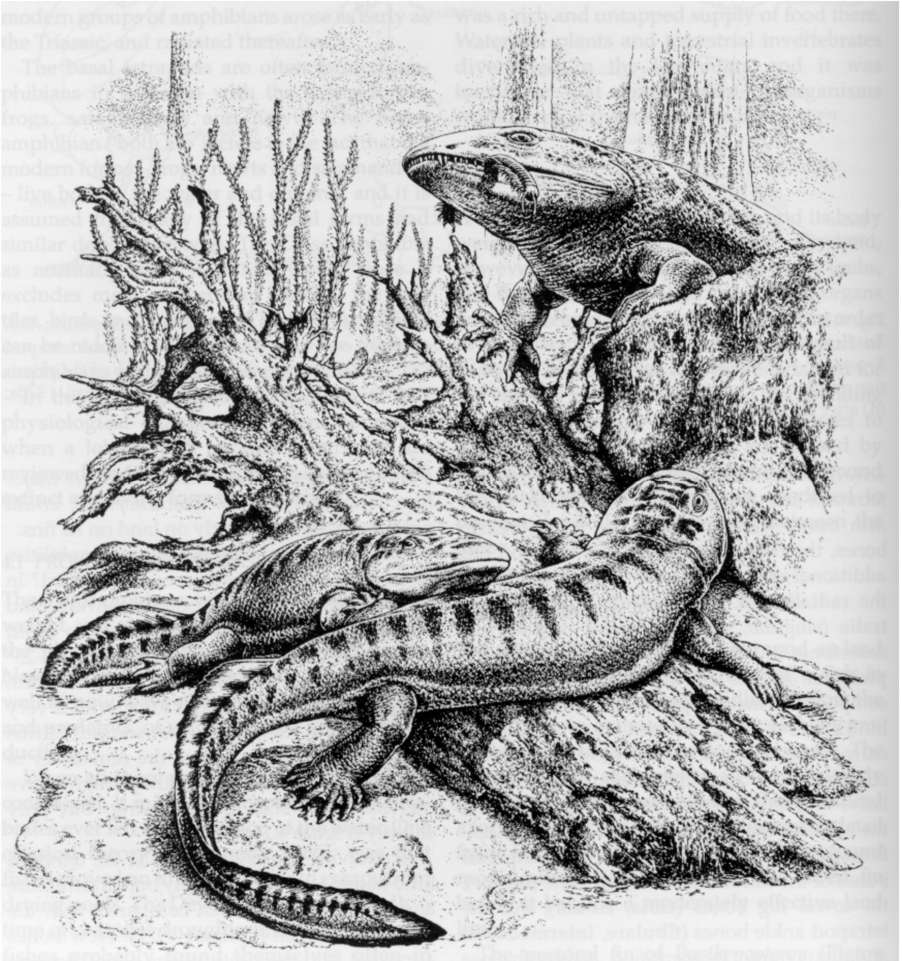
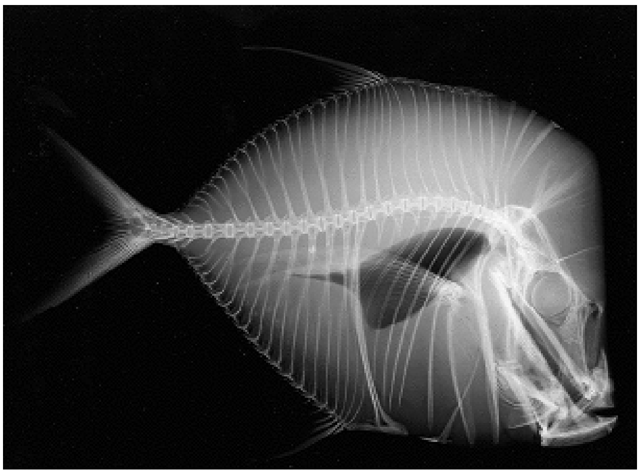
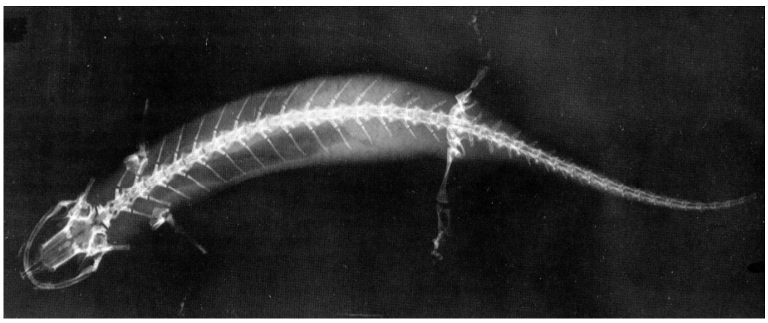


Legged Terrestrial Locomotion in (vertebrate) **Animals**

Peter Aerts & Kristiaan D'Août
University of Antwerp, BE

Aquatic organisms :
neutrally buoyant

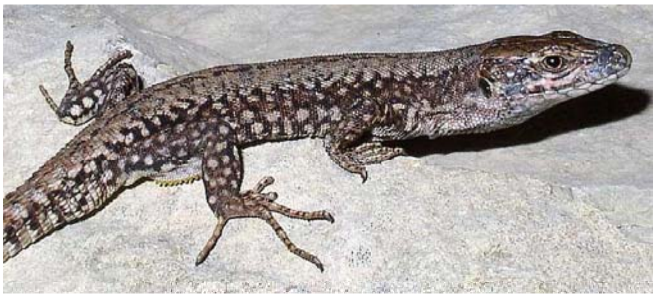




Terrestrial organisms :
Locomotion means
=> Support (against gravity)
=> Propulsion
=> Balance (postural control)

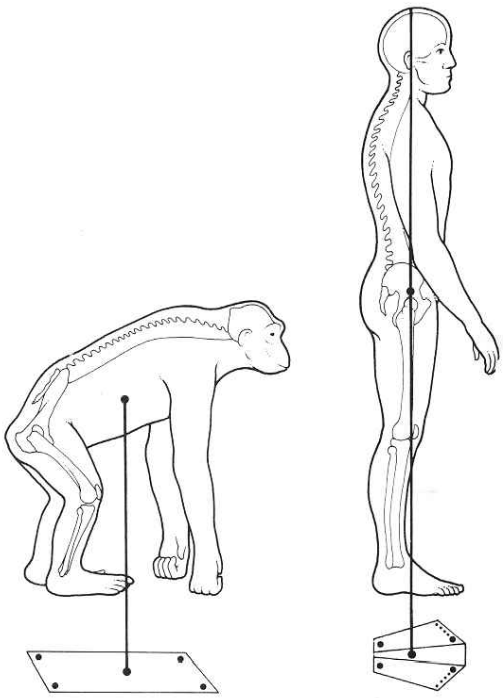
Propulsion & Support

transversal limb posture



parasagittal limb posture

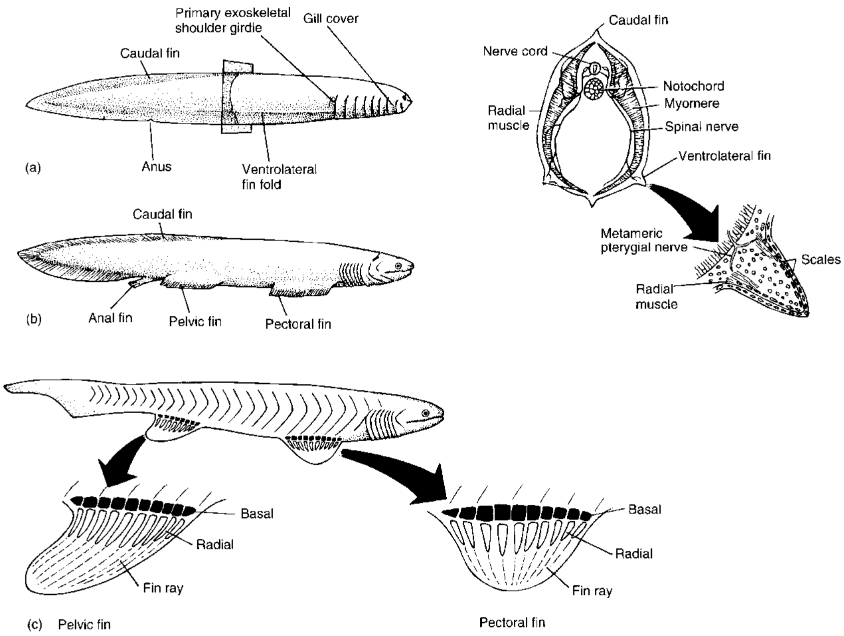
Balance



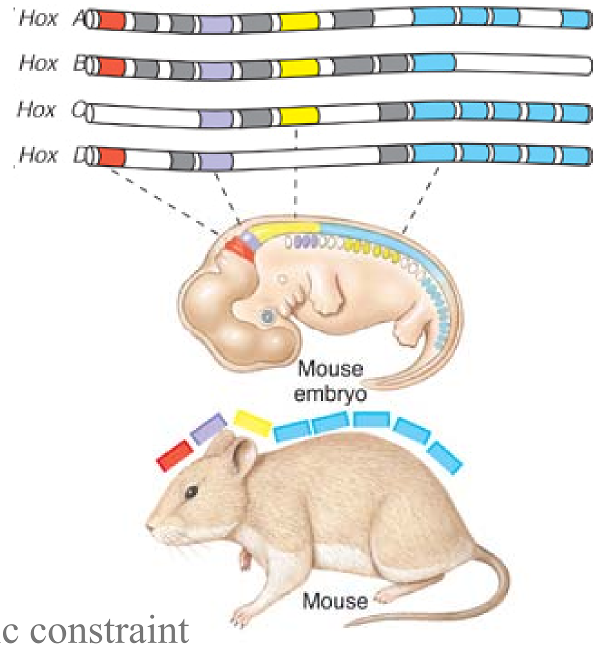
static equilibrium

dynamic equilibrium

Why 4 ?

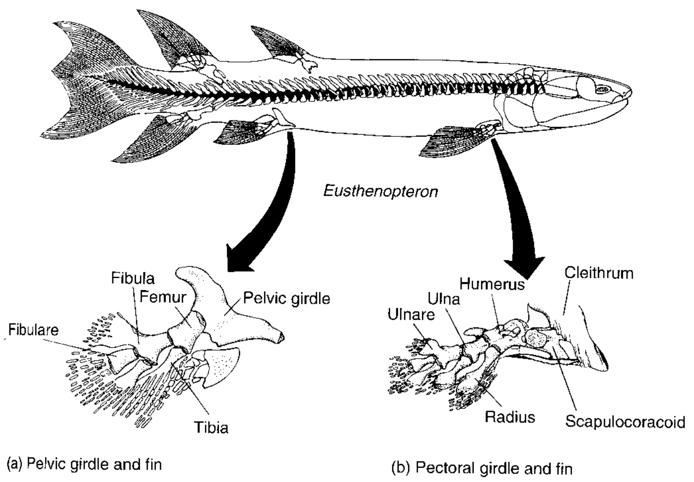


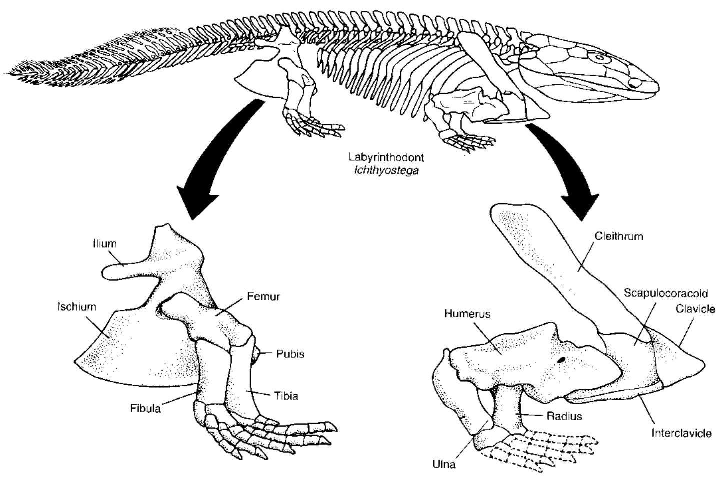
phylogenetic constraint

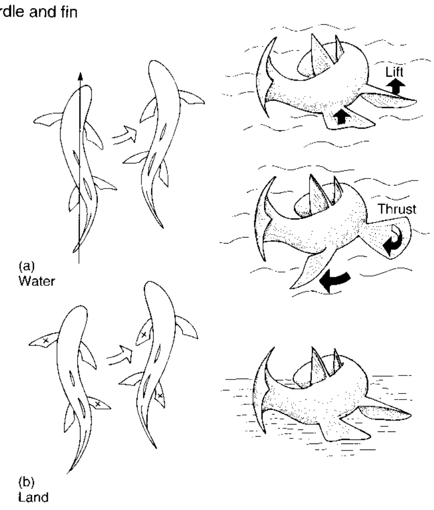


ontogenetic constraint

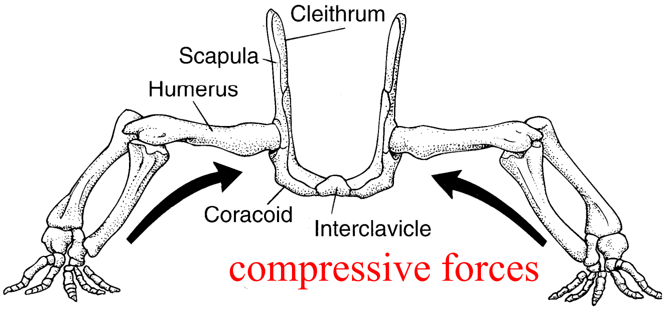
Locomorph Summer School
Odense 23 – 27 August 2012
ANIMAL LOCOMOTION





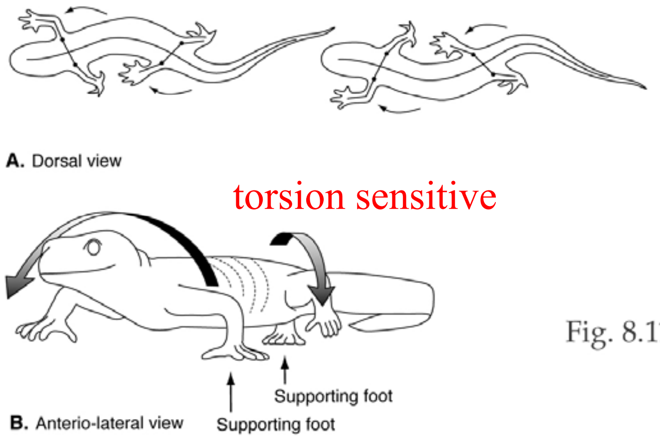


Transversal limbs: benefits and drawbacks



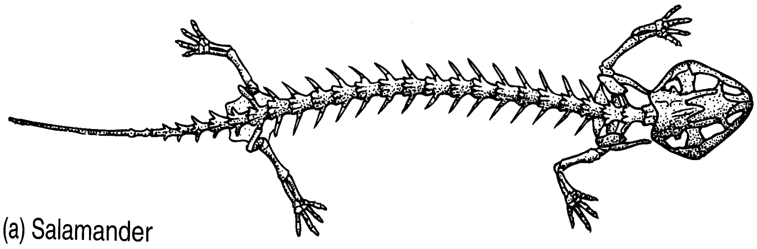
compressive forces

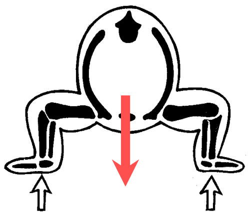
static equilibrium



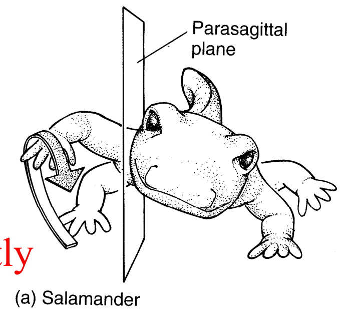
torsion sensitive

Fig. 8.11





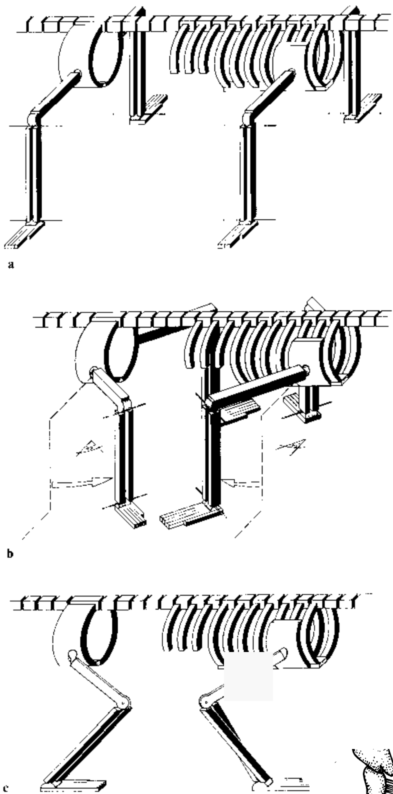
support : costly

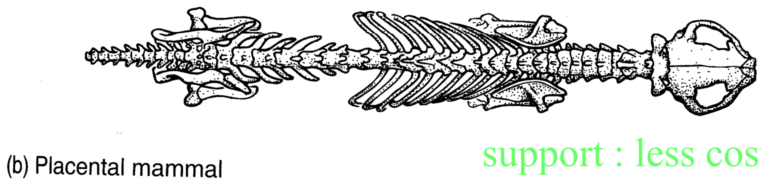


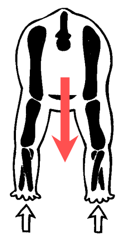
swing phase : costly

Locomorph Summer School
Odense 23 – 27 August 2012
ANIMAL LOCOMOTION

towards parasagittal limbs

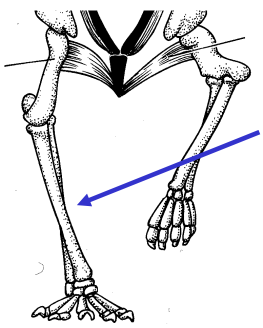


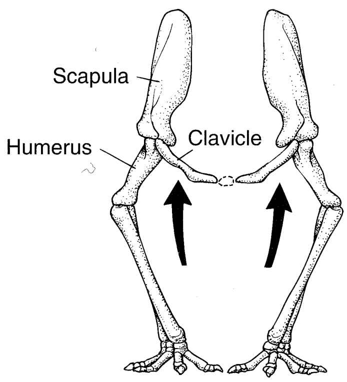




support : less costly

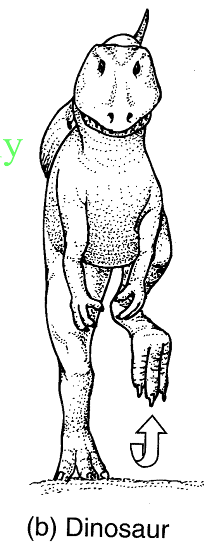
balance : focus more on dynamic equilibrium
(control cost)





