Walking

Central Pattern Generation

Gaits in insect walking:
tripod gait

- cockroach (*Periplaneta americana*)
  - 0.44-1.1 m/s alternating tripod gait
  - 1-1.5 m/s quadruped gait or bipedal

adult stick insects use tetrapod gait
(like “walk”, tripod gait like “trot”)

Walking: cycle of movements

stance phase:
- tarsi in contact with the ground
- backward movement of legs
- extensor motoneurons and muscles active
  - body moves forward

swing phase
- tarsi not in contact with ground
- forward movement of legs
- flexor motoneurons and muscles active

Walking: typical for insects:
you don’t fall over as long as your center of gravity is between 3 points
- use of insect walking as model for robot manoeuvring in rough terrain
Pattern generators in walking

alternative hypotheses:
- one central pattern generator for all legs?
- one central pattern generator for each leg?

Coordination between legs in the stick insect

1. swing phase inhibits swing (anterior)
2. start of stance excites start of swing (anterior, lateral)
3. caudal positions excite start of swing (posterior, lateral)
4. targeting (starn go to last position of anterior tarsi, lateral)
5a. increased resistance increases force (coactivation; all directions)
5b. increased load prolongs stance (all directions)
6. do not step on your own toes

“The temporal sequence of the movements of all legs can be explained by the actions of a distributed command structure consisting of six more or less independent walking-pattern generators and at least three different kinds of coordinating pathways between them.” (Bender, Buschges 1998)
Control of movements of a single leg

- Leg motor neurons
- Each muscle: 1-9 motoneurons
- All muscles of all joints of the leg: about 70
- Fast and slow motor neurons, usually also innervate fast and slow muscle fibers
- Inhibitory neurons (common inhibitory neurons supply several muscles)

Constant activity here: common inhibitor neurons.
They speed up walking by relaxing tonically active posture muscles, inhibition speeds up relaxation of muscles.

Central pattern generators in walking

Does walking depend on sensory feedback or by activity from the central nervous system?

- Fast walking cockroach: basic pattern produced by CNS
- Slow walking stick insect: sensory feedback dominant role; walking pattern as long as sensory feedback from at least one leg.

Feedback through sensory systems

- Sense organs measuring position
- Sense organs measuring load

- Sensory information modulates and coordinates motor neuron activity
- System is highly redundant