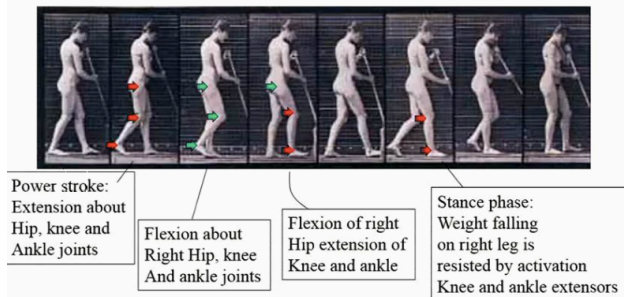


Lecture 6 Locomotion

- Early 20th century experiments showed that the basic rhythm of walking is set up in spinal segments
- Sequential activation of muscles during stepping
- *Interneurons* involved in alternating activation of flexor and extensor motor neurons
- Ways in which afferent feedback regulate the pace of stepping
- Pattern generators and coordination of stepping

Human locomotion (note movement of right leg)

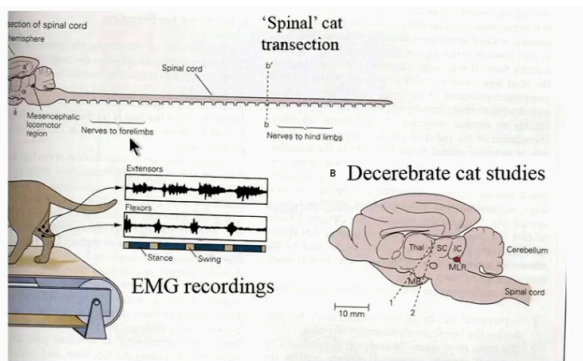


The process behind walking has been looked at since the start of cameras and film.

Three phases:

1. Power stroke
2. Swing
3. Stance

Lesions to spinal cord



Lesions studies have shown that lesioning the spinal cord at an area that affects the lower limbs causes the absence of walking.

Proving that descending inputs have a regulatory effect in stepping.

'Spinal Cat'

- Spinal transection in cat eliminates descending inputs
- Initial acute immobility
- But rhythmic walking could be re-established by applying a tonic electrical stimulation to the cut end of the spinal cord.
- Pace of walking could be adjusted by the increase in electrical stimulus.

De-afferented cord (cutting the dorsal roots)

- Eliminated sensory afferent feedback
- Reduced tonic excitatory synaptic input to the motor neuron making the MN less excitable
- However rhythmic walking movement could still be produced even in the absence of sensory feedback by drugs etc
- Immobilising the limb later found to be a better way of removing cyclical feedback from afferents
- Role of afferent feedback: to adjust/modify step in response (eg to lift paw over an obstacle)

There is still an alternating contraction of the gastrocnemius and tibialis anterior even when the dorsal roots have been cut, therefore signifying that afferents are not important in stepping!!

SUMMARY of early studies

- Supra-spinal structures not needed for producing basic stepping sequence
- Rhythmicity of stepping must be generated within the spinal segments
- These spinal pattern generating circuits can be activated or suppressed according to the level/frequency of descending tonic signals
- Pattern generating circuits do not require afferent feedback information but:
 - Afferents confer excitatory tone to MN's
 - Proprioceptor afferents normally act to modify stepping

Four phases of the stepping cycle in cats (and humans)

SWING

F- flexion of hip, knee and ankle (leg comes off the ground)

E1- hip still flexes but knee and ankle extend, pushing foot forward

STANCE

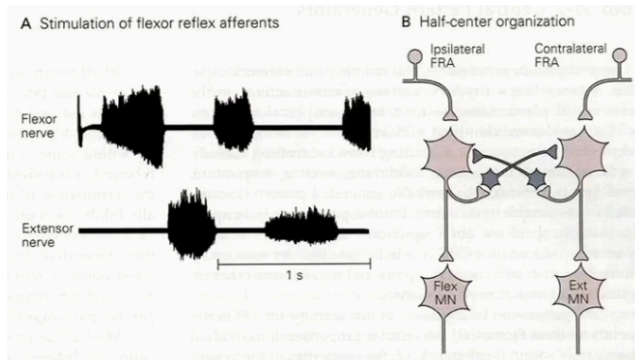
E2- foot makes contact with ground again and body weight flexes knee and ankle joints even though the extensors are still being strongly activated

E3- all three joints extend as their extensor muscles contract strongly in unison to push back against ground

Alternating bursts of flexor and extensors

- Reciprocal innervation of antagonists muscles can facilitate reflex responses but cannot explain prolonged bursts of flexor and extensor activity
- In spinal cats treated with **L-DOPA**, brief stimulation of high threshold (muscle and cutaneous) *flexor reflex afferents (FRA)* triggered sustained bursts of activity in either flexor or extensor MNs depending on whether ipsi- contra-lateral nerve stimulated

Half centre hypothesis



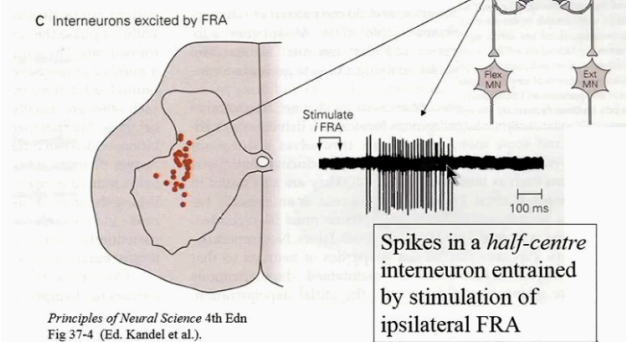
This states that extensors and flexor neurons controlling the limb are activated with prolonged bursts.