less compressive forces

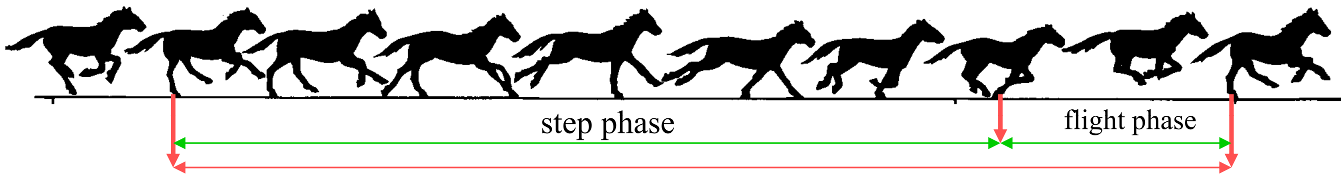
swing :
less costly



Terrestrial legged locomotion: cyclical movement pattern

- one cycle = stride;
- distance covered (by BCOM) in one cycle = stride length;
- # cycles per second = stride frequency

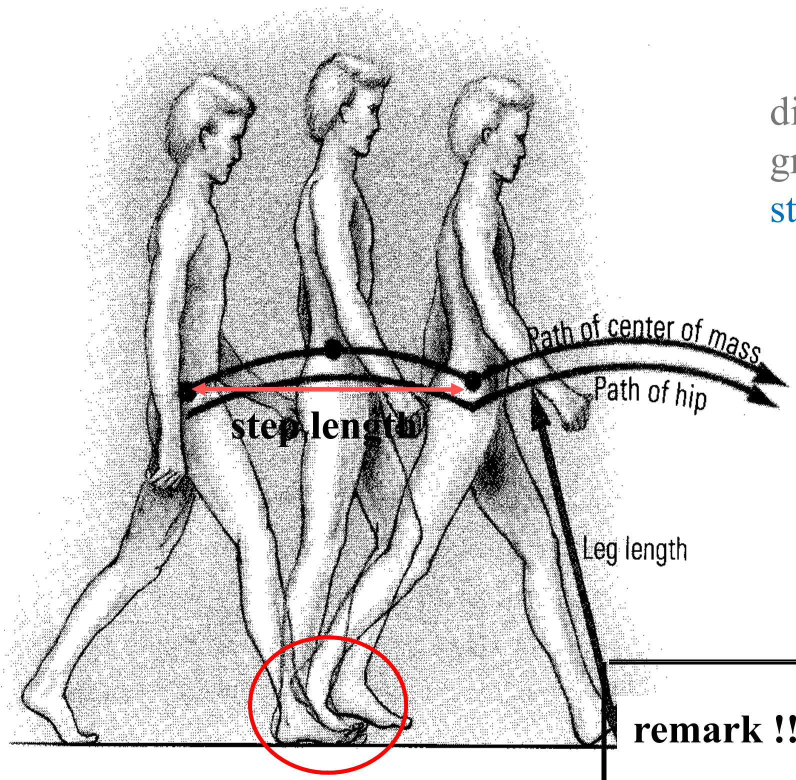
consequently : locomotion speed = stride length x stride frequency



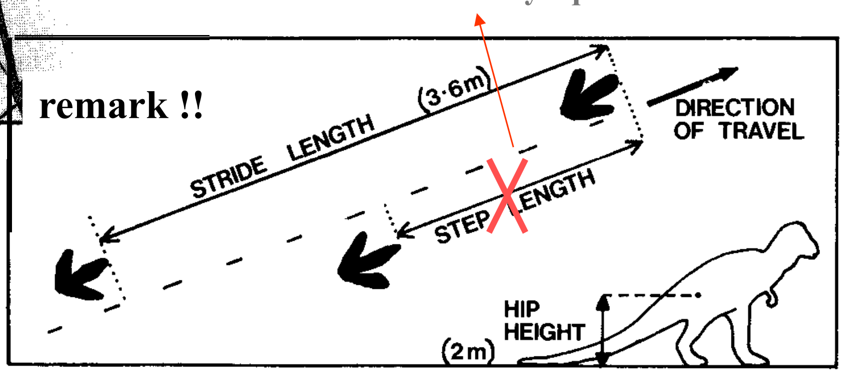
-stride can (eventually, depending on gait) be split in a step phase & flight phase

Locomorph Summer School
Odense 23 – 27 August 2012
ANIMAL LOCOMOTION

distance covered (by BCOM) during ground contact of one limb = step length



Definitions only equivalent at df = .5



options to increase speed (m/s) = stride frequency (1/s) x stride length (m)

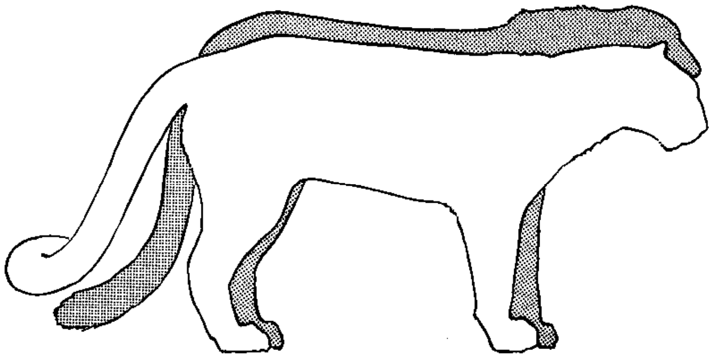
-increase frequency

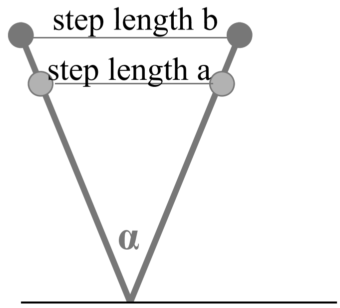
and/or

-increase length

1) Increase stride length : larger step and/or flight phase

a) larger relative limb length

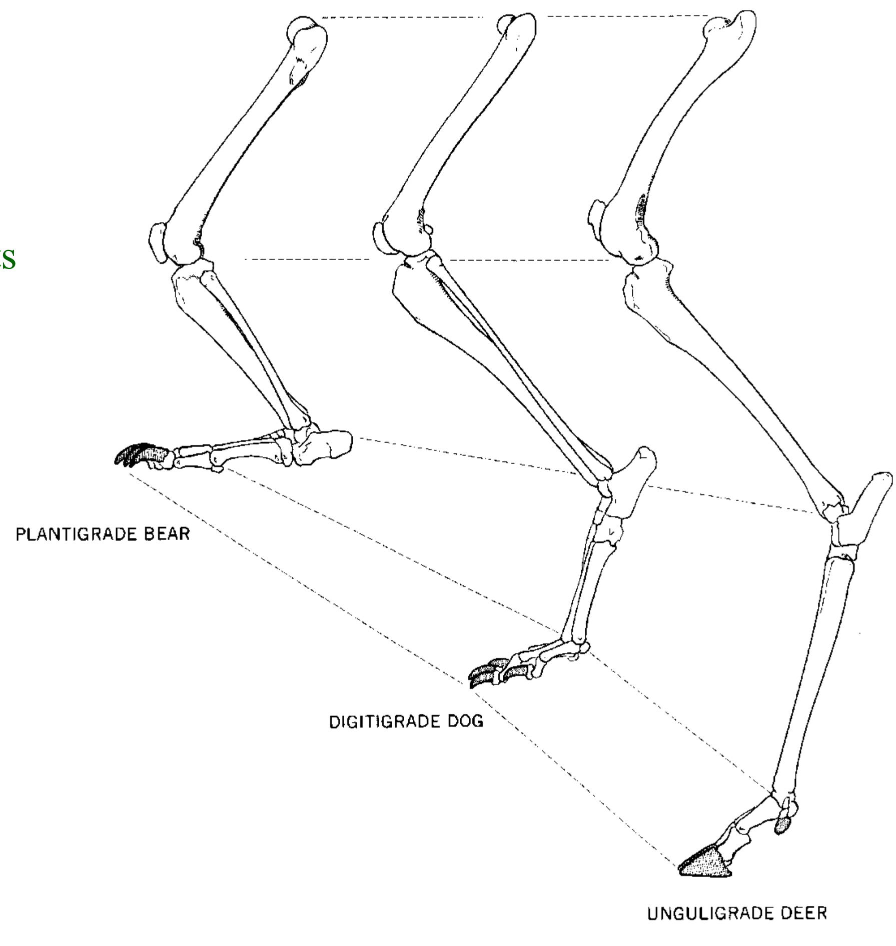




b) larger distal limb segments

c) adjust limb posture

-plantigrade
-digitigrade
-unguligrade

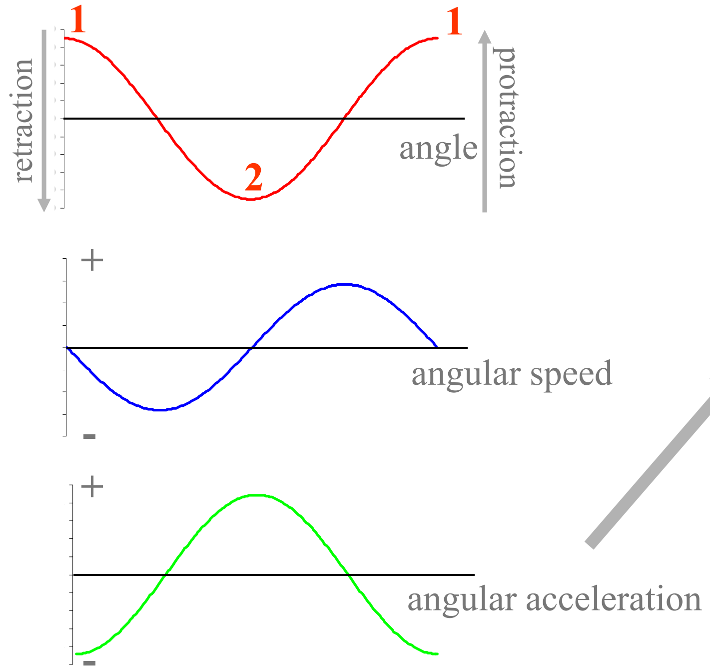


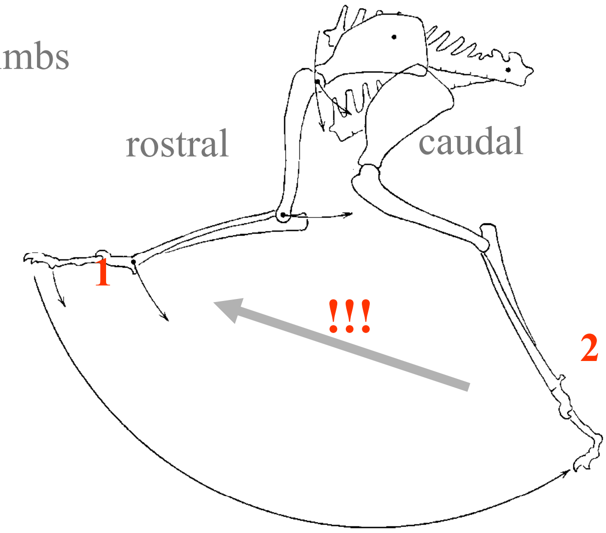
but:

locomotion = cyclic re- and protraction of limbs

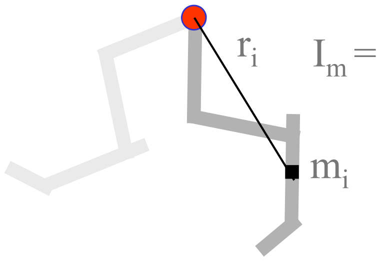
↓

implies angular speed fluctuations





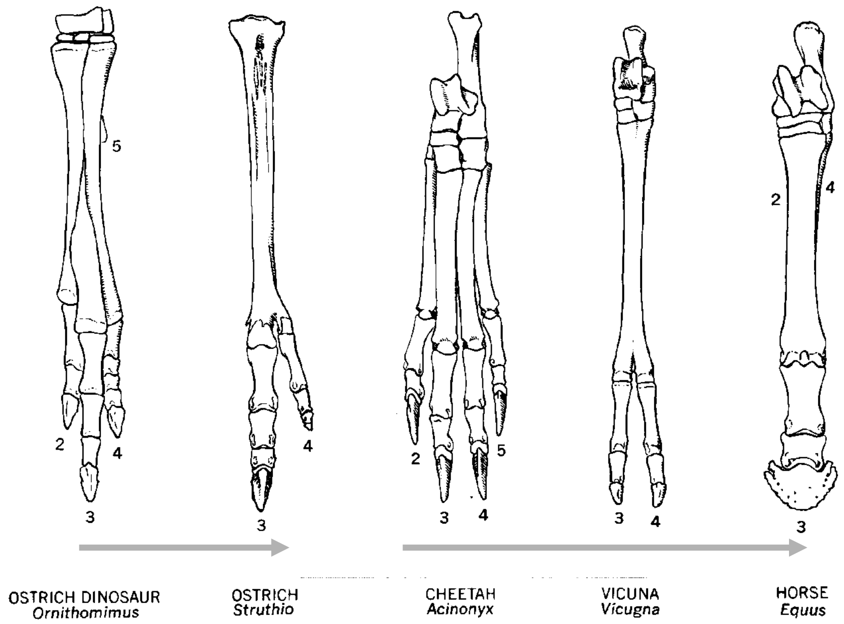
$I_m \ddot{\alpha} = \Sigma M_{ext}$ (I = moment of inertia)
(I = resistance against rotation)

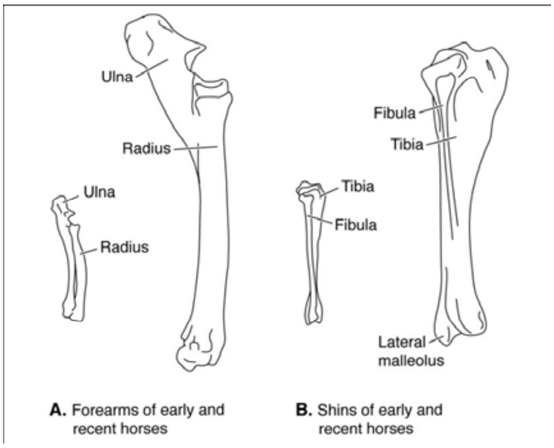


$I_m = \Sigma m_i r_i^2$

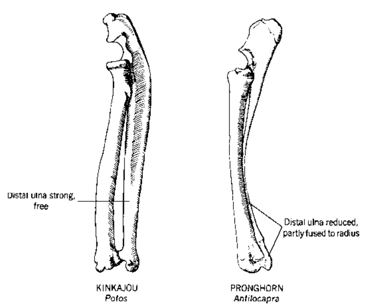
Longer limbs: increase of I_m because of larger r_i ⟶ higher costs

solution 1: reduce distal limb mass ($I_m = \Sigma m_i r_i^2$)

