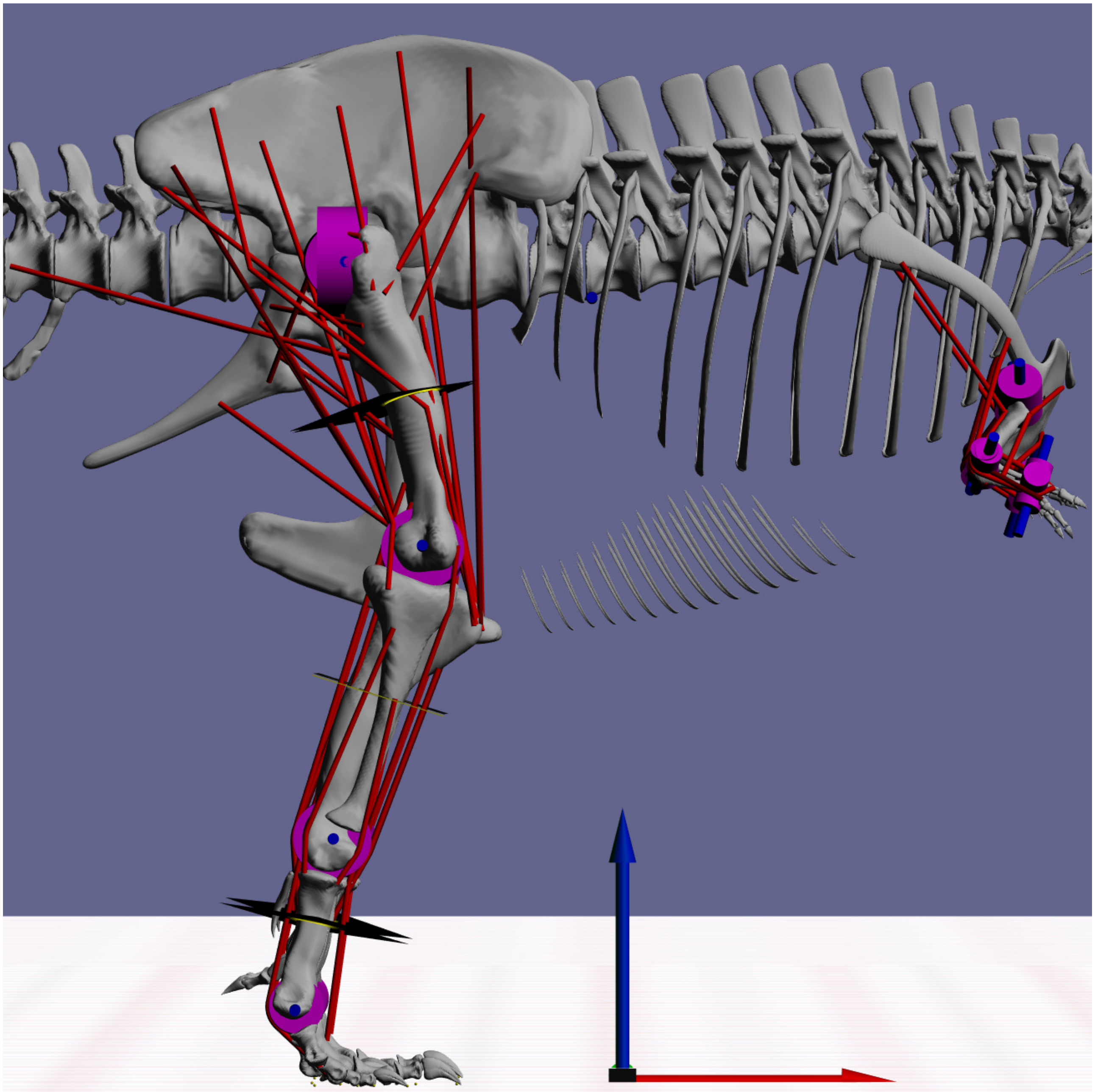
Figure 2. Graphs showing the effects of changing the peak stress limit on gait parameters. A, maximum velocity; B, Froude Number; C, stride length; D, gait cycle duration.

