Motor control and muscles

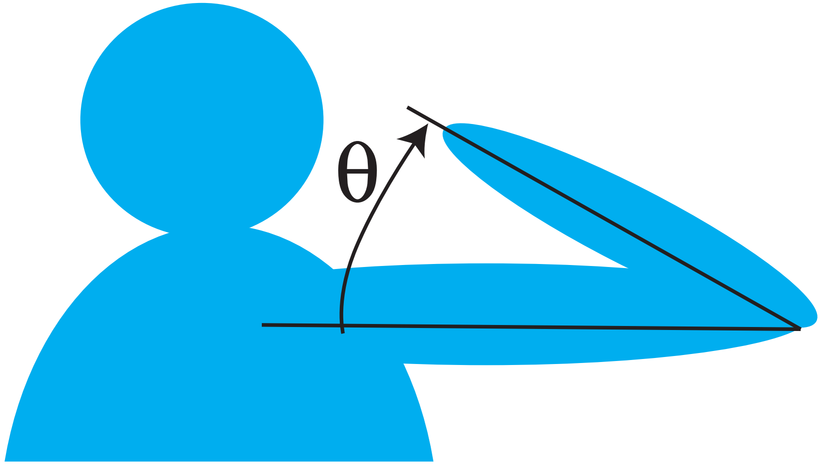
Gregor Schöner

motor control

- how are forces generated that move effectors?
- by muscles, obviously...
- ... and by gravity
- ... and by inertia...

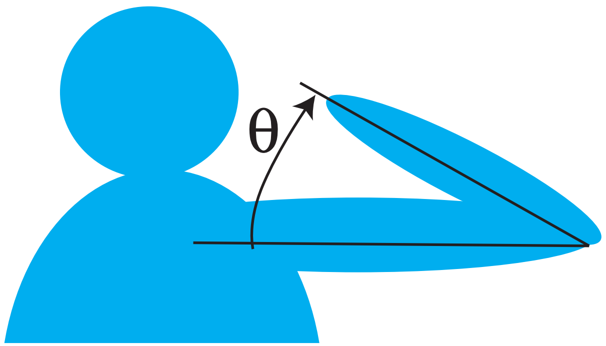
motor control

- posture of the elbow joint with the arm in horizontal position



what about the elbow is "controlled"?

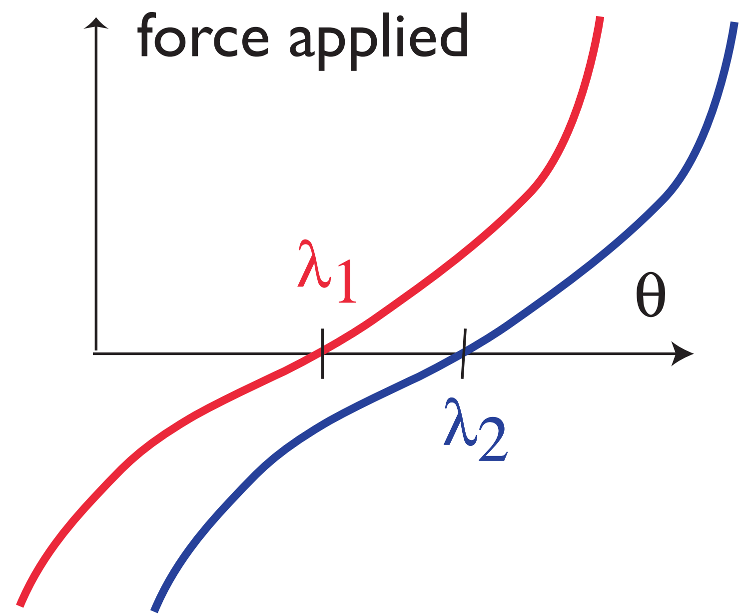
- the elbow does not behave like a passive mechanical system with a free joint at the elbow: $J\ddot{\theta} = 0$
- where J is inertial moment of forearm (if upper arm is held fixed)
- Instead, the elbow resists, when pushed => there is active control= stabilization of the joint



=>experiment

the mass spring model

- Anatol Feldman has figured out, what the macroscopic description of this stabilization is
- the invariant characteristic



the mass-spring model

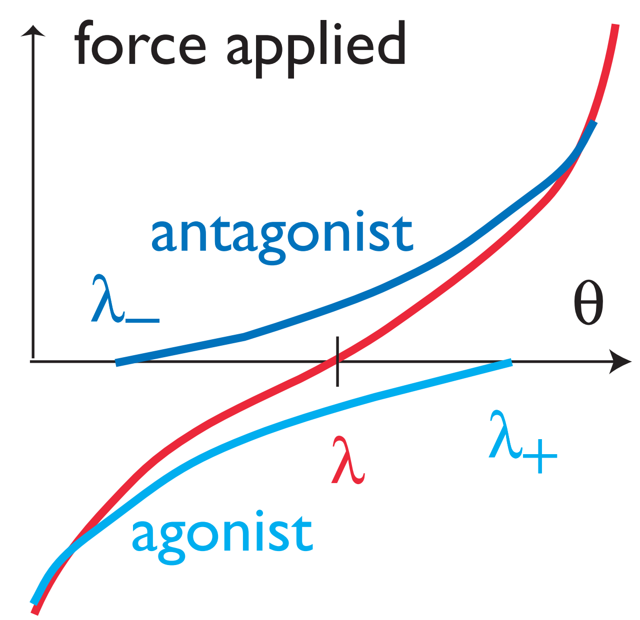
- this is an elastic force (because it is proportional to position)
- there is also a viscous component (resistance depends on joint velocity)

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

active torques generated by the muscle

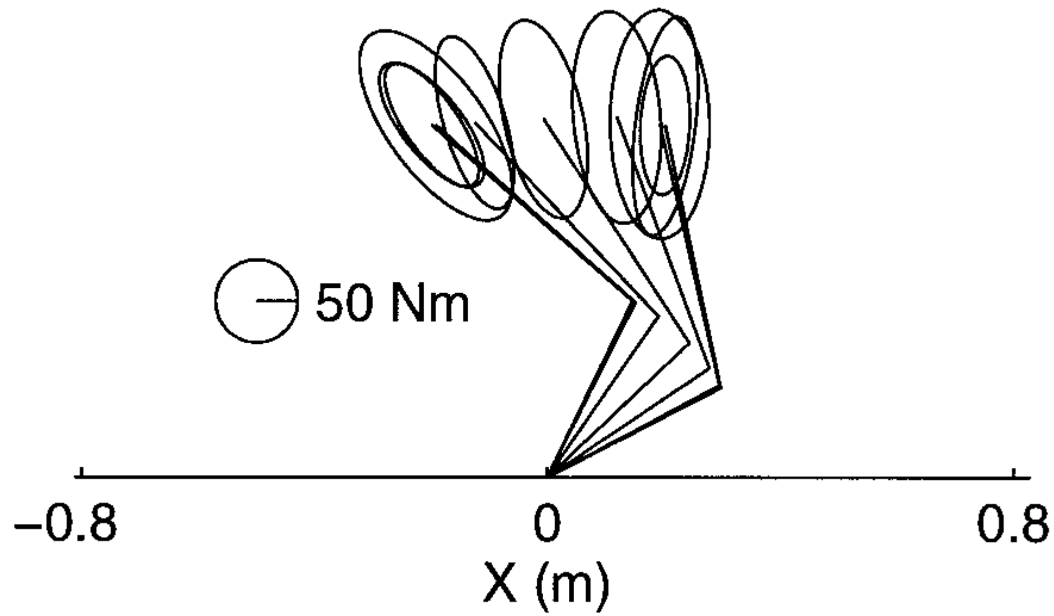
agonist-antagonist action

- one lambda per muscle
- tested on muscles detached at one end
- co-contraction controls stiffness



