Human motor control

Gregor Schöner

Movement generation in animals

- movement generation adapted to and directed at a sensed environment is the core of animal experience… and a key evolutionary factor
- => animal are amazing autonomous movement machines..
- => the brain is strongly organized around movement generation… (the basis of a tradition of thought called “embodied cognition”)

Human movement

- humans are particularly skilled at movement directed at objects
    - manipulation, compliant acting on objects
- humans are particularly flexible, versatile in their movement generation
    - while some other animals excel at particular specialized motor acts

A landscape of human movement

- looking: eye and head movements (gaze)
- orienting the body in space, upright stance
- legged locomotion
- navigation
- steering
- reach, grasp, manipulate
- sequences of motor acts
- speech articulatory movement

Qualities of human movement

- involuntary (reflexive)
- automatic/habitual (requires little attention)
- voluntary/intentional

Qualities of human movement

- whole body movements in space
- movements of hand/arm or other extremities while anchored in space

Qualities of human movement

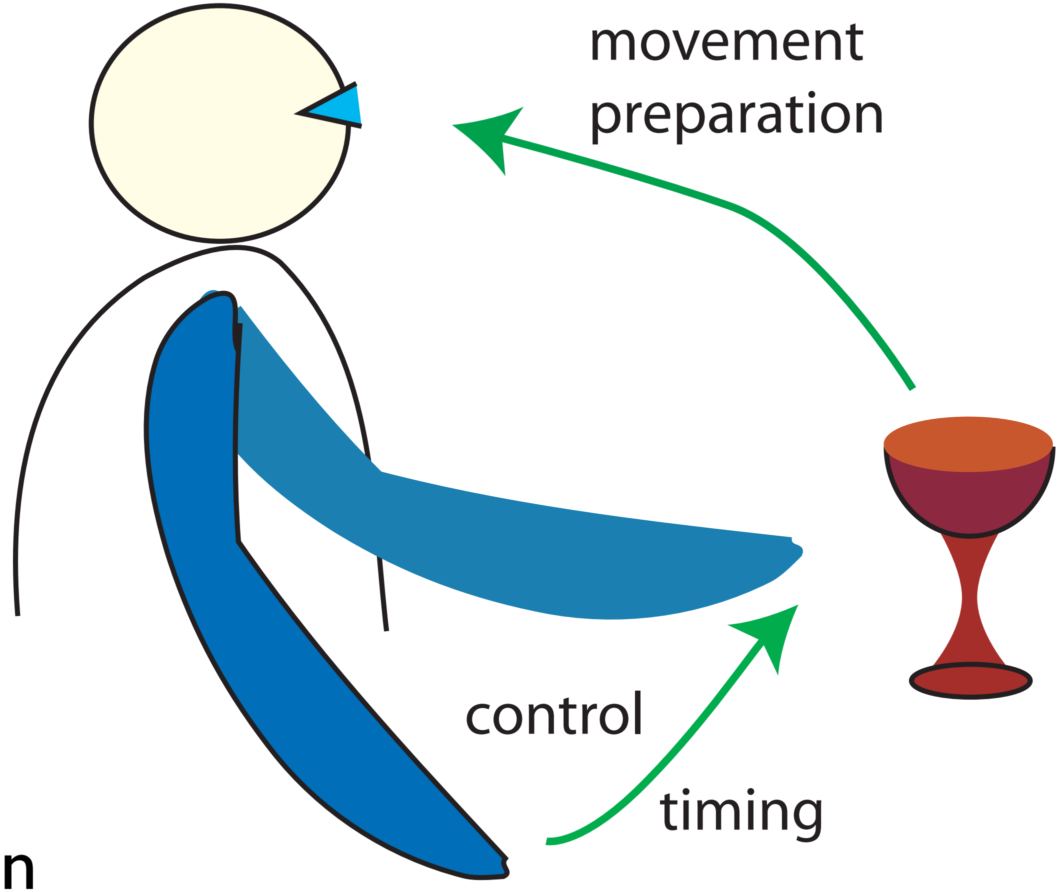
- rhythmic
- discrete (in time)

Textbooks

- David Rosenbaum: Human motor control, Academic Press, 2009 (2nd edition)
- Richard A Schmidt, Timothy D Lee: Motor Control and Learning, Human Kinematics, 2011 (5th edition)
- James Tresilian: Sensorimotor Control & Learning. Palgrave McMillan, 2012

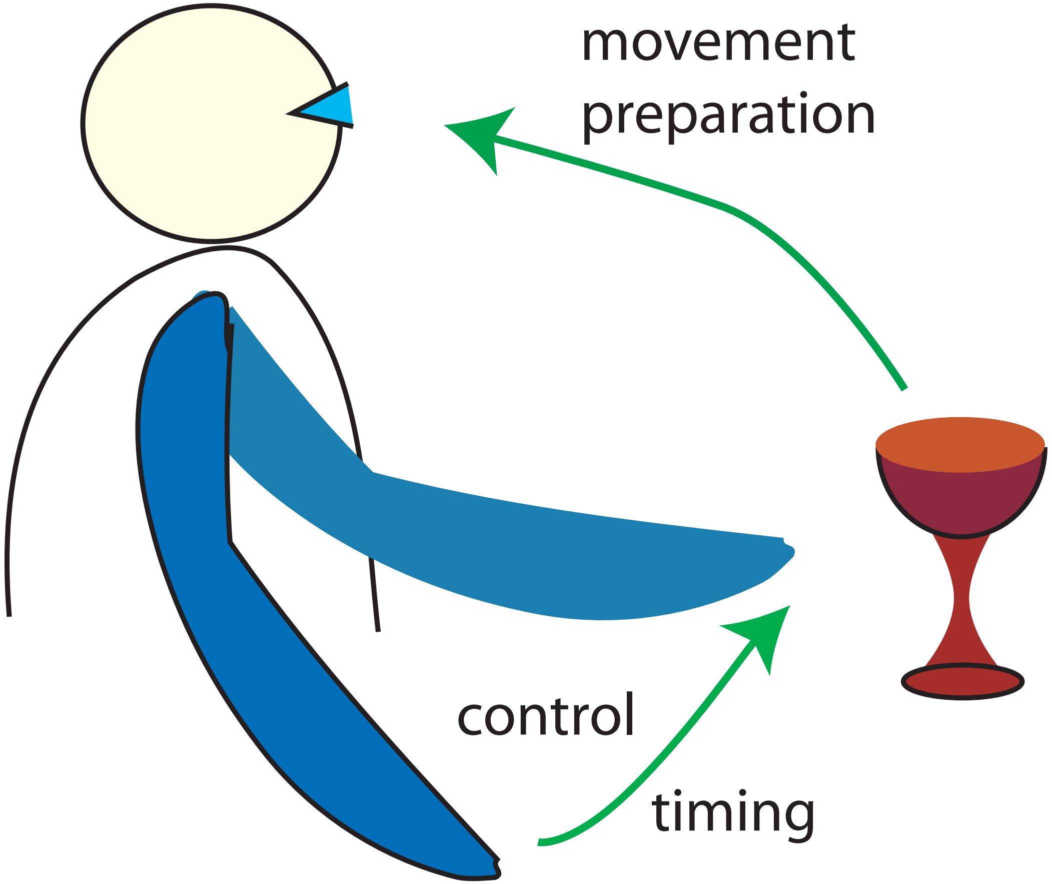
What is entailed in generating an object-oriented movement?

- scene and object perception
- movement preparation
- movement initiation and termination
- movement timing and coordination
- motor control
- degree of freedom problem
- => spans perception, cognition and control

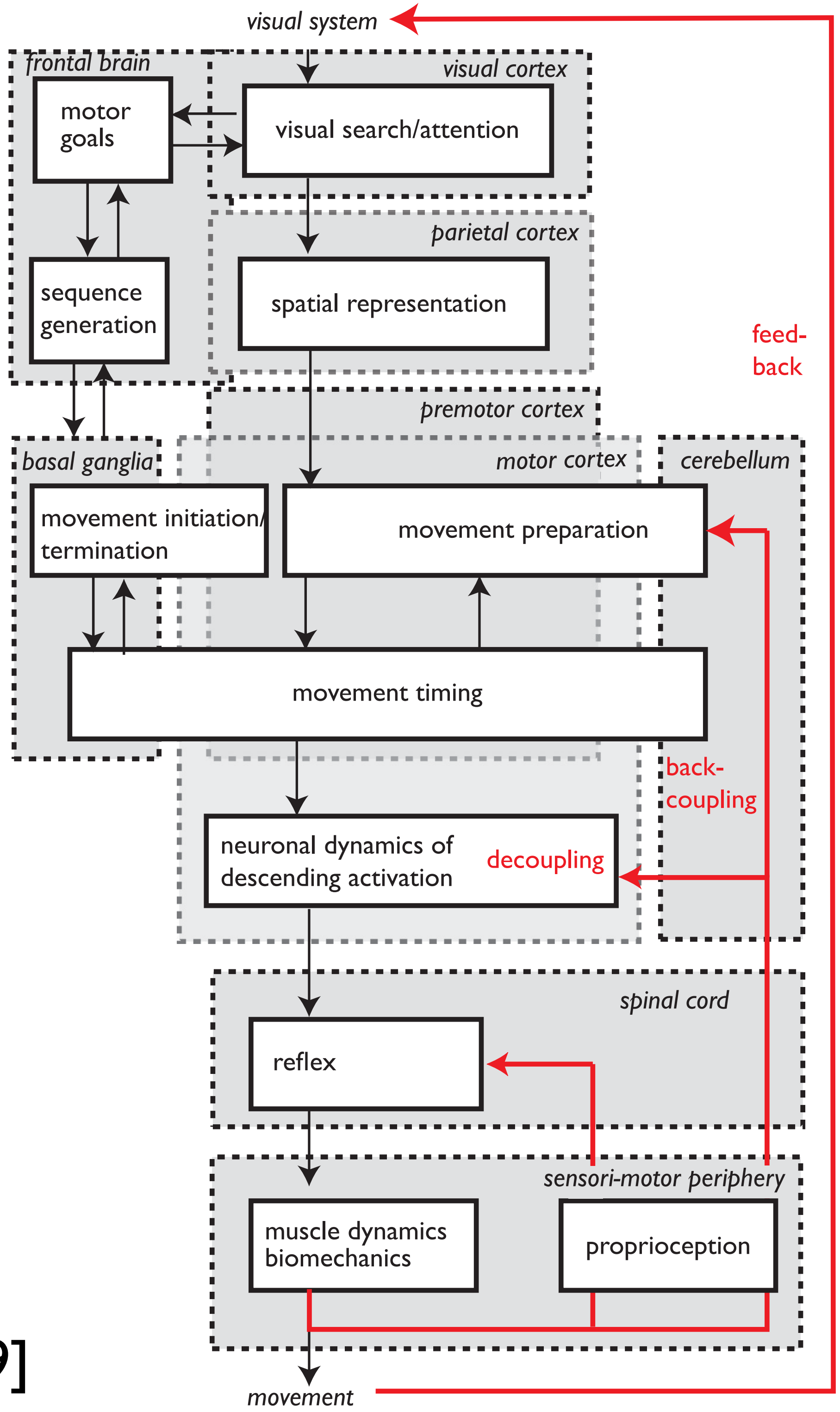


What is entailed in generating an object-oriented movement?

- tightly interconnected processes
- which this is why movement is so hard to study
- critical to understand integration

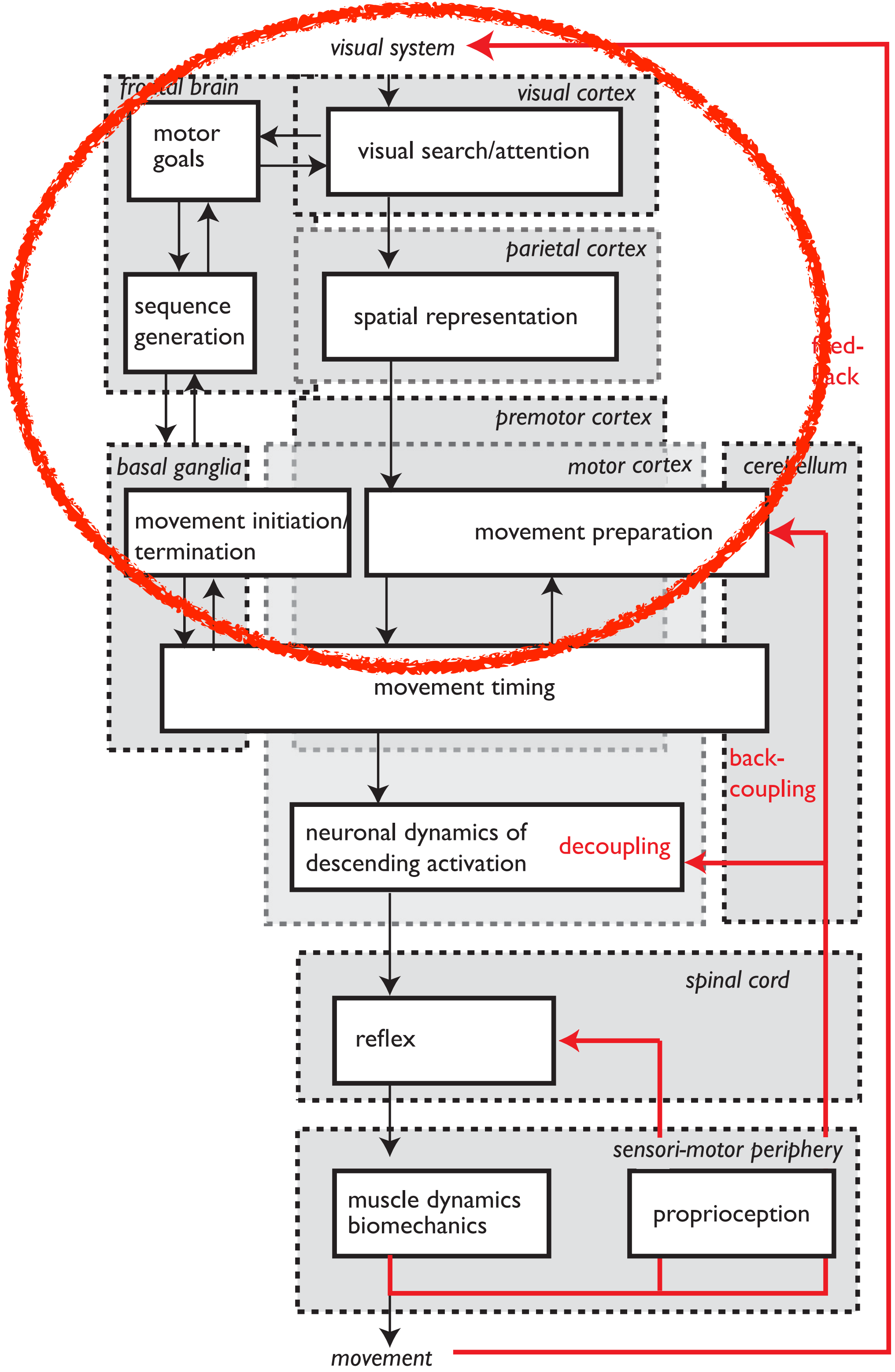


A neural architecture of reaching



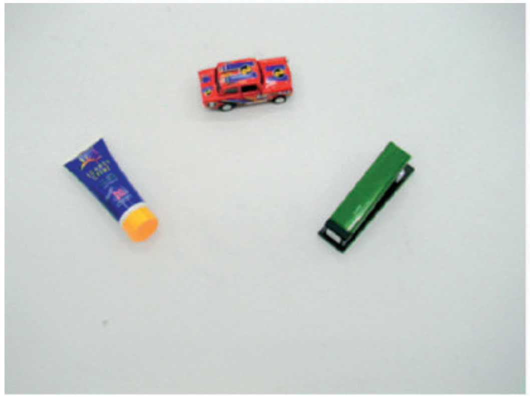
[adapted from: Martin, Scholz, Schöner. *Neural Computation* 21, 1371–1414 (2009)]

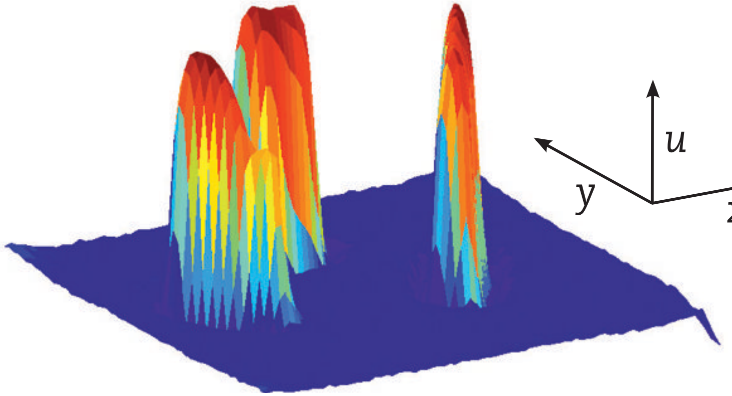
- the perception and cognition on which object-oriented action is based…. topic of my course in the WS



Scene perception

- neural fields… dynamic field theory

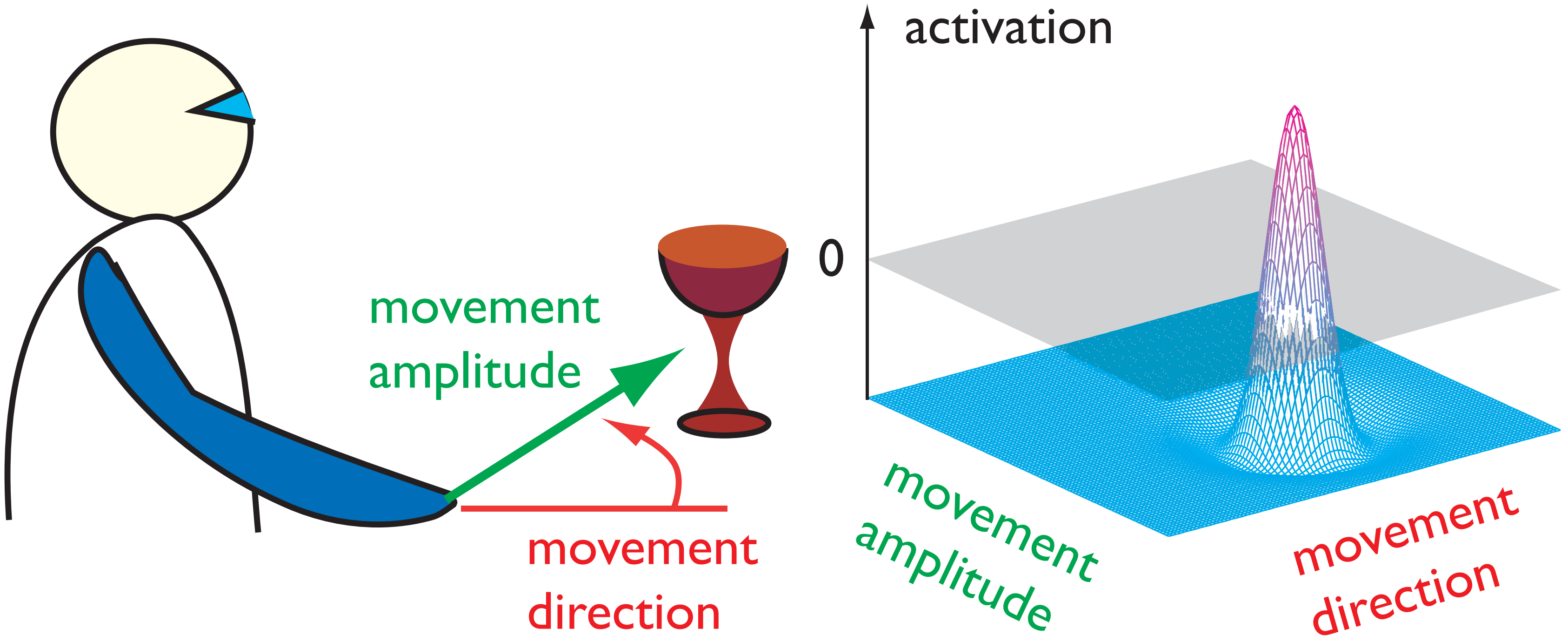




[Zibner, Faubel: In DFT Primer (2016)]

