Prediction of performance from muscle models

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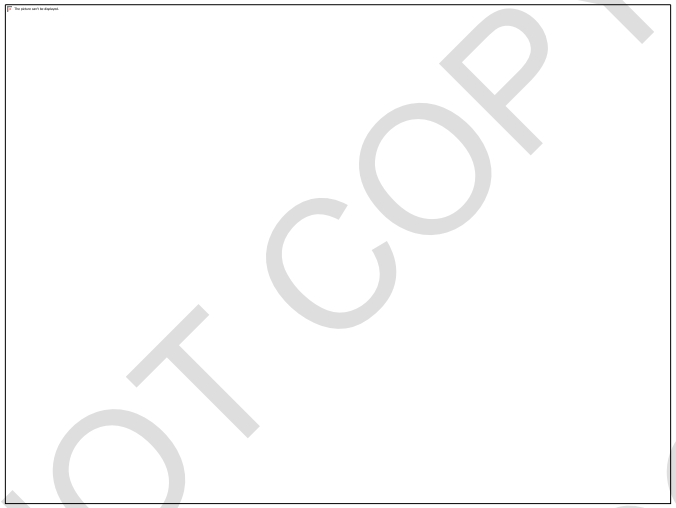
Muscles are used for mobility, stability and posture



Mechanical function of muscle

Length

Work = Force x Δ Length

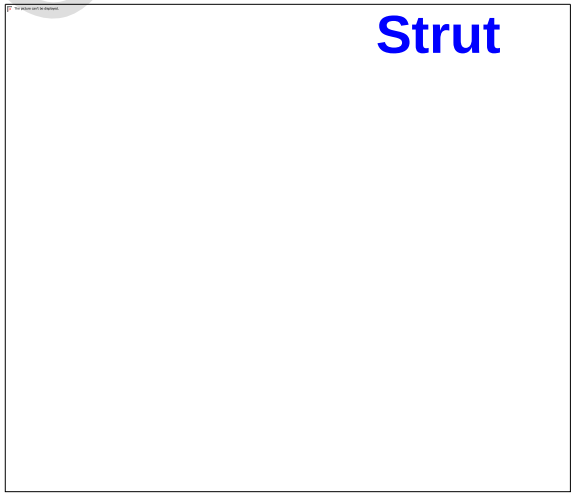
Power = Force x Velocity

Force

Motor

Brake

Strut



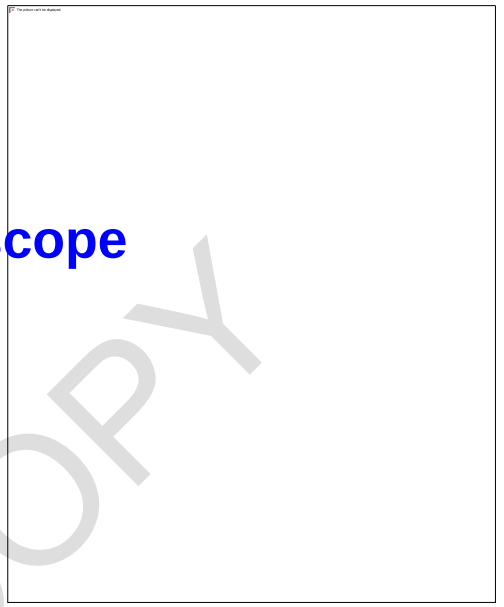
Dickinson et al., *Science* 2000

Length measurements in human muscle

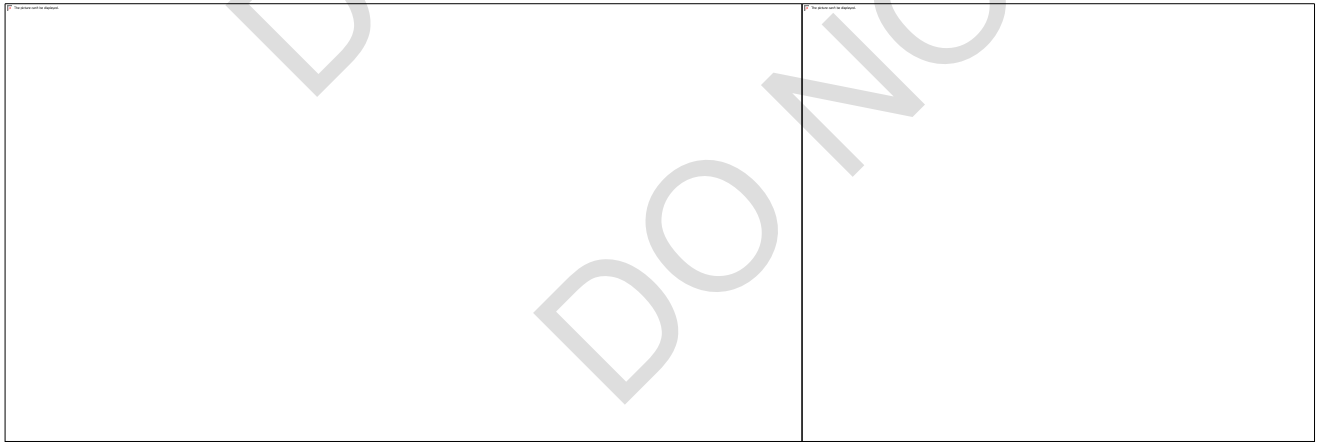
Intraoperative laser diffraction

Lieber et al. *J.Neurophysiol.* 1994

Optical microendoscope



Llewellyn et al. *Nature* 2008



Sarcomere and fascicle lengths

Lichtwark et al.
J. Appl. Physiol. 2018

Muscle force cannot be directly measured

Muscle redundancy – biomechanical indeterminacy

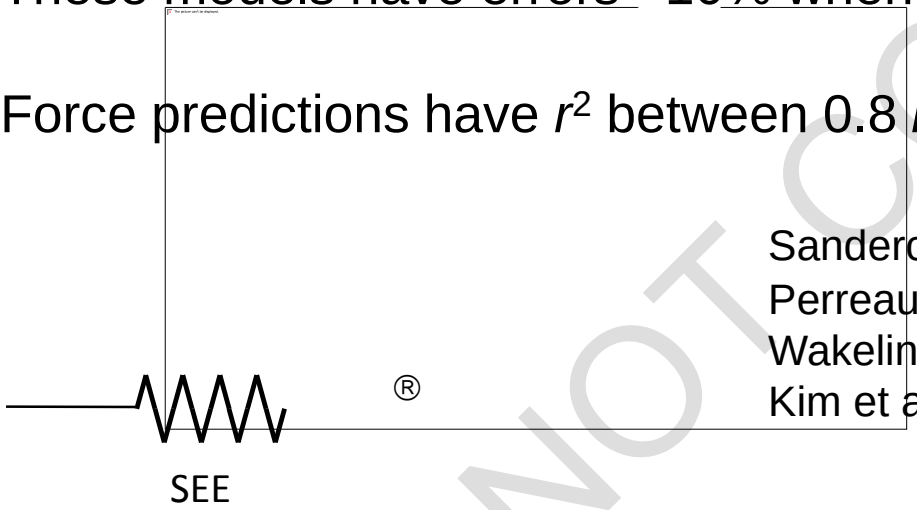
- More force-carrying structures (including muscles) crossing joint than degrees of freedom
- Mathematical description of joint mechanics is underdetermined
- Muscle force must be estimated by numerical optimization

Crowninshield & Brand, *J. Biomech.* 1981

Hill-type muscle models are not perfect

These models have errors >10% when predicting force from whole muscle.

Force predictions have r^2 between 0.8 *in situ* and 0.4 *in vivo*.



Sandercock and Heckman, 1997;
Perreault et al., 2003
Wakeling et al., 2012; Lee et al., 2013
Kim et al., 2015; Dick et al. 2017

Assumptions in Hill-type models

- Muscle force depends on instantaneous activation, length and velocity
- Muscles contain a single contractile element whose properties are scaled in size
- Muscles are linear, mass-less actuators with constant thickness

Muscle force depends on contraction history

- Does muscle force depend on instantaneous activation, length and velocity ?

Force enhancement: muscle force is elevated if it is actively stretched.