stiffness

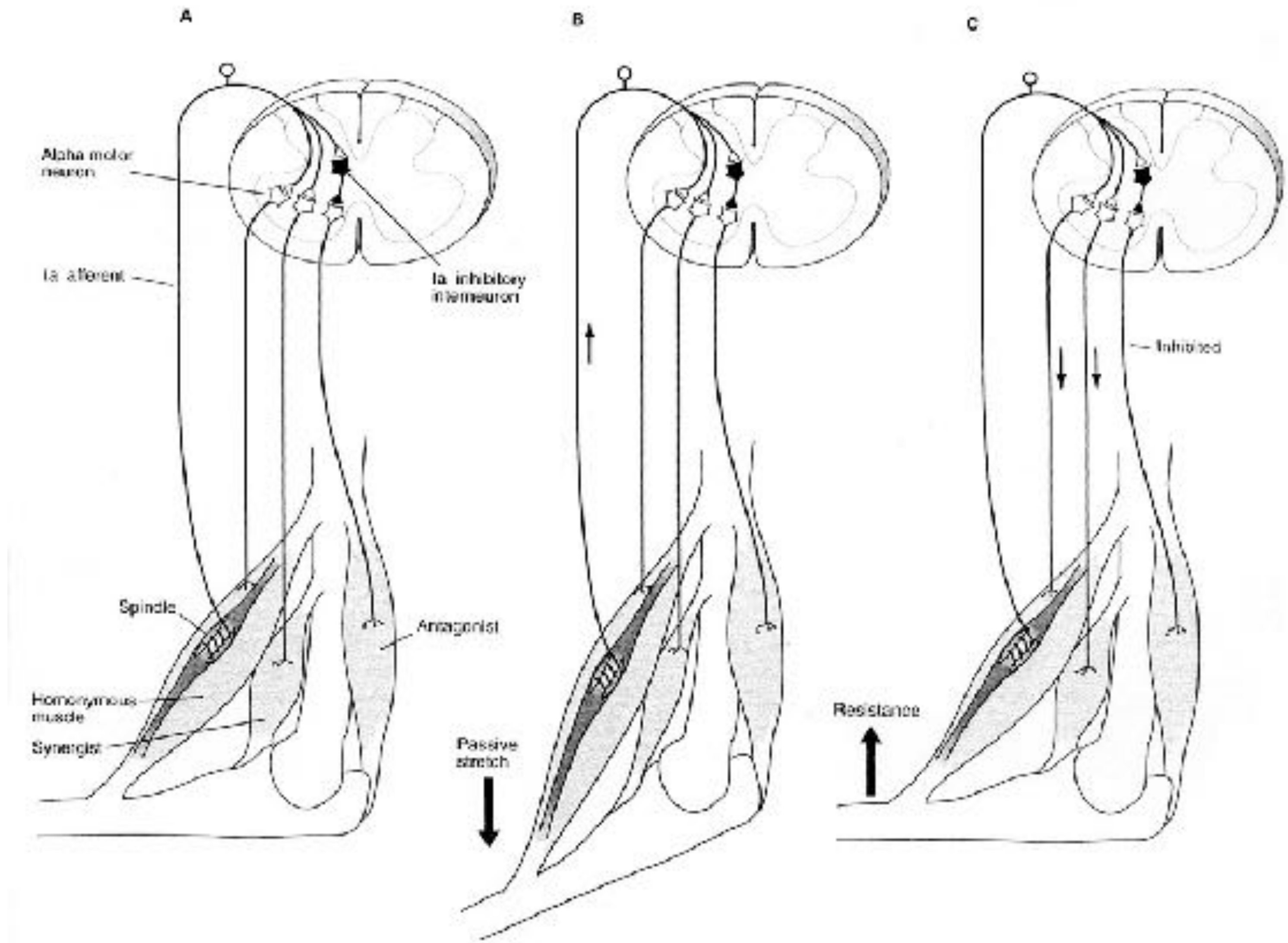
- the stiffness, k, can be measured from perturbations
- the viscosity "mu" is more difficult to determine



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

neural basis of EP model: spinal reflex loops

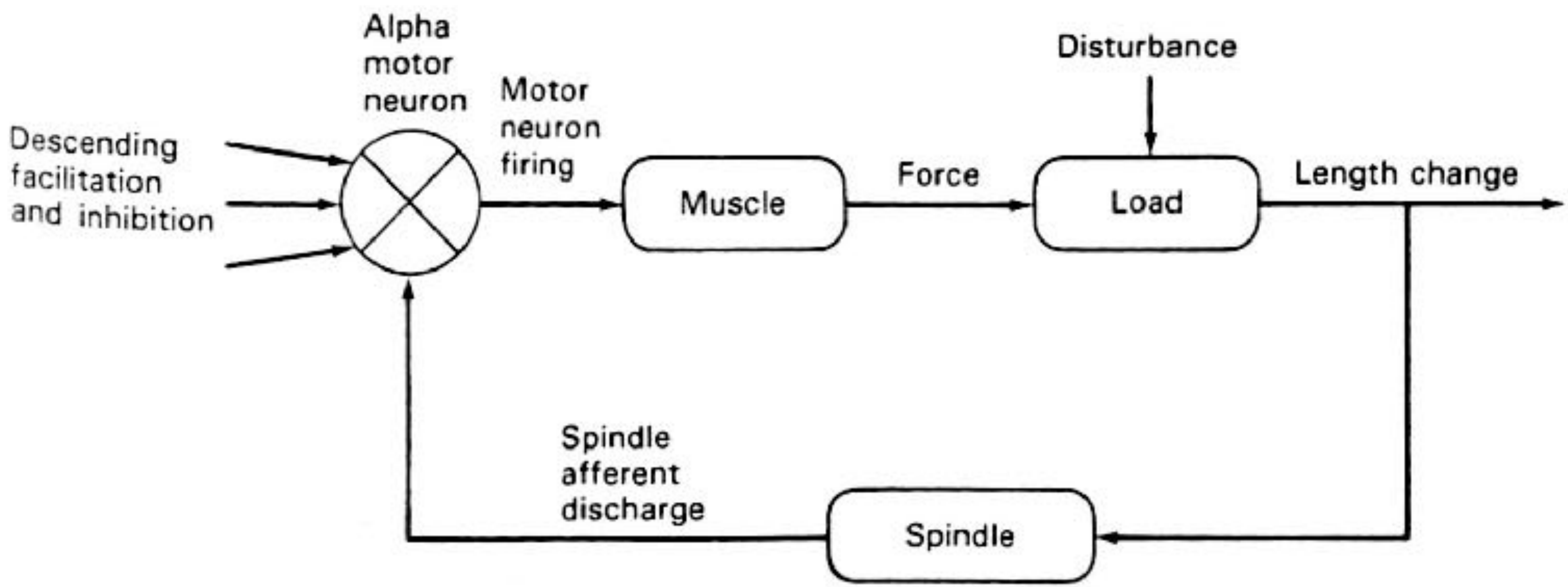
- alpha-gamma reflex loop generates the stretch reflex



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

spinal cord: reflex loops

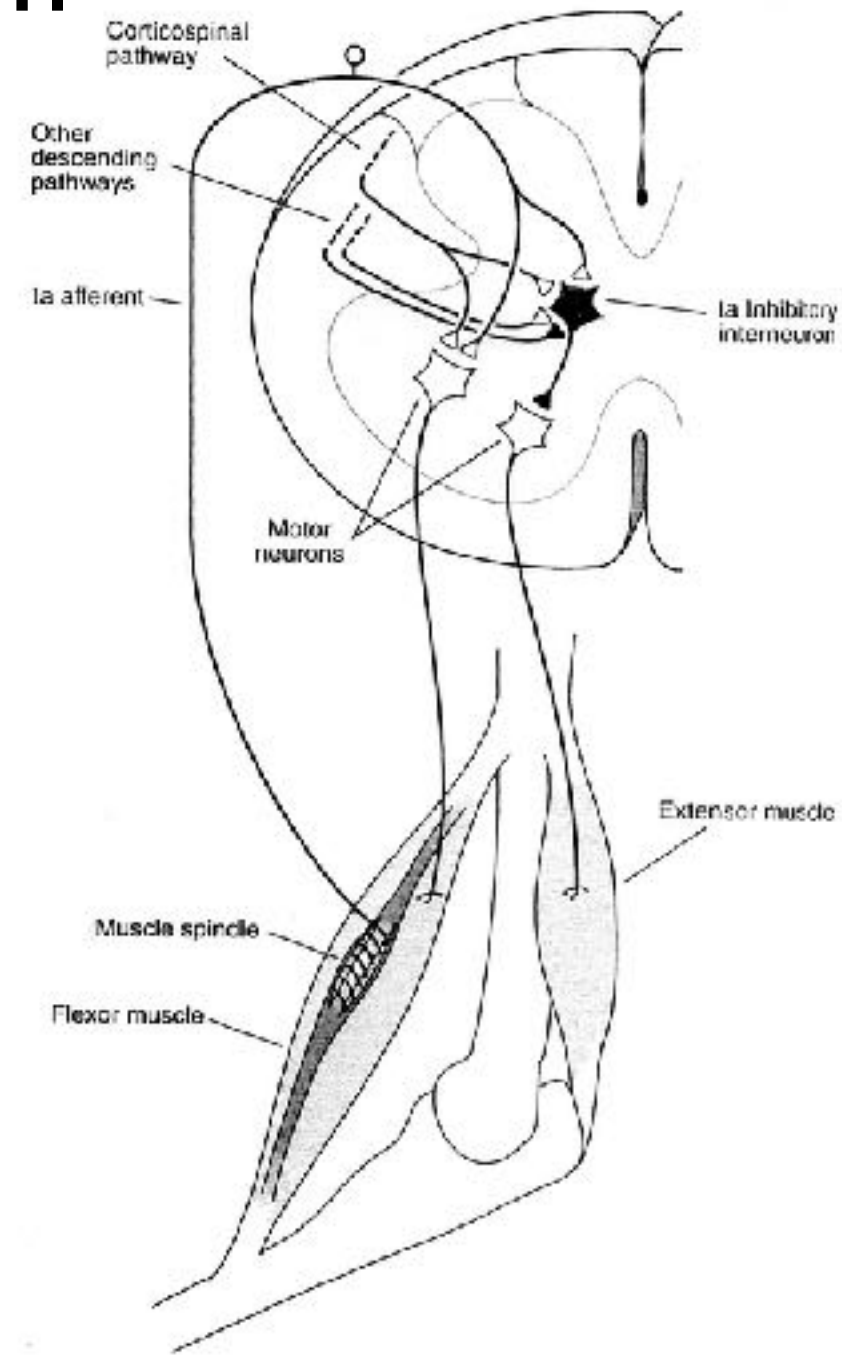
- the stretch reflex acts as a negative feedback loop