Movement preparation

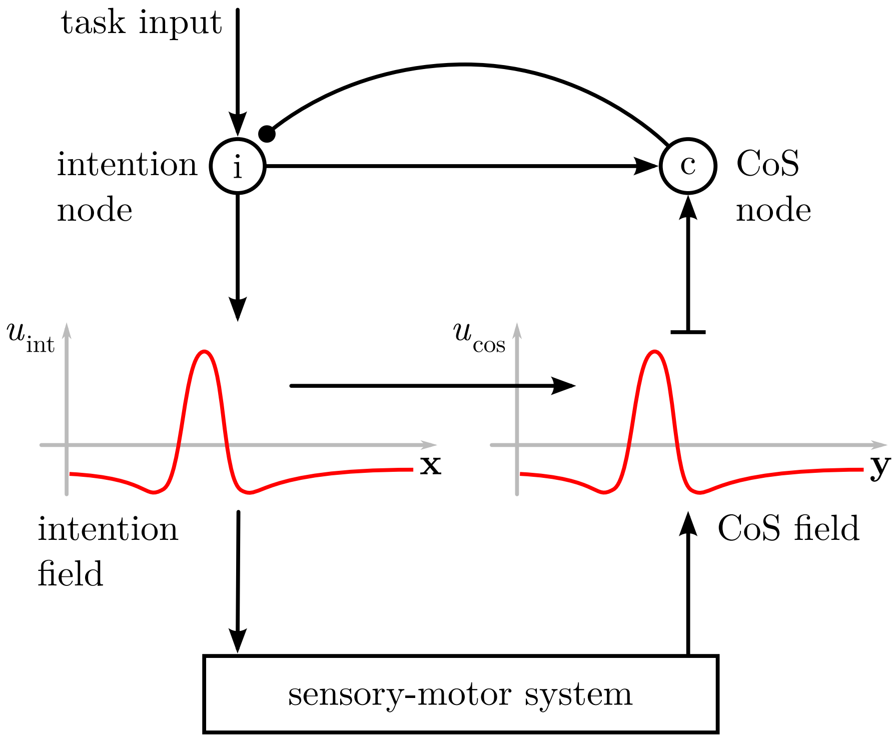
- coordinate transform into initial position of hand



[Erlhagen Schöner, Psych Rev 2002]

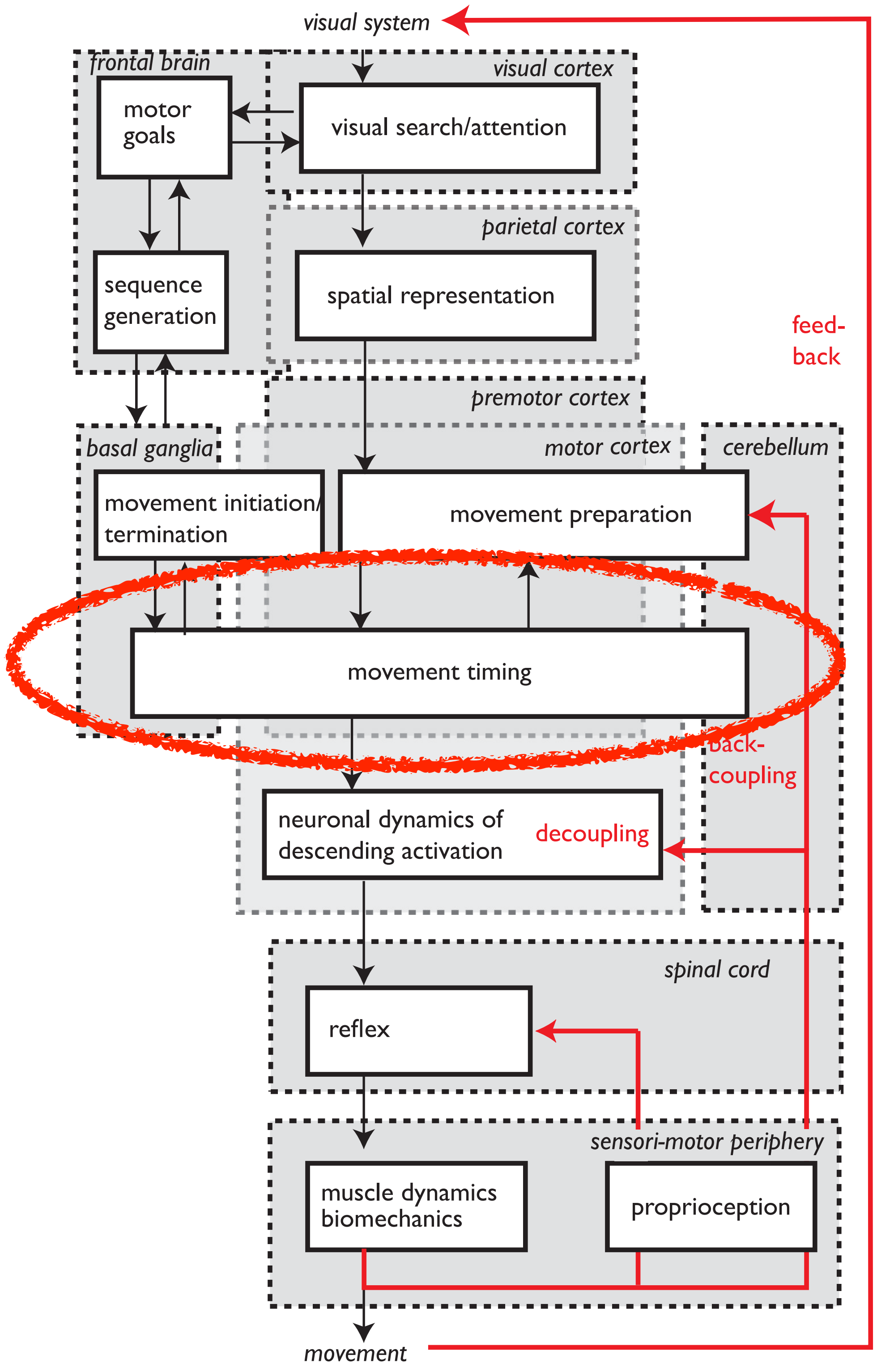
Sequence generation

- every action is represented as a stable activation sate in an "intentional field"
- that predicts its "condition of satisfaction"
- instabilities drive the transition from one intention to another

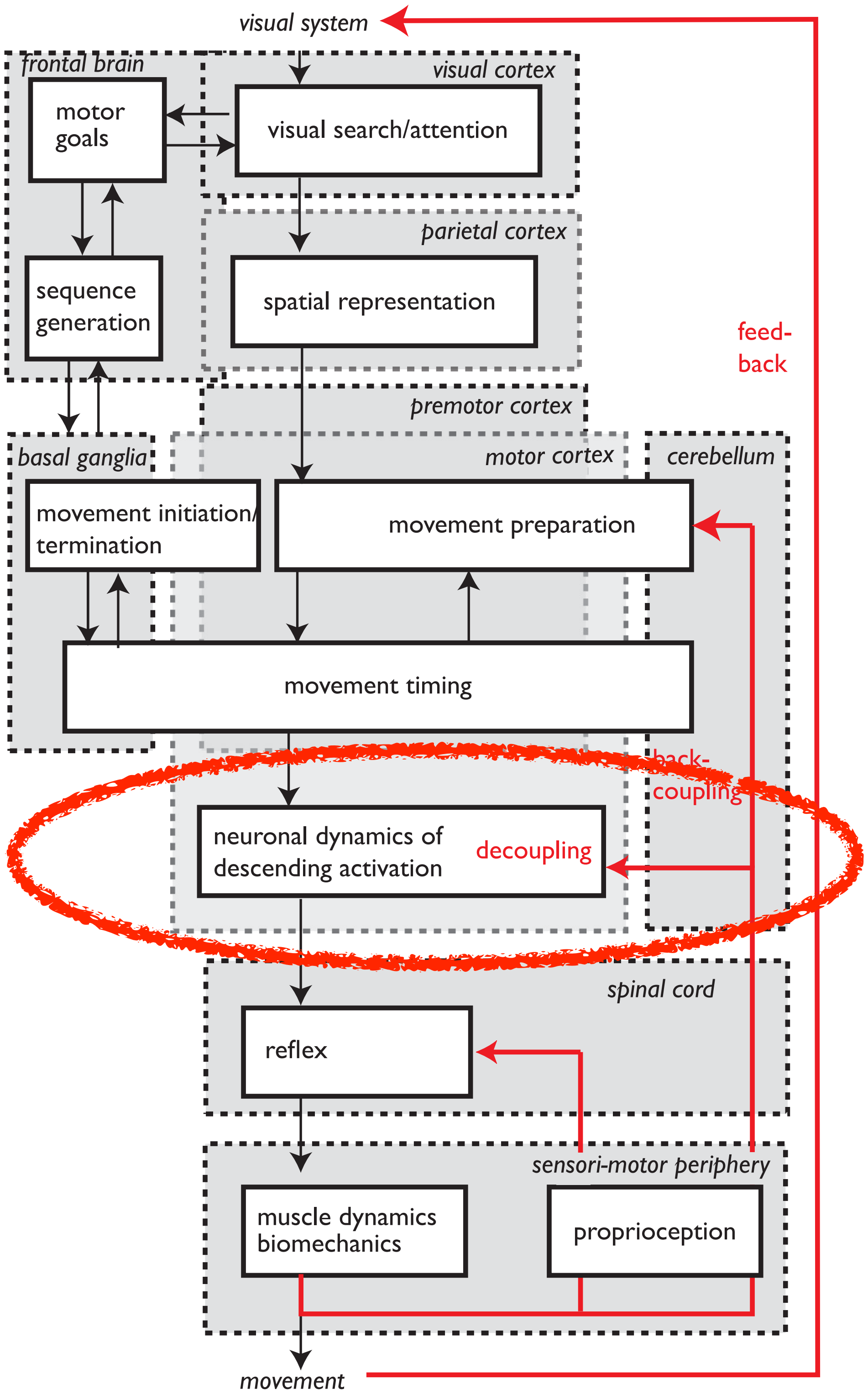


[Sandamirskaya, Zibner, Schneegans, Schöner: New Ideas in Psychology (2013)]

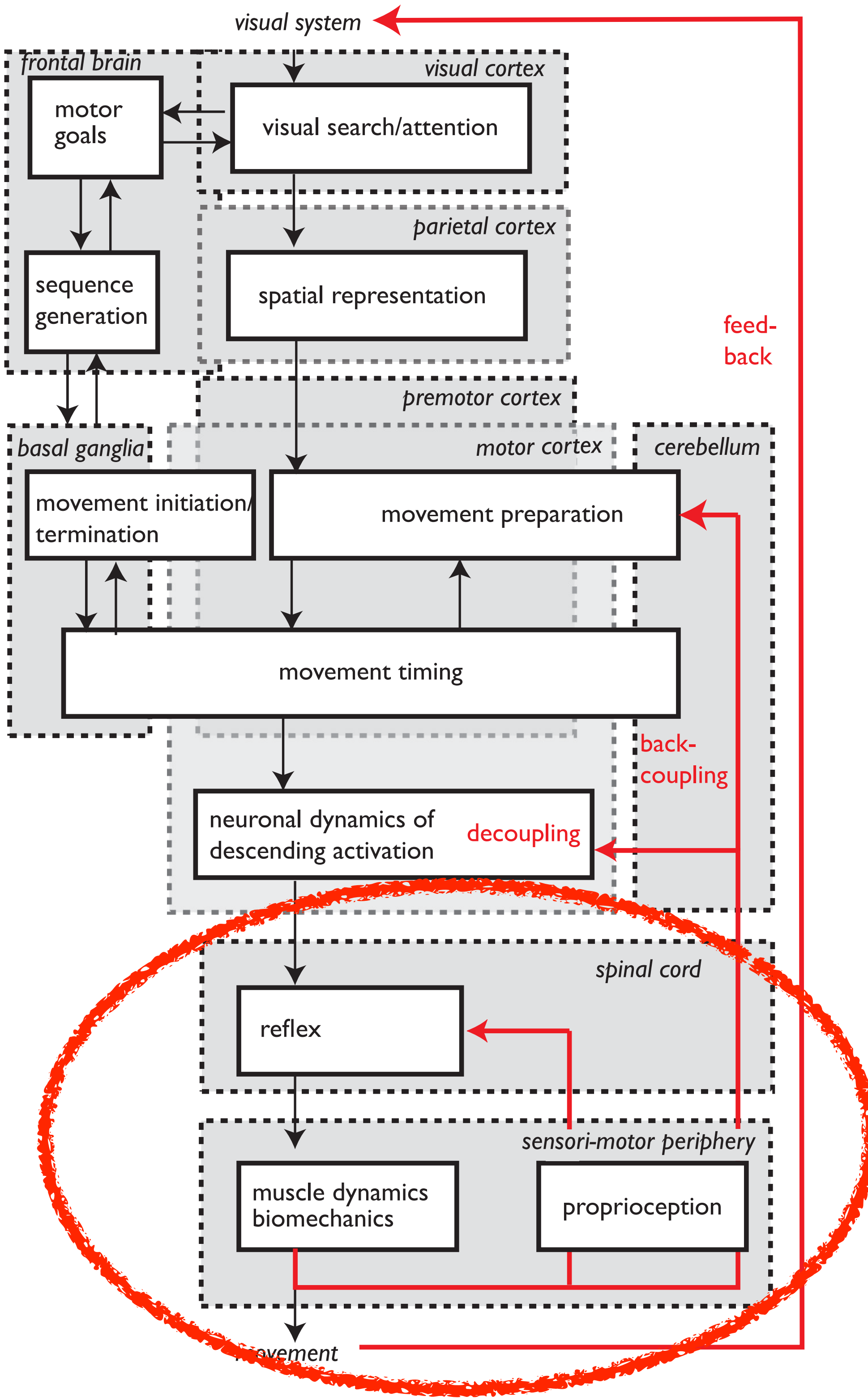
- timing and coordination: Lecture 7/Exercise 6



- degree of freedom problem: Lecture 6/ Exercise 5



- human motor control: how forces are generated and regulated



visual system

frontal brain

motor goals

sequence generation

visual cortex

visual search/attention

parietal cortex

spatial representation

feed-back

premotor cortex

basal ganglia

motor cortex

cerebellum

movement initiation/ termination

movement preparation

movement timing

back-coupling

neuronal dynamics of descending activation

decoupling

spinal cord

reflex

sensori-motor periphery

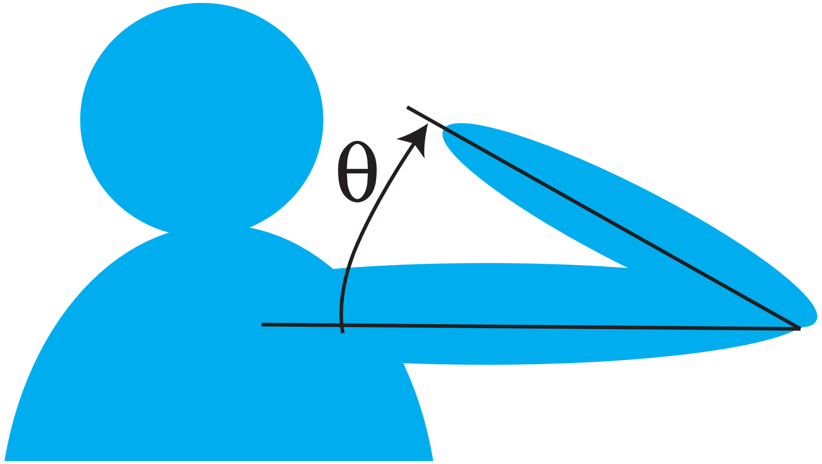
muscle dynamics biomechanics

proprioception

movement

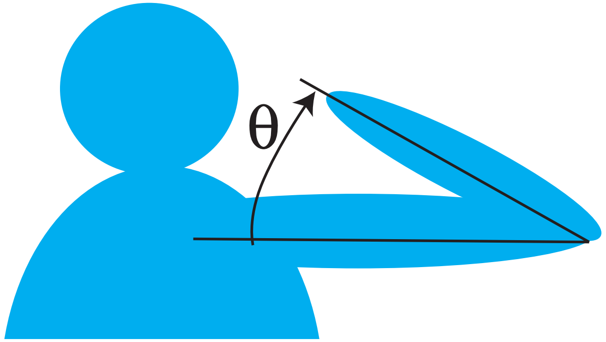
Human motor control

- consider a single DoF, the elbow angle..
- in a fixed posture



Posture is controlled

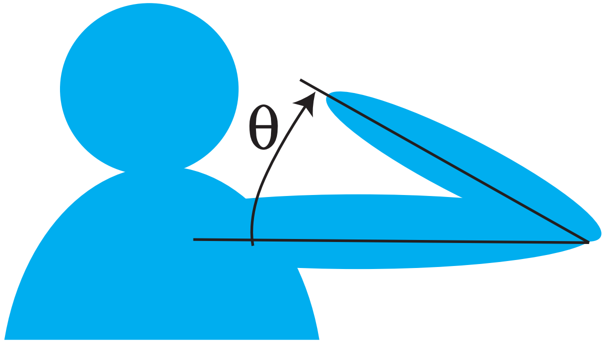
- the elbow does not behave like a passive mechanical system with a free joint at the elbow: $J\ddot{\theta} = 0$
  - where J is inertial moment of forearm (if upper arm is held fixed)
- Instead, the elbow resists, when pushed => there is active control= stabilization of the joint



=>experiment

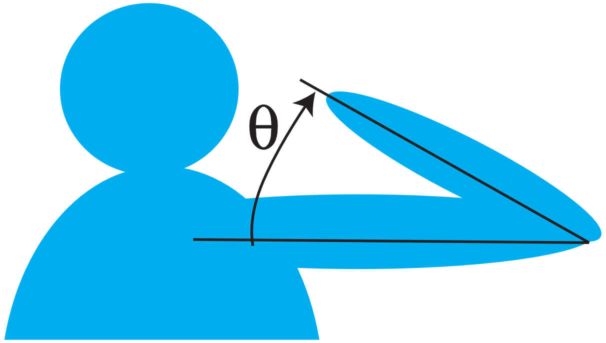
Posture is controlled

- human effectors are not very stiff…. unlike robotic actuators
- stiffness expressed in Eigenfrequency => time scale ~ of the same order of magnitude as movement time
- => human movement is highly compliant…



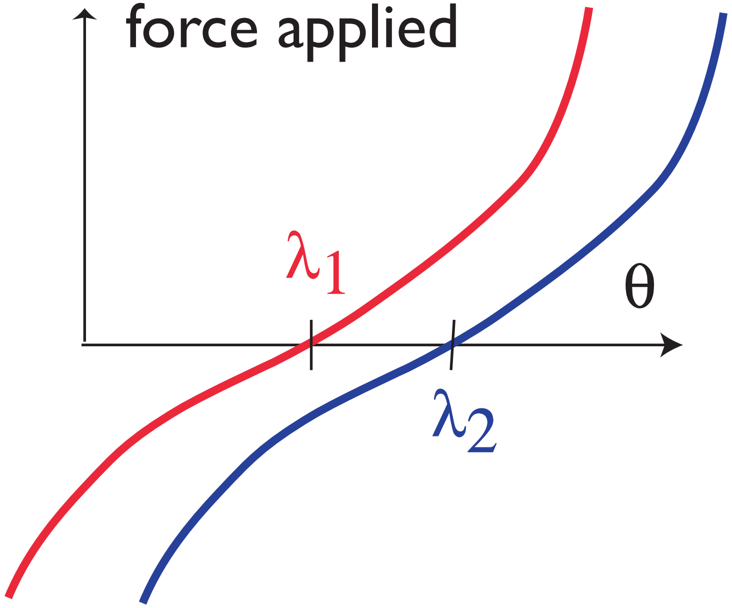
The problem of human motor control

- => leads to major problems in human motor control: how to make a soft spring move fast to precisely reach a target and softly stop there…