Abbott and Aubert, 1952; Cavagna and Citterio, 1974
Herzog and Leonard, 2002

Force depression: muscle force is depressed if it actively shortens

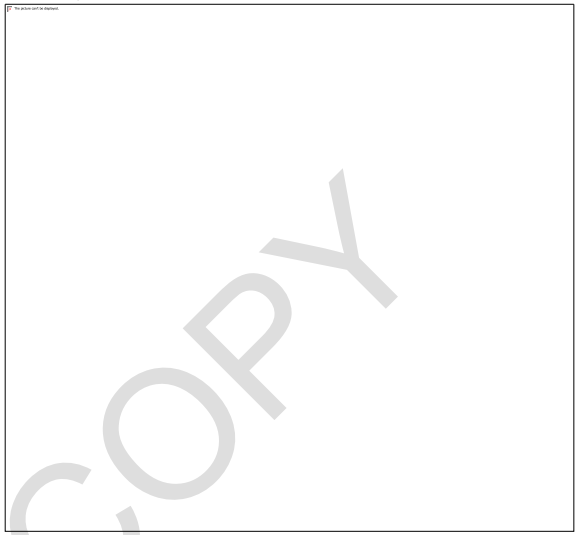
Abbott and Aubert, 1952; Marechal and Plaghki, 1979
Meijeretal., 1998; Herzog et al., 2000; McGowan et al. 2010

Muscle force depends on contraction history

'Sticky-spring' mechanism

Rode et al. 2009

'Three-filament' model



Herzog et al. 2012

'Winding filament' hypothesis

Nishikawa et al. 2011

Muscle force depends on fibre recruitment

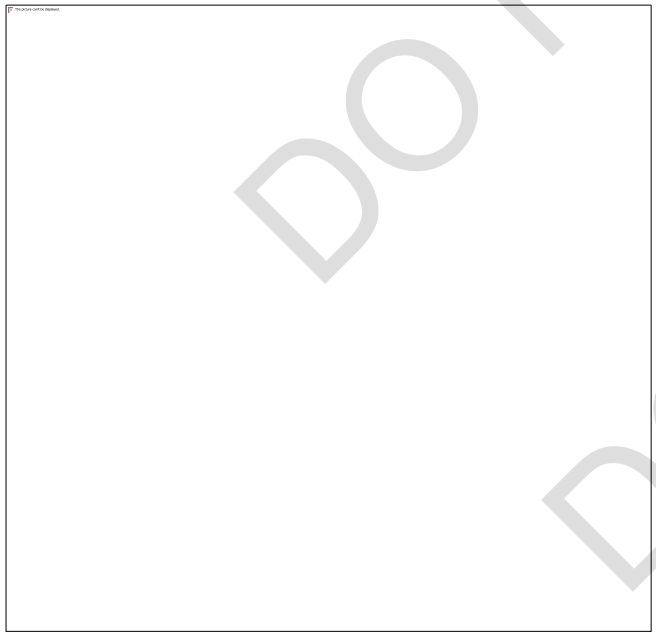
- Do muscles contain a single fibre whose properties are scaled in size ?

Heterogeneity of fibre-types within muscle:

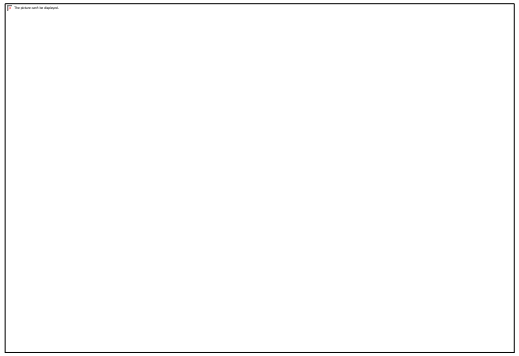
- Muscle contains many different fibres, that have a range of mechanical and metabolic fibre-type properties
- Recruitment patterns of different types of fibre affects force predictions

Wakeling et al. 2012; Lee et al. 2013; Dick et al. 2017

Motor unit activation, derived from EMG decomposition



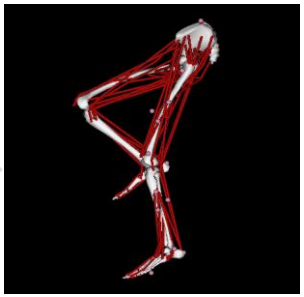
Two (contractile-) element model



Muscle force depends on fibre recruitment

Cadence [r.p.m.]	Torque [N m]	
60	44	
60	13	
100	13	
140	13	

- Do muscles contain a single fibre whose properties are scaled in size ?