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

spinal cord: coordination

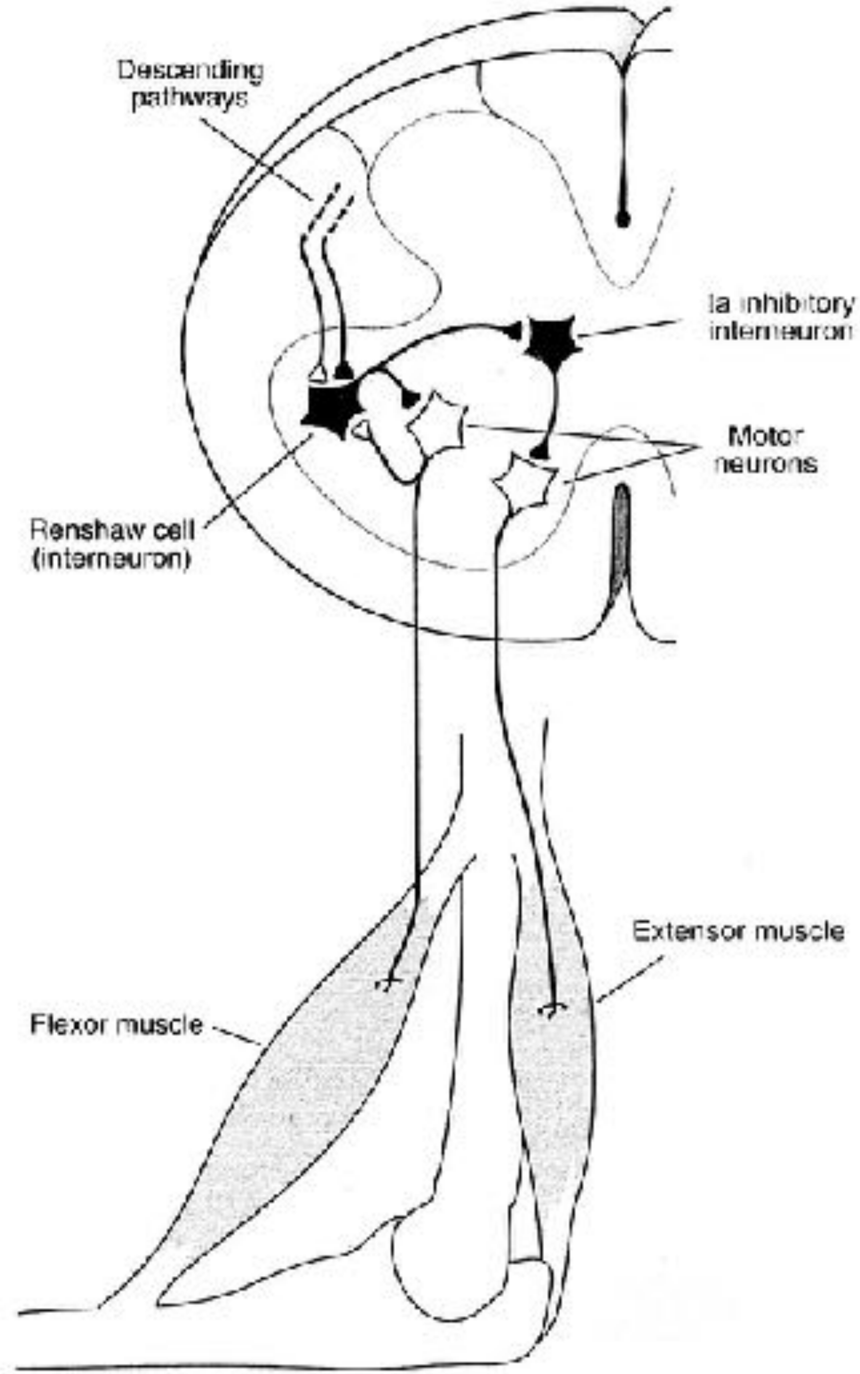
- Ia inhibitory interneuron mediates reciprocal innervation in stretch reflex, leading to automatic relaxation of antagonist on activation of agonist



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

spinal cord: synergies

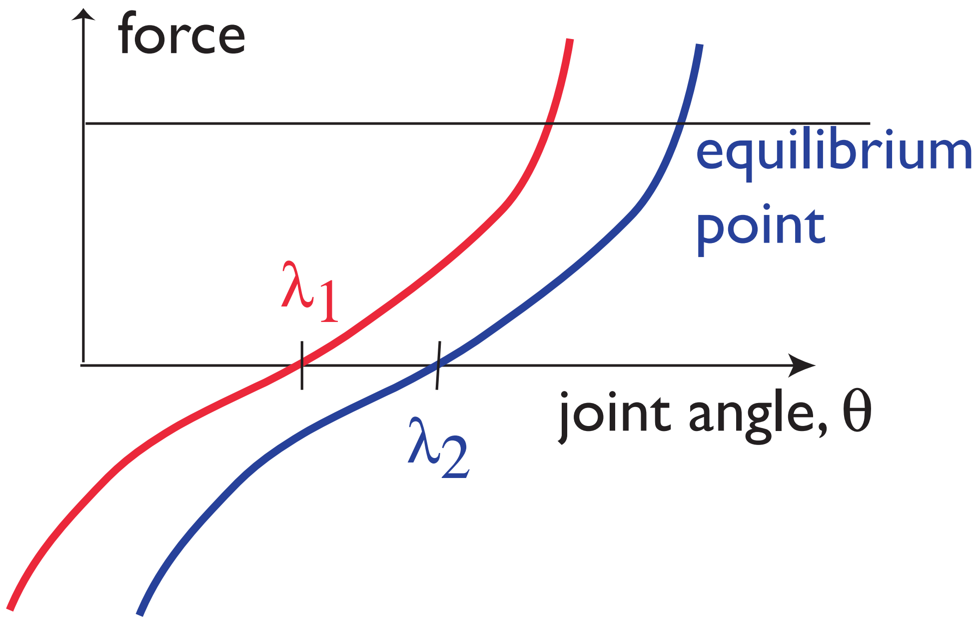
- Renshaw cells produce recurrent inhibition, regulating total activation in local pool of muscles (synergy)



[Kandel, Schartz, Jessell, Fig. 38-3]

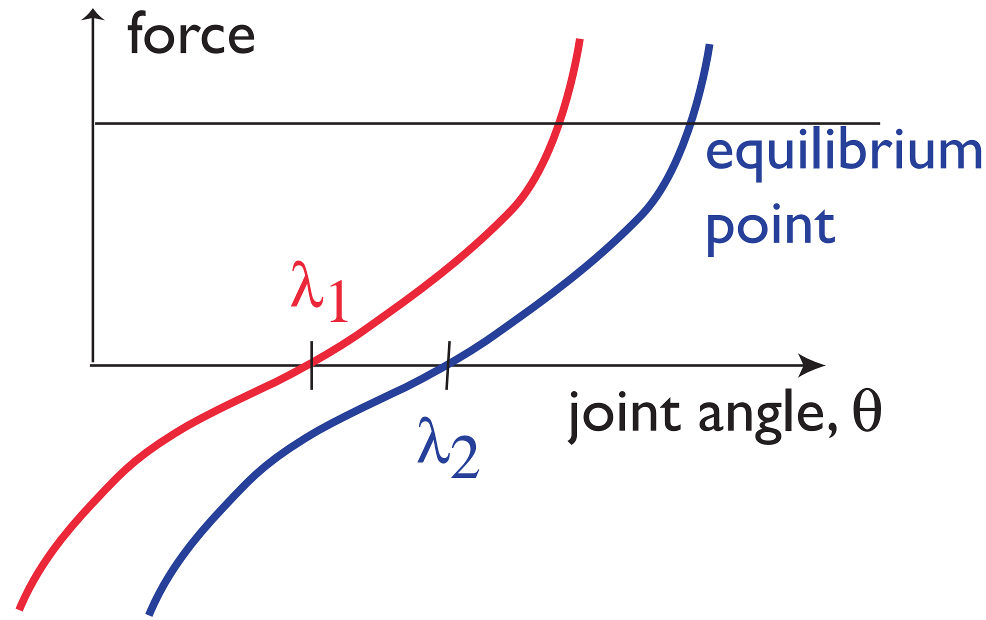
Posture

- muscle-joint systems have an equilibrium point during posture that is stable against transient perturbation



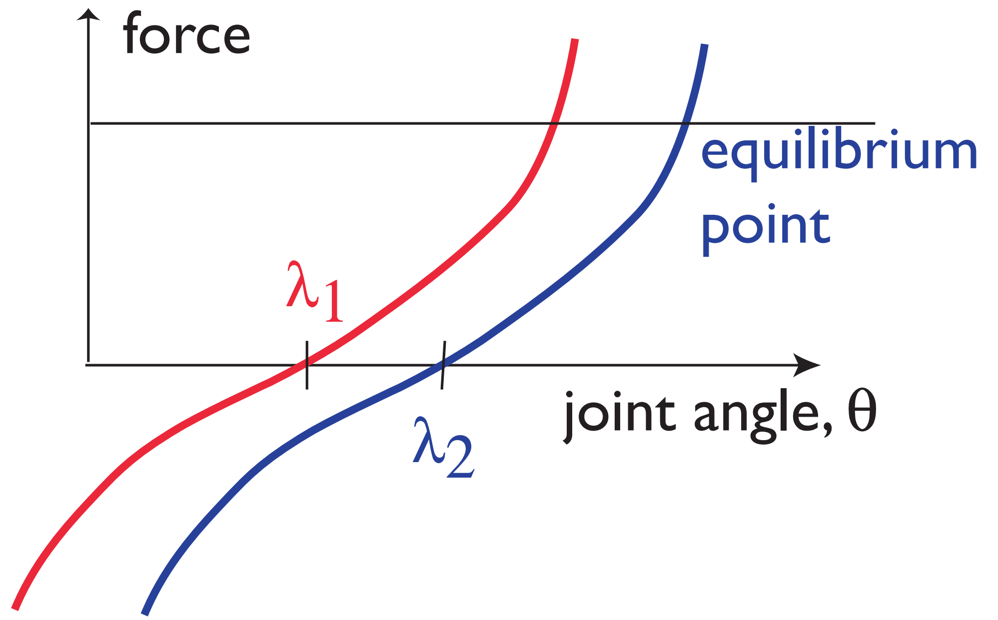
Movement entails change of posture

- that equilibrium point is shifted during movement so that after the movement, the postural state exists around a new combination of muscle lengths/joint configurations