Figure 3. Graphs showing the peak stress (2nd order Butterworth low-pass filtered at 5Hz) calculated at the functional mid-point of the hindlimb segments at different peak stress cutoffs. Foot contact times are also shown (black is ipselateral limb, grey is contralateral limb). The time axis represents two complete gait cycles, and the dashed line is drawn at 100 MPa which is the nominal stress limit for a safety factor of 2.

Figure 4. These graphs show the centre of mass horizontal velocities and the centre of mass vertical positions in the different peak load simulations.

Figure 5. These graphs show the energy transformations within the simulation: horizontal kinetic energy, gravitational potential energy, and also the sum of these two energy values.

Figures



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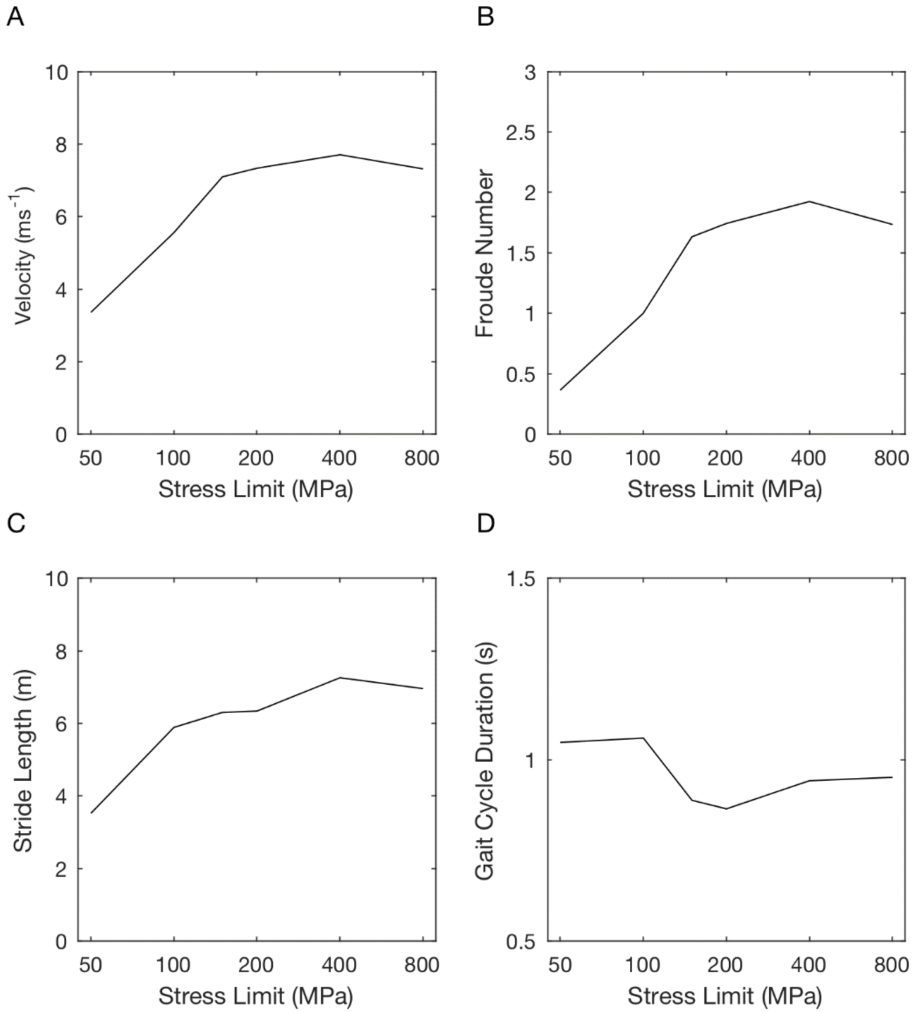