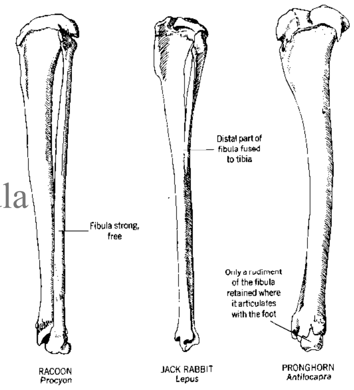




reduction ulna

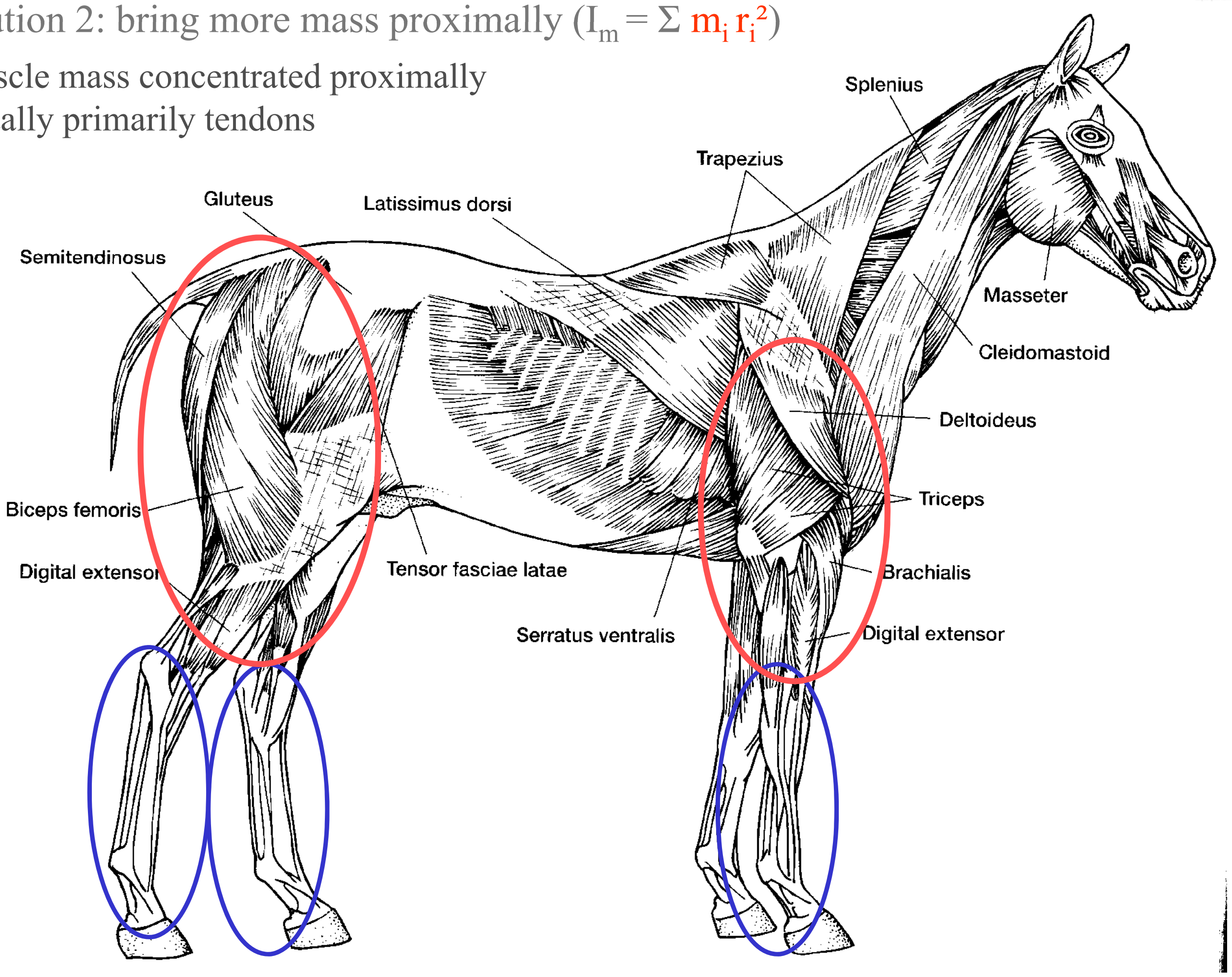


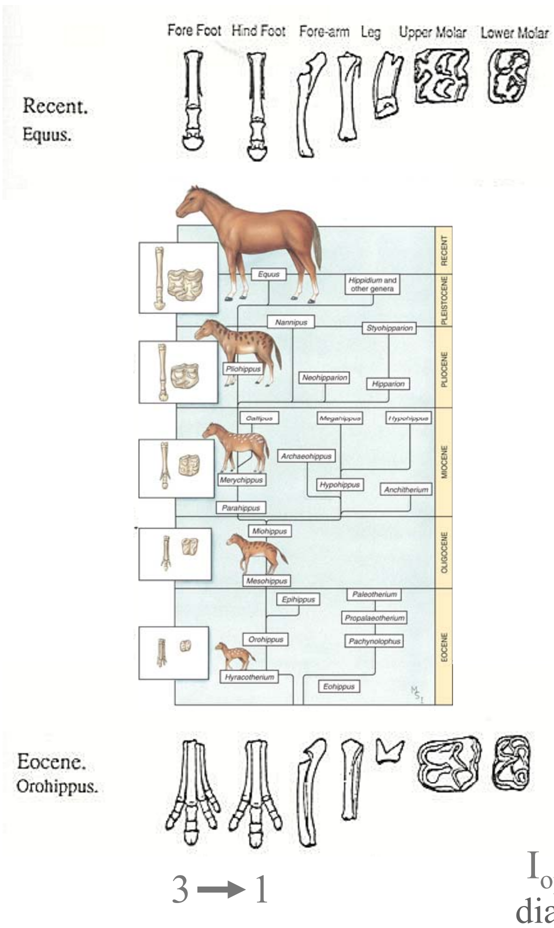
reduction fibula



solution 2: bring more mass proximally ($I_m = \Sigma\, m_i\, r_i^2$)

- muscle mass concentrated proximally
- distally primarily tendons





but: running faster

↓

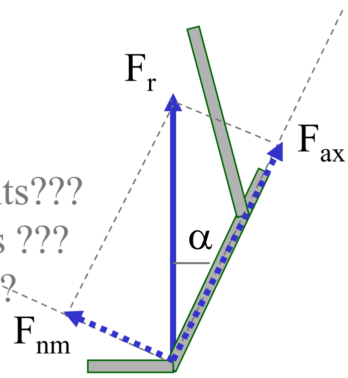
higher forces

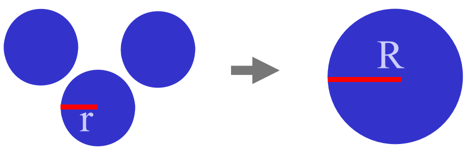
↓

??? reduction of distal segments???

??? lighter & longer segments ???

??? (bending)strength ???





similar axial strength = identical ∅-surface

$$3\pi r^2 = \pi R^2$$

$$r = (R^2/3)^{1/2}$$

I_{opp} = measure for resistence against bending

$I_{opp} = \pi\,(\text{diameter}^2 / 8)^2 = \boldsymbol{\pi R^4/4}$ (recent horse)

!!for eocene ancestor!!:

$I_{opp} = 3[\pi\,((R^2/3)^{1/2})^4/4] = 3[\pi\,(R^2/3)^2/4] = \boldsymbol{\pi R^4/12}$

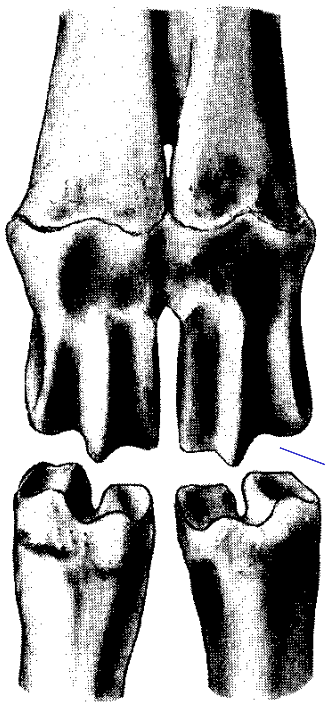
diameter recent metatarsal can be 0.76 x smaller (=lighter)

without loss of bending strength

but: longer segments linked to reduced distal muscle mass

↓

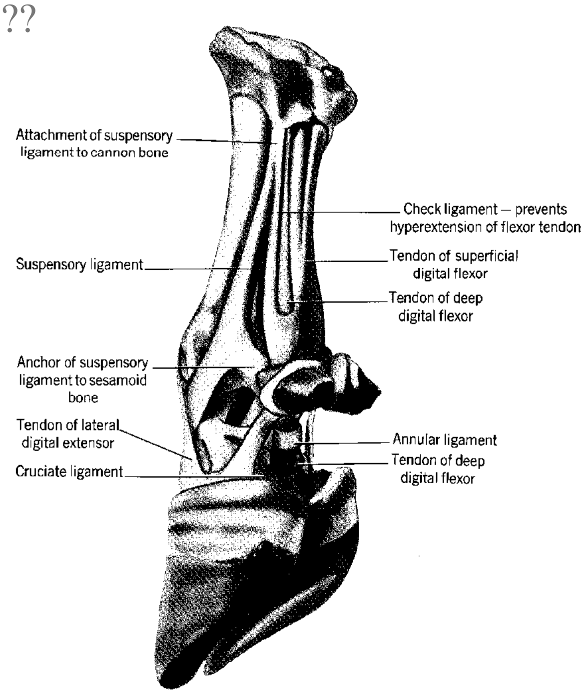
???loss of joint stability???



development of complex joint surfaces
(with loss of DOFs)

‘hinge’ (1 DOF)

(fetlock pronghorn)

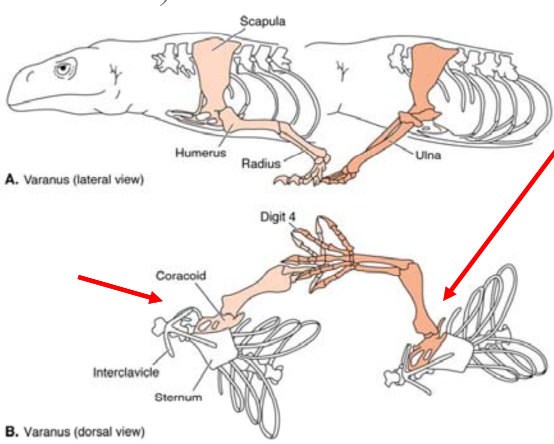


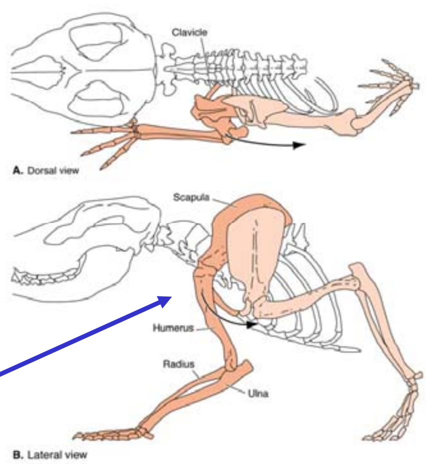
stabilization by ligaments

Locomorph Summer School
Odense 23 – 27 August 2012
ANIMAL LOCOMOTION

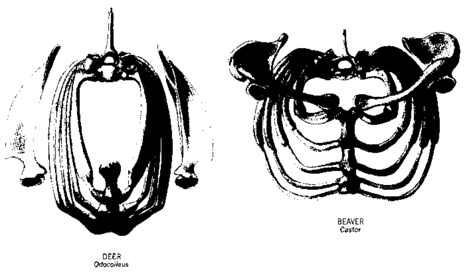
d) increase functional limb length

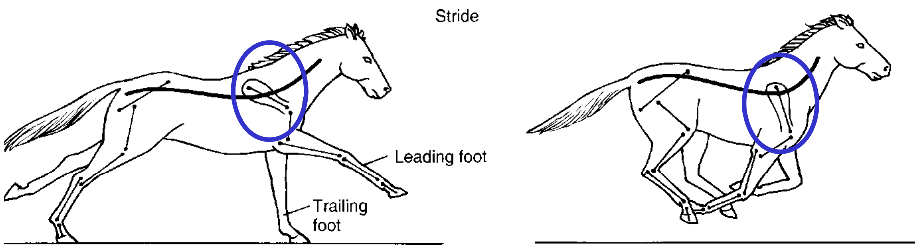
1) Transversal limbs: shift coracoid ⟶ longer step lengths





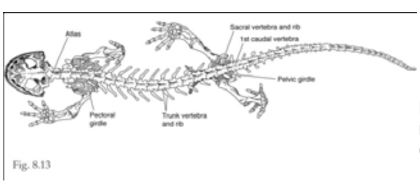
2) Parasagittal limbs: free scapula ⟶ longer step lengths

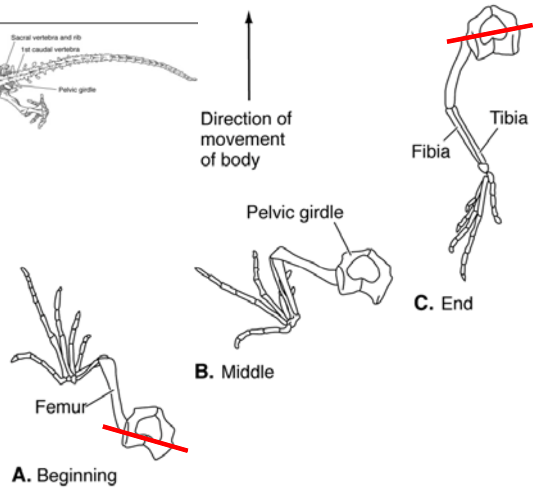


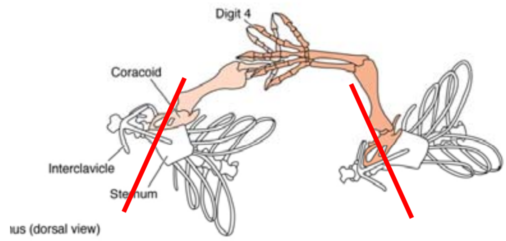


e) undulation vertebral column : longer step length

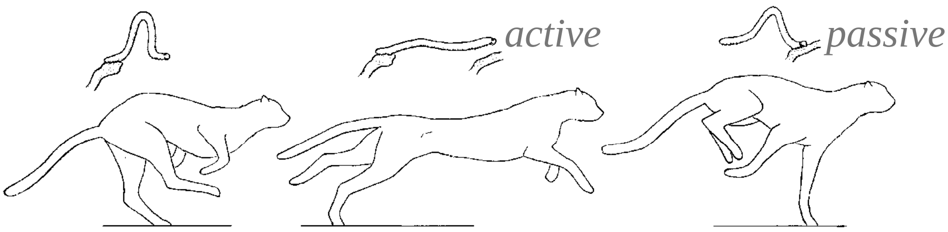
1) Transversal limbs: lateral undulation + girdle rotation







2) Parasagittal limbs: dorso-ventral undulation

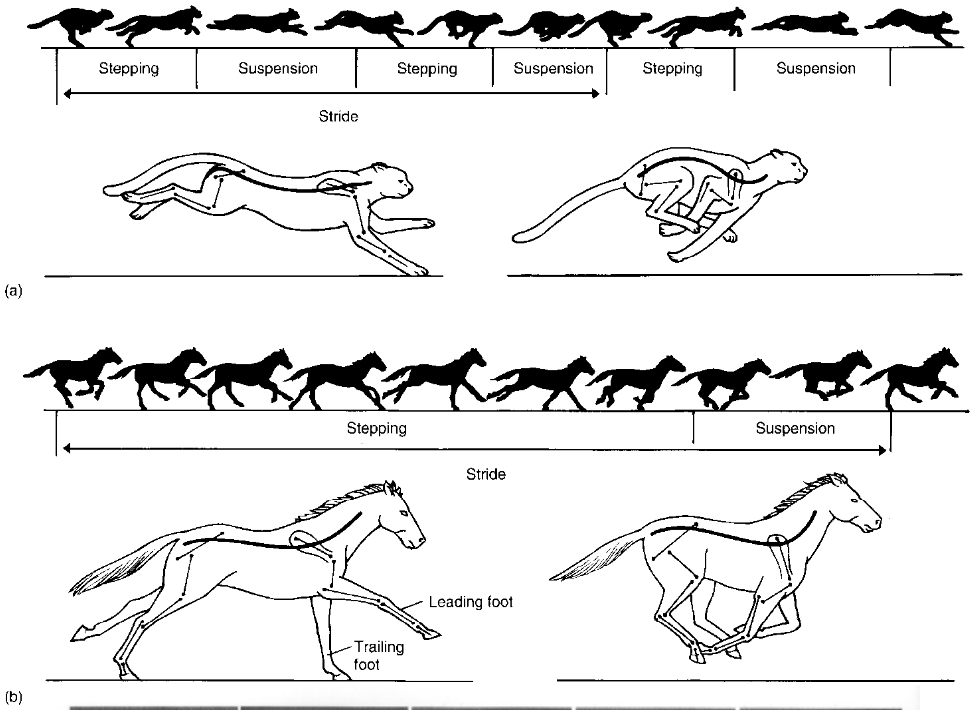


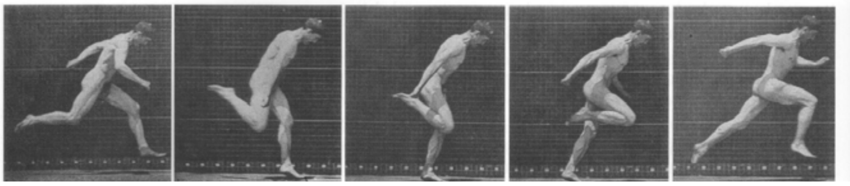
determines 10% of speed

f) include a (double) flight phase

↓

requires sufficient force

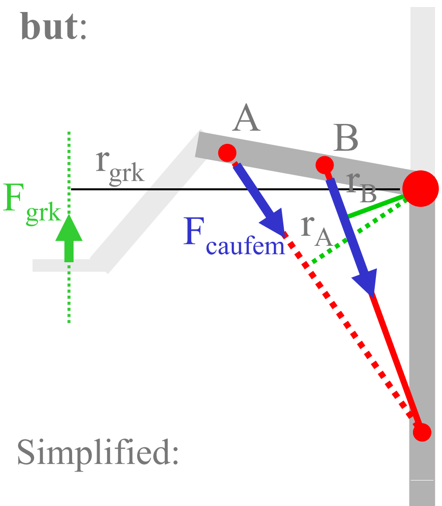




Locomorph Summer School
Odense 23 – 27 August 2012
ANIMAL LOCOMOTION

g) Move muscle insertion site towards joint to increase step length for a given muscle shortening