To generate limb swing by two opposing groups of interneurons (two half-centres) that mutually inhibits each other.

It's believed that when a half centre neuron is activated, it **simultaneously activates an inhibitory interneuron** that inhibits the opposing muscle.

FRA's

Interneurons with similar burst firing can be found in intermediate Grey matter (spatially distinct from Ia interneurons and Renshaw cells)



Receptors in skin and muscles

High threshold – small diameter sensory fibres (distinct from the large diameter Ia fibres)

Activation of ipsilateral FRA triggers ipsilateral flexor activation

Does contralateral FRA activation help adjust the timing of the switch from swing to stance?

Beat generator neurons

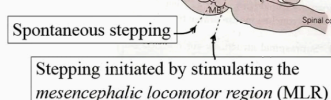
- The spinal segments of mice, can produce an alternated rhythmic burst firing of flexor and extensor MNs
- A class of excitatory interneurons has been identified in relevant parts of spinal cord by their expression of distinct transcription factors genes (**Hb9- positive neurons**)

Hb9- positive = express a particular transcription factor

- Excitatory interneurons in medial lamina VIII of lower thoracic and upper lumbar segments
- Display burst firing in-phase with the burst firing of flexor MN's (L1-L3 ventral root axons during swing phase)
- Burst activity patterns can still be elicited in Hb9 neurons by neurochemical treatment, even when excitatory and inhibitory inputs to the neuron are blocked. This shows that these neurons are beat generators.
- Hb9 +ve neurons are *electrically coupled*, coordinating their firing as a group

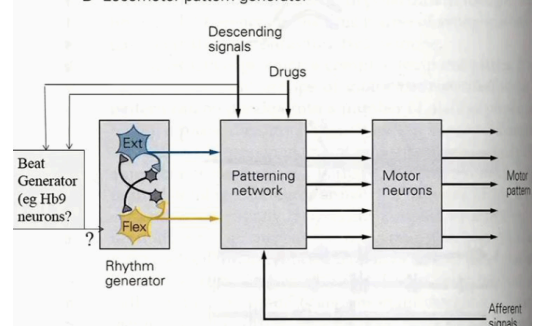
Decerebrate cat experiments reveal brainstem regions involved in initiation/regulation of stepping

Transection of the brainstem at different levels elicited:



Thus, descending pathways from different brain regions must have both positive and negative influences on stepping behavior.

D Locomotor pattern generator

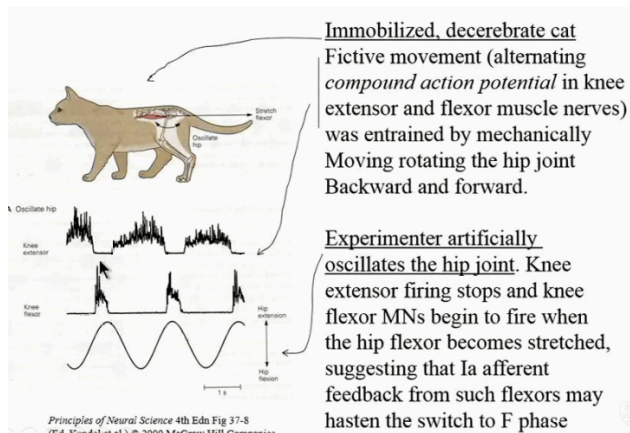


Sensory afferent can modify stepping

- **Proprioceptors** – in muscles and joints provides information to brain about limb position
- **Cutaneous receptors** – spinal level reflex response to external obstacles (rocks etc)

The spinal cat can speed up its rate of walking to match changes in the speed of the treadmill by **foreshortening the stance phase of stepping**

What determines the change in stepping phase? 2 ways:



By stimulating the stretch receptor in the hip joint of a cat, they were able to show that the knee extensor prematurely stopped and the knee flexor occurred earlier in the cycle.

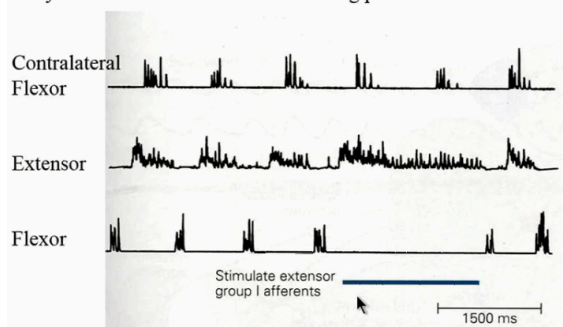
This proves the information from the Ia afferents is important in changes the stages of the cycle by making the muscle make their transition.

Ankle Extensor afferents

Are also believed to have an influence in switch to swing phase

- Ankle extensor afferents are most active when the ankle active extending
- Output of class I afferents from ankle extensors drops off at the end of the power stroke when tension eases off the foot
- Prolonging the activity of the ankle extensors (power stroke not completed) can delay the switch to swing phase

Ankle extensor spindle (and other) afferent activity delays the transition from stance to swing phase



Extensor Ia spindle (and other) afferent activity can delay the transition from stance to swing phase