The “mass spring” model

- a simplified macroscopic description
  - of the mechanics of the muscles
  - and the reflex control of the muscles
- the invariant characteristic



The mass-spring model

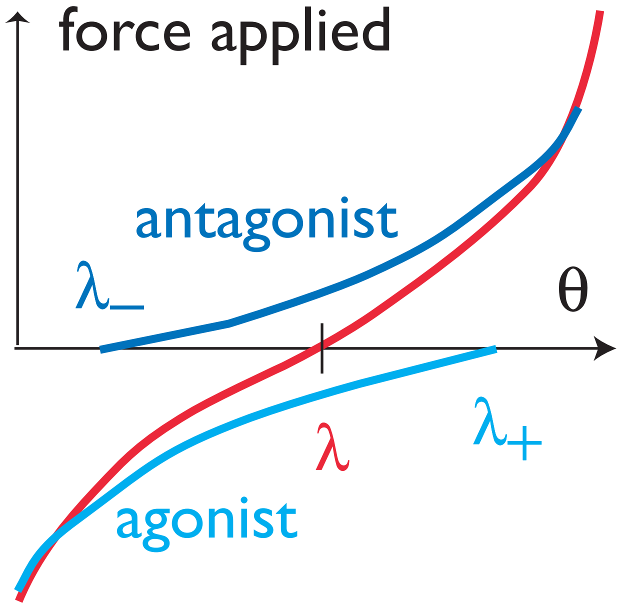
- elastic component: proportional to position
- viscous component: resistance depends on joint velocity

$$J\ddot{\theta} = \boxed{-k(\theta-\lambda)-\mu\dot{\theta}}$$

active torques generated by the muscle

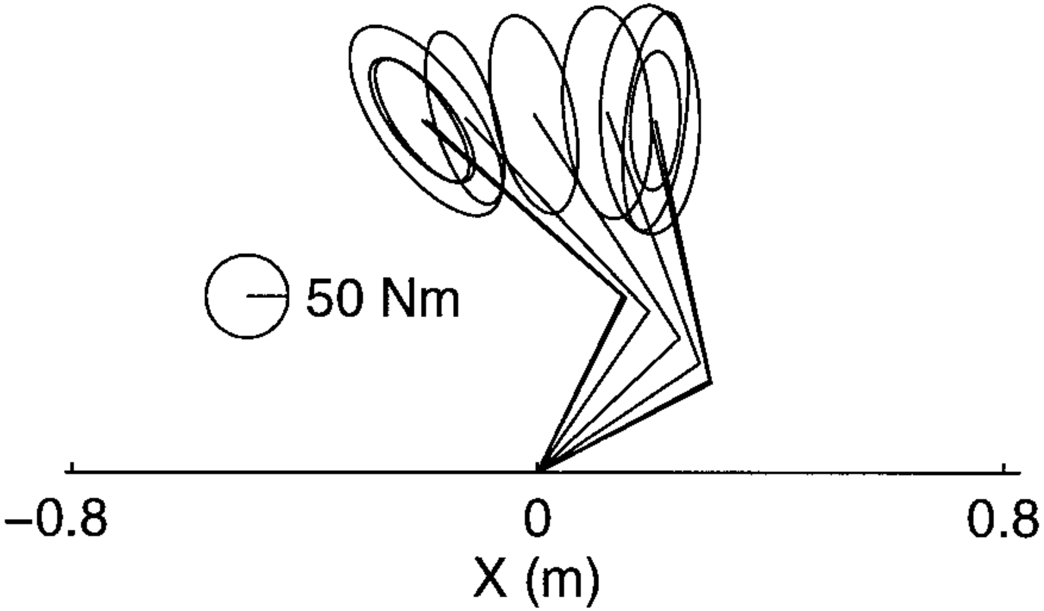
Agonist-antagonist action

- muscles only pull, so the invariant characteristic comes from pairs of muscle groups
- one lambda per muscle
- co-contraction varies stiffness



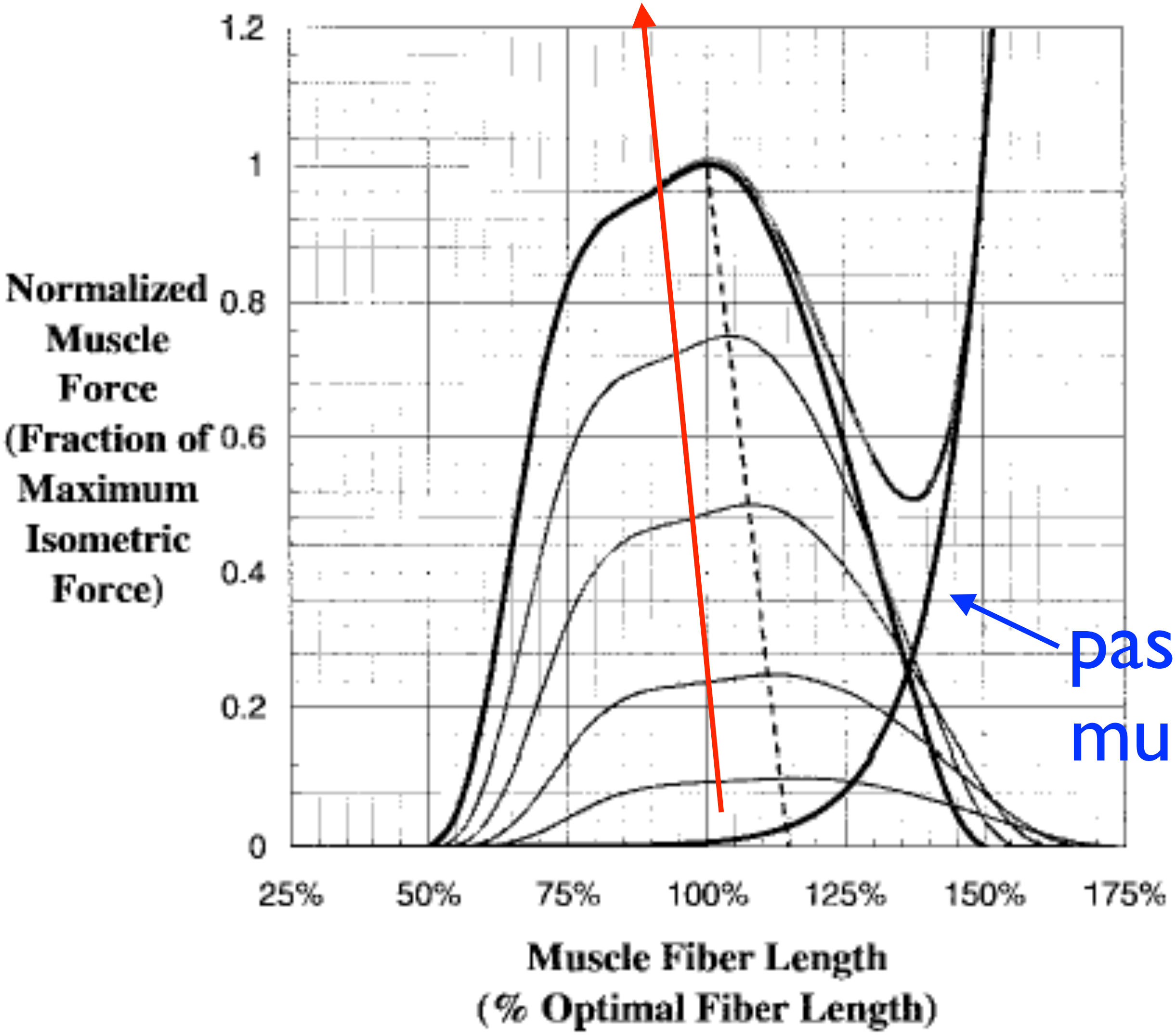
Stiffness

- the stiffness, k, can be measured from perturbations
- the viscosity "mu" is more difficult to determine



$$J\ddot{\theta} = -k(\theta - \lambda) - \mu\dot{\theta}$$

Muscle dynamics



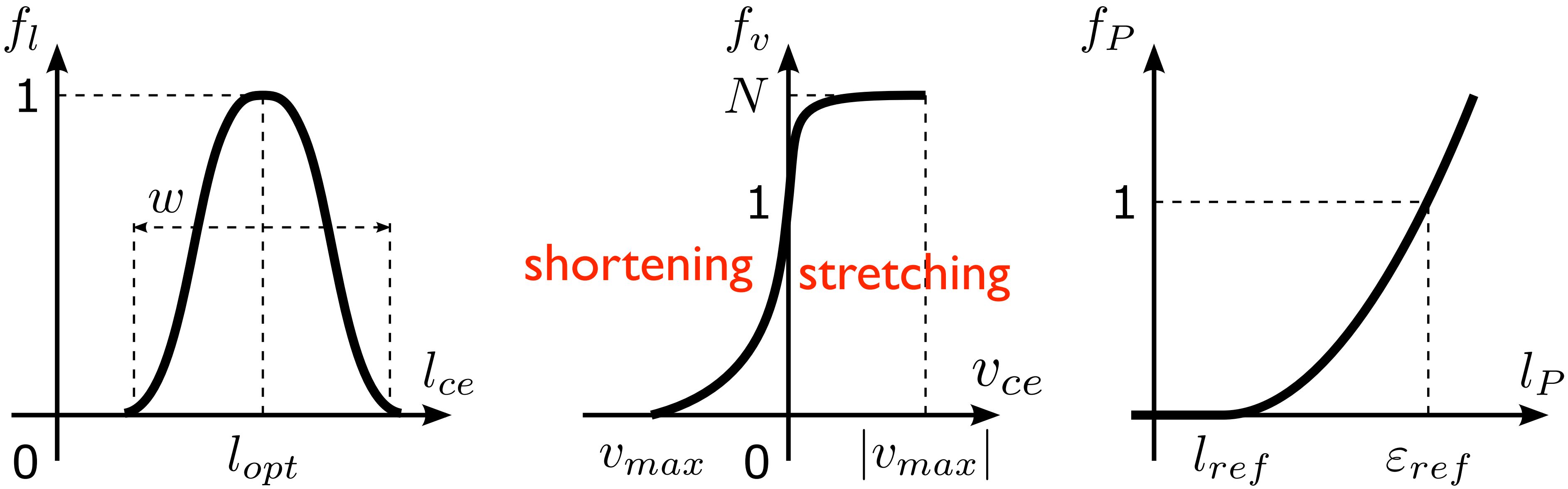
increasing level of muscle activation

passive muscle

[Buchanan et al. 2014]

Muscle dynamics

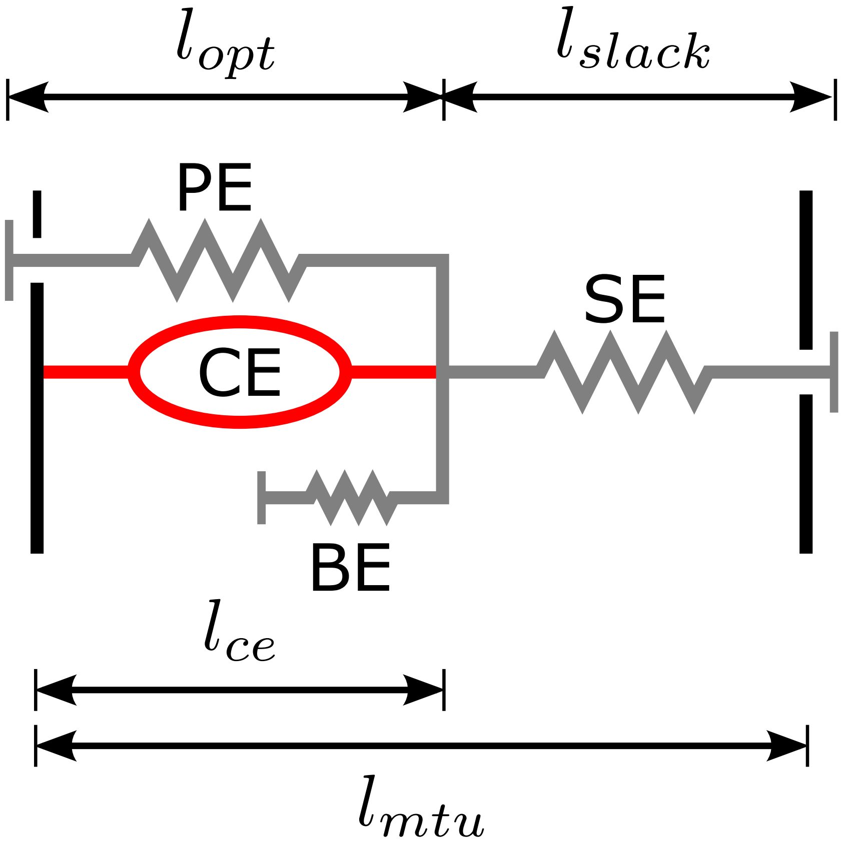
- force generated depends on speed of lengthening / shortening
    - less force for shortening
    - more for stretching



[Song 2017]

Muscle dynamics

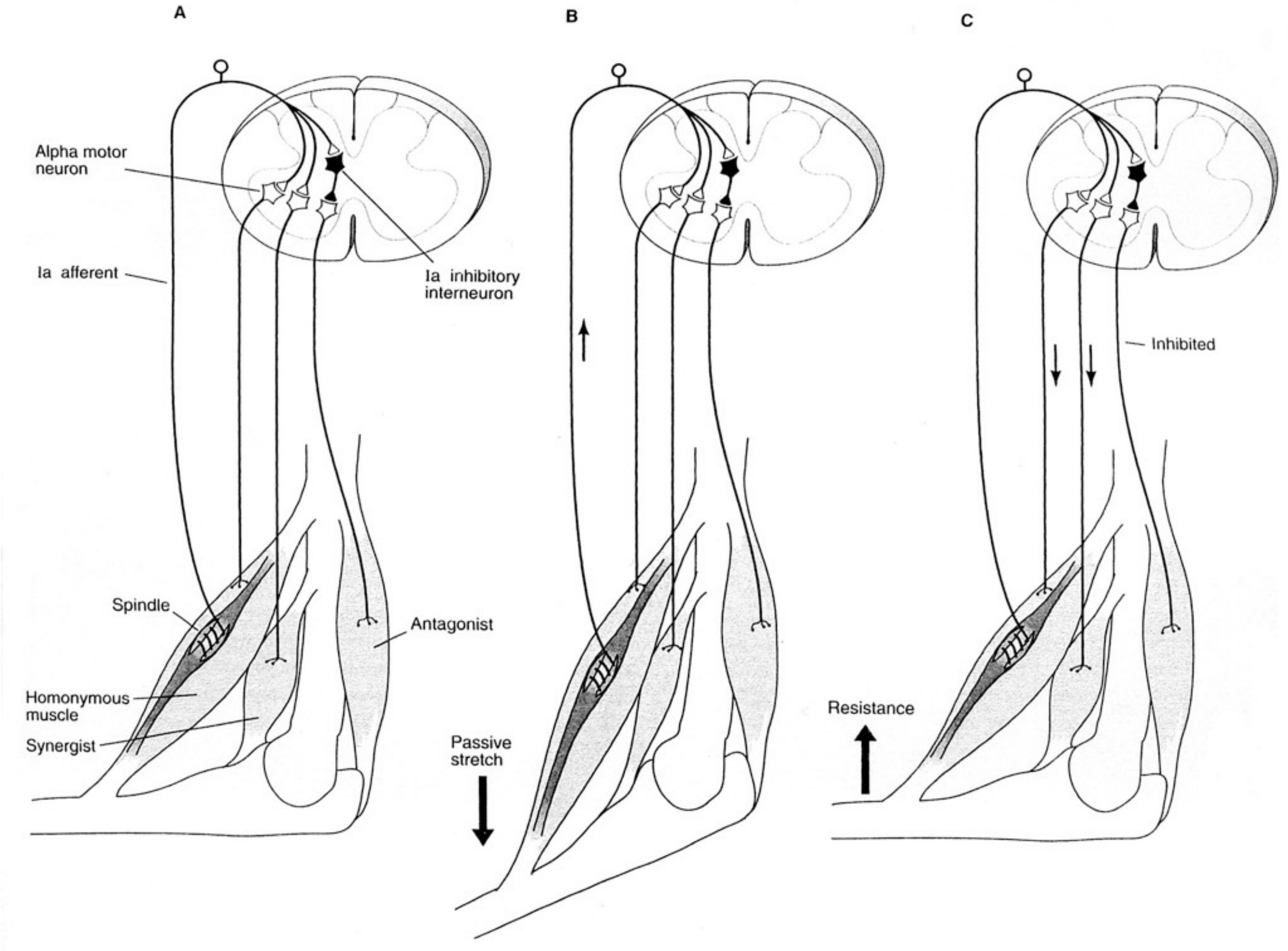
- Hill type models



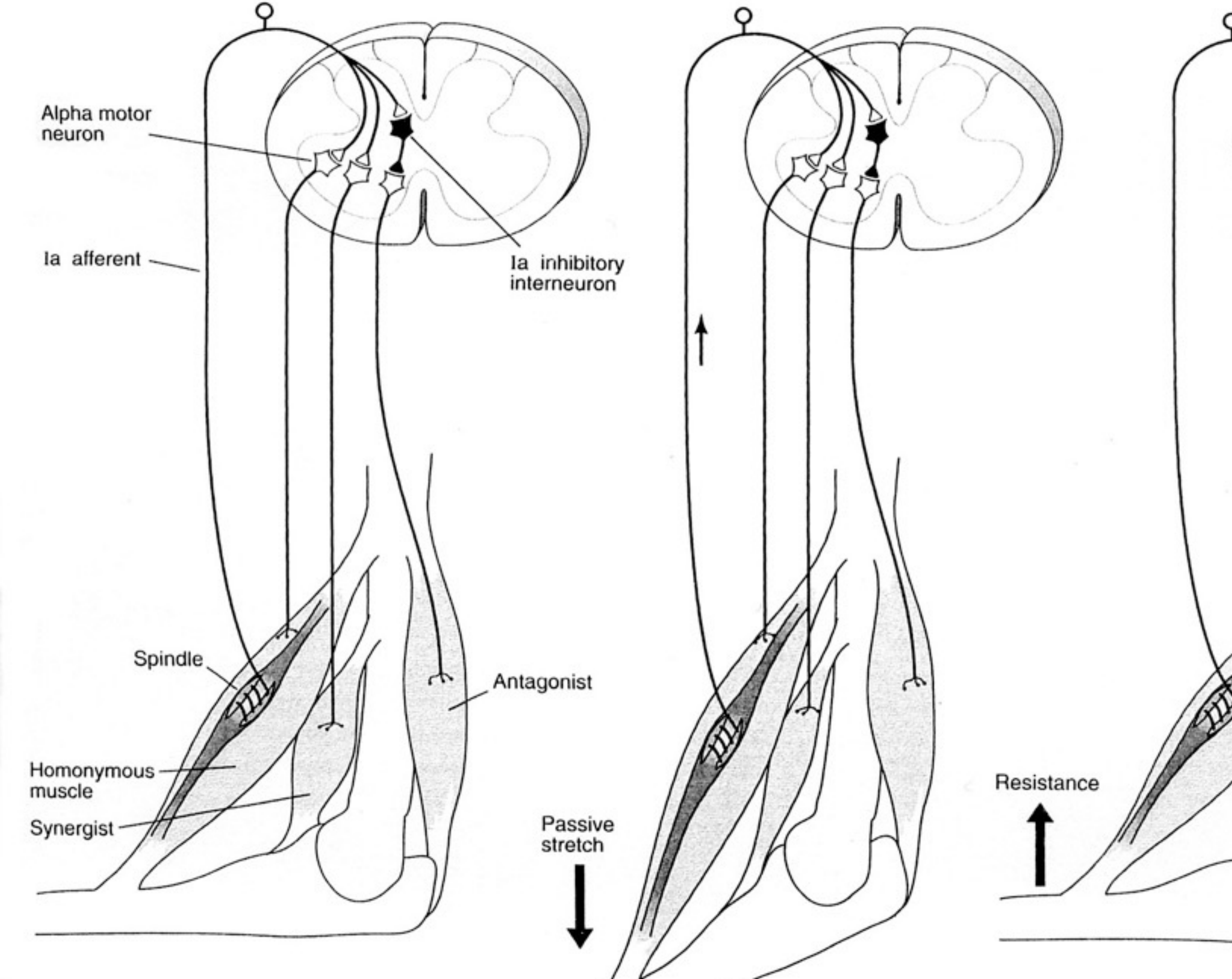
[Song 2017]