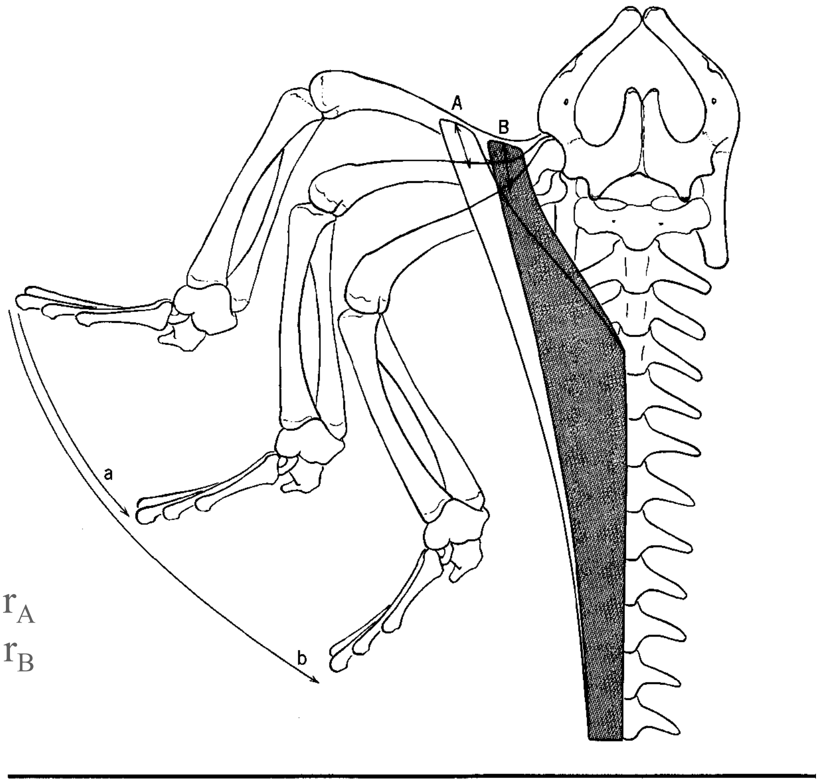
but:



Simplified:

$$Mgrk = F_{grk}\, r_{grk} = -M_A = -F_{caufemA}\, r_A$$
$$Mgrk = F_{grk}\, r_{grk} = -M_B = -F_{caufemB}\, r_B$$

same muscle shortening requires more force = larger muscle-∅
(or at least more activated fibres)

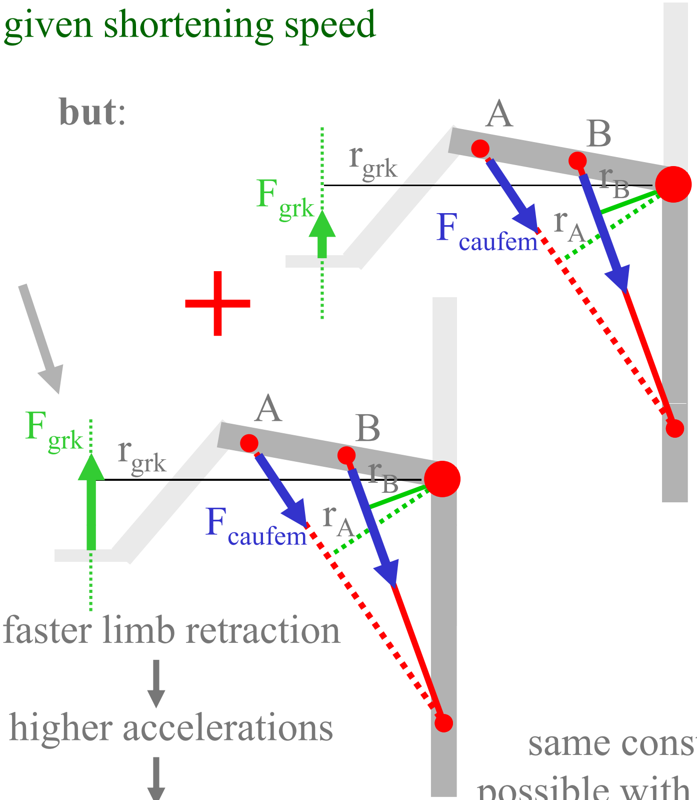


(vb: caudofemoralis)

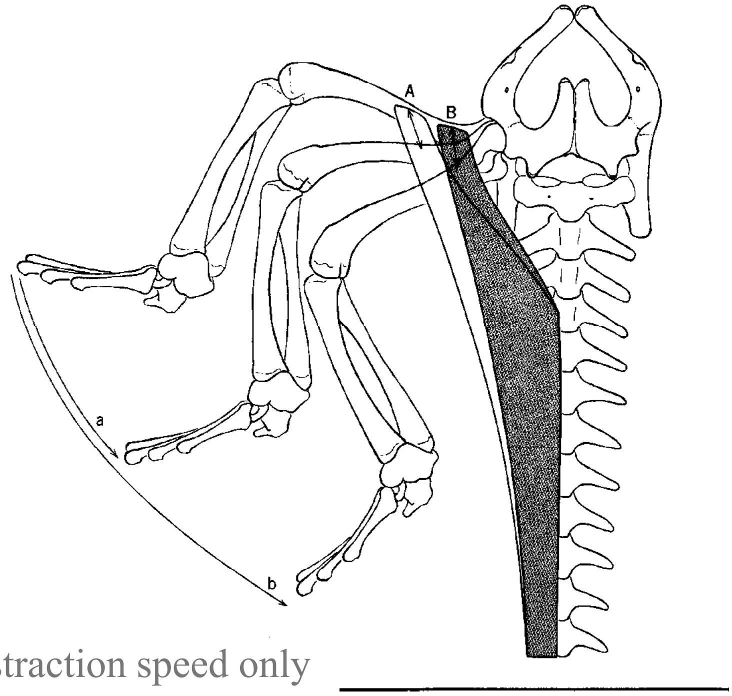
2) increase of the stride frequency : faster limb movements (cycling)

a) move muscle insertion site towards joint to increase the swing velocity for a given given shortening speed

but:



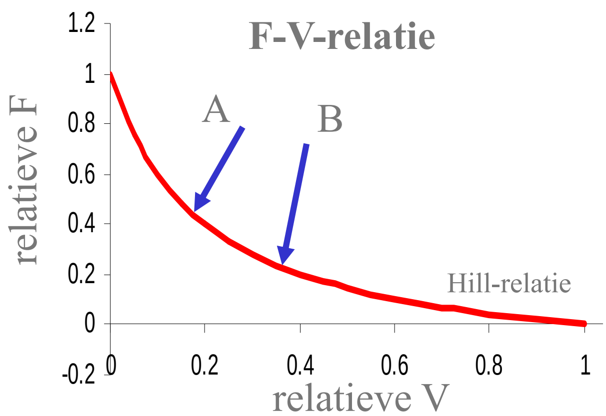
faster limb retraction
↓
higher accelerations
↓
higher F_{grk}



same constraction speed only possible with even larger muscle-∅
(or even more activated fibres)

(vb: caudofemoralis)

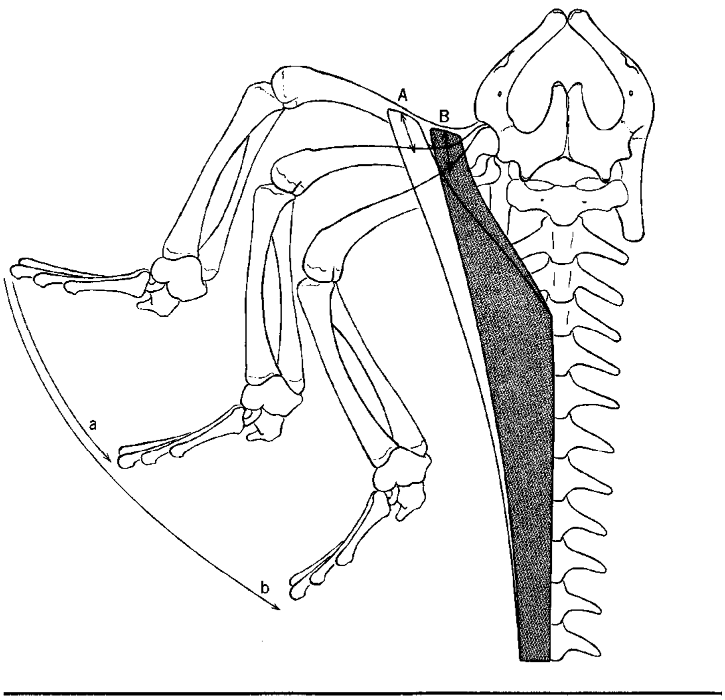
remark 1



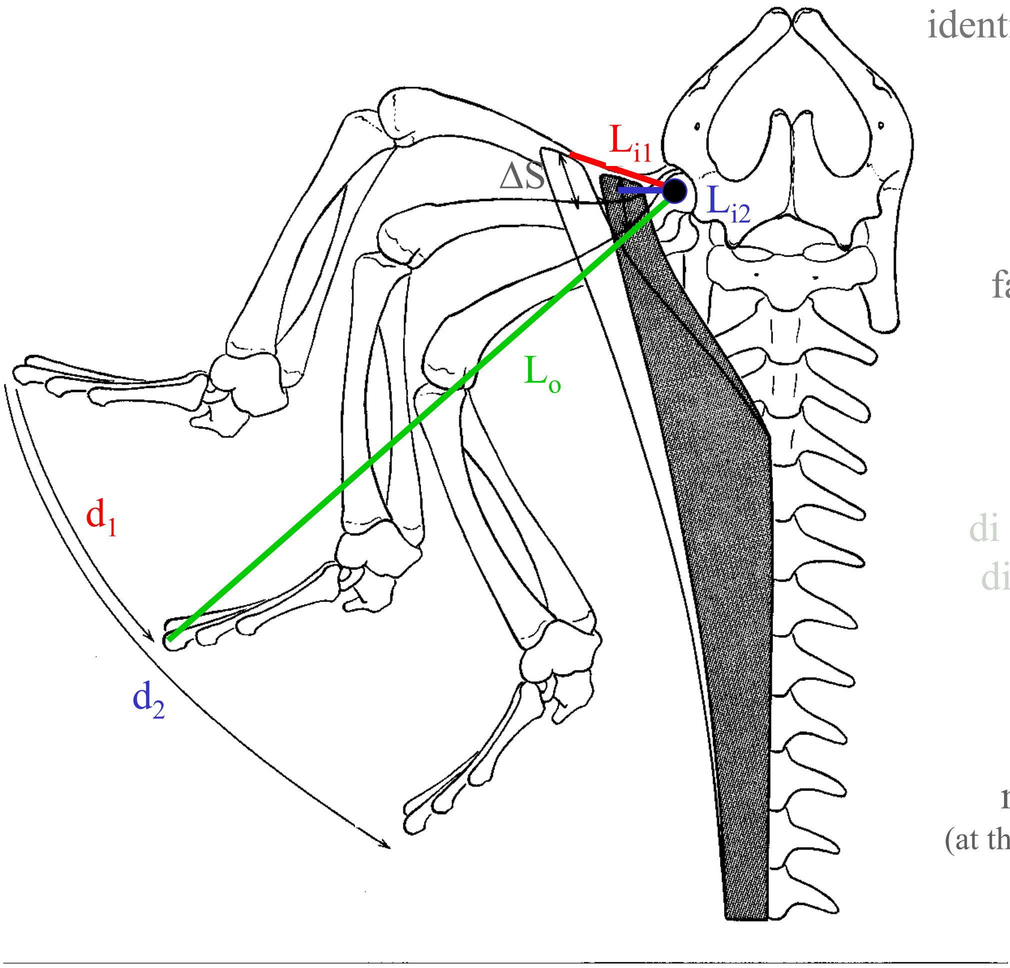
when all fibres are activated
force output *must* drop

remark 2

larger muscle-∅ implies higher mass;
higher mass implies higher inertia;
higher inertia implies higher F_{grk}
higher F_{grk} requires more muscle force….
…..



(vb: caudofemoralis)



identical muscle contraction
(shortening + speed)

ΔS ↓ ΔS/ Δt

faster limb retraction

||

$d_2/\Delta t > d_1/\Delta t$

since:

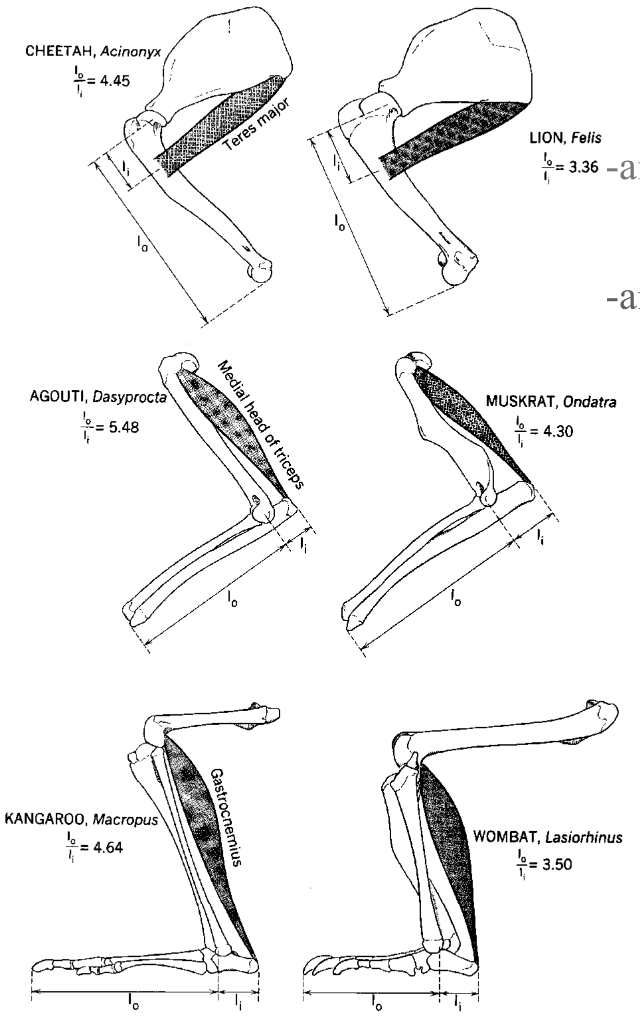
$di = Lo\ \Delta\ \alpha = Lo\ \Delta S/Li$

$di/\ \Delta t = Lo/Li * \Delta S/\ \Delta t$

$d_i/\Delta t \approx L_{out}/L_{in}$

L_{out}/L_{in} =
gear ratio =
measure for speed
(at the cost of reduced force!!!)