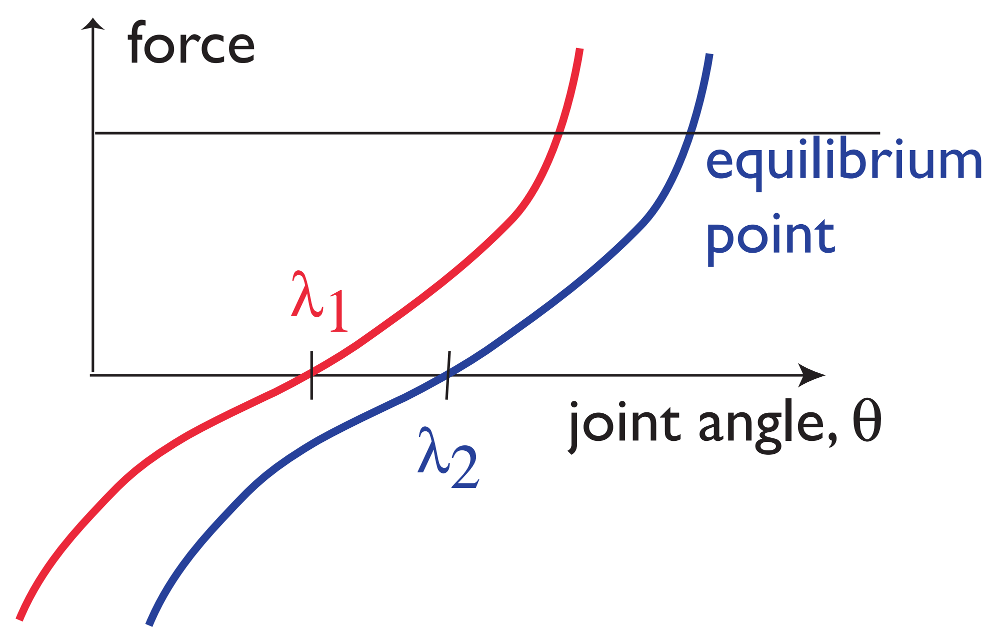
Movement entails change of posture

- most models account for movement in terms of generation of joint torques….
- => the shift of the EP is the single most overlooked fact in control models of movement generation



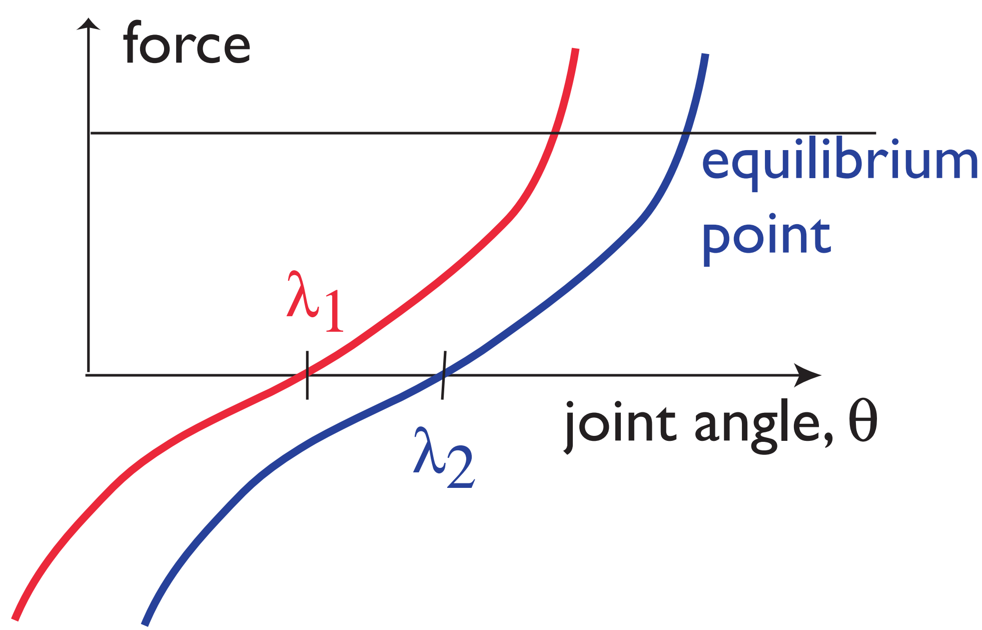
Does the "motor command" specify force/torque?

- no! Because the same descendent neural command generates different levels of force depending on the initial length of



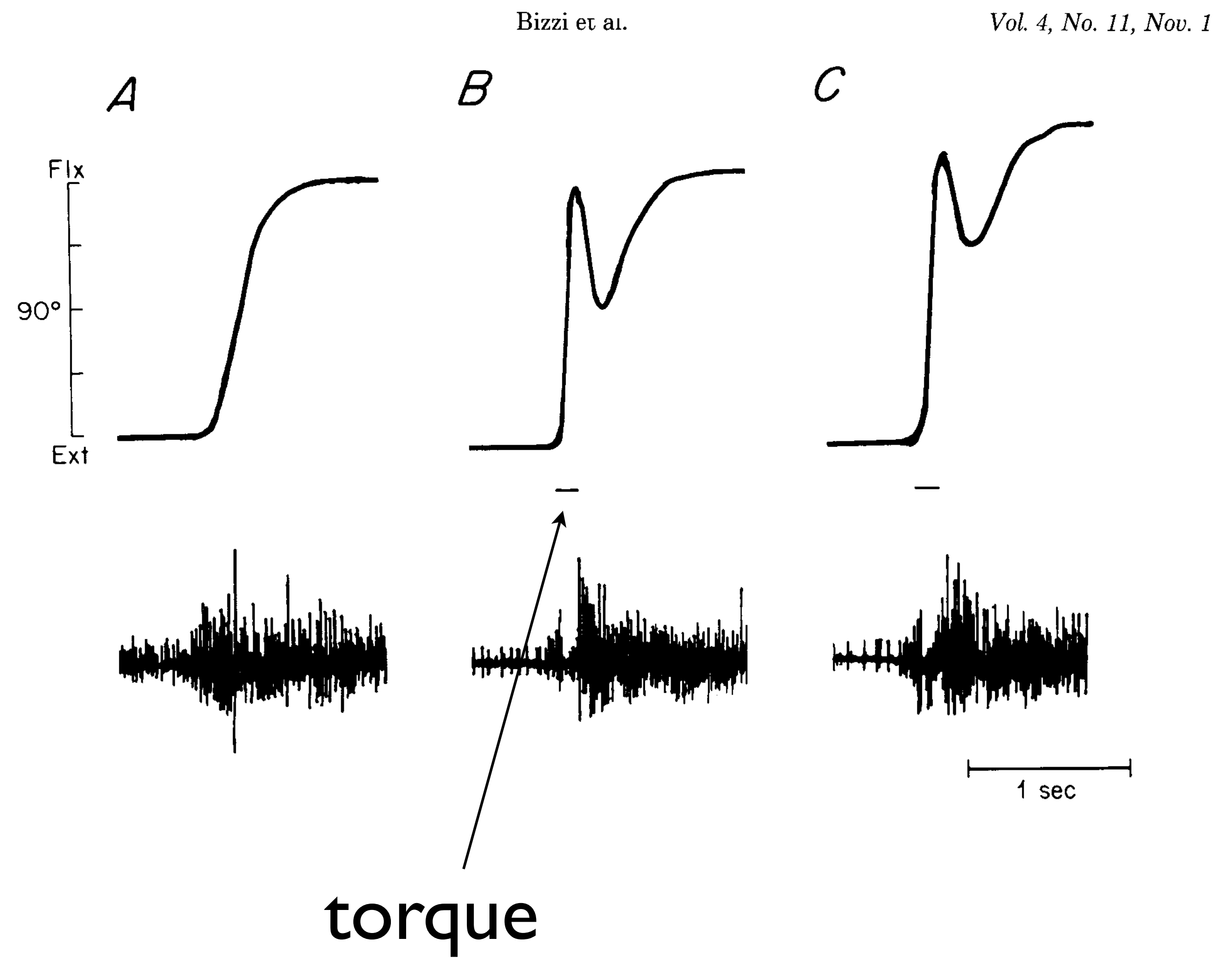
Virtual trajectory

- shifting the equilibrium point is necessary, but is it also sufficient?
- first answer: yes… simple ramp-like trajectories of the "r" command ("virtual trajectories") shift the equilibrium point smoothly in time…



time continuous shift of the equilibrium point

- during movement an external torque moves a joint to the target position
- in the deafferented animal, the joint returns to the "virtual trajectory"



[from Bizzi et al., J. Neurophys. 1984]

Virtual trajectory

- This view of movement generation is "quasi-static": the effector "tracks" the attractor that is shifted by the virtual trajectory
- This seems to trivialize the "optimal control" problem = generating the right time course of motor commands so that the effector arrives at the target in the desired time with zero velocity (and has some desired smooth temporal shape).