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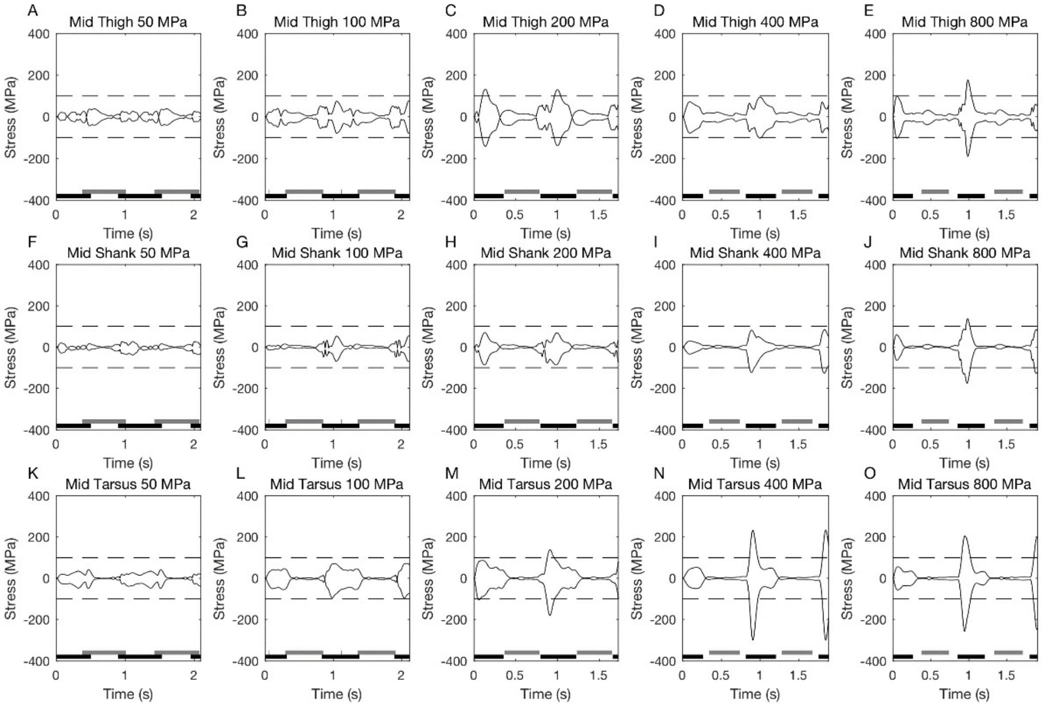

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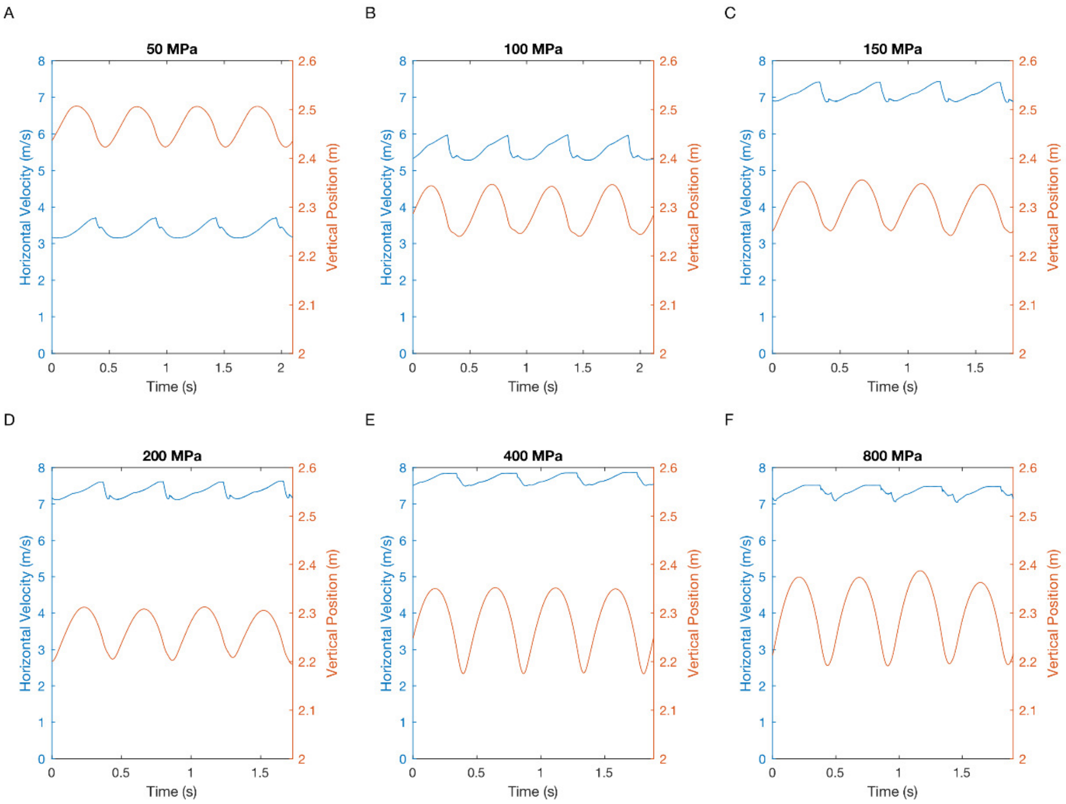