Neural basis of invariant characteristic: stretch reflex

- alpha-gamma reflex loop generates the stretch reflex

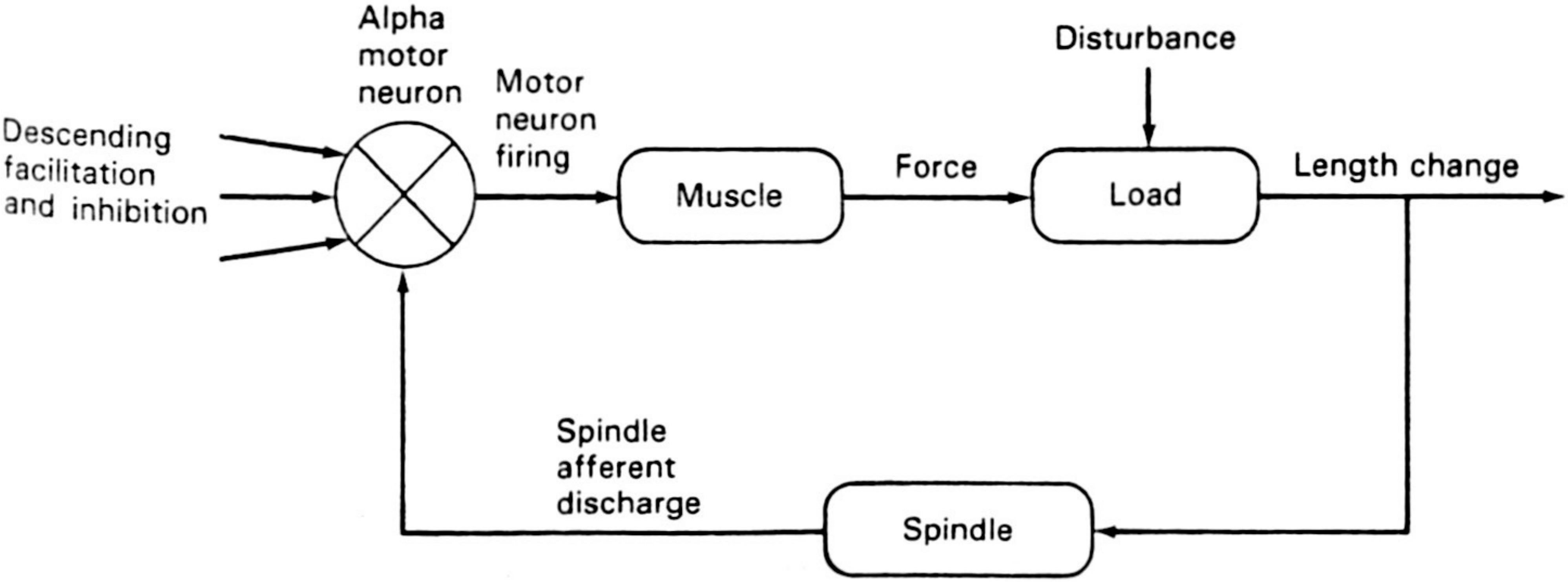


[Kandel, Schartz, Jessell, Fig. 37-11]


Alpha motor neuron
Ia afferent
Ia inhibitory interneuron
Spindle
Antagonist
Homonymous muscle
Synergist
Passive stretch
Resistance

spinal cord: reflex loops

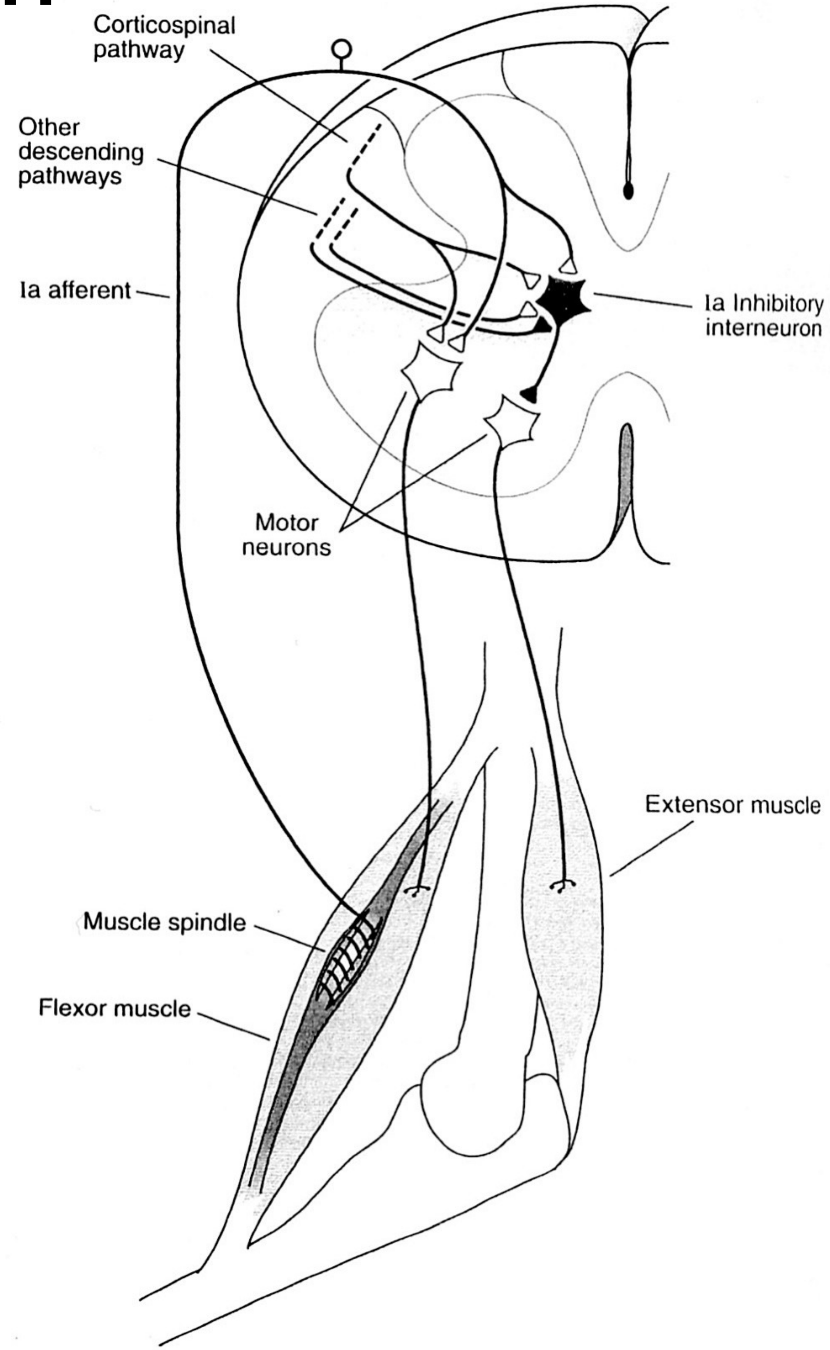
- the stretch reflex acts as a negative feedback loop



[Kandel, Schartz, Jessell, Fig. 31-12]

spinal cord: coordination

- Ia inhibitory interneuron mediates reciprocal innervation in stretch reflex, leading to automatic relaxation of antagonist on activation of agonist

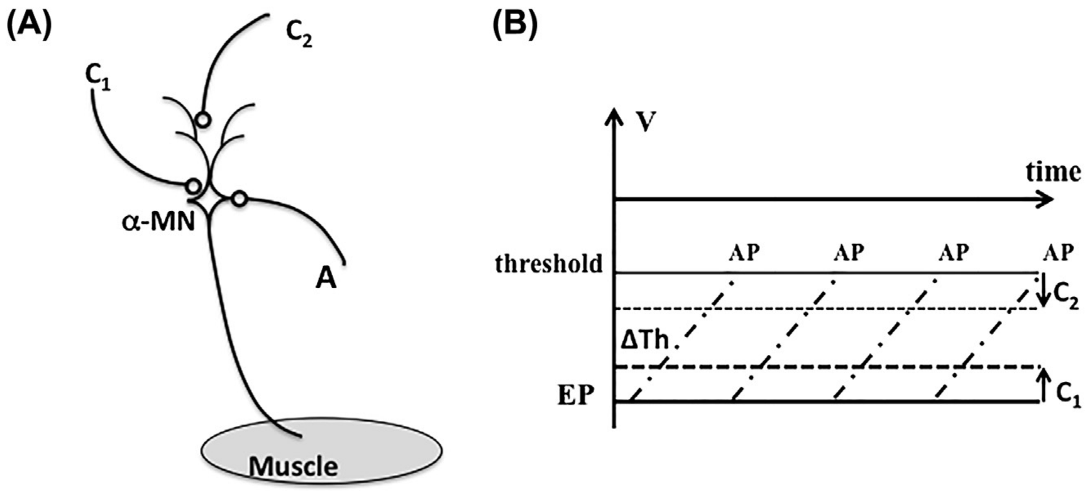


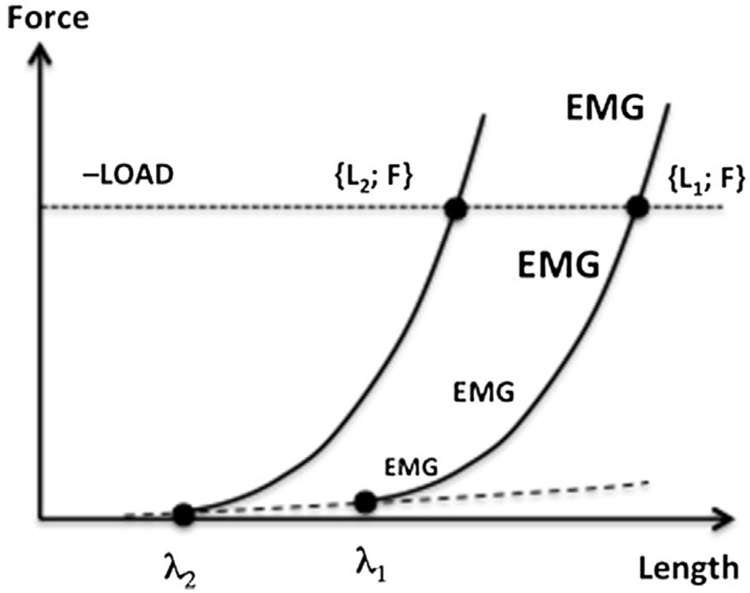
[Kandel, Schartz, Jessell, Fig. 38-2]

Reflex model

- monotonic relationship force-length
- reflex threshold can be varied by descending activation signals

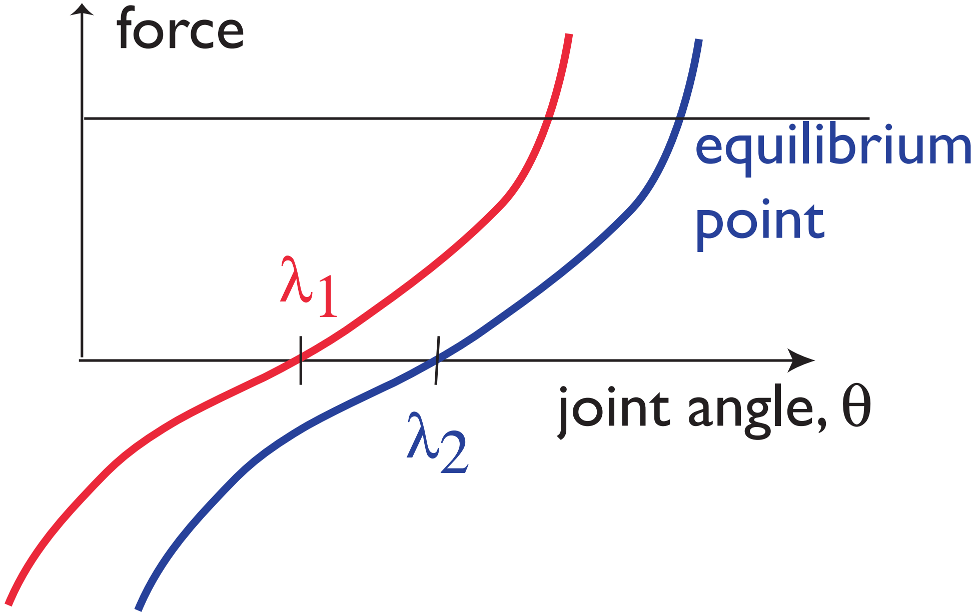
[Latash, Zatsiorsky, 2016]





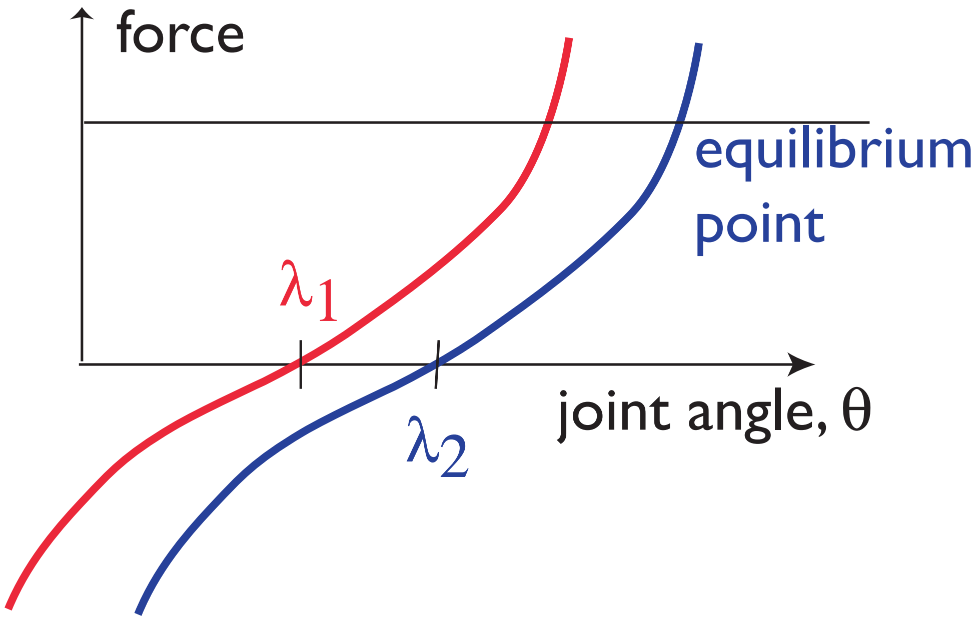
Movement entails change of posture

- the threshold lengths of the muscles must be shifted during movement so that after the movement, the postural state exists around a new combination of muscle lengths (<=> joint configuration)



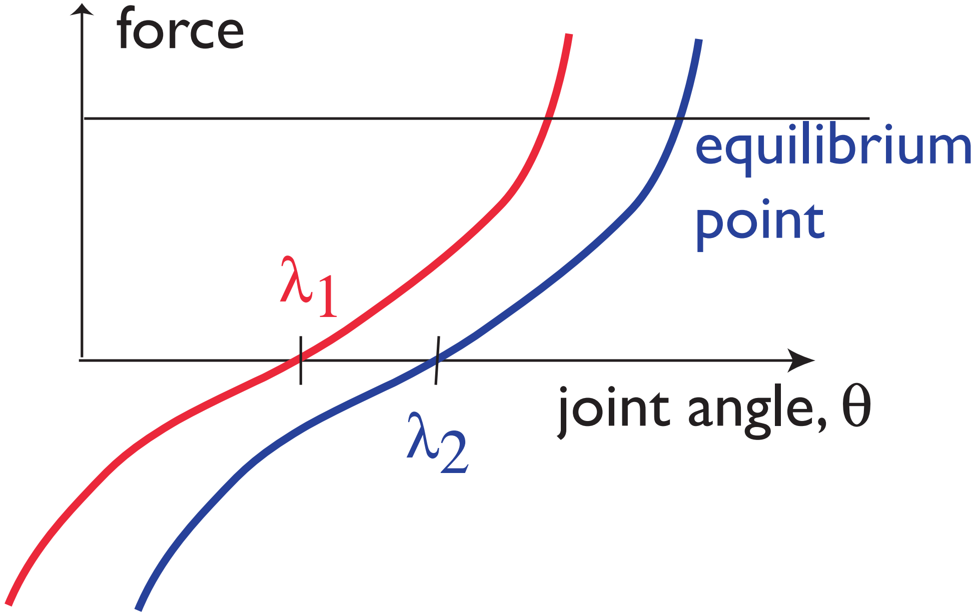
Movement entails change of posture

- many models account for movement in terms of muscle activation/desired torques….
- => the shift of the EP is the single most overlooked fact in control models of movement generation



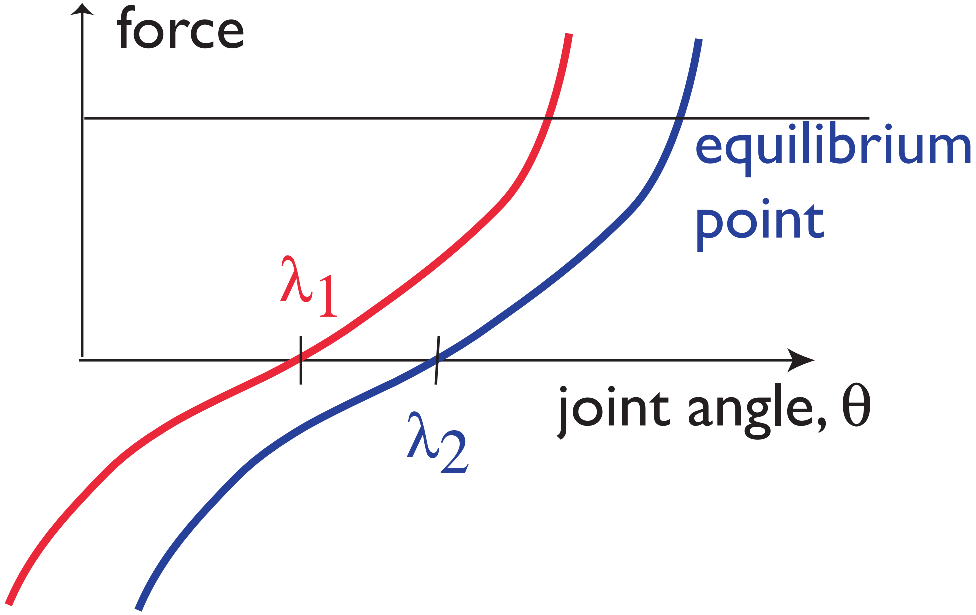
Does the "motor command" specify force/torque?