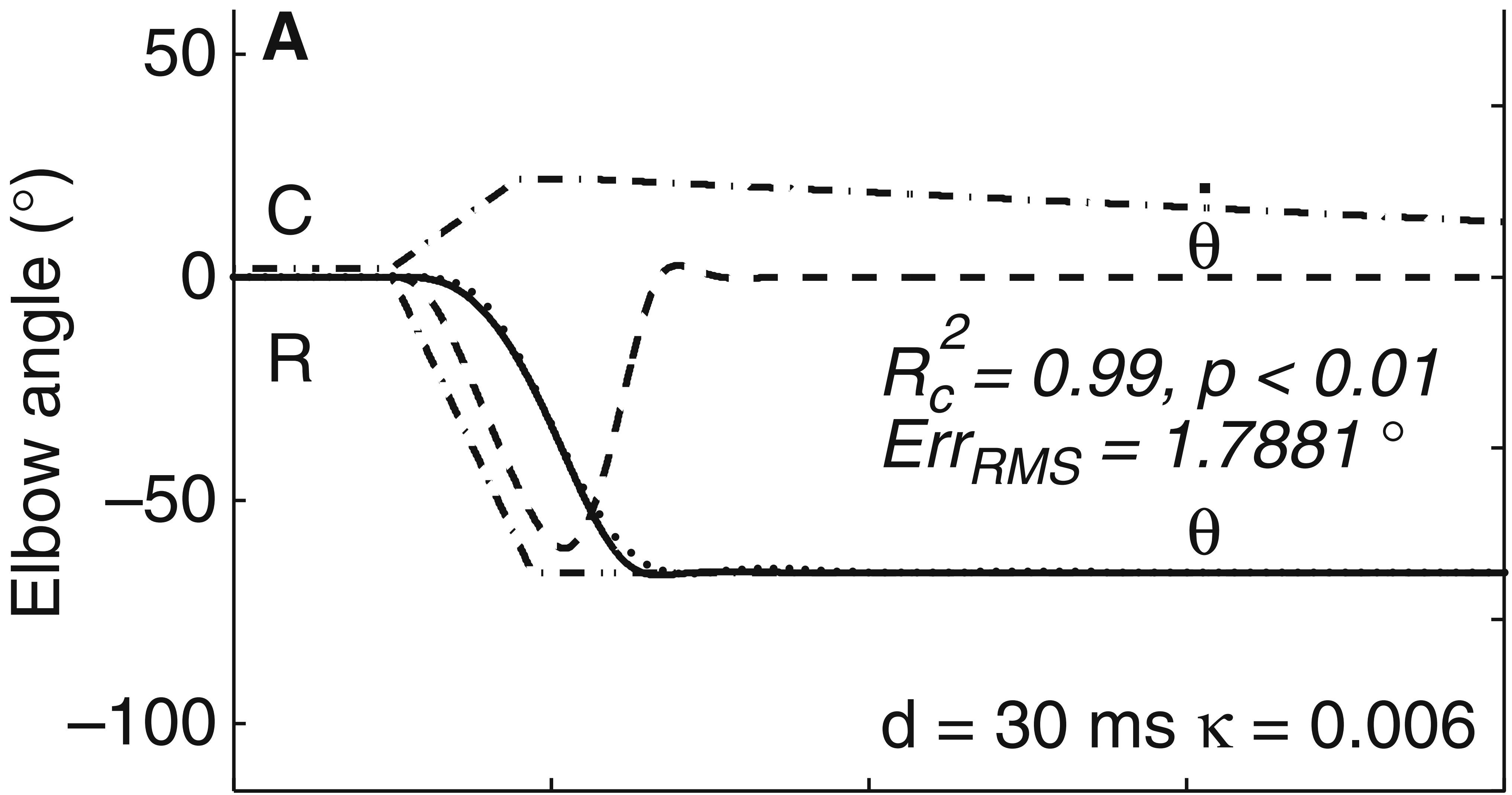
But

- is this simplification of movement generation as a "quasi-postural" system feasible for fast movements given the relatively soft muscles, the time delays involved in generating torque from muscles, etc. ?
    - the strong time delay between the command and the movement is a hint that this needs investigation

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

- first answer: yes =>
- simple ramp-like trajectories of the “r” command (“virtual trajectories”) shift the equilibrium point smoothly in time…

Pilon, Feldman, 2006



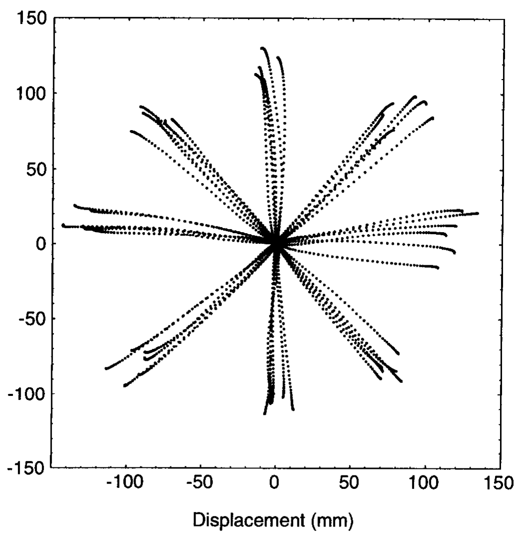
Shifting the equilibrium point is necessary, but is it also sufficient?

- such simple ramp-like trajectories of the “r” command (“virtual trajectories”) will be sufficient when movements
  - are sufficiently slow
  - interaction torques/mechanical conditions unchallenging
- but is this generally true?

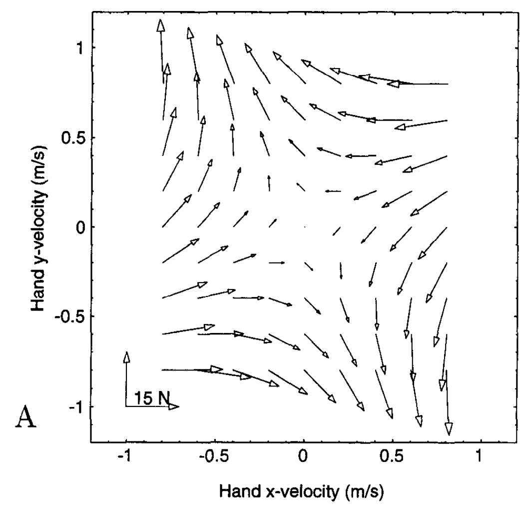
Limit case: velocity dependent force field

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

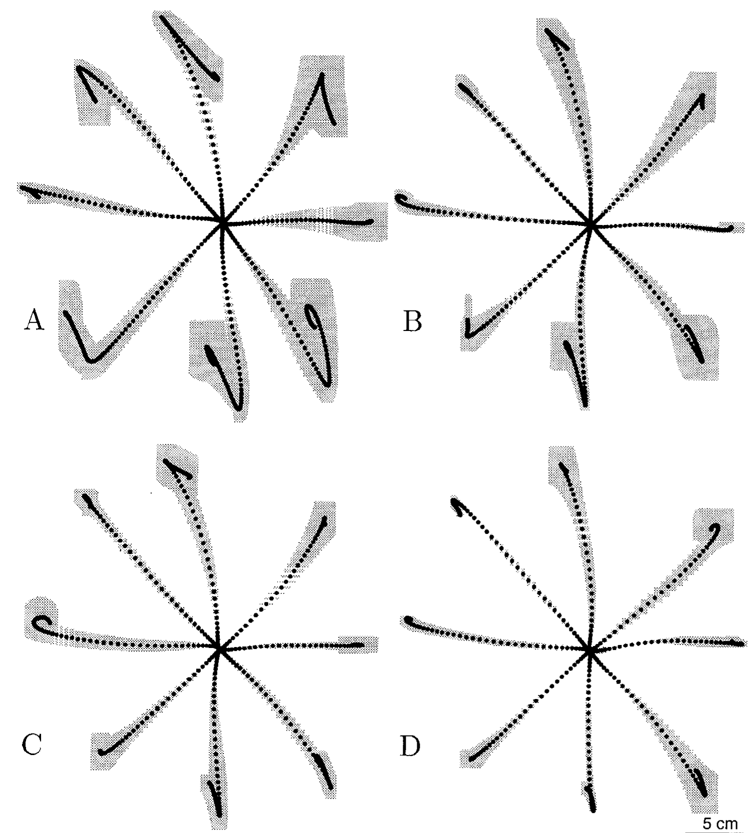
[Shadmehr, Mussa-Ivaldi, 1994]



center-out movements before force-field adaptation



velocity dependent force-field = zero at rest



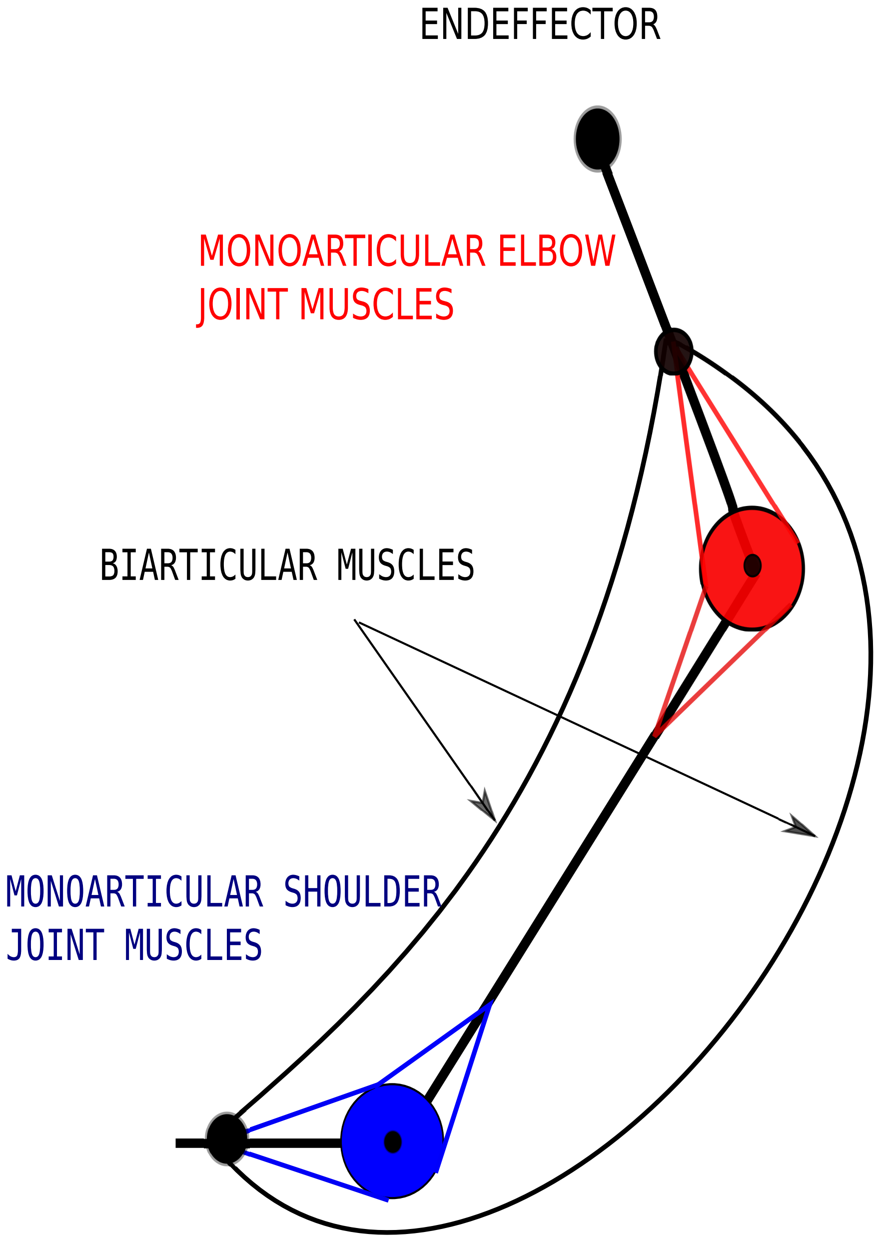
center-out movements at four stages during force-field adaptation