Locomorph Summer School
Odense 23 – 27 August 2012
ANIMAL LOCOMOTION

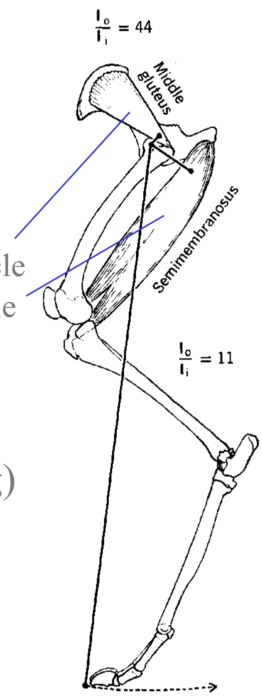


'gear ratio' reflected in behaviour

-aiming for (constante) high speed :
high L_{out}/L_{in}

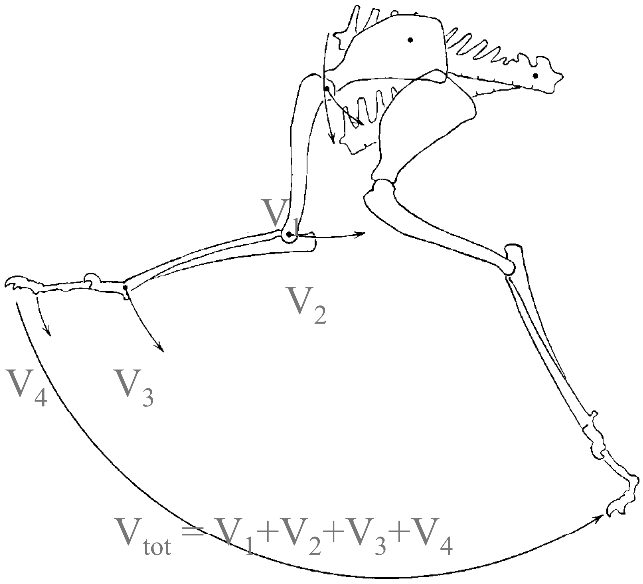
-aiming for force (e.g. digging, inertia):
low L_{out}/L_{in}

gearing is possible
- high gear muscle
- low gear muscle



(note: dynamic gearing)

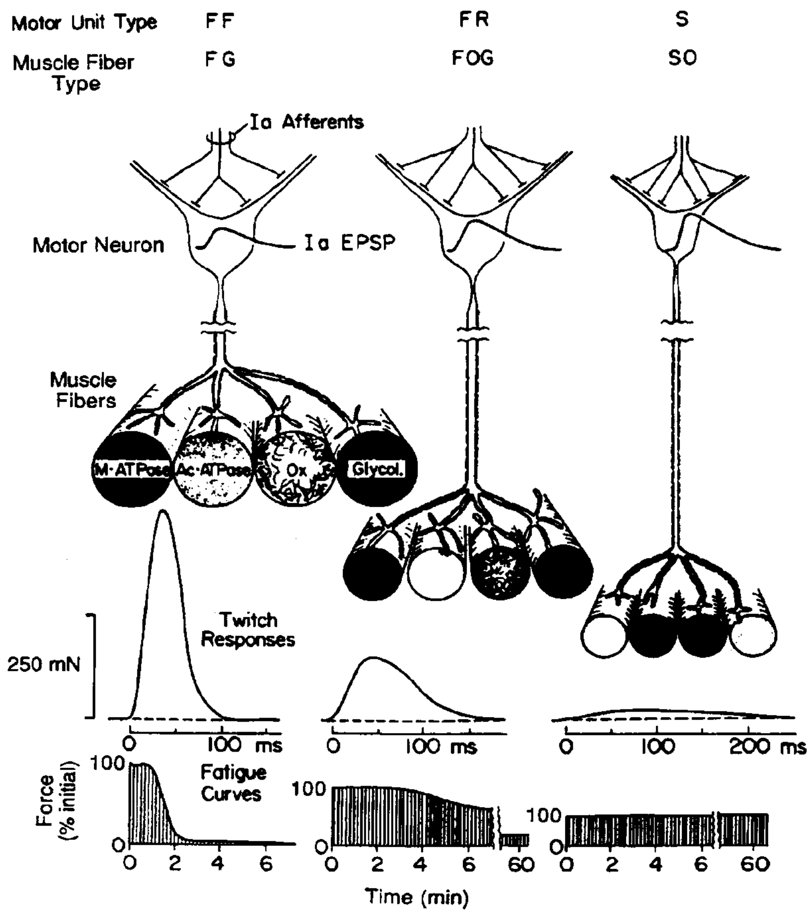
b) summation of joint rotation speeds (when independently actuated)

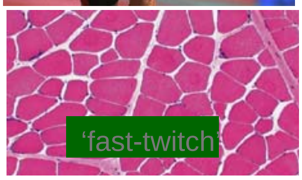


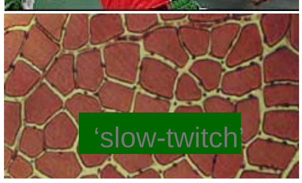
Locomorph Summer School
Odense 23 – 27 August 2012
ANIMAL LOCOMOTION

c) switching to faster muscle fibre types ('white fibres')

but: much more sensitive to fatigue !!



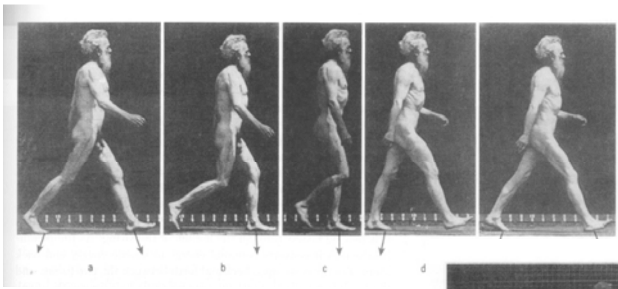




Gait: specific pattern of locomotor movements and inter limb coordination (often changing with speed)
Gaits can be classified on a kinematic or a dynamic basis

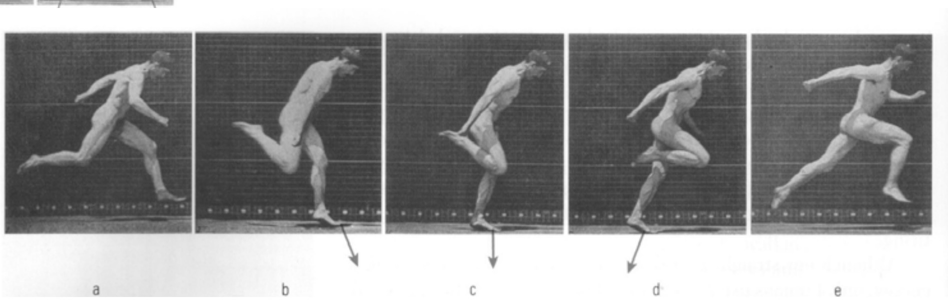
1) kinematically(or spatio-temporally) : based on **duty factor** and **relative phase**

- **duty factor DF** = ground contact time of a (specific) limb / stride duration
- DF > 0.5 ⟶ walking gaits
  < 0.5 ⟶ running gaits



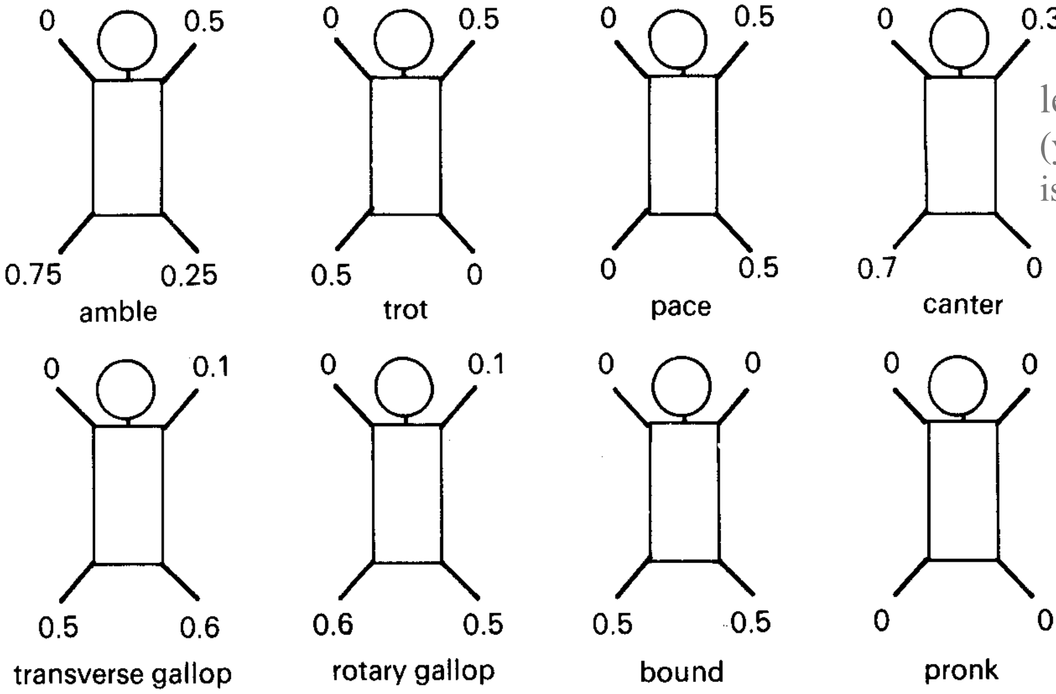
for bipedal locomotion, walking is characterised by a double support phase
DF > 0.5

running by a flight phase
DF < 0.5



Locomorph Summer School
Odense 23 – 27 August 2012
ANIMAL LOCOMOTION

further division on the basis of **relative phase** (RF)
RF = relative timing within a stride of the foot falls with respect to a reference limb



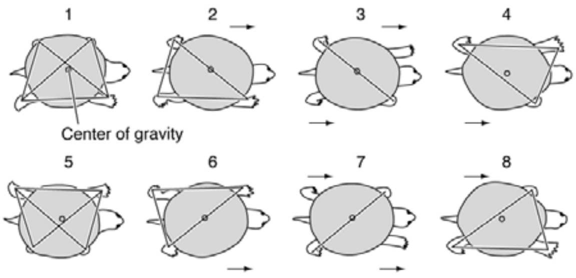
left-front = reference (yet, most often left-hind is used)

normal walking and running in humans : RF = 0.5

- if RF = 0.5 **within** a girdle: symmetrical gait
- all other cases: asymmetrical gaits

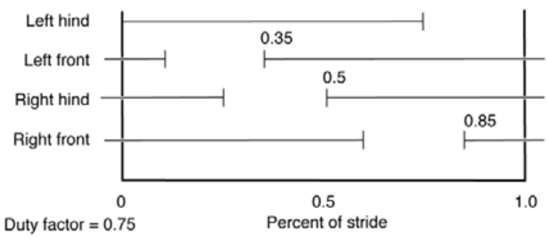
[remark : refers to time symmetry ! (listen to cadans)]

symmetric



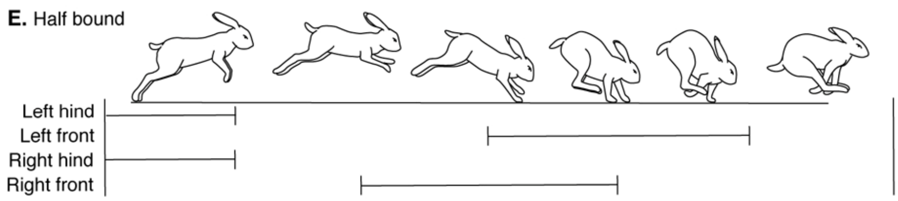
A. Limb movements and foot placements during one stride of a turtle

use of 'footfall'-patterns

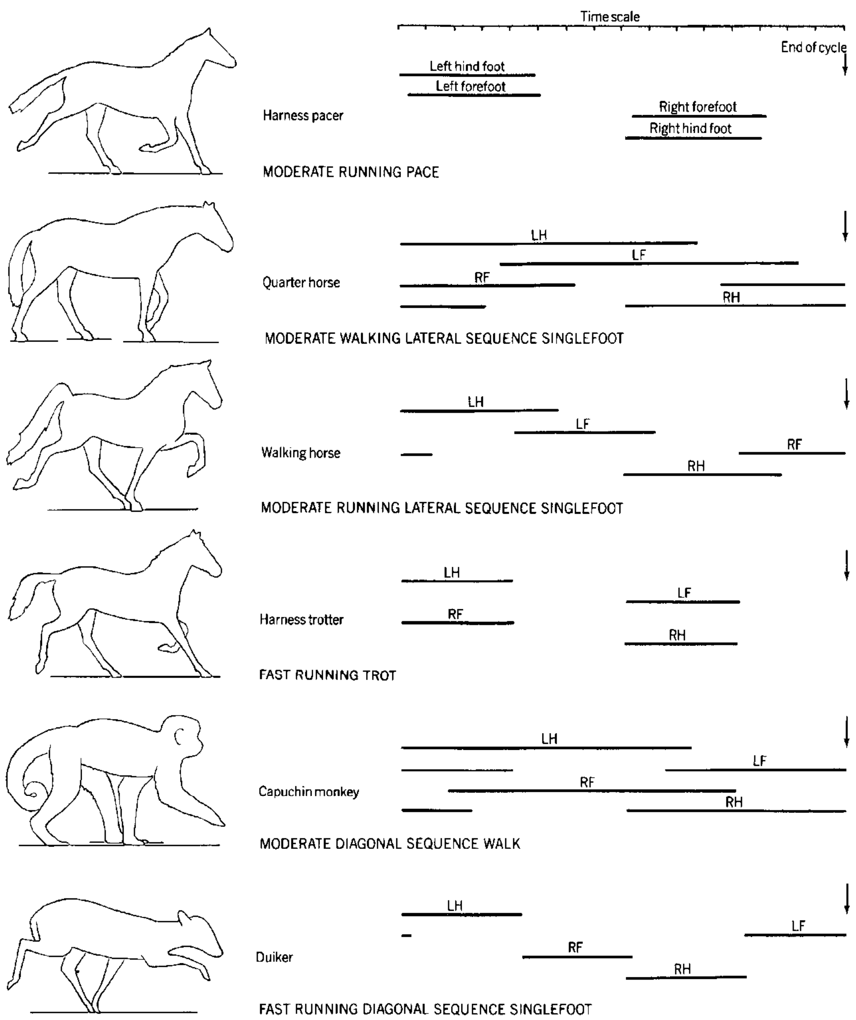


B. Gait diagram of the stride shown in A

asymmetric

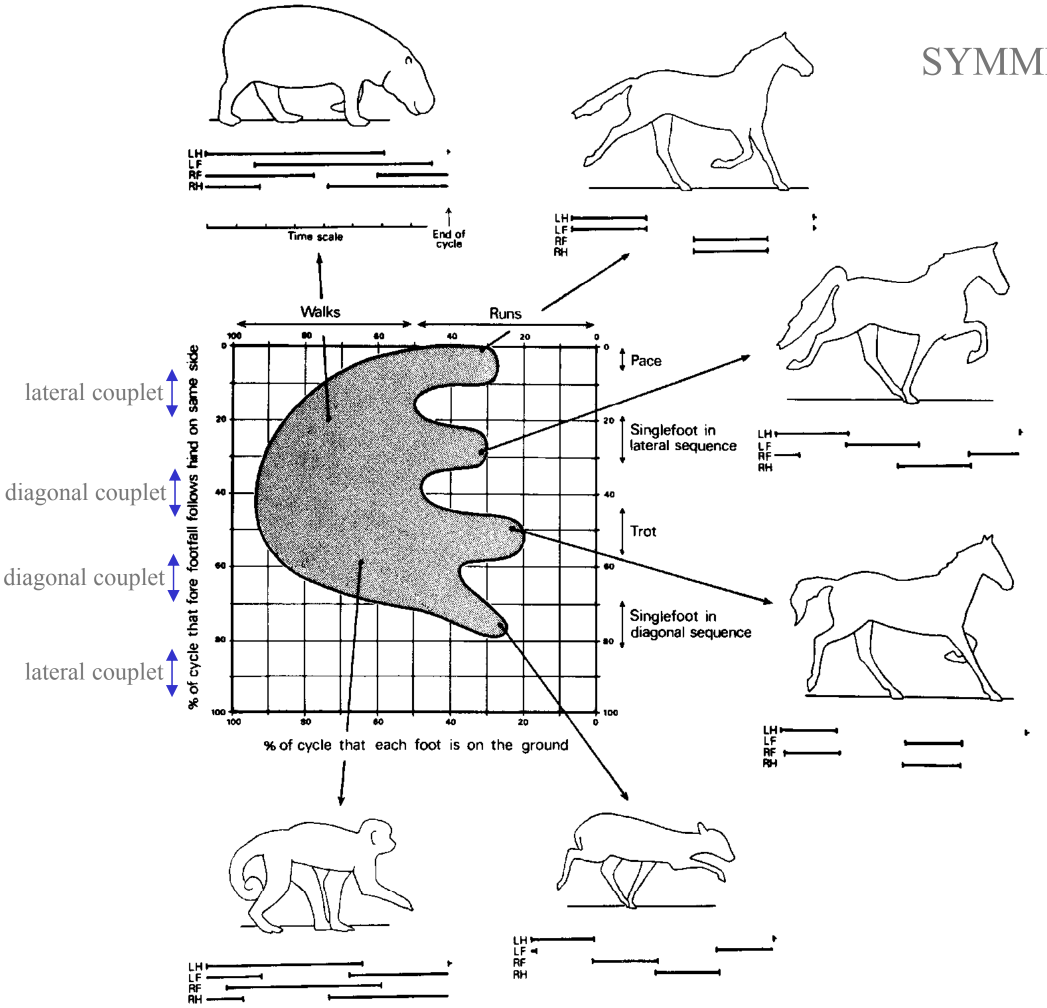


Locomorph Summer School
Odense 23 – 27 August 2012
ANIMAL LOCOMOTION



SYMMETRICAL GAITS

SYMMETRICAL GAITS



RF ipsilateral (fore –aft)