- Not necessarily ..
- because the same descendent neural command generates different levels of force depending on the initial length of the muscle

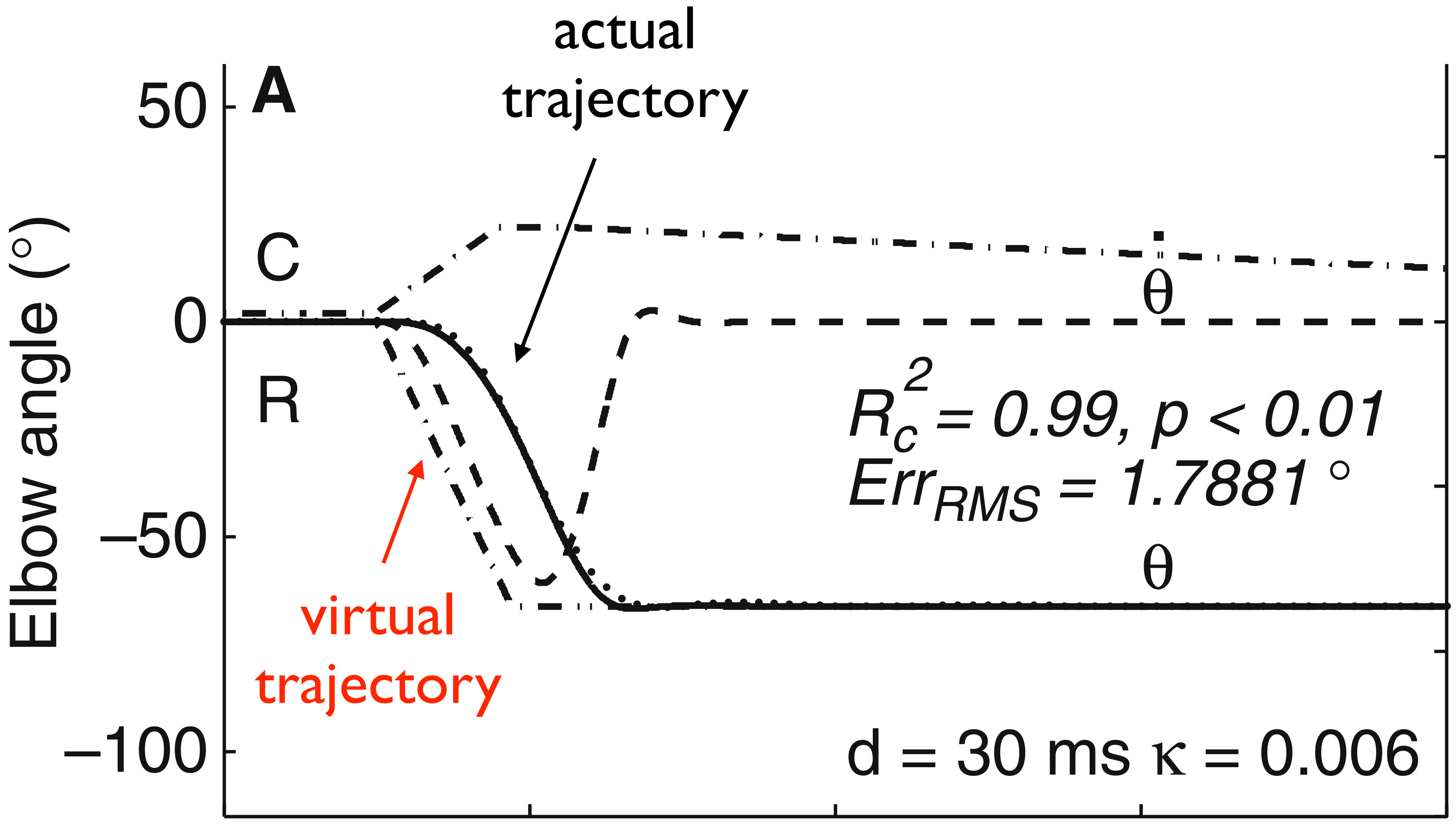


Virtual trajectory

- Shifting the threshold lengths is necessary, but is it also sufficient?
- first answer: yes… simple ramp-like trajectories of the combined threshold lengths of the antagonistic muscles ("r" command ~ virtual trajectory) may model movement



Pilon, Feldman, 2006



actual trajectory

virtual trajectory

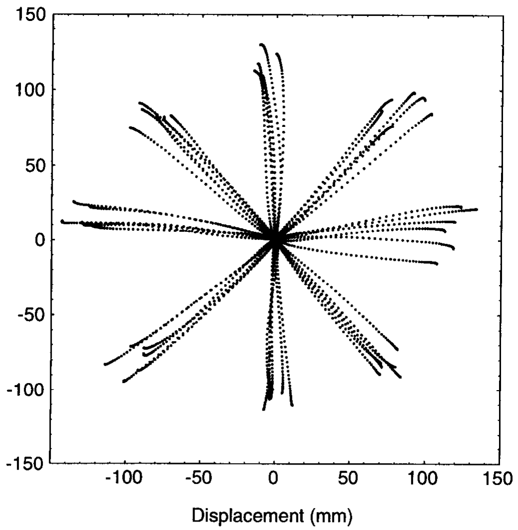
Shifting the equilibrium point is necessary, but is it also sufficient?

- such simple ramp-like trajectories of the “r” command (“virtual trajectories”) may be sufficient when movements
  - are sufficiently slow
  - interaction torques/mechanical conditions unchallenging
- but is this generally true?
- (answer: no)

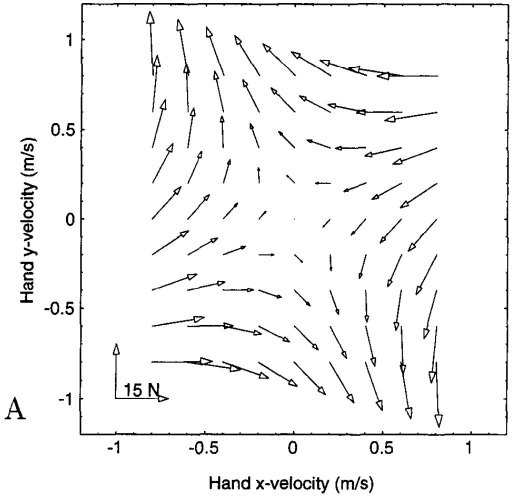
Limit case: velocity dependent force field

- after adapting to a velocity dependent force field the hand reproduces the “natural” path, but must generate compensatory forces on the way

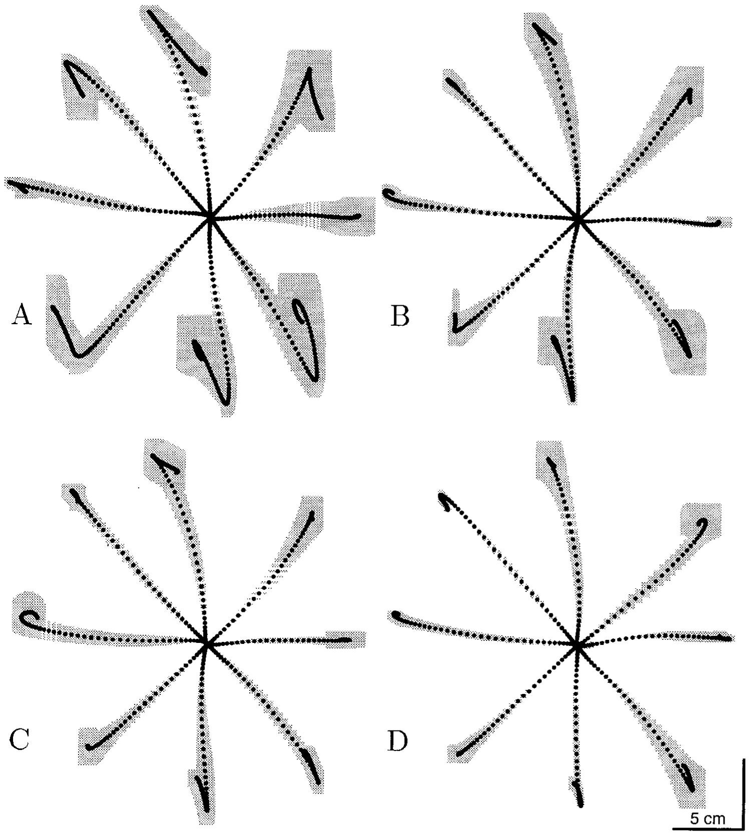
[Shadmehr, Mussa-Ivaldi, 1994]



center-out movements before force-field adaptation



velocity dependent force-field = zero at rest

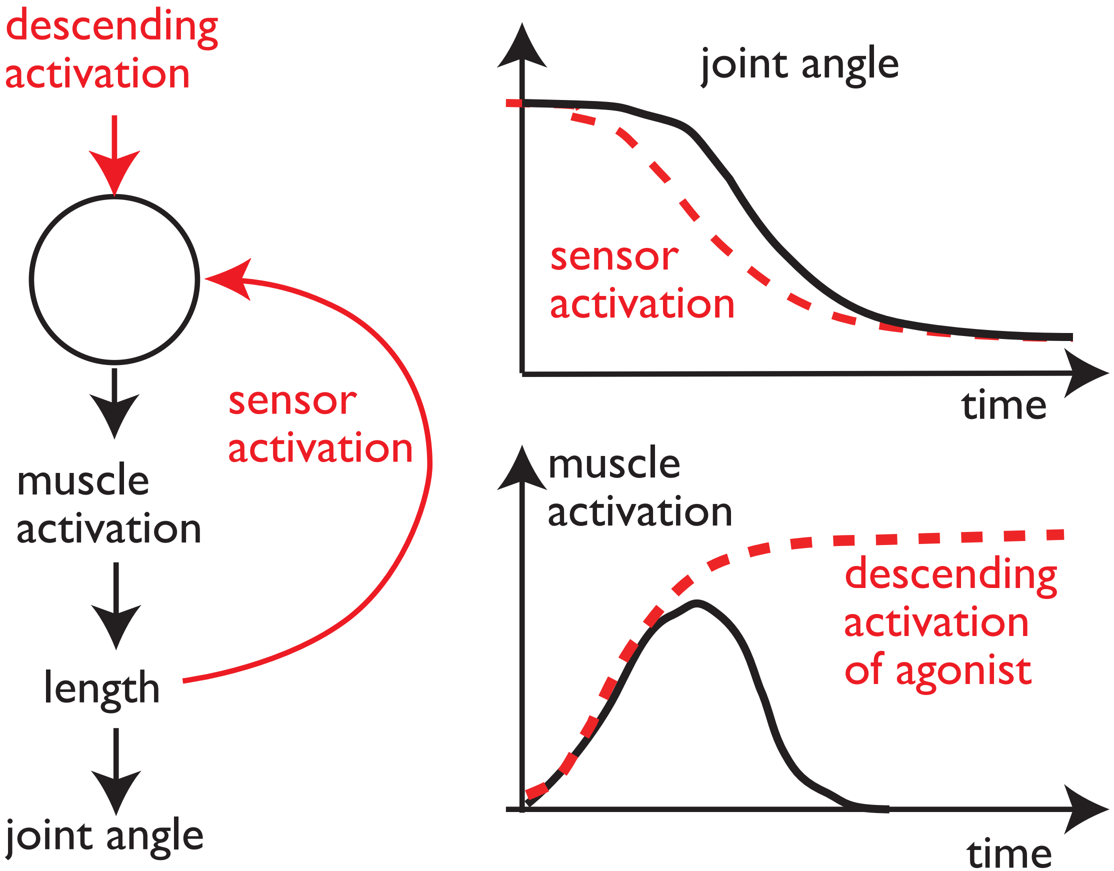


center-out movements at four stages during force-field adaptation

Shifting the equilibrium point is necessary, but is it also sufficient?

- => r-command must still shift from initial to final posture, but must also generate the forces to compensate for the force field during the movement
- that probably takes the form of non-monotonic, “complex” time courses…
- are such temporally complex (e.g,. non-monotonic) r-commands necessary during unperturbed movement

Estimating the descending signal (~virtual trajectory)



(1) Estimate the descending activation by inverting a neuro-muscular model

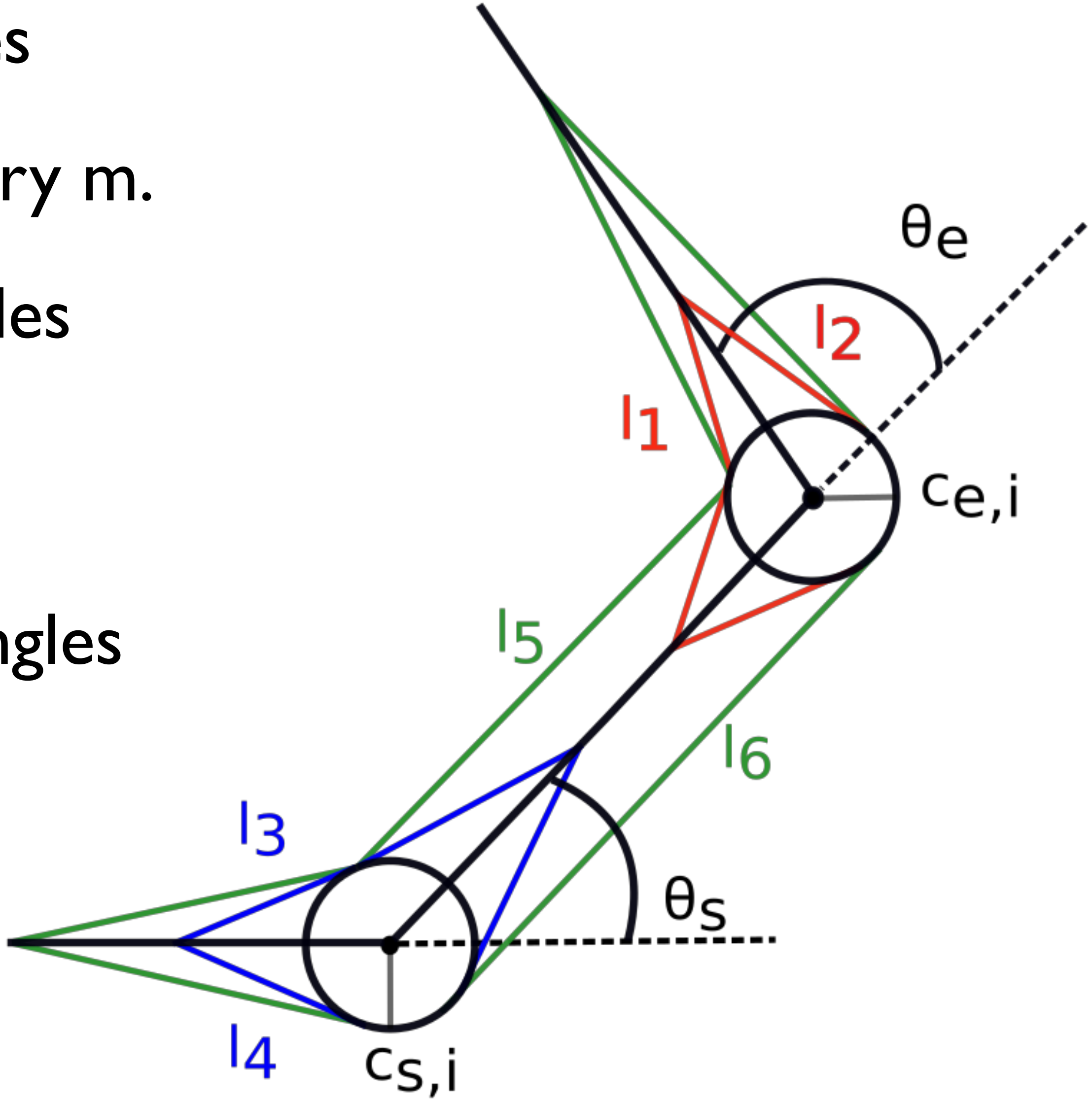
- simplified version Hill type mode:[Gribble, Ostry et al., 98] .. 4 muscles

[Hummert, Zhang, Schöner]

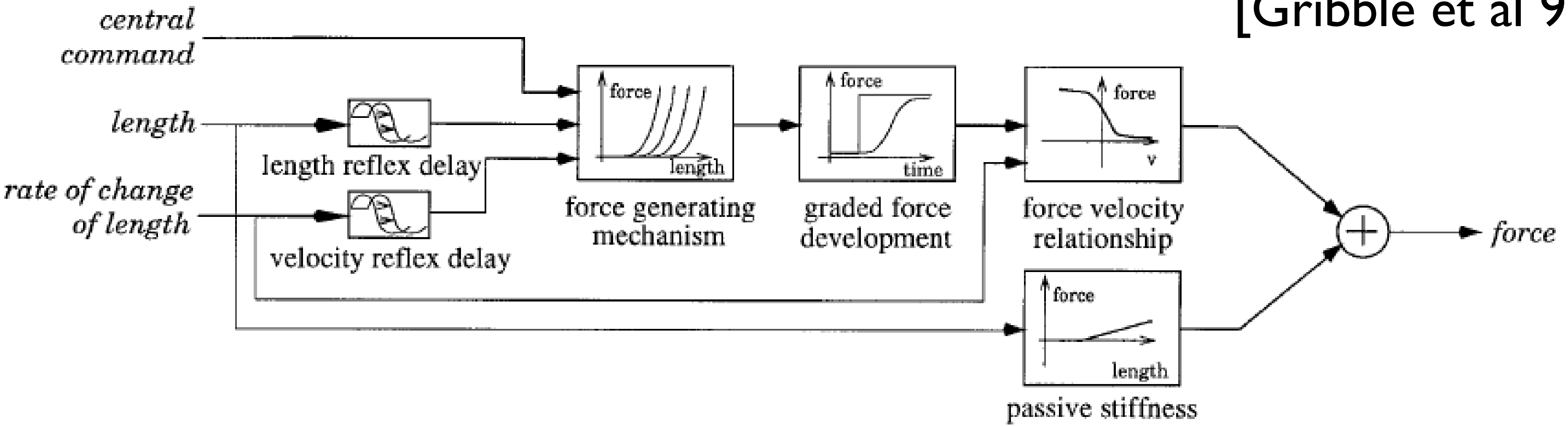
Kinematics

- two joint limb with 4 muscles
- = 2 pairs of mono-articulatory m.
- neglect: bi-articulatory muscles
- muscle length link to joint angles

$$l_i = c_i + c'_{\mathrm{i,s}}\theta_{\mathrm{s}} + c'_{\mathrm{i,e}}\theta_{\mathrm{e}}$$