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
- => Poster of Rachid Ramadan

Rachid Ramadan

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



- muscle length link to joint angles

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

Rachid Ramadan

- Neuro-muscular model based on Gribble, Ostry et al., 98… consistent with EP hypothesis

$$A_{\mathrm{i}} = [l_{\mathrm{i}} - \lambda_{\mathrm{i}} + \mu \cdot \dot{l}_{\mathrm{i}}]^+$$

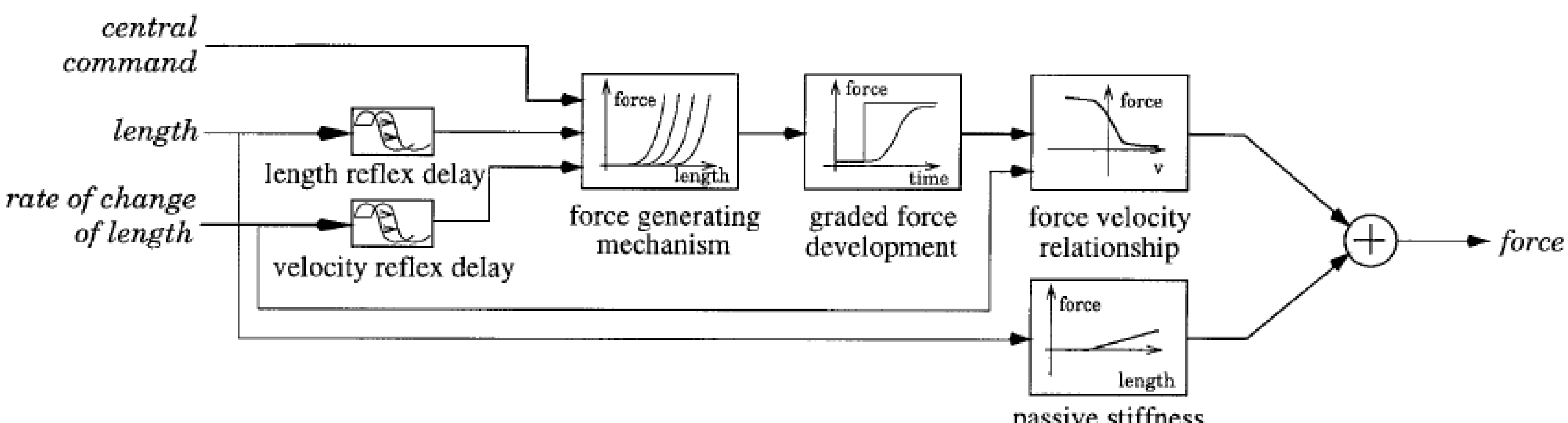
$$[x]^+ = \begin{cases} x, & \text{if } x > 0 \\ 0, & \text{if } x \le 0 \end{cases}$$

$$\tilde{M}_{\mathrm{i}} = \rho_{\mathrm{i}} \cdot (e^{sA_{\mathrm{i}}} - 1).$$

$$\tau^2 \ddot{M} + 2\tau \dot{M} + M = \tilde{M}$$

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

neglect delay



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- Biomechanical dynamics… standard…

$$T = -H \cdot F$$

with H defined as

$$H = \frac{\partial l}{\partial \theta} = \begin{pmatrix} \frac{\partial l}{\partial \theta_1} & \frac{\partial l}{\partial \theta_2} \end{pmatrix}$$

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

$$x = \cos(\theta_1) \cdot l_1 + \cos(\theta_1 + \theta_2) \cdot l_2$$
$$y = \sin(\theta_1) \cdot l_1 + \sin(\theta_1 + \theta_2) \cdot l_2$$

back to muscle:

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

Rachid Ramadan

- determine the "minimal" motor command that changes all lamda's the least possible:

$$\min_{\vec{\lambda}} \Psi(\vec{\lambda}) = \int_0^{t_f} \dot{\vec{\lambda}}(t)^2 \, \mathrm{d}t.$$

- given that the EP shifts: with boundary conditions

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

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

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

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

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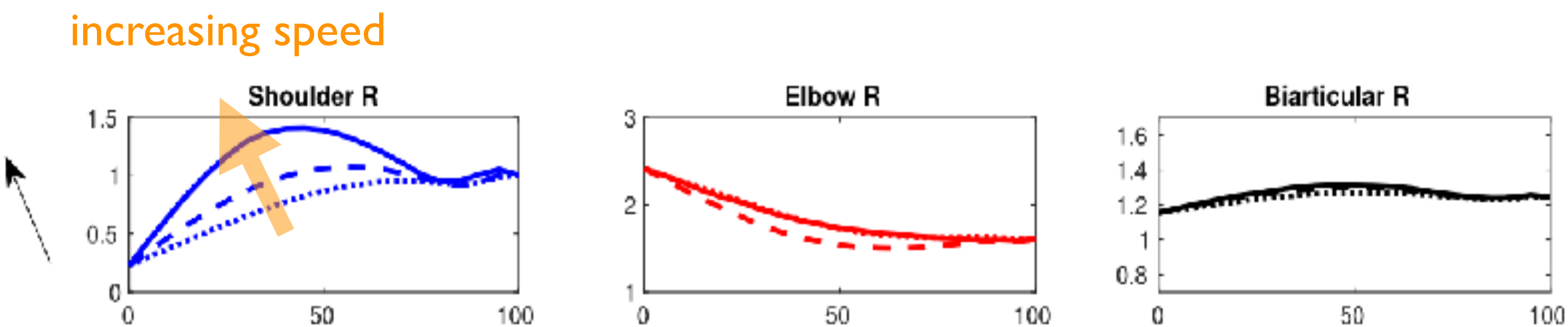
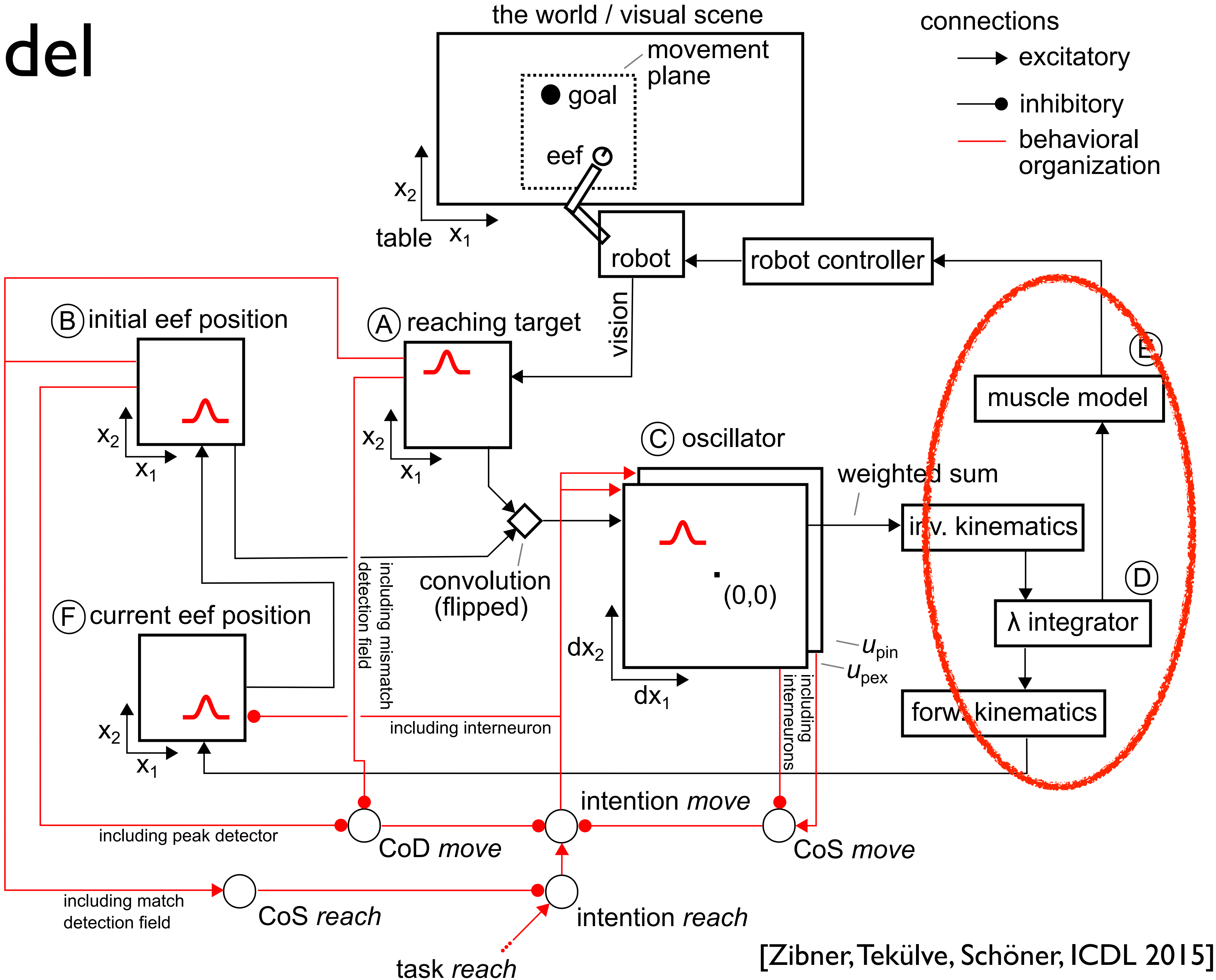
- minimal r-commands at increasing movement speeds