≅0 : pace
≅15 : lateral couplet
≅25 : lateral 'single foot'
≅35 : diagonal couplet
≅50 : trot
≅65 : diagonal couplet
≅75 : diagonal single foot'
≅85 : lateral couplet
≅100 : pace

SYMMETRICAL GAITS: lateral couplet => pace

SYMMETRICAL GAITS : laterale sequence (couplet)

SYMMETRICAL GAITS laterale sequence single foot

SYMMETRICAL GAITS: diagonal sequence (couplet) => walking trot

Locomorph Summer School
Odense 23 – 27 August 2012
ANIMAL LOCOMOTION

SYMMETRICAL GAITS : trot

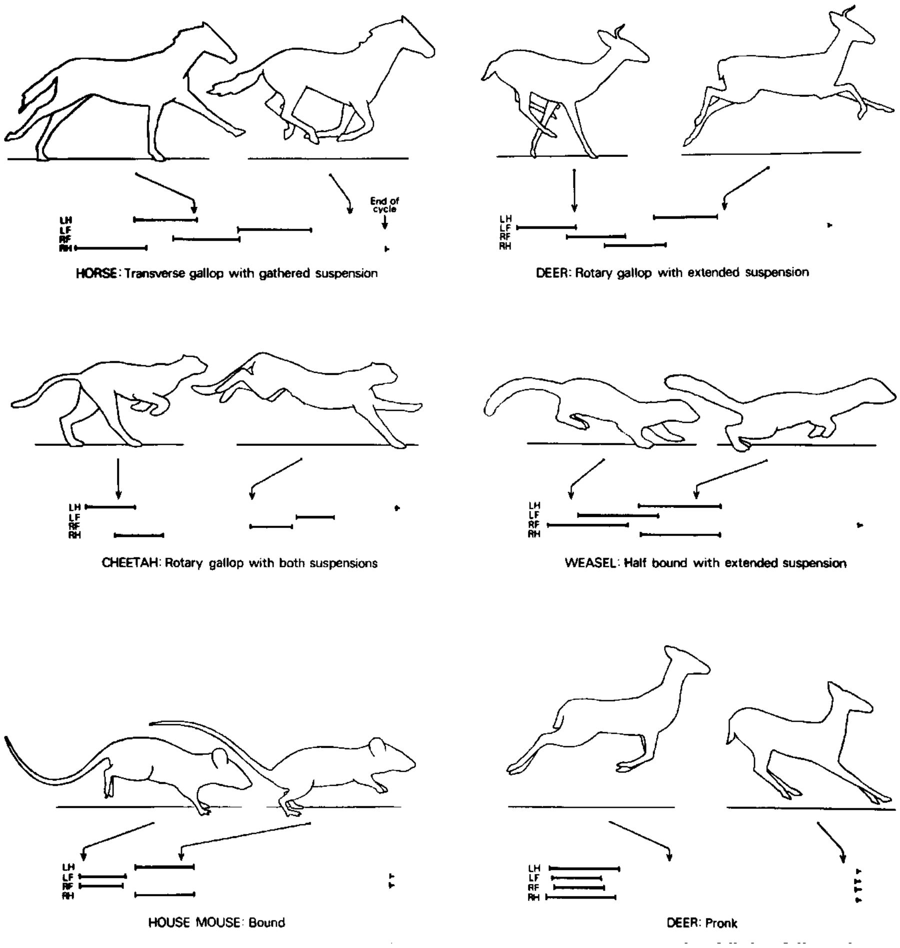
SYMMETRICAL GAITS : walking trot

SYMMETRICAL GAITS : bipedal running

SYMMETRICAL GAITS : bipedal running

SYMMETRICAL GAITS : bipedal walking

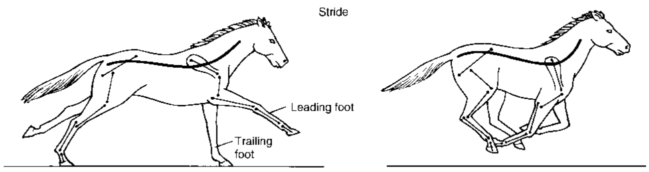
ASYMMETRICAL GAITS



ASYMMETRICAL GAITS : gallop

ASYMMETRICAL GAITS : bound

ASYMMETRICAL GAITS



'rotary' gallop

⇅

'transverse' gallop

ASYMMETRICAL GAITS : bipedal gallop

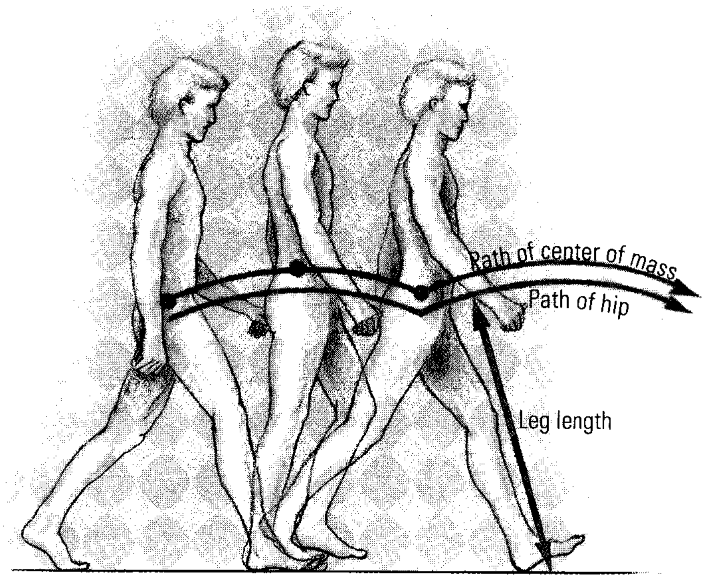
Locomorph Summer School
Odense 23 – 27 August 2012
ANIMAL LOCOMOTION

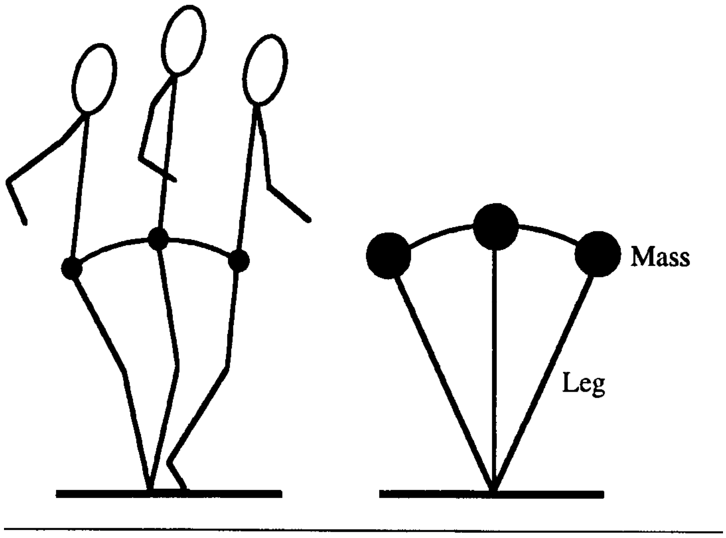
ASYMMETRICAL GAITS : ricochet

alternative for kinematical classification

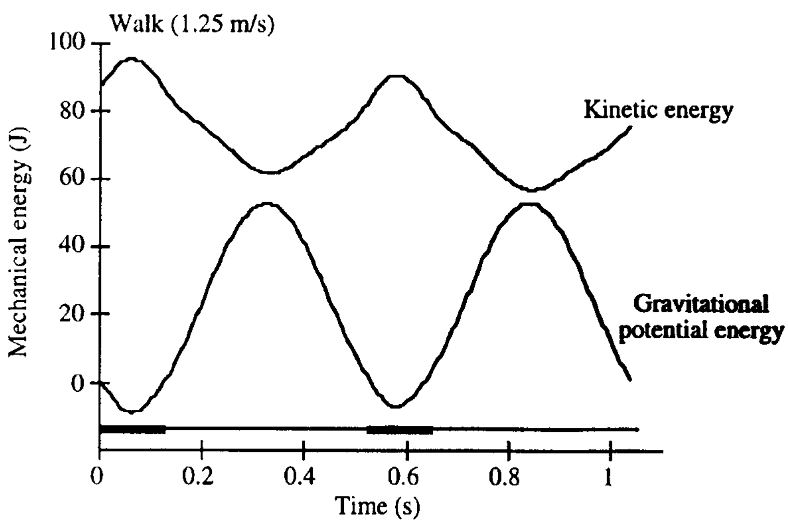
2) dynamically (according mechanical behaviour of support limb)

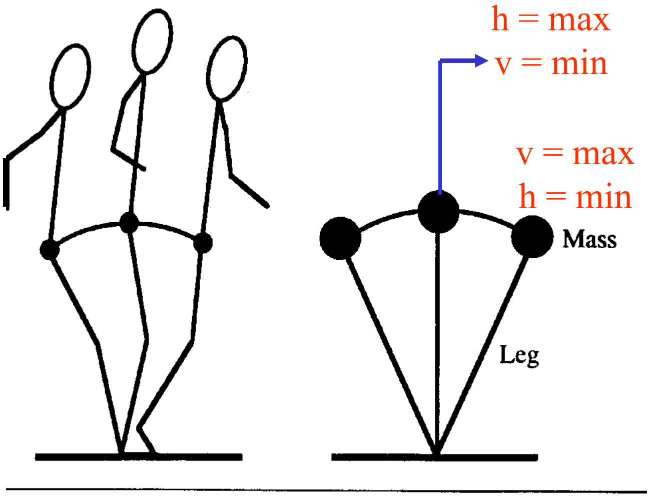
paradigm for walking gaits: inverted pendulum:
organism pivots about (relatively) stiff support limb



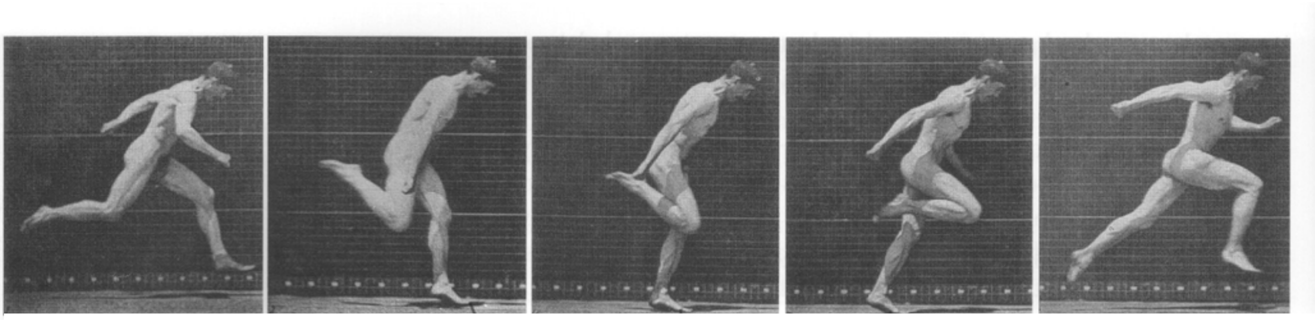


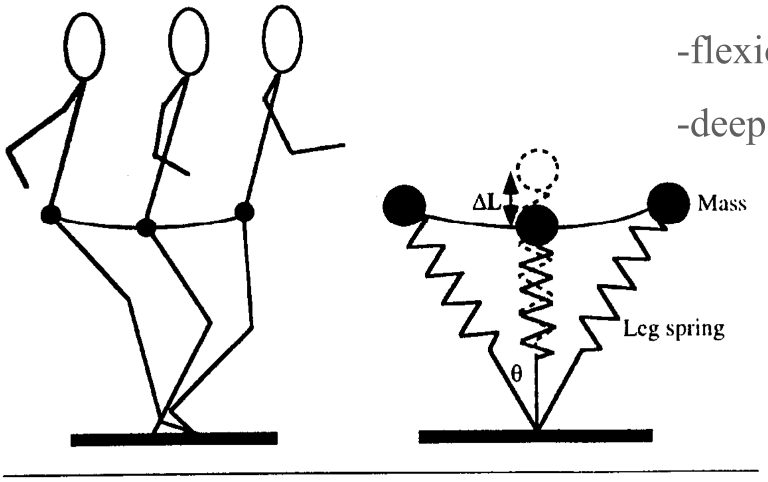
Locomorph Summer School
Odense 23 – 27 August 2012
ANIMAL LOCOMOTION





-potential (mgh) and kinetic ($mv^2/2$) energy fluctuations are out of phase fase (cf. pendulum): energy conversion saves up to 70% of the mechanical (!!) costs paradigm for running : spring mass system

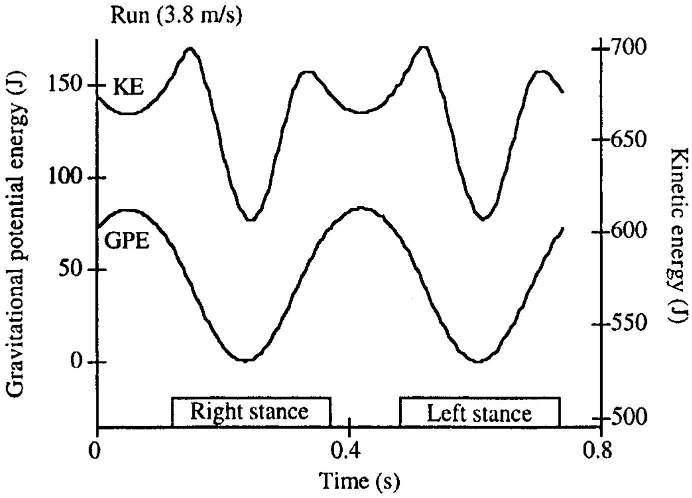


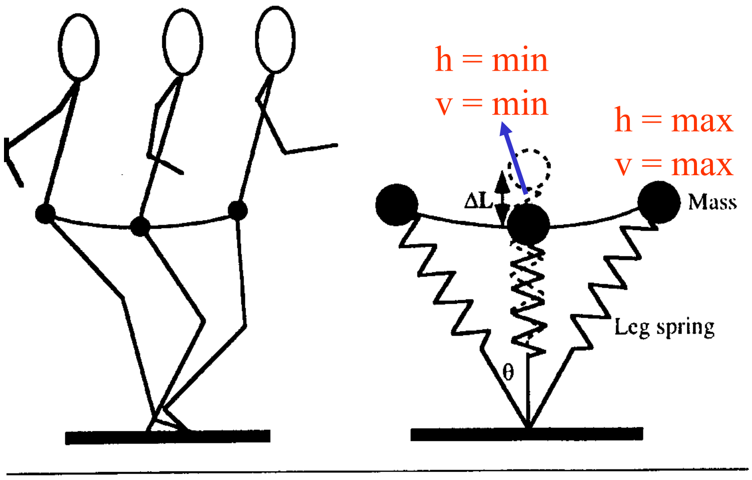


-flexion-extension of support limb

-deepest point at midstance

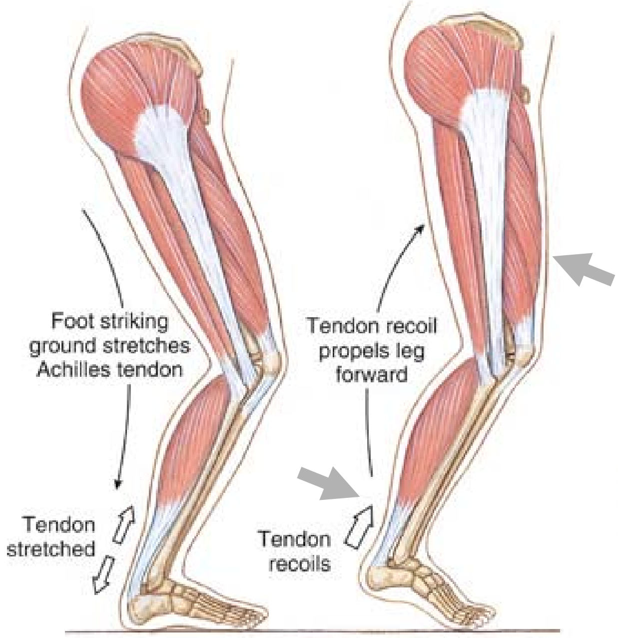
Locomorph Summer School
Odense 23 – 27 August 2012
ANIMAL LOCOMOTION

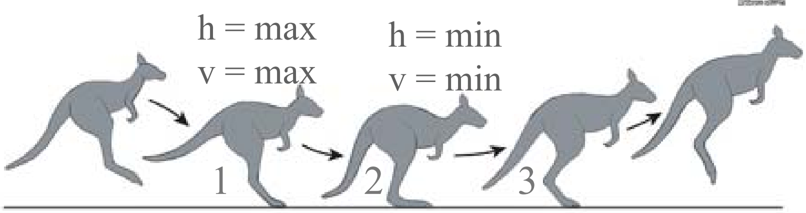




potential and kinetic energy fluctuate in phase :
no conversion

But !!!