[Gribble et al 98]



muscle activation from descending command

$$A_i = [u_i + l_i + \mu \dot{l}_i]^+ \qquad [x]^+ = \begin{cases} x, & \text{if } x > 0 \\ 0, & \text{if } x \leq 0 \end{cases}$$

forces from muscle activation

$$F_i = M_i[(f_1 + f_2 \cdot \arctan(f_3 + f_4 \cdot \dot{l}_i)] + k(l_i - c_i).$$

$$\tau^2 \ddot{M} + 2\tau \dot{M} + M = \tilde{M} \qquad \tilde{M}_{\mathrm{i}} = \rho_{\mathrm{i}} \cdot (e^{sA_{\mathrm{i}}} - 1).$$

torques from forces

$$T_i = -H_i * F_i$$

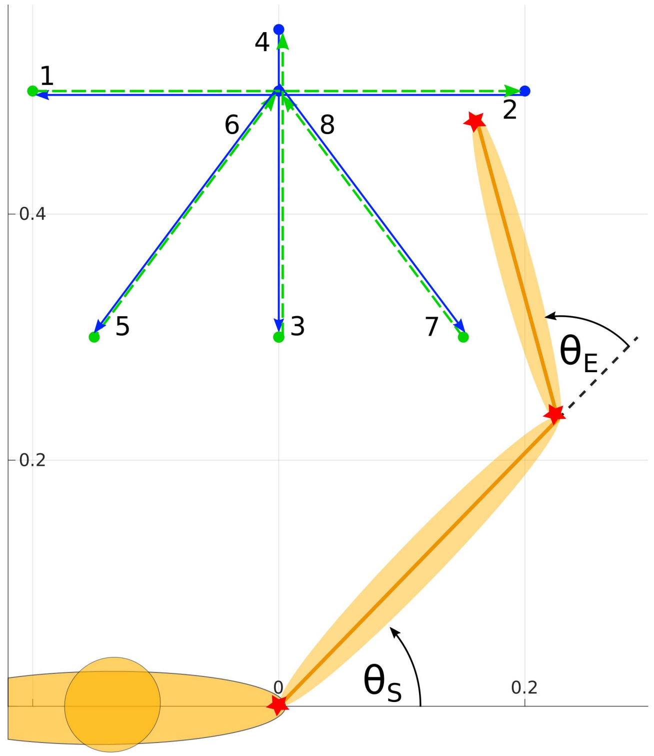
motion from torques

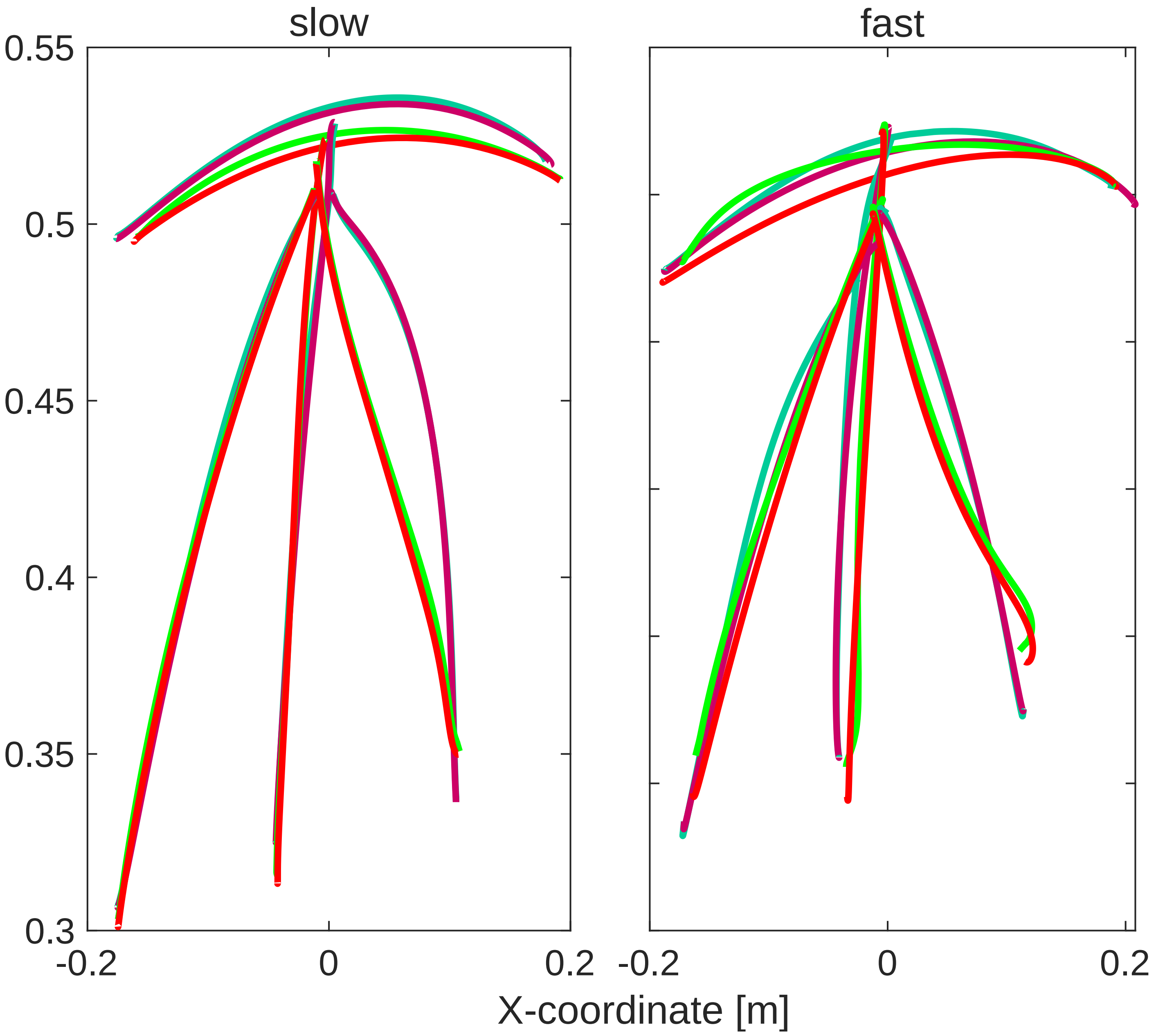
$$\ddot{\theta} = I^{-1}(T - T_{ext} - C\dot{\theta})$$

[Hummert, Zhang, Schöner]

Comparing data to movements predicted from estimated descending activation

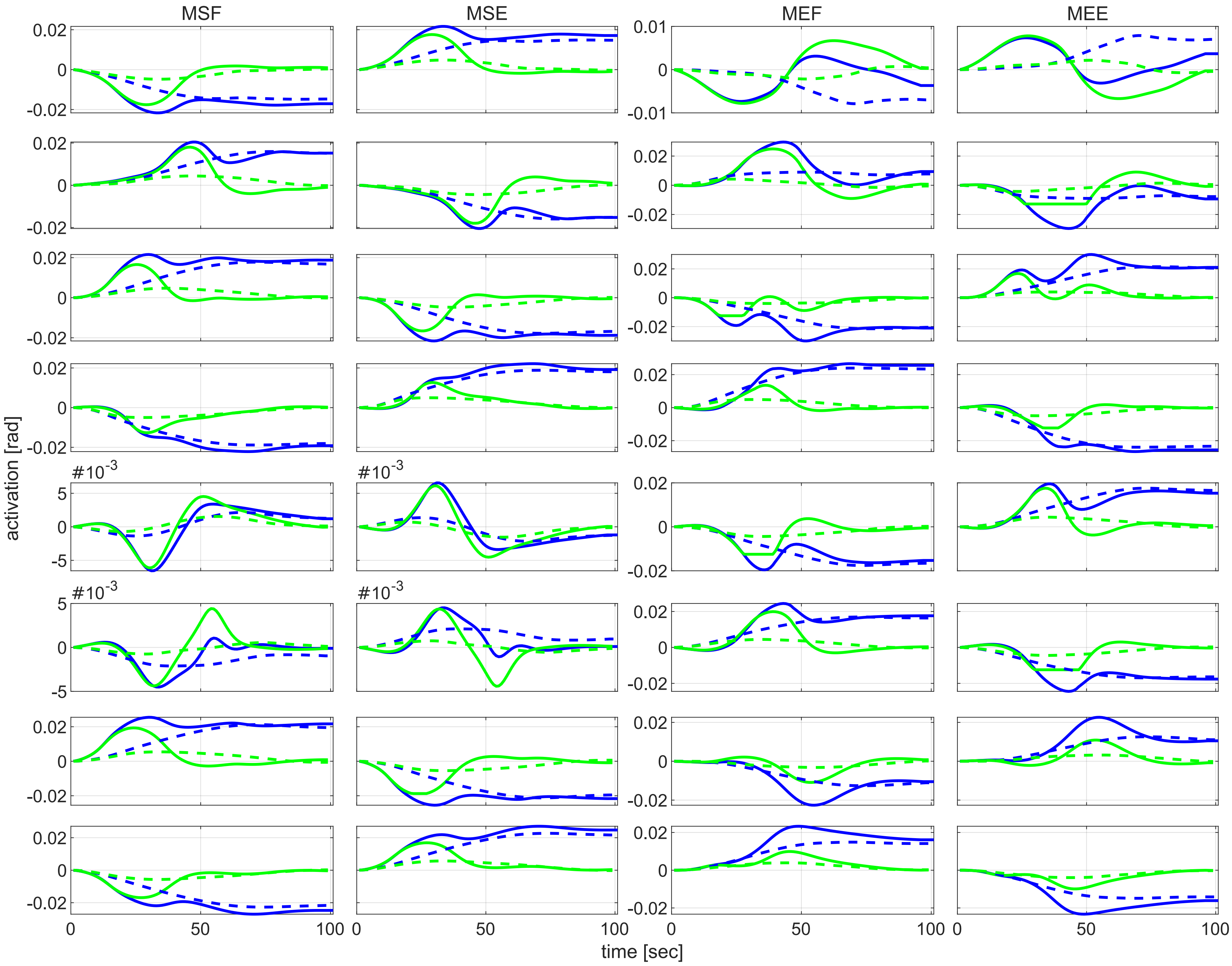
data: red/magenta
(for the two directions)
model: green/cyan





green: muscle activation

blue: descending activation

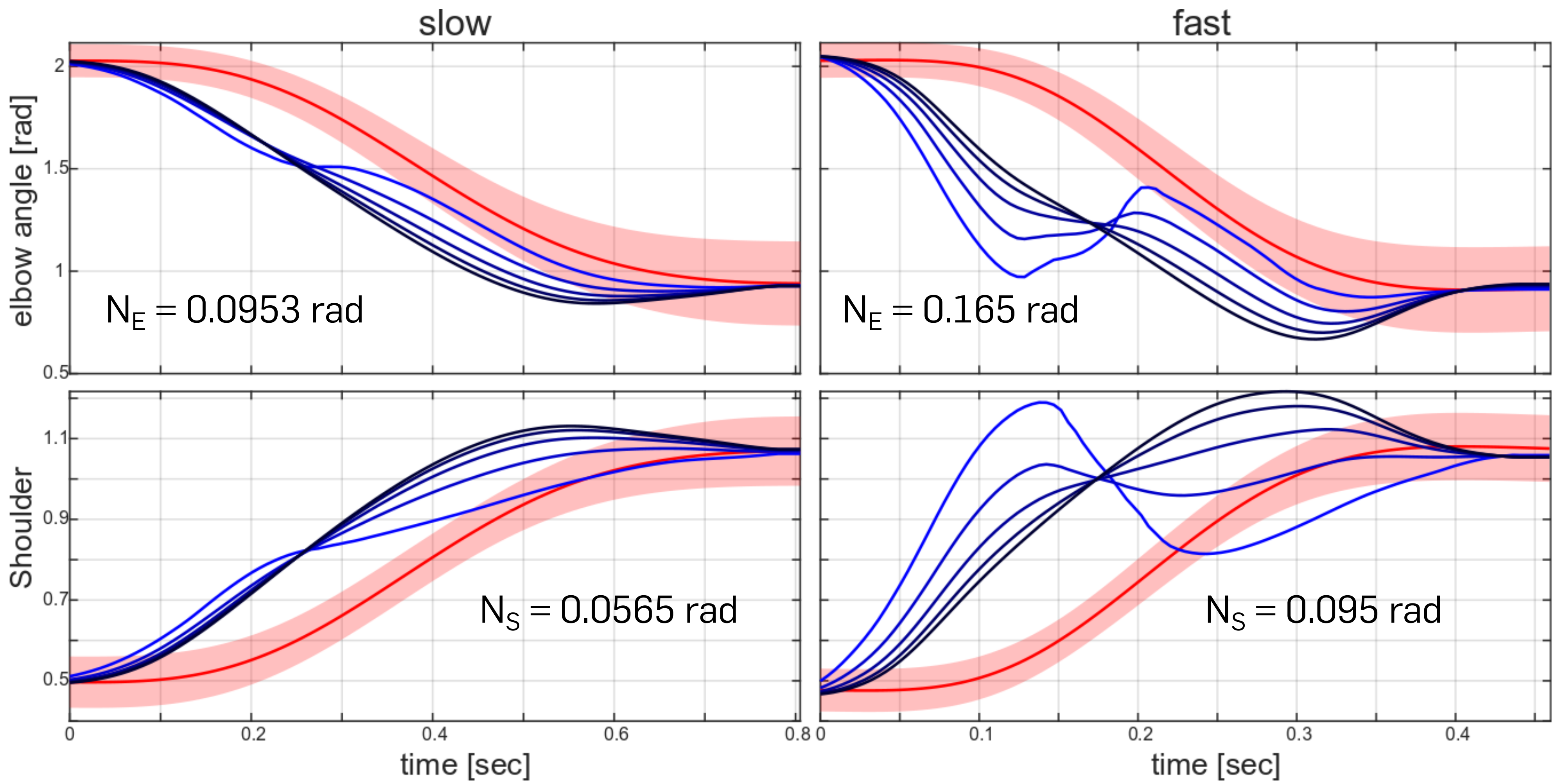


solid: fast

dashed: slow

time course of descending activation

- … as a virtual trajectory



(2) Estimate minimal descending activation

- "minimal" change of descending activation

$$\min_{\vec{u}} \Psi(\vec{u}) = \int_0^T \dot{\vec{u}}(t)^2 dt$$

- to bring about the movement

$$\vec{\theta}(t_0) - \vec{\theta}_{\text{start}} = 0, \qquad \dot{\vec{\theta}}(t_0) = 0, \qquad \ddot{\vec{\theta}}(t_0) = 0,$$

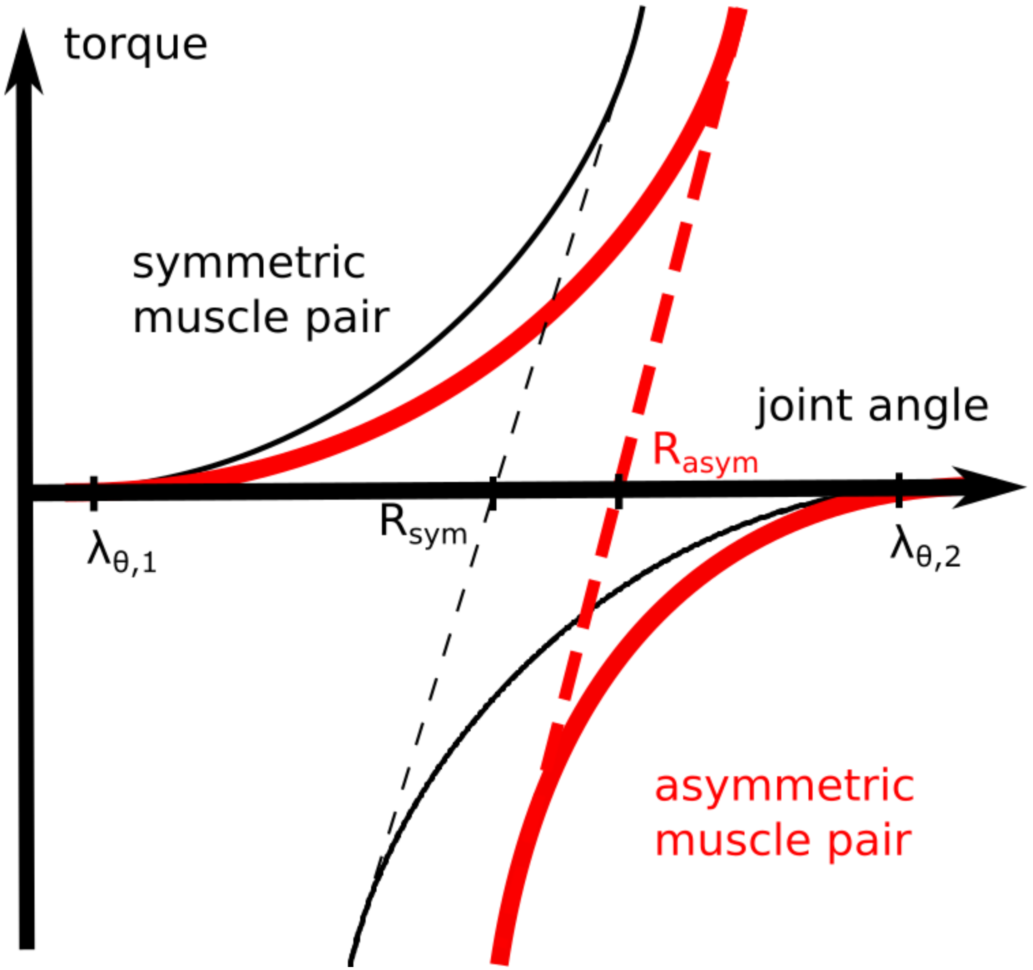
$$\vec{\theta}(t_f) - \vec{\theta}_{\text{final}} = 0. \qquad \dot{\vec{\theta}}(t_f) = 0. \qquad \ddot{\vec{\theta}}(t_f) = 0.$$

$$\vec{\theta}(t) < \vec{\theta}_{\text{max}}, \qquad \lambda_{\text{min}} \leq \vec{\lambda}(t) \leq \lambda_{\text{max}} \qquad t \in [t_0, t_f].$$

$$\dot{\vec{\theta}}(t) < \dot{\vec{\theta}}_{\text{max}}.$$

[Ramadan, Hummert, Jokeit, Schöner (under revision)]

Why “lambda” rather than “r”?

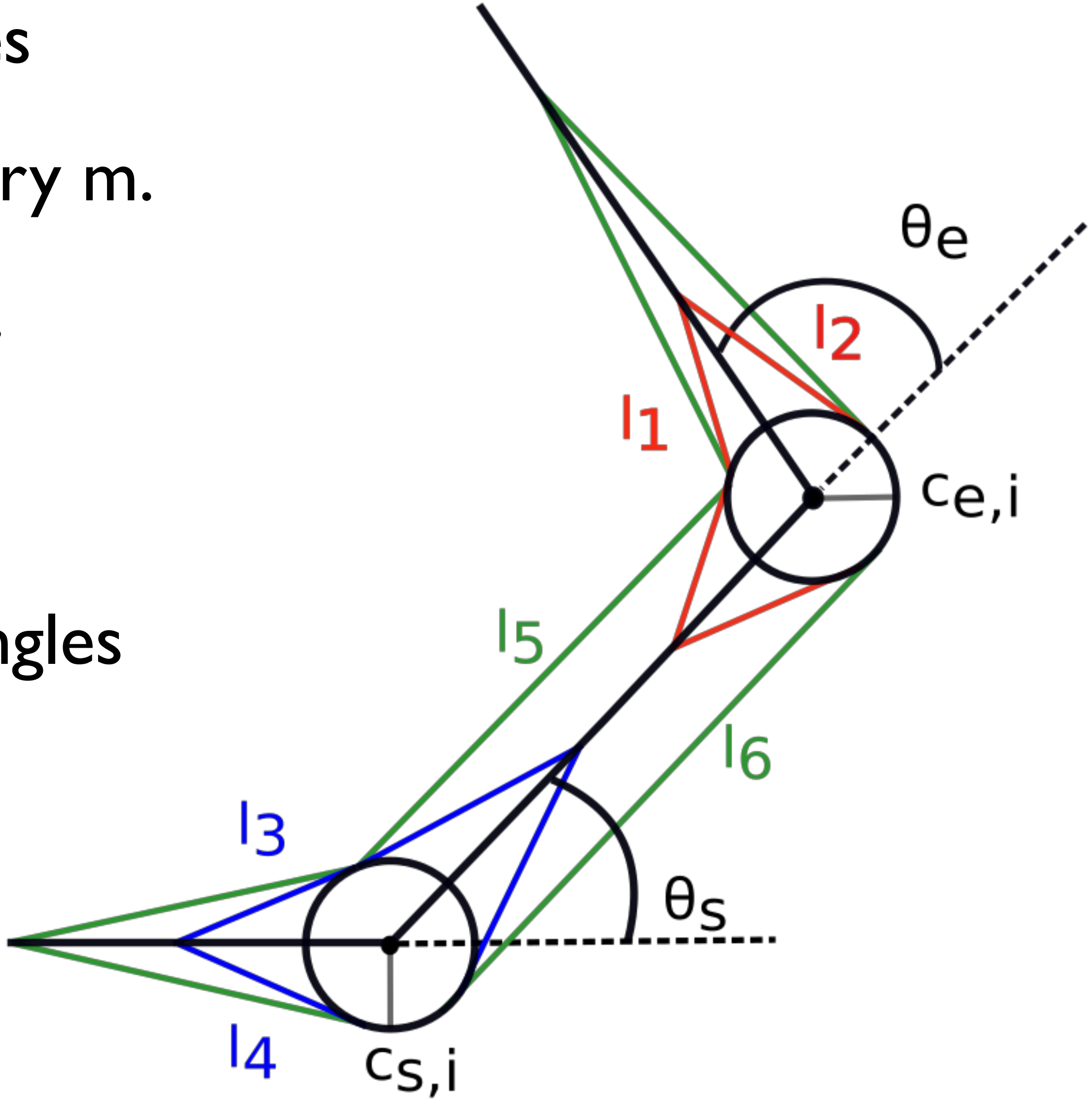


Kinematics

- two joint limb with 6 muscles
- = 2 pairs of mono-articulatory m.
- + 1 pair of bi-articulatory m.