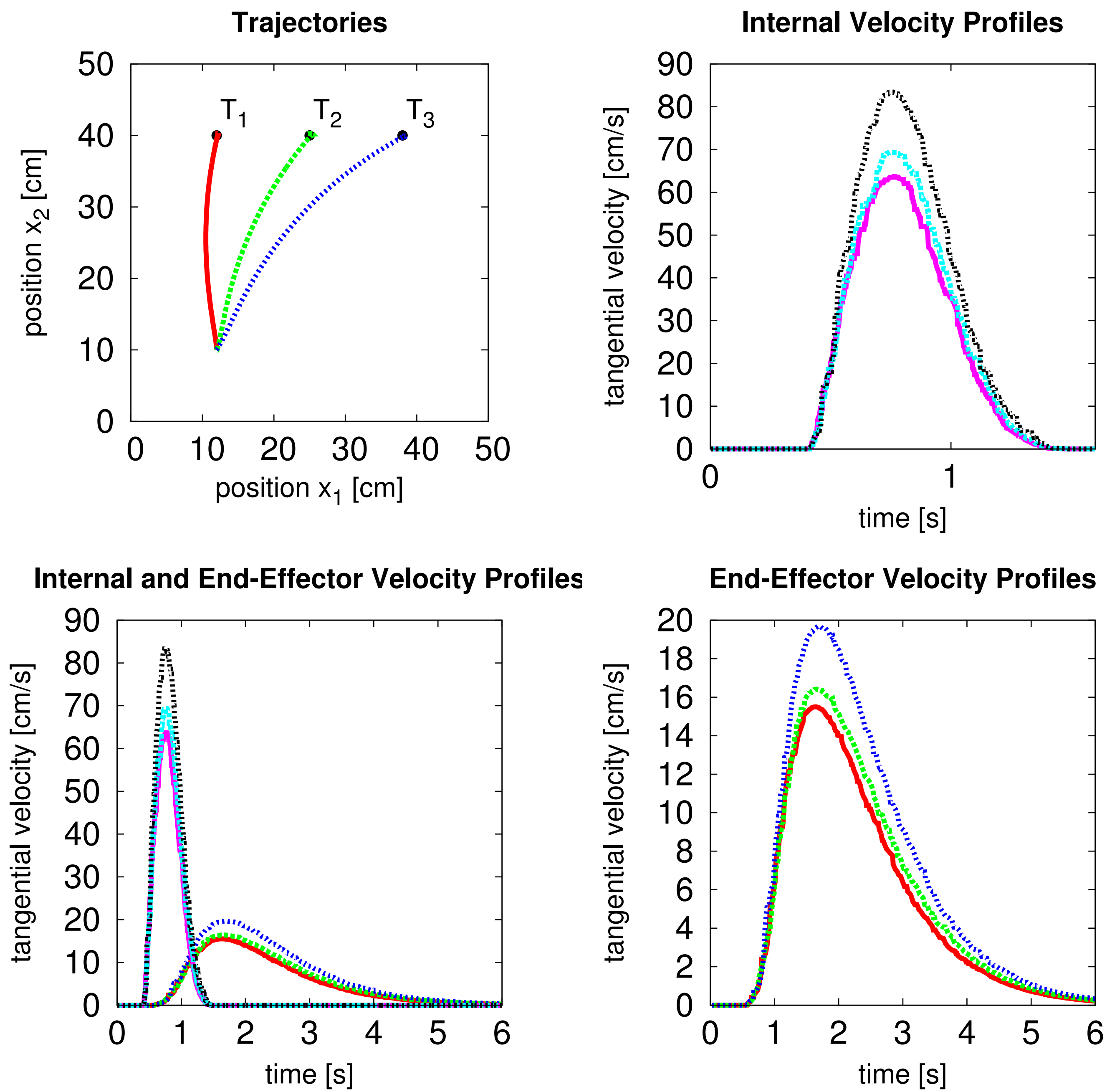


Model



[Zibner, Tekülve, Schöner, ICDL 2015]

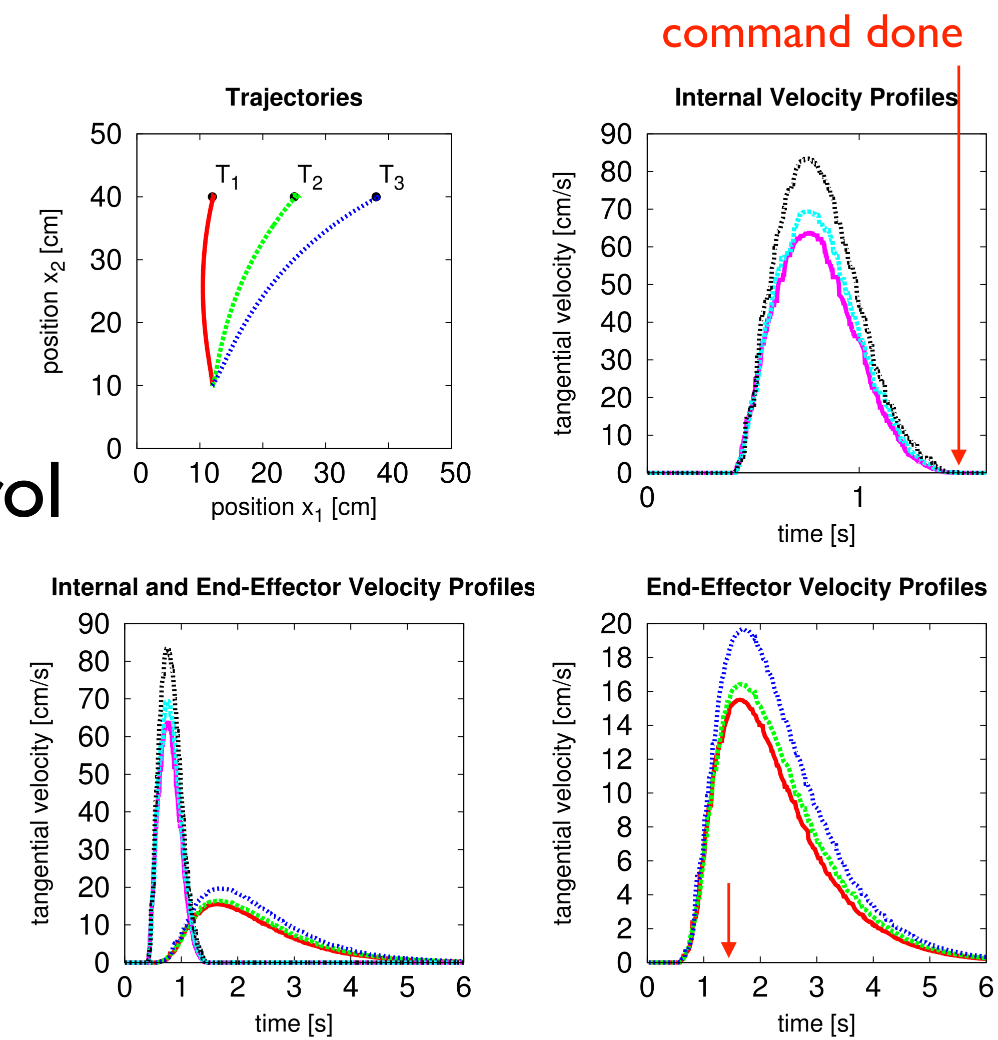
Architecture



[Zibner, Tekülve, Schöner, ICDL 2015]

Architecture

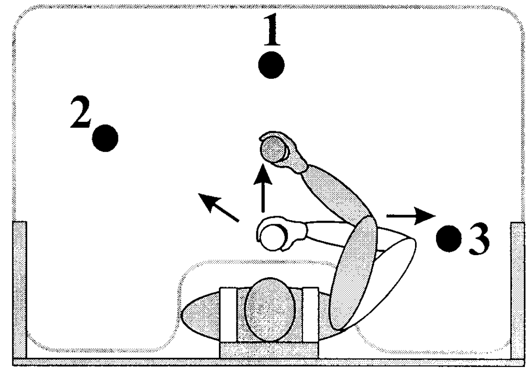
- time delay between "command' and movement
- broad implications for control
  - for coordination
  - for sequential organization
  - non-isomorphic control signals?