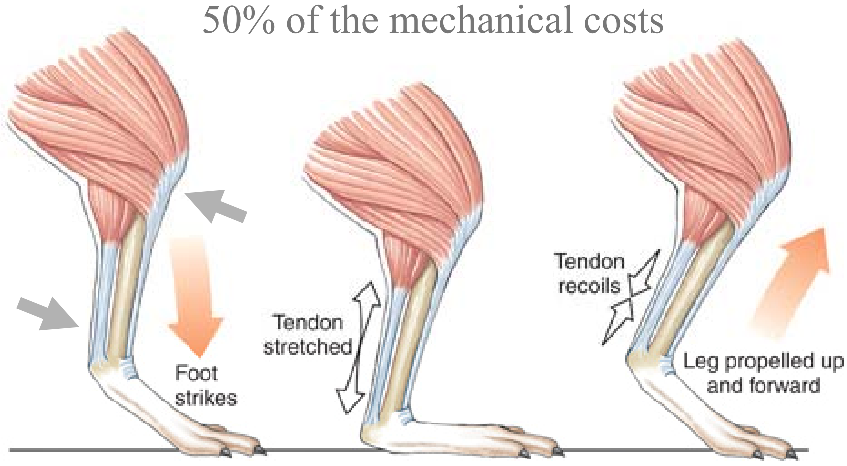


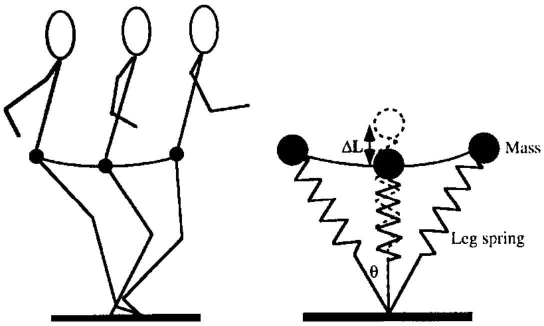


$$t_2 - t_1: m(\Delta V)^2/2 + mg\,\Delta h \longrightarrow E_{elast}$$

$$t_3 - t_2: E_{elast} \longrightarrow m(\Delta V)^2/2 + mg\,\Delta h$$

Energy conversion saves up to 50% of the mechanical costs



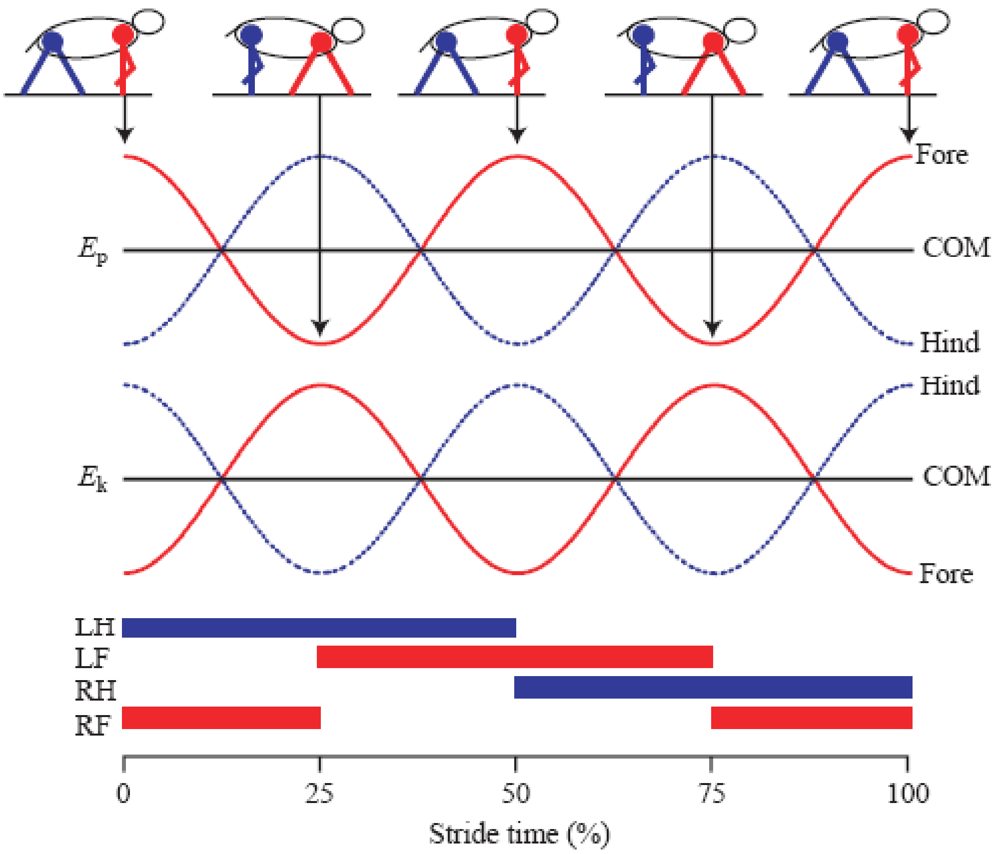


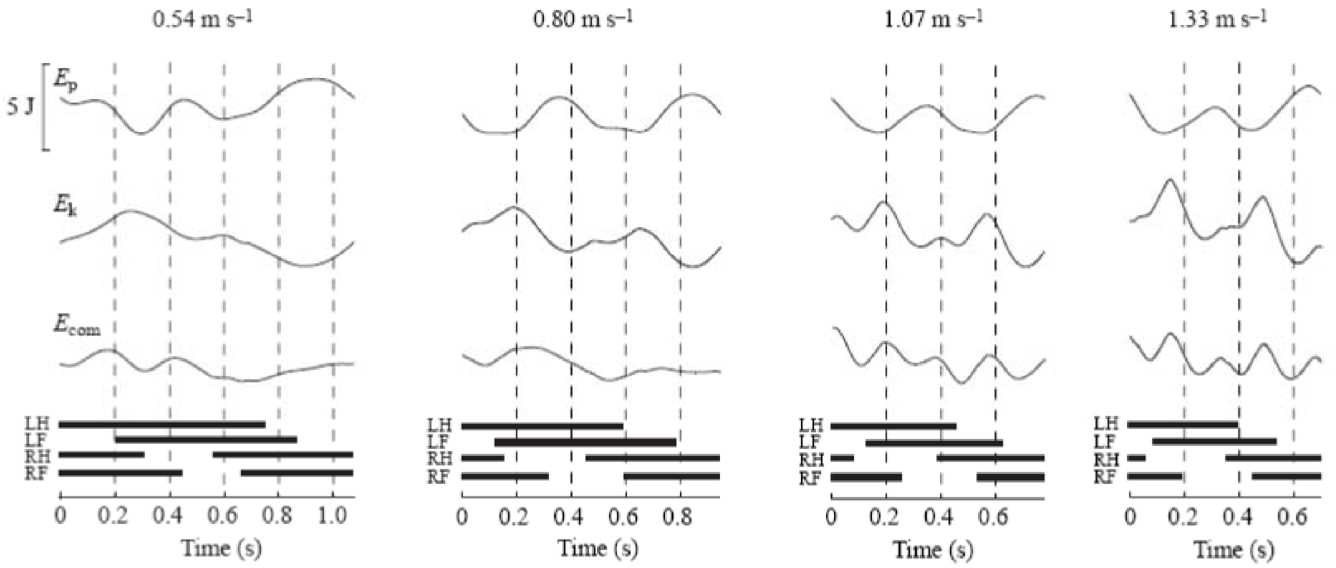
Muscle-tendon-systems behave as elastic springs

(!! extensors : achilles tendon, quadriceps, triceps surae)

Locomorph Summer School
Odense 23 – 27 August 2012
ANIMAL LOCOMOTION

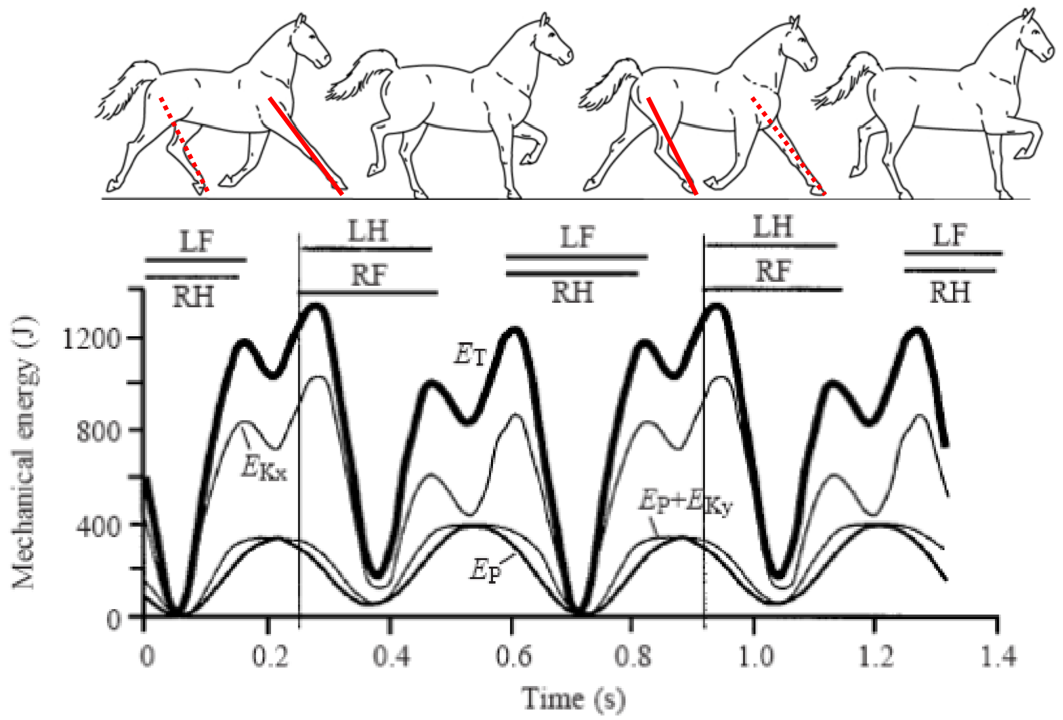
‘inverted pendulum’ mechanism holds for quadrupeds, too
2 ‘bipedalen’ in tandem



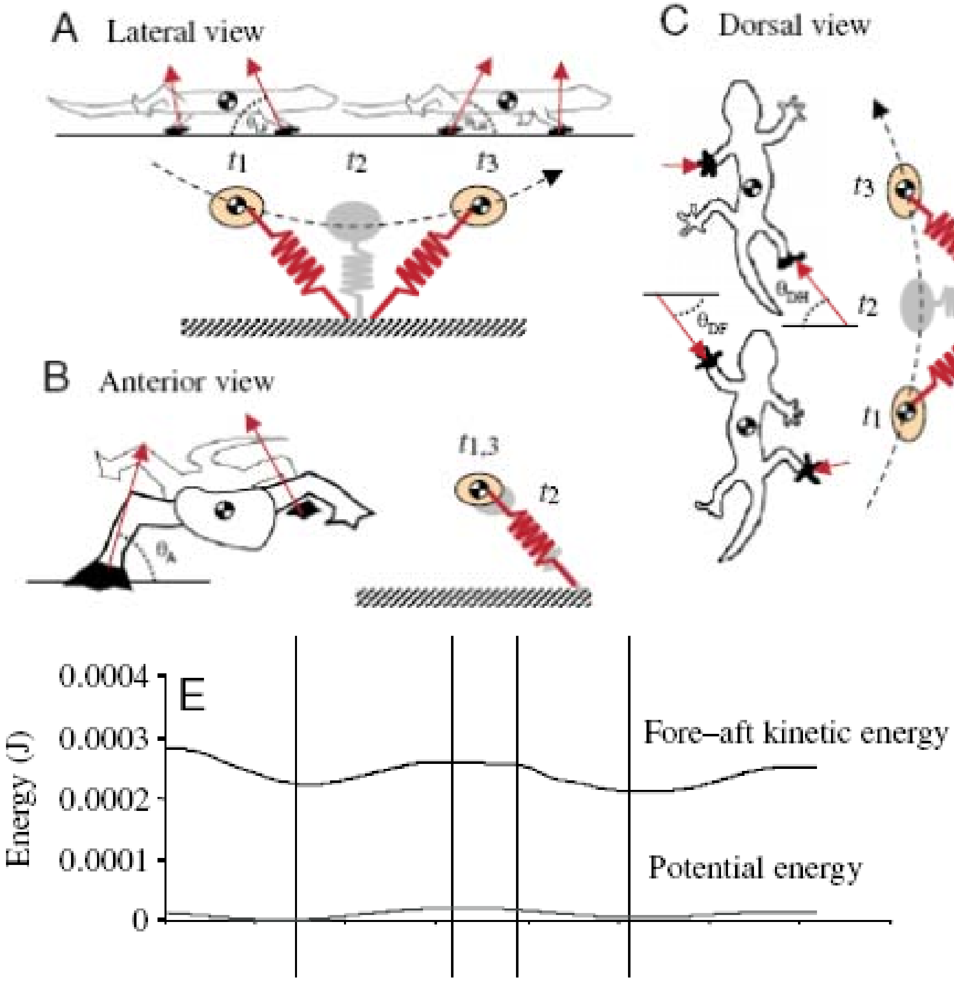


dog walking at different speeds:
Epot en Ekin largely out of phase → 70% recovery

‘spring-mass’ mechanism holds for quadrupedal trotting
diagonal limb pairs behave as a ‘biped‘



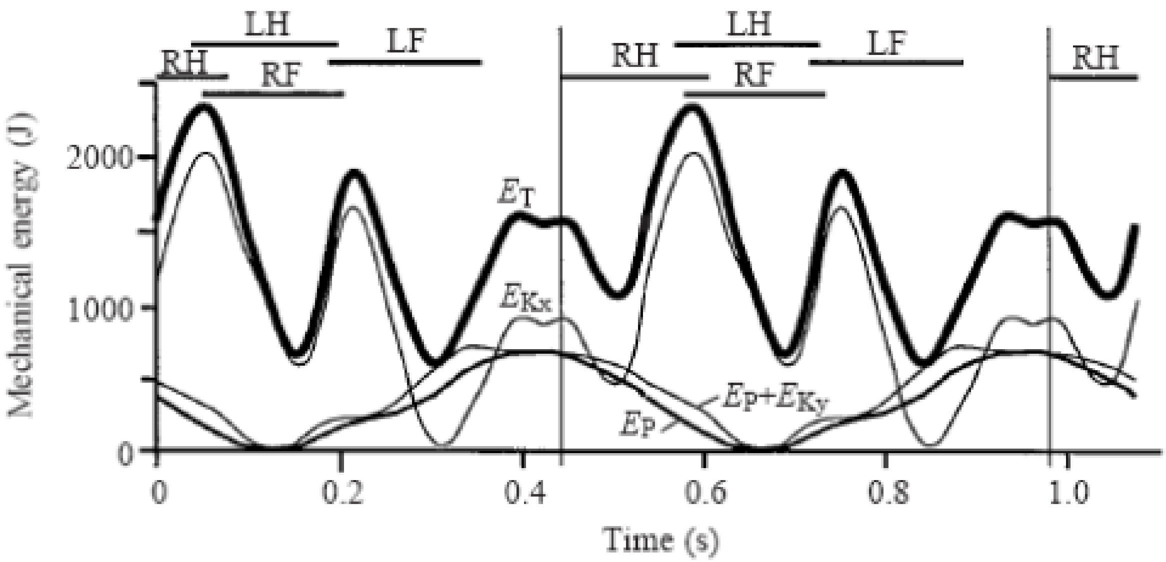
Epot en Ekin largely in phase during diagonal limb contact