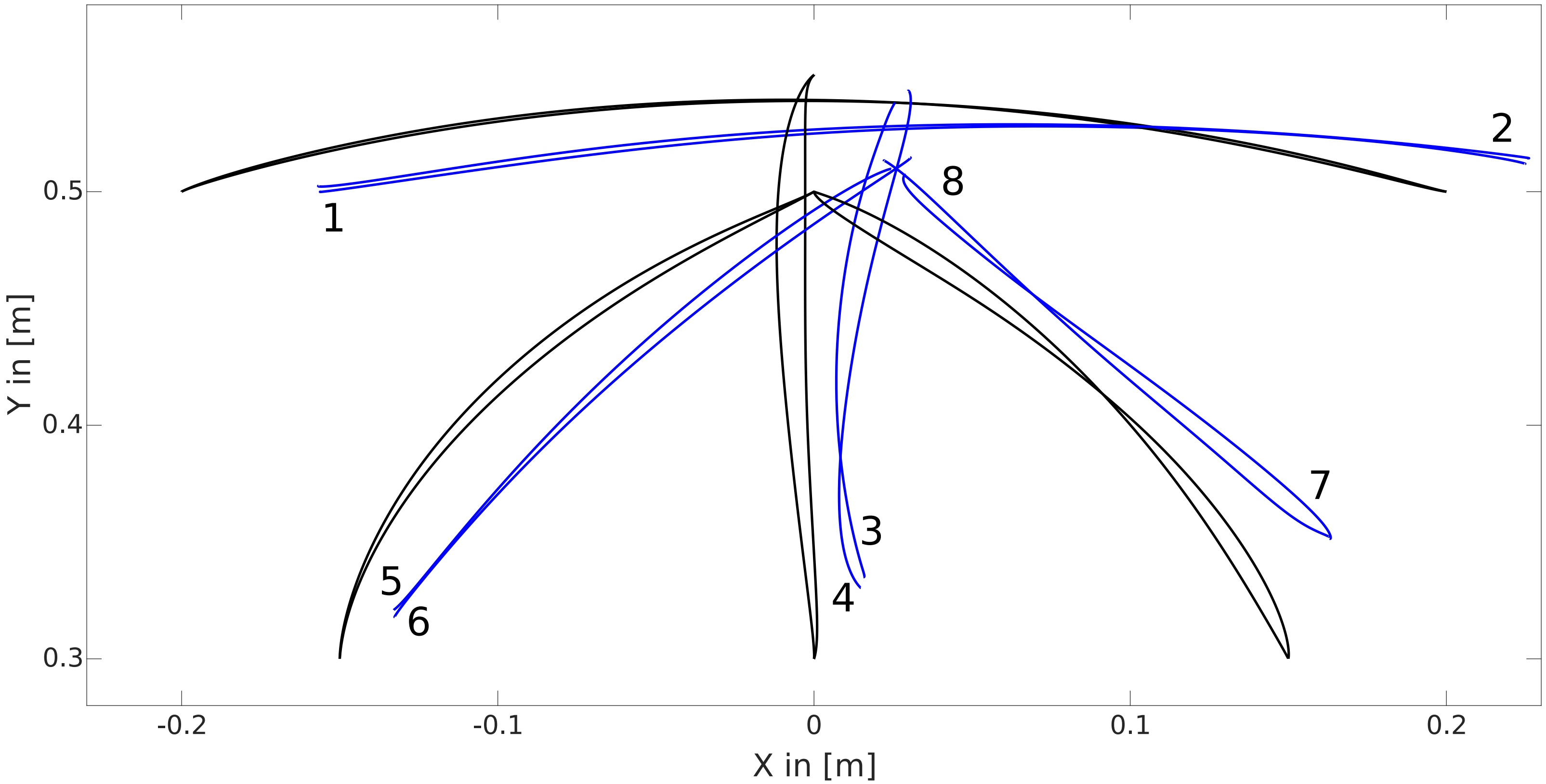
- muscle length link to joint angles

$$l_i = c_i + c'_{\mathrm{i,s}}\theta_{\mathrm{s}} + c'_{\mathrm{i,e}}\theta_{\mathrm{e}}$$



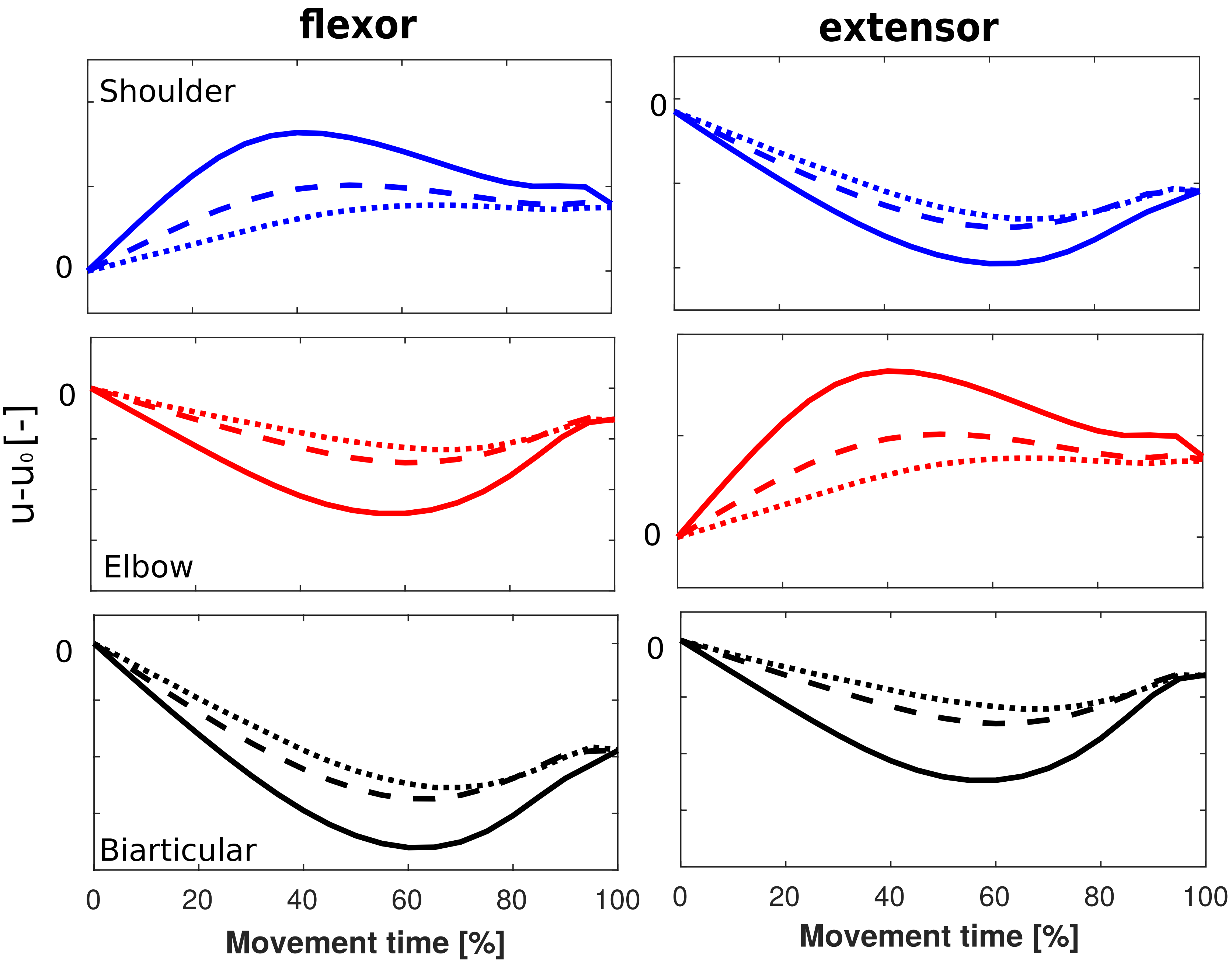
[Ramadan, Hummert, Jokeit, Schöner, under revision]

Paths data vs. model



blue: experiment
black: model

Minimal descending activation



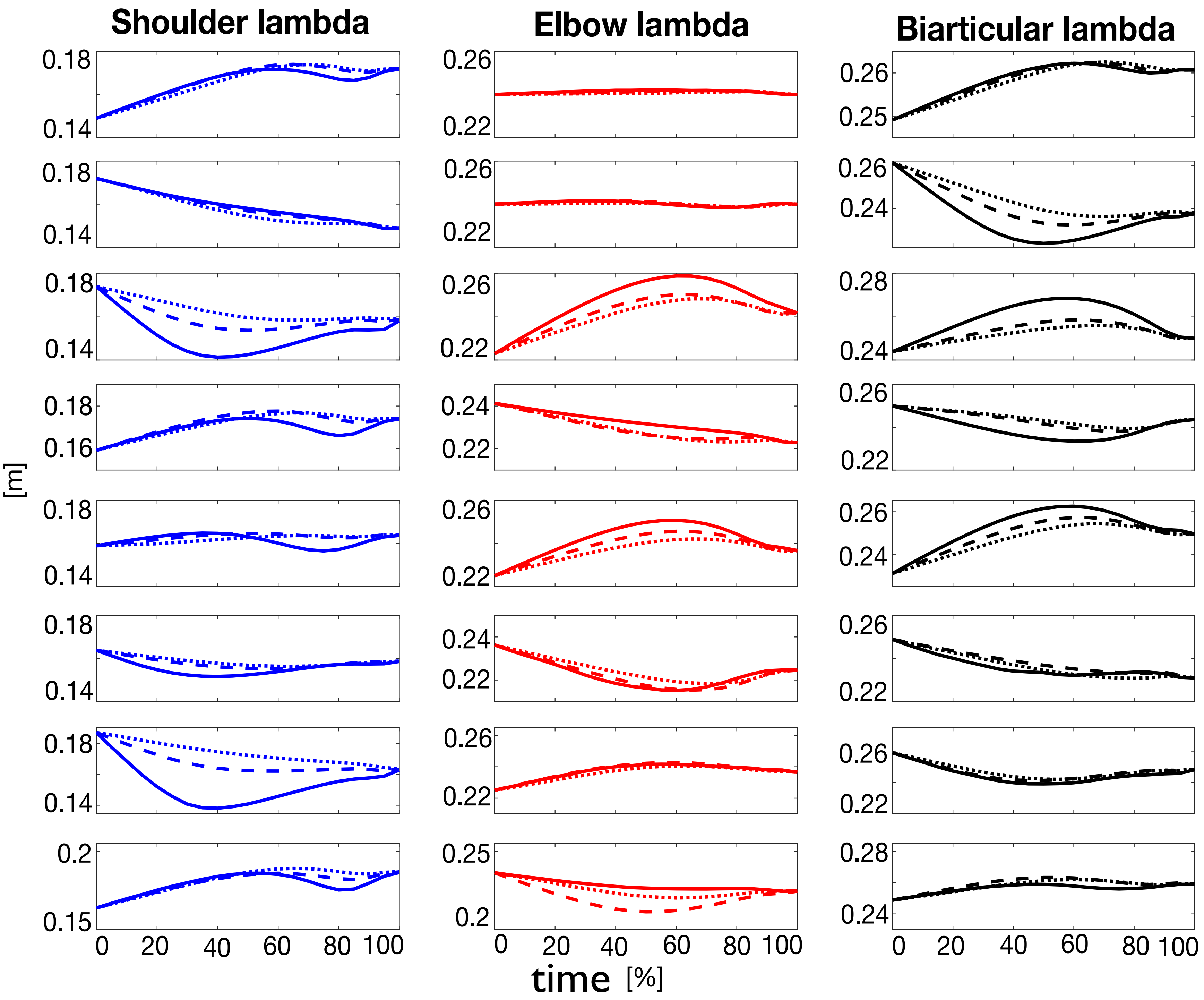
slow:
dotted

medium:
dashed

fast:
solid

Minimal lambda trajectories

flexors



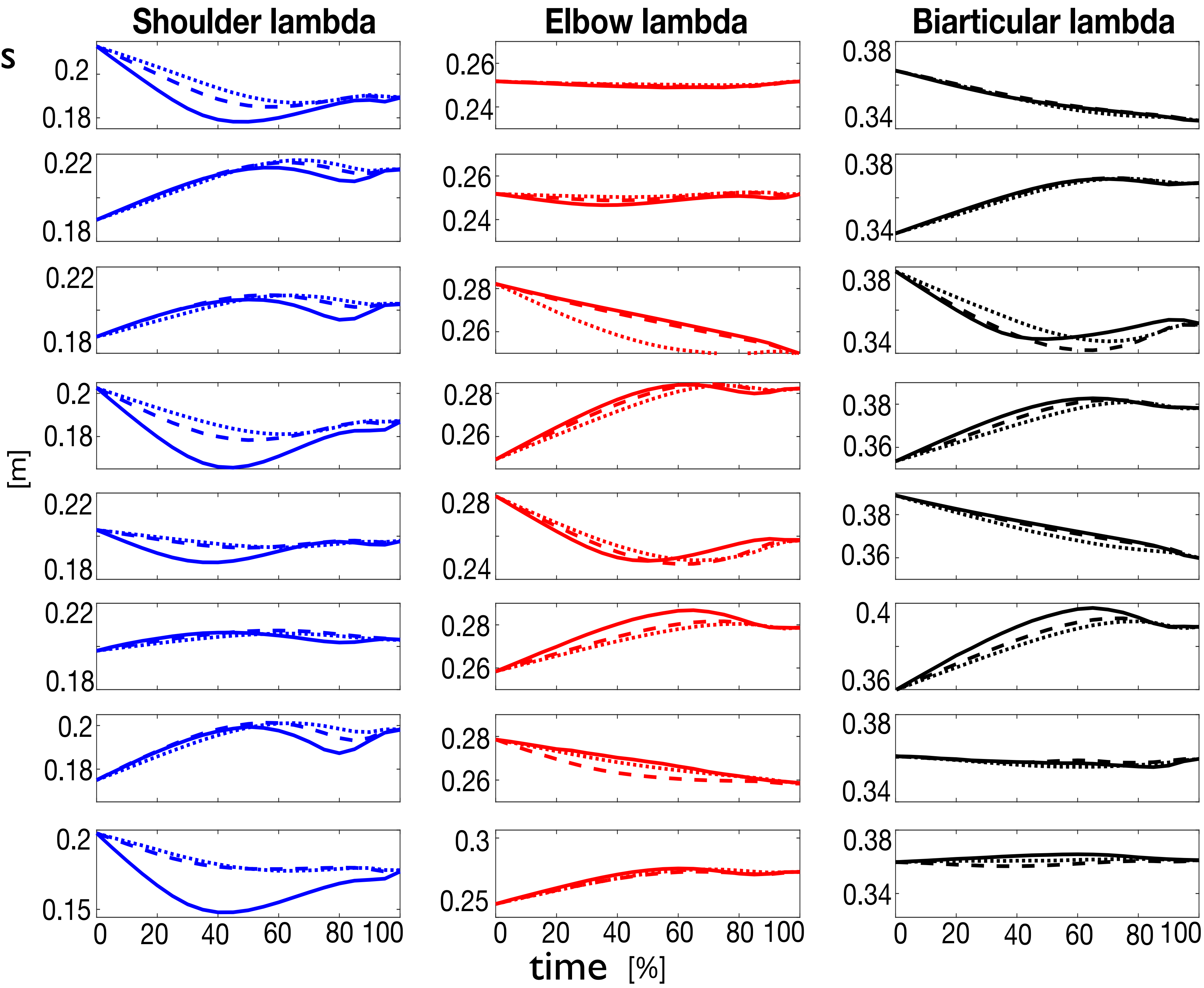
slow: dotted

medium: dashed

fast: solid

Minimal lambda trajectories

extensors



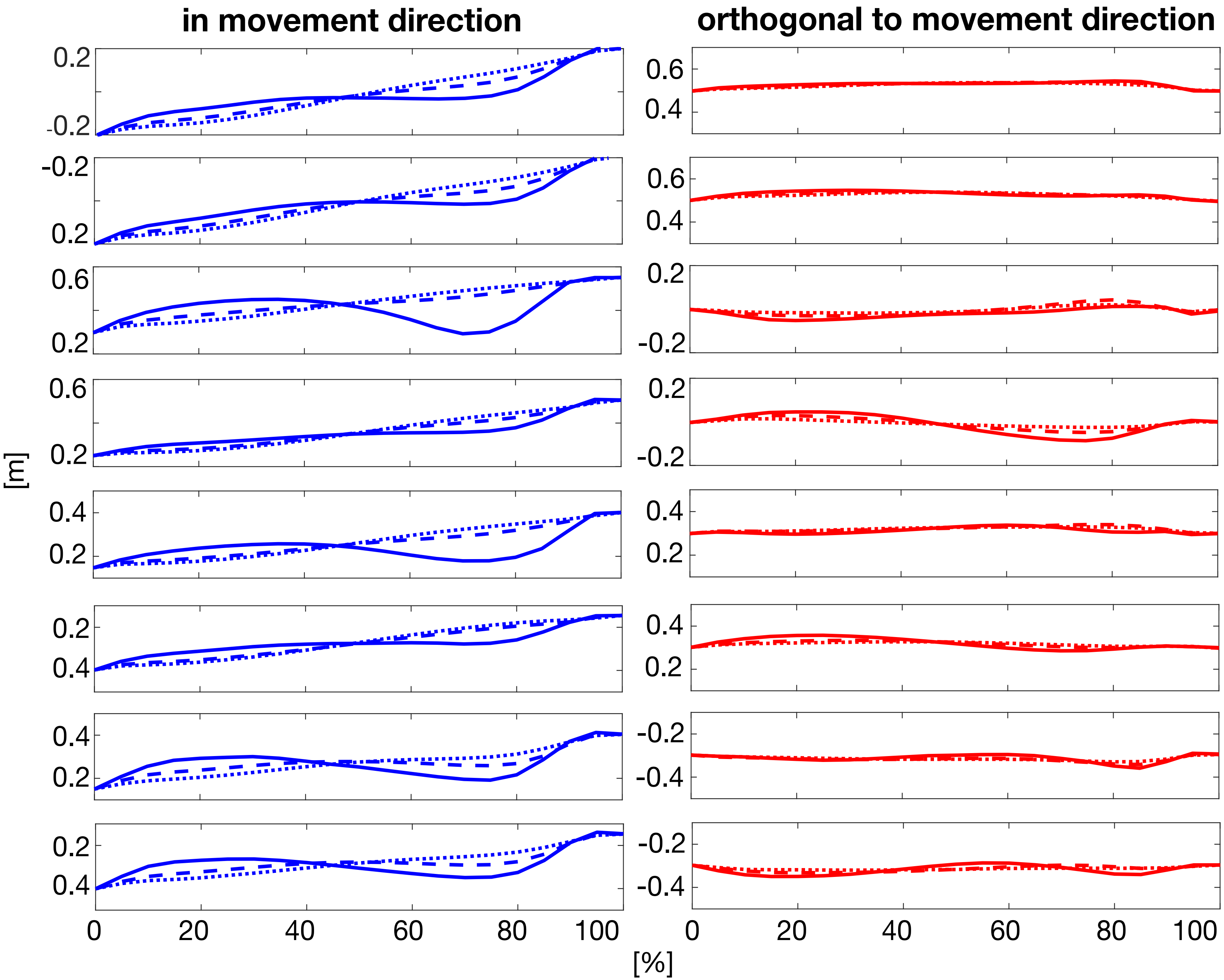
slow: dotted

medium: dashed

fast: solid

Hodgson-Hogan attractor trajectories

in end-effector space!