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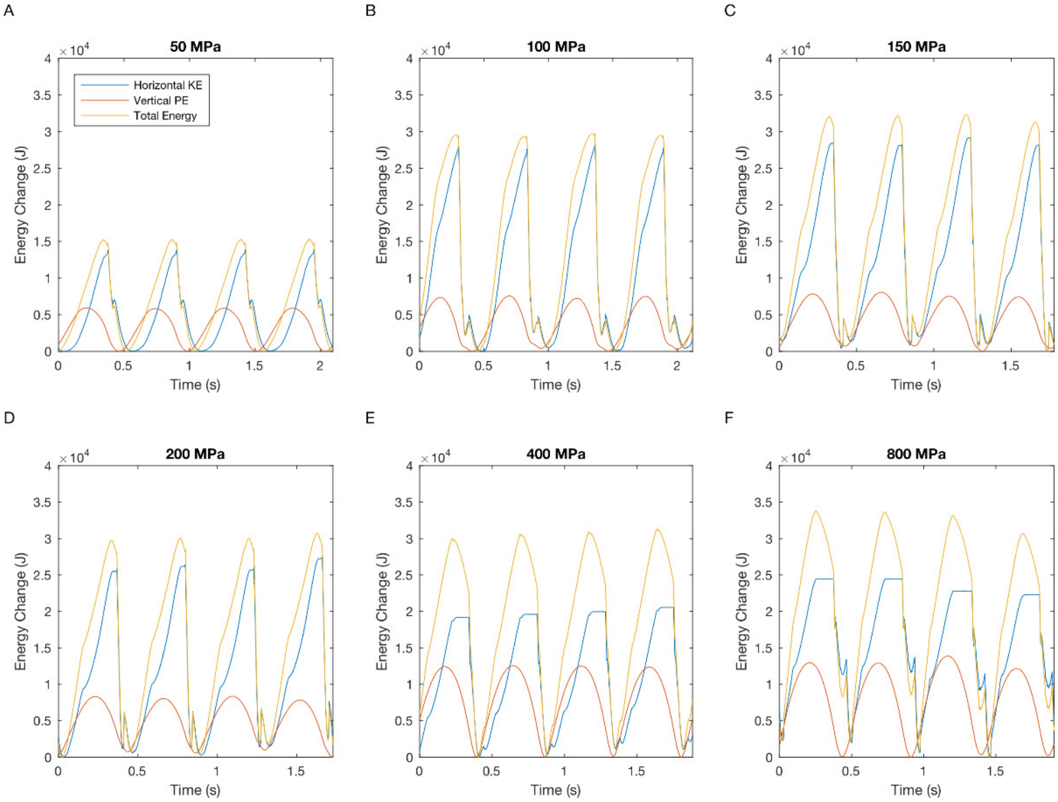

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