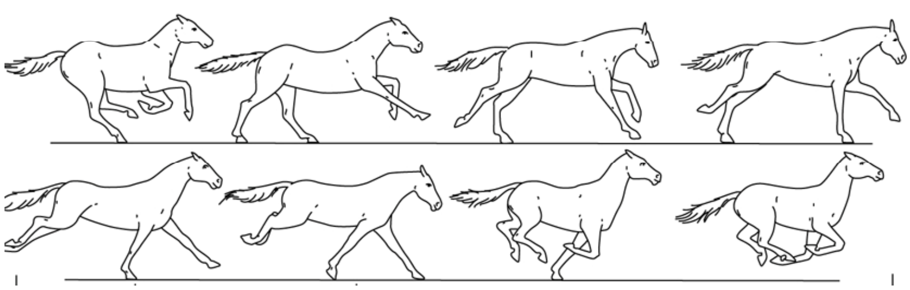


also ‘sprawling’-gaits (= transversal limbs) behave as spring-mass system

Locomorph Summer School
Odense 23 – 27 August 2012
ANIMAL LOCOMOTION

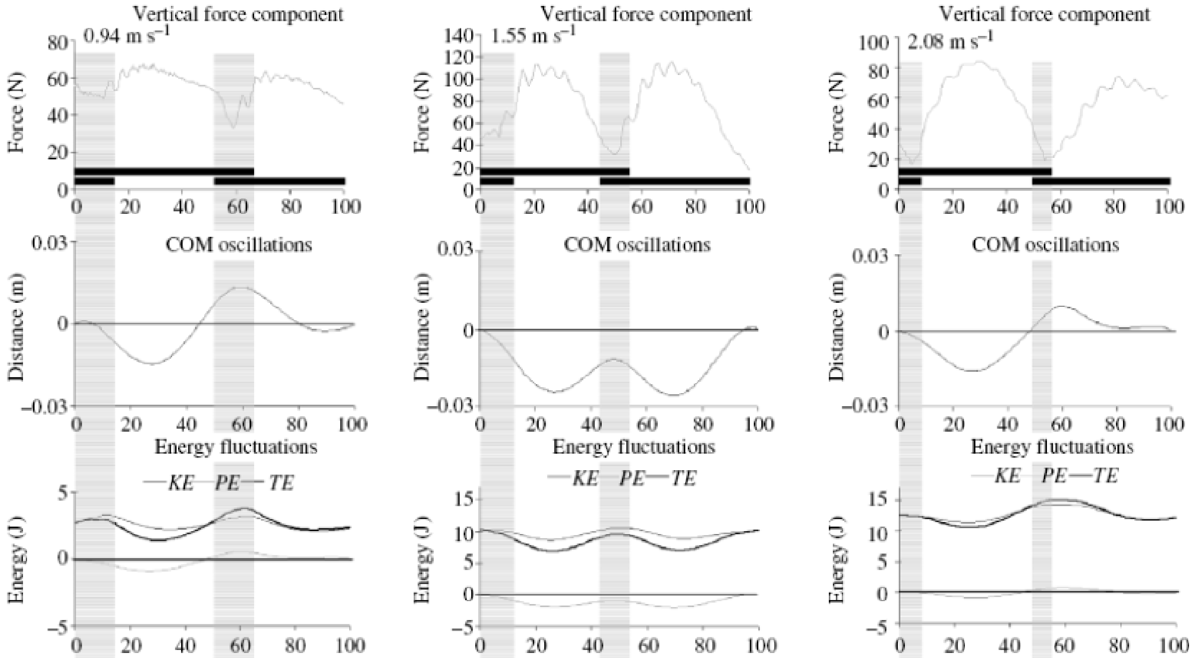
gallop is likely a complex mix of inverted pendulum & mass-spring mechanism



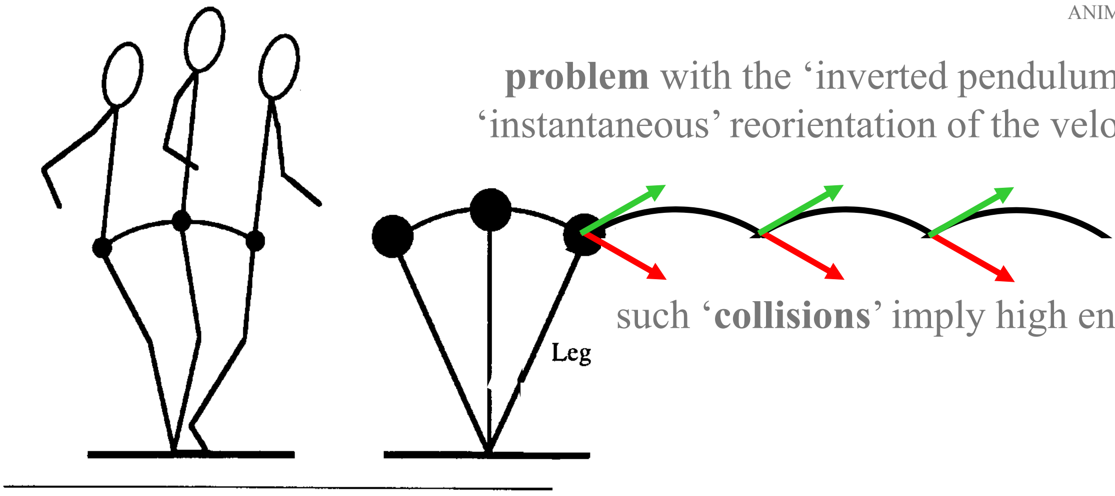


kinematical and dynamical classifications do not neccessarily overlap : DF > 0.5 + 'spring-mass' mechanism = 'groucho running' (grounded running)

gibbon bipedal 'grounded running'

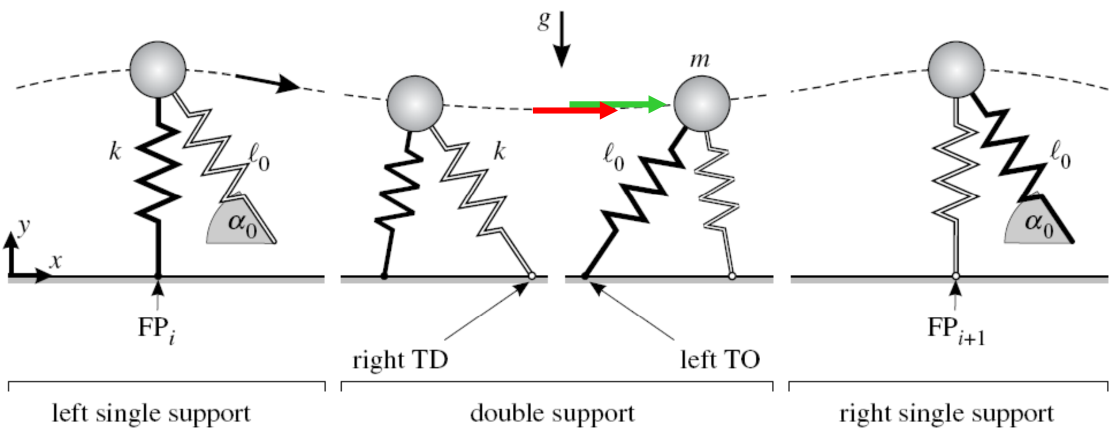


problem with the 'inverted pendulum' model: 'instantaneous' reorientation of the velocity vector

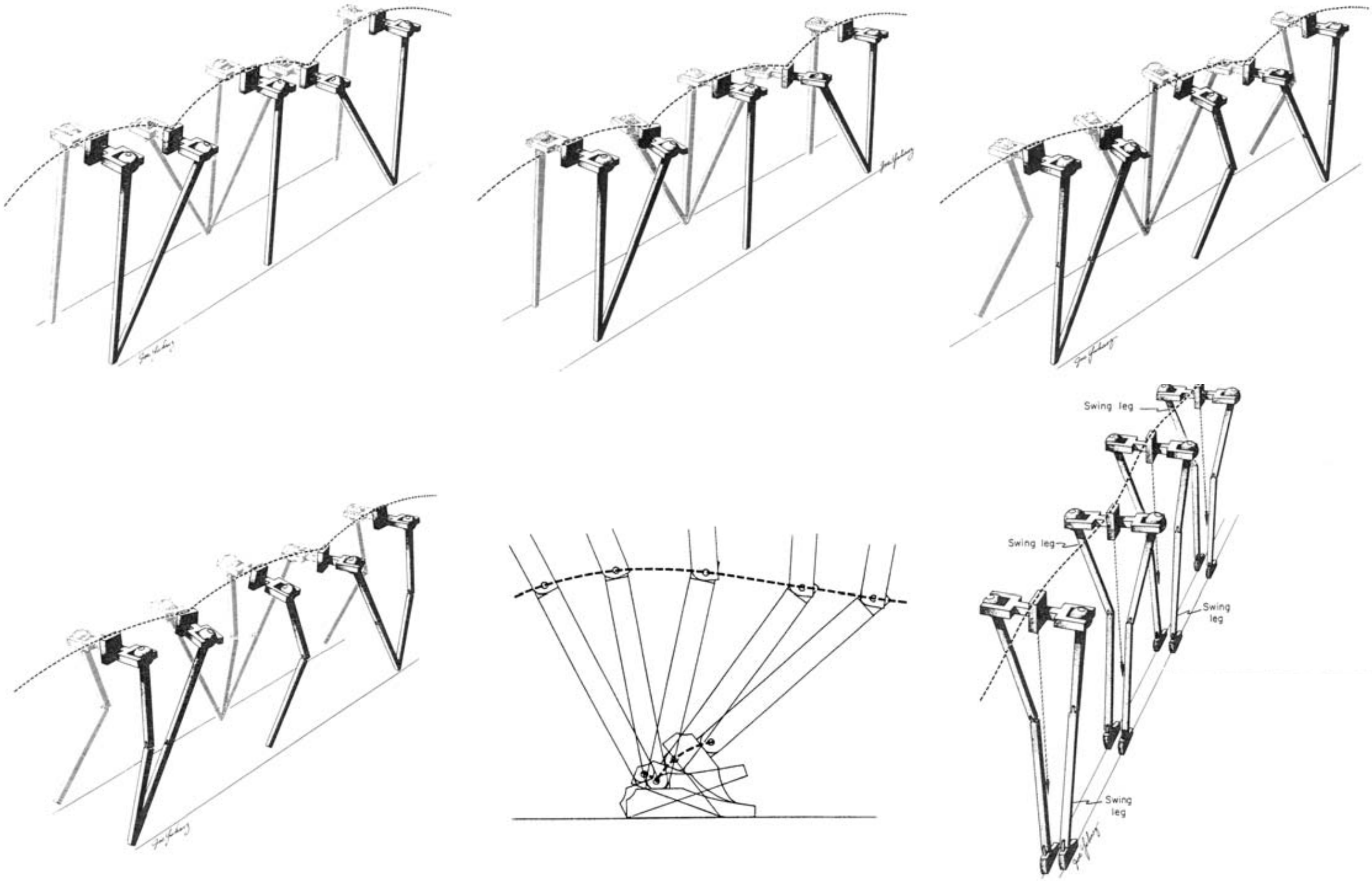


such '**collisions**' imply high energy losses

combining both models reduces collisions

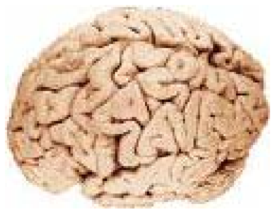


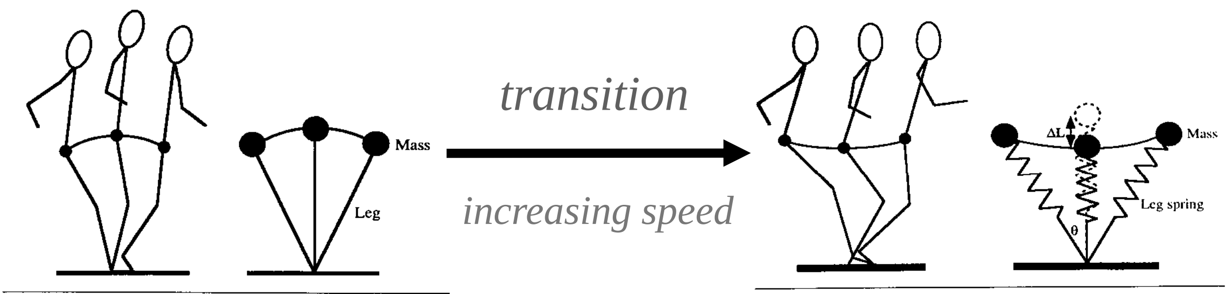
in humans this accords to the 6 gait determinants for efficient walking as proposed by Saunders (1953)



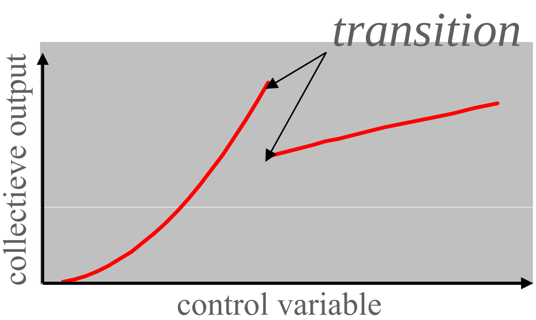
Transitions between gaits : 1) proximat explanation (answer to 'how' ?)

Central programming approach



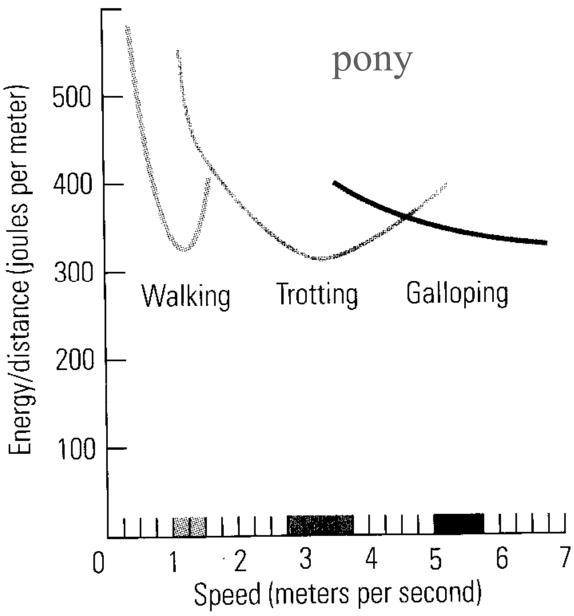


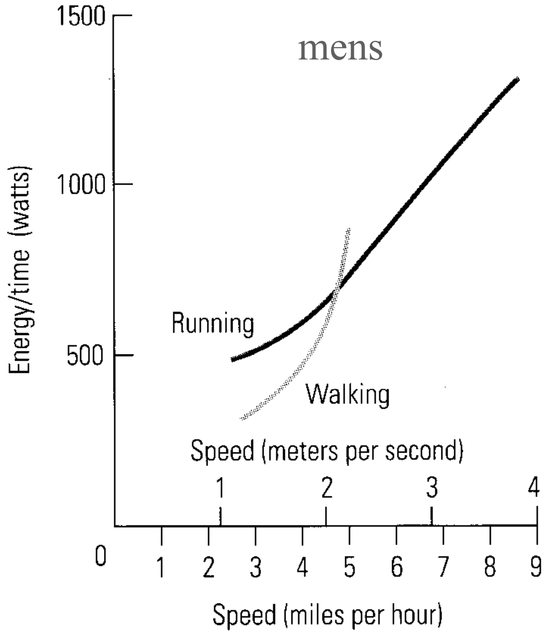
Dynamic systems Approach
(self-organising)

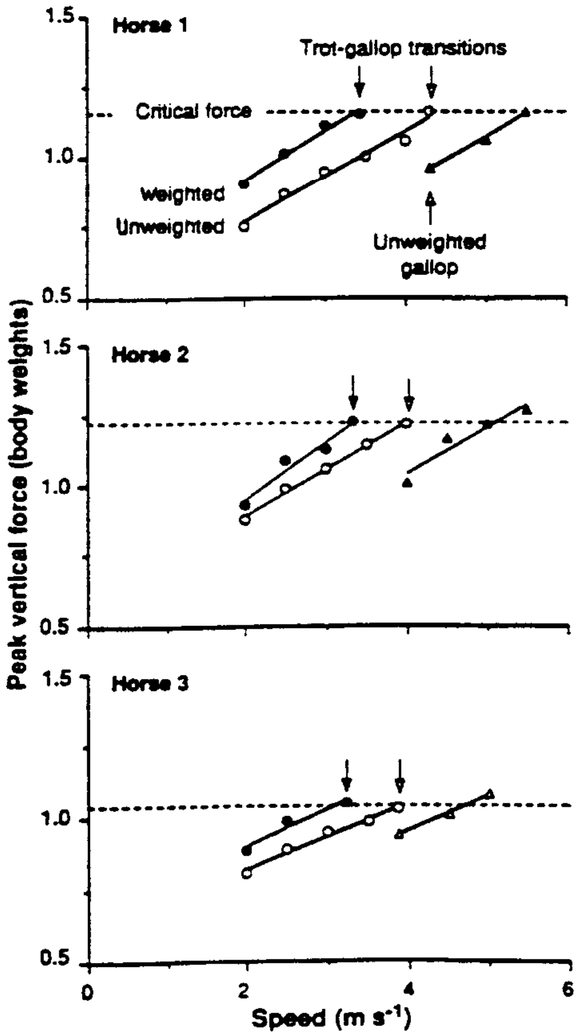


Transitions between gaits : 2) ultimate explanation (answer to 'why' ?)

two general hypotheses : **a)** to minimize costs







b) to minimize stress