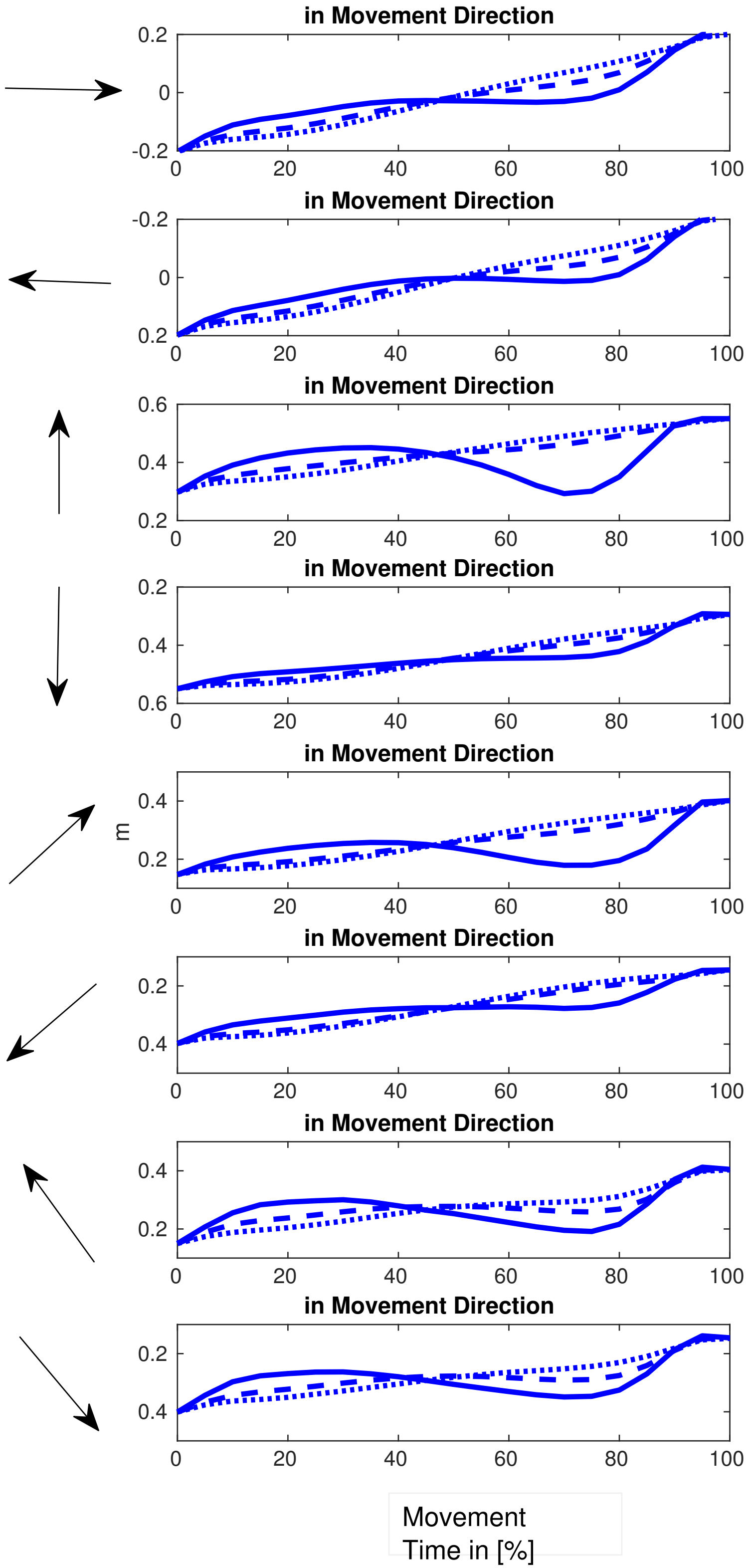
slow: dotted

medium: dashed

fast: solid

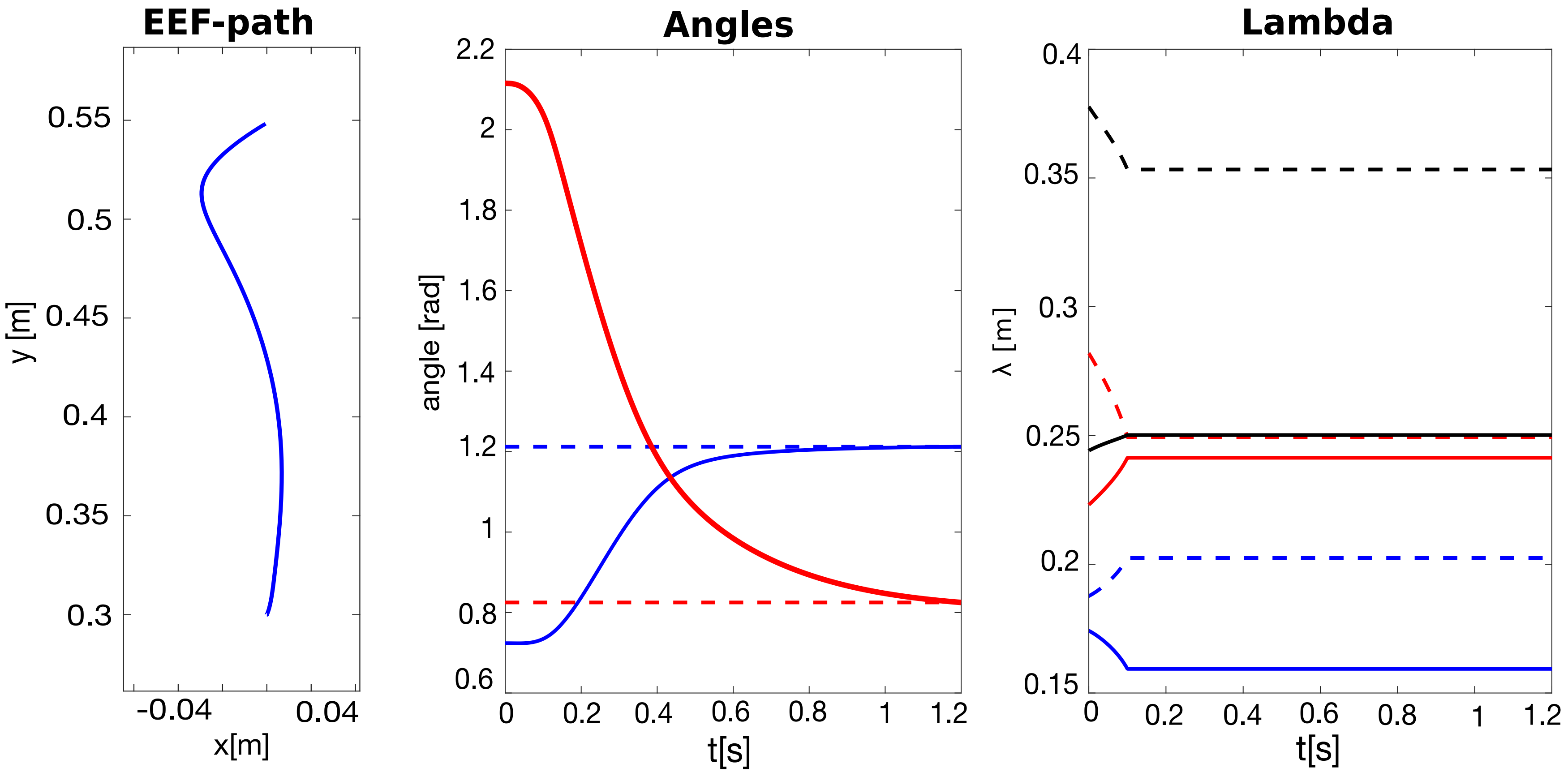
attractor trajectory in hand-space

- at higher speeds (solid line), attractor trajectories are temporally structured “just right” for the hand to reach the target



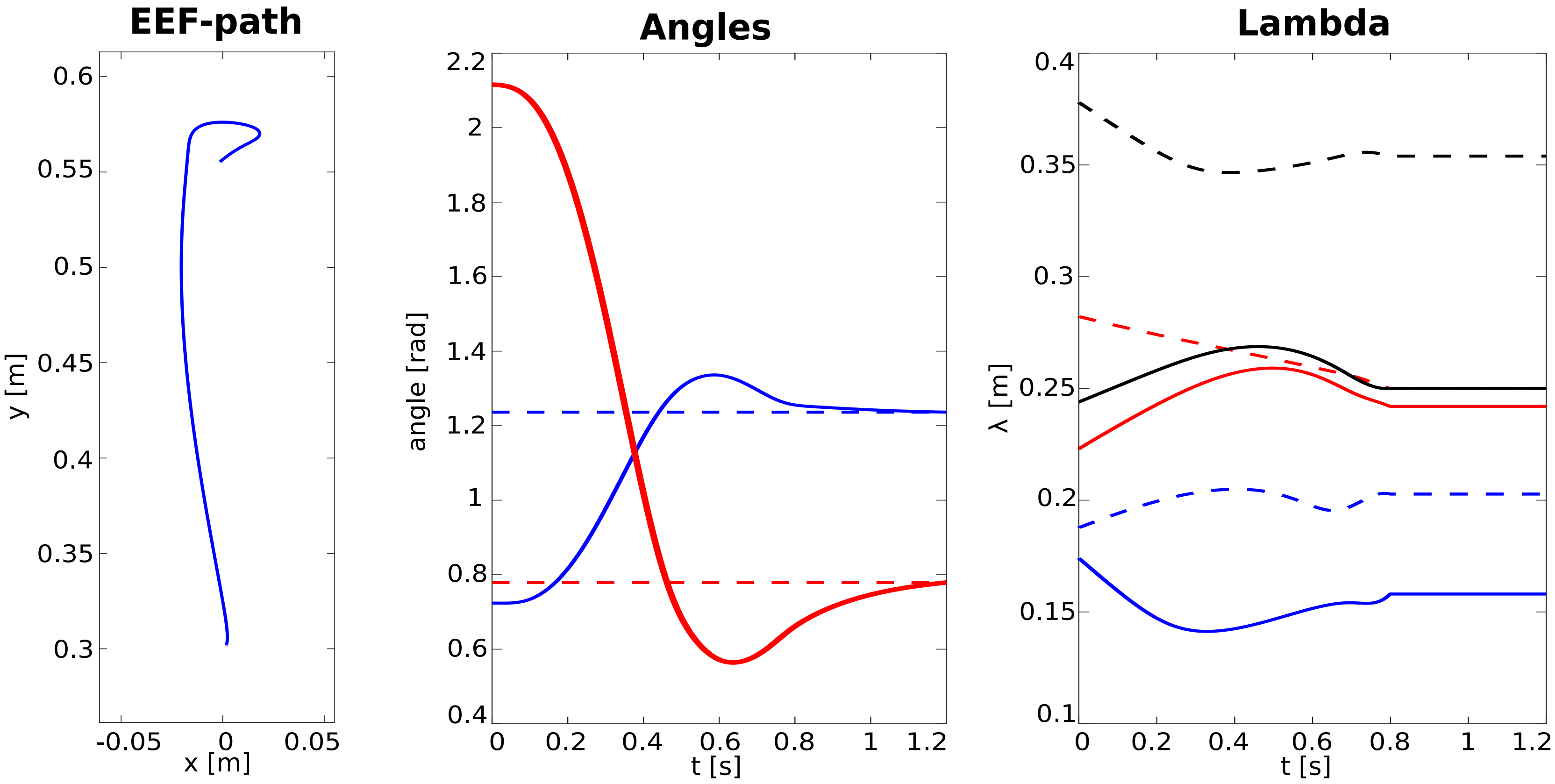
Do the time courses of lambda matter?

- making a slow lambda (ramp in hand space) fast => doesn't make movement fast



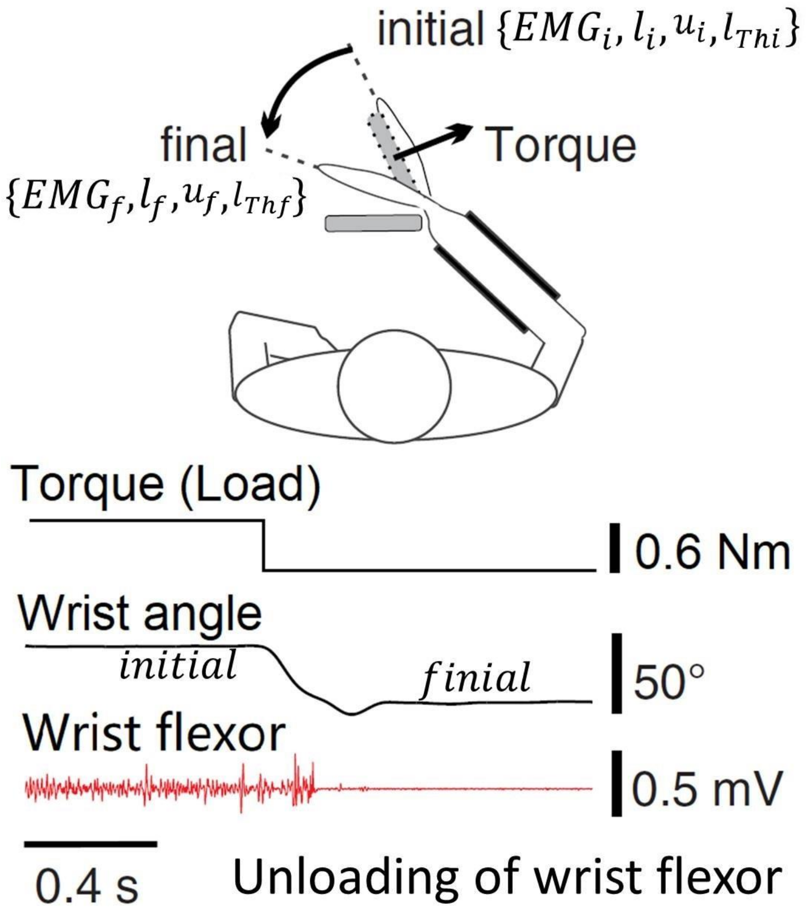
Do the time courses of lambda matter?

- making a fast lambda slow: doesn't make a good slow movement



(3) Estimate descending activation from EMG

- unloading experiment to determine linear relationship between EMG and descending activation
- (by estimating threshold length in unloading)



[Zhang, Feldman, Schöner]

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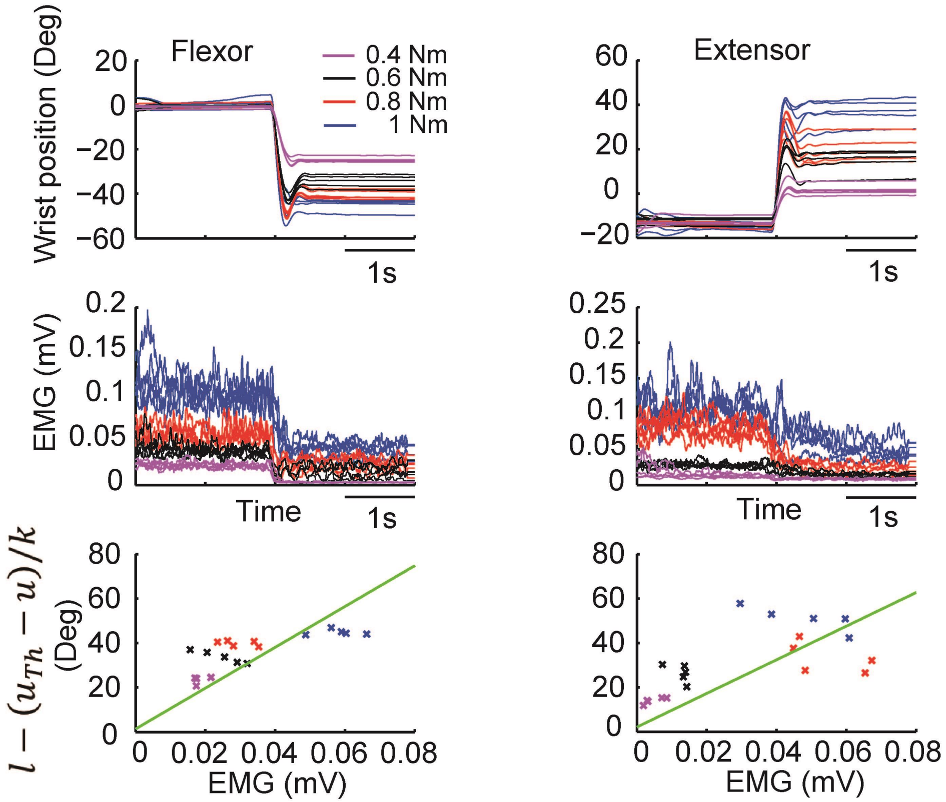


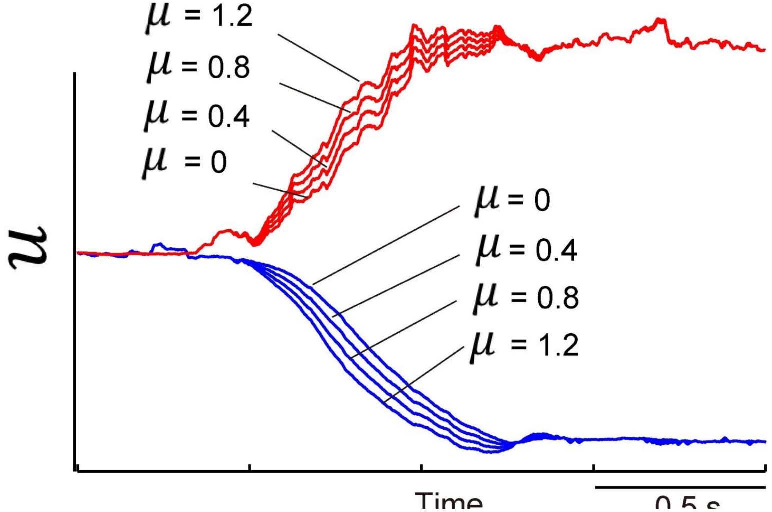
For flexor: $p_1 = 0.0011$; $p_2 = -0.0015$

For extensor: $p_1 = 0.0014$; $p_2 = -0.0028$

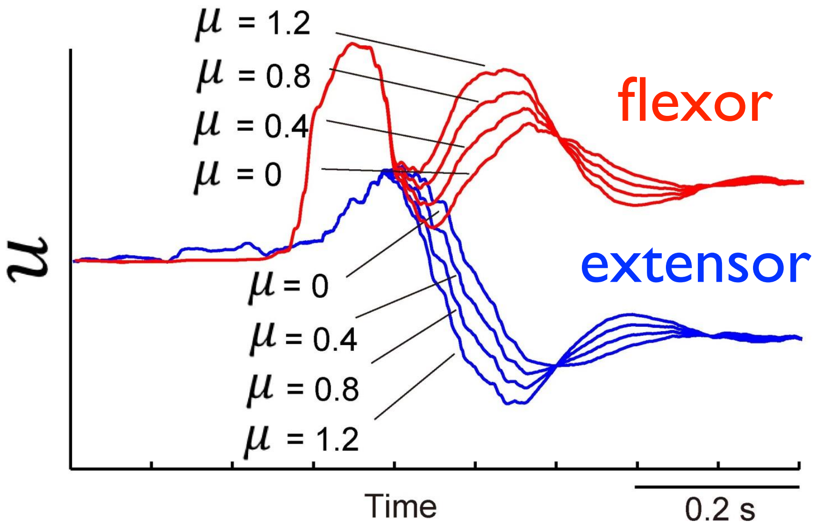
$$EMG = p1 \times (l - l_{Th}) + p2 = p1 \times (l - (u_{Th} - u)/k\ ) + p2$$

[Zhang, Feldman, Schöner]

slow



fast



$$A = \left[k(l + \mu\dot{l}) - (u_{Th} - u)\right]^{+} = k\left[l + \mu\dot{l} - l_{Th}\right]^{+}$$

Why is this important ?

- quasi-postural picture
  - target is an attractor….
- optimal control picture
  - a precise time course of a motor command must be computed and generated to move to the target and reach zero velocity there
- => demands on the neural computations
- => demands on learning

Conclusion: Human motor control

- Human movement uses "soft" muscles that have nonlinear muscle dynamics
- Postures are stabilized by reflexes, whose thresholds must be shifted during movement
- Those shifts by descending commands so solve the "optimal control" problem = the right time course so that the effector arrives at the target in the desired time with small velocity and a smooth temporal shape