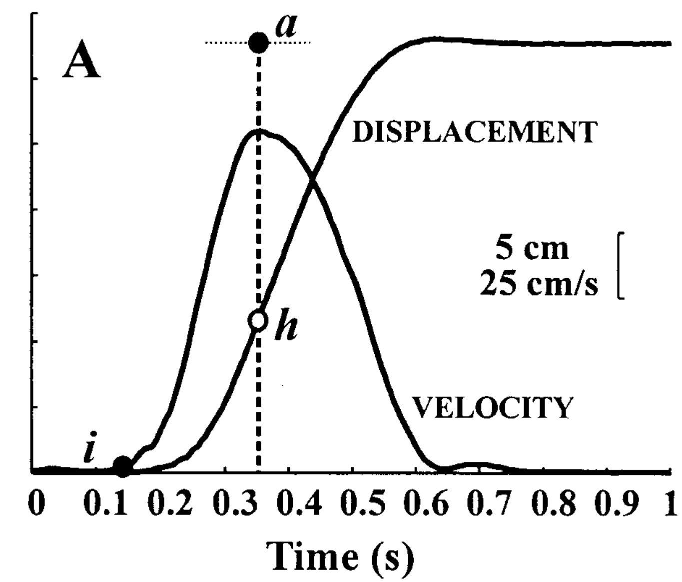


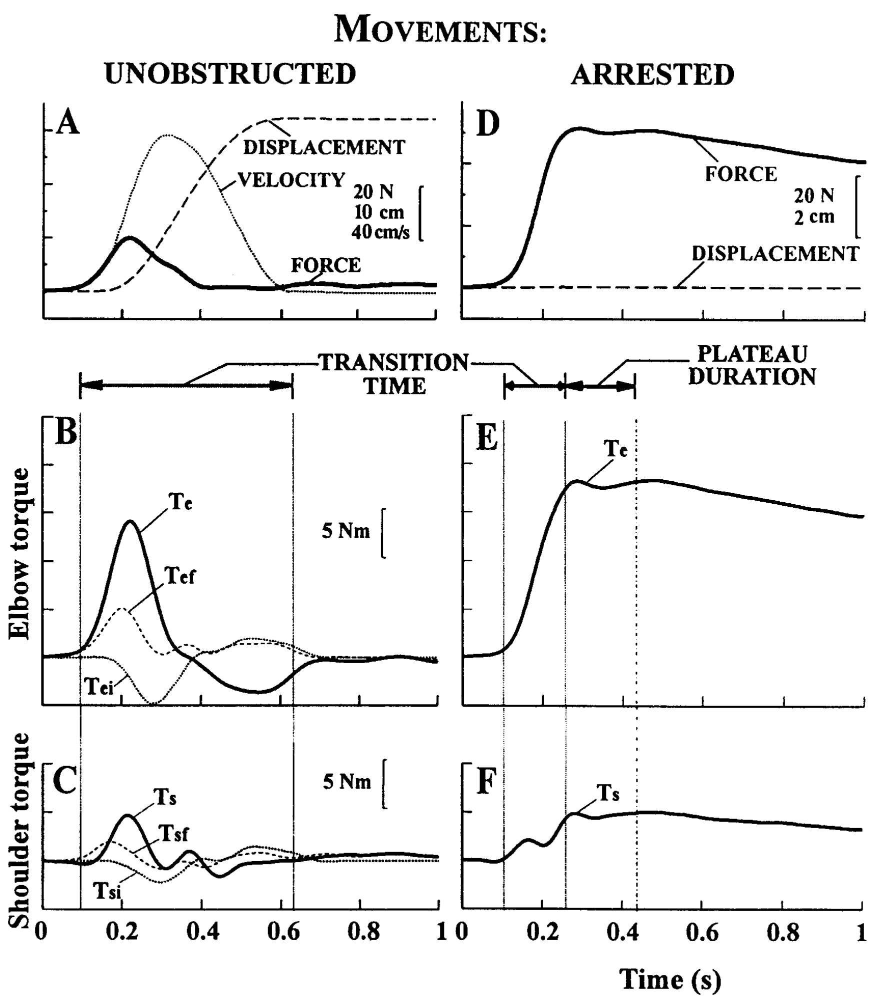
[Zibner, Tekülve, Schöner, ICDL 2015]

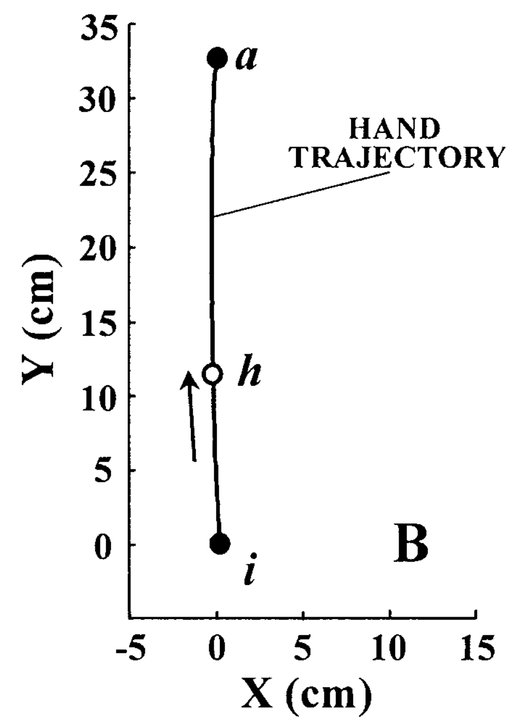
Experimental data

[Ghafouri Feldman, 2001]

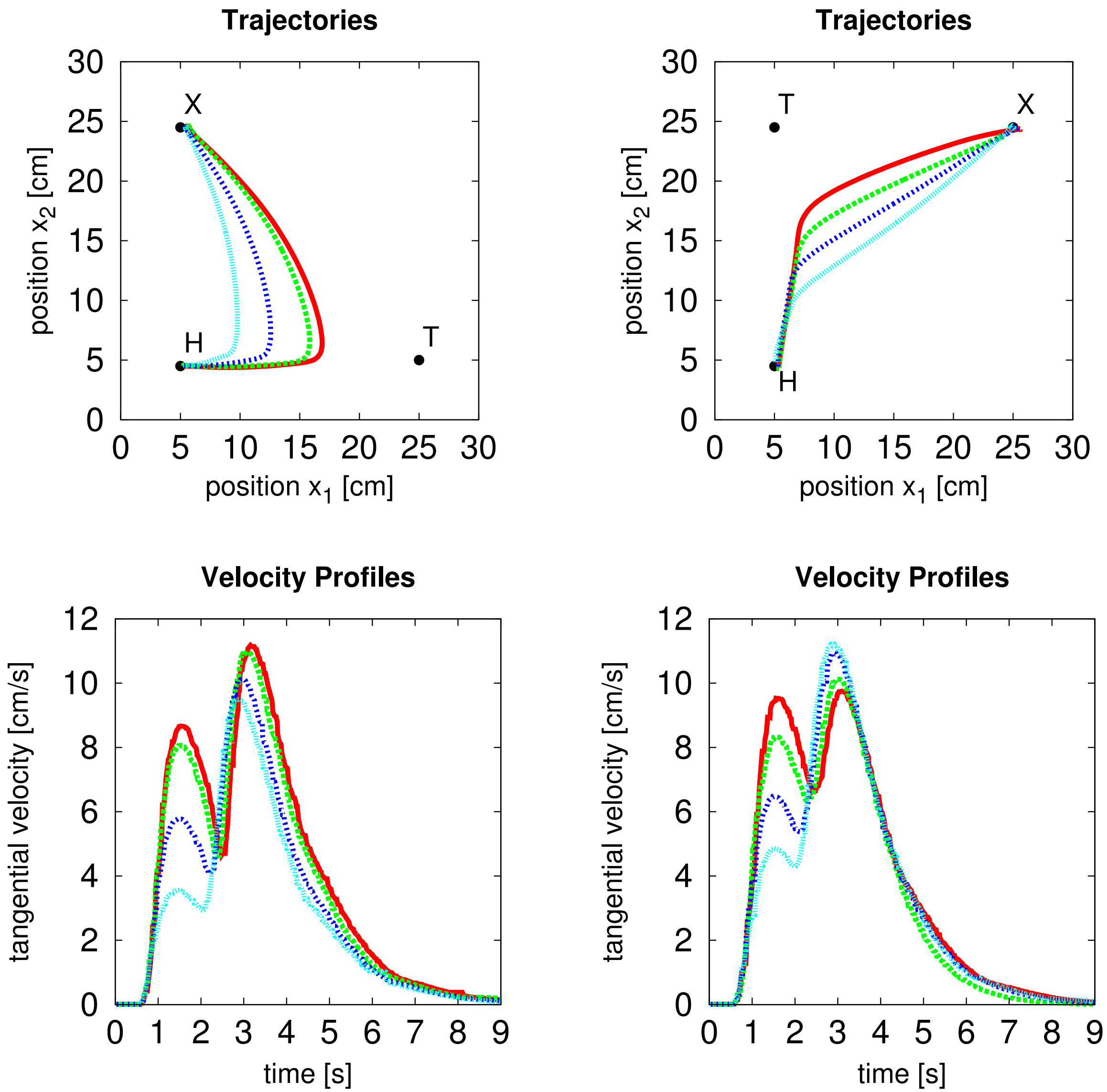








Architecture: online updating



[Zibner, Tekülve, Schöner, ICDL 2015]

Conclusion

- muscle dynamics and biomechanical dynamics make that the optimal control problem cannot be entirely trivialized: appropriate space-time virtual trajectories are needed to generate realistic movement behavior