Orderly recruitment of slow MUs and preferential recruitment of fast MUs emerge from predictive simulations with two-element muscle models.

These match decompositions of experimental of EMG.

Lai et al. 2017, 2018

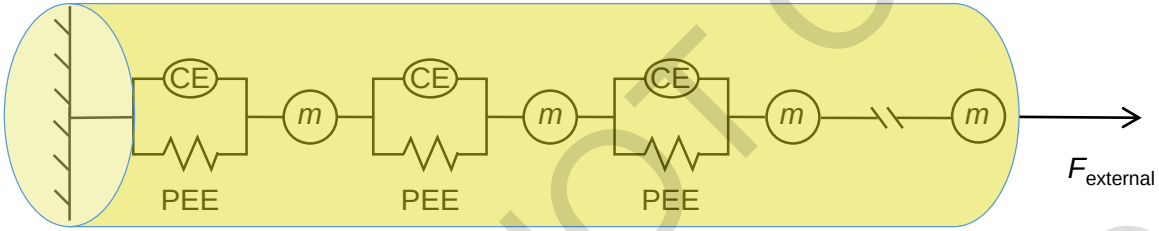
Size matters too

- Are muscles mass-less actuators ?

Muscle mass affects dynamics of contraction at larger sizes:

- Whole muscles contract differently from constituent fibres

Günther et al. 2012; Ross and Wakeling 2016; Ross et al. 2017, 2018



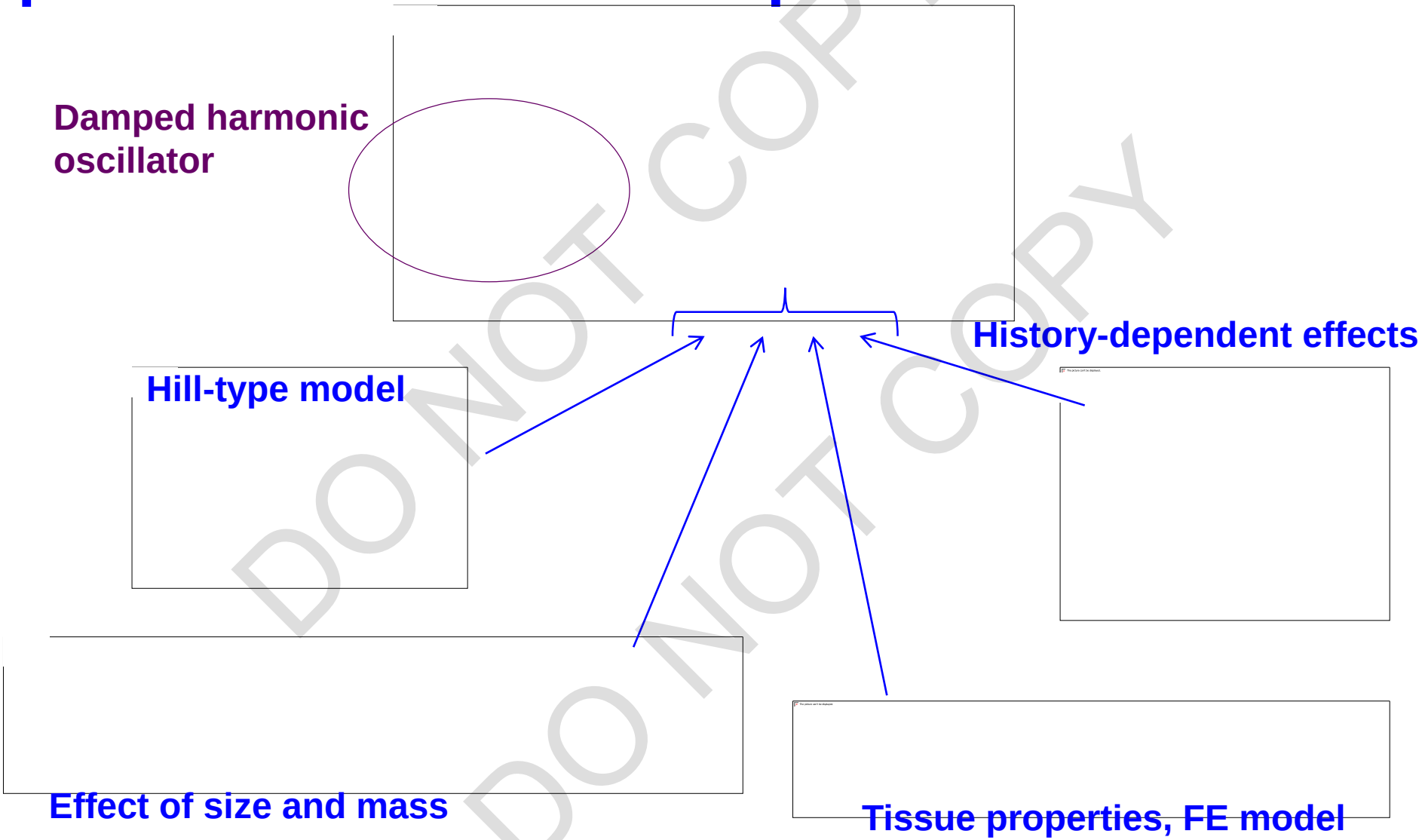
Geometric scaling: increase mass

	increase
Length	2
Force	4
Inertial mass	8

Decrease in activation

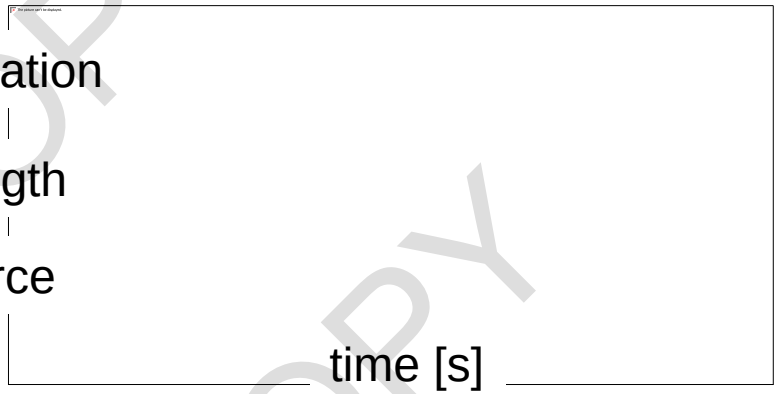
Submaximal contraction yields decreased force for same inertial mass

Relative effects of muscle properties on predictions of force and power



Ross et al. 2018

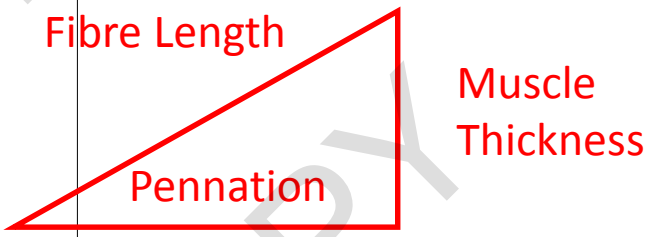
Relative effects of muscle properties on predictions of force and power



Ross et al. 2018

Muscles as linear actuators

- Are muscles linear actuators with constant thickness ?



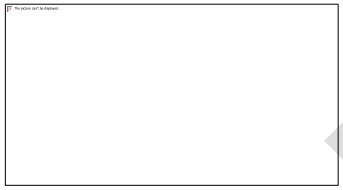
Zajac, 1989; Rajagopal et al. 2016

Constant thickness assumption:

- Simplifies prediction of pennation angle given a fibre length

- Implicitly constrains the gearing to be constant and independent of load
  - ➢ Not supported by: experimental observations of variable gearing

Azizi et al. 2008; Wakeling et al. 2011

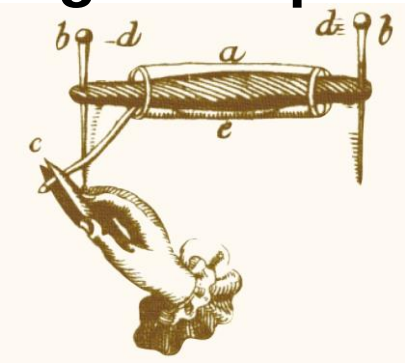


ultrasound images of contracting muscle

Maganaris et al. 1998; Randhawa et al. 2012

Muscles bulge during contraction

Muscle girth expands



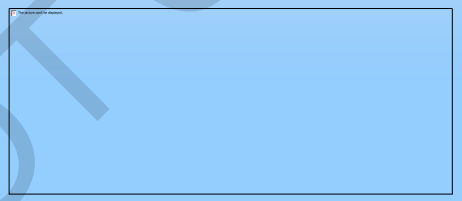
Swammerdam, 1758; Baskin & Paolini, 1967

Maganaris et al. 1998; Randhawa & Wakeling, 2012, 2018

Bolsterlee et al., 2017

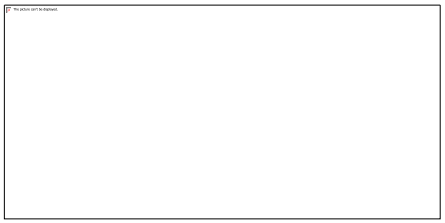
Myofilament lattice expands

Huxley, 1969; Williams et al. 2013; Daniel et al. 2013



Muscle fibre bundles expand

Smith et al. 2011



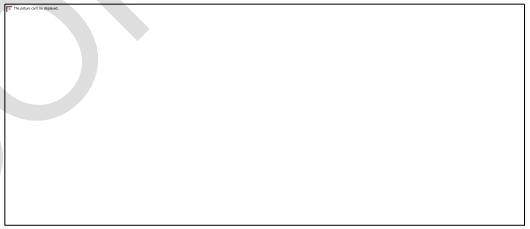
1D constant thickness models may be OK

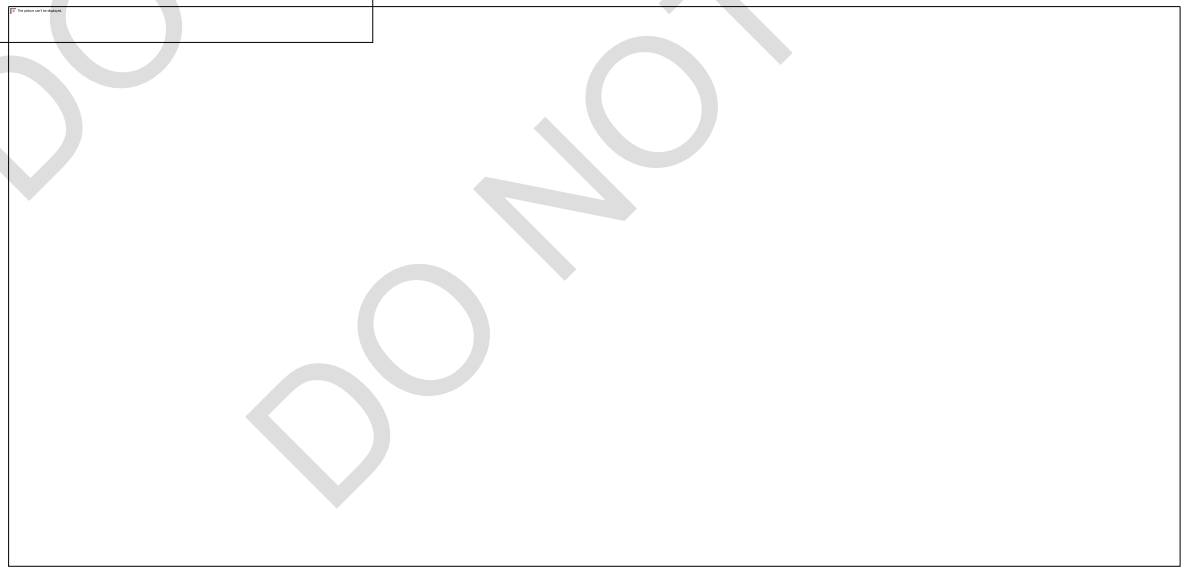
1D

2D

3D

- Provided they are only used to predict pennation from fibre length





Dick et al. 2018

Conclusions

- Muscle force cannot be experimentally measured in humans, but is necessary to understand function and dysfunction

- Models must be used to predict forces, and thus function

- Hill-type models are common,
  - in part due to computational simplicity
  - but, still lack desirable accuracy

- Current progress is being made in understanding the effects of:
  - titins and history-dependent properties
  - recruitment of different types of motor unit
  - size effects for understanding whole muscle function
  - 3D effects and tissue properties and their effect on muscle quality

- These combined factors will be needed for future models to improve their ability to predict muscle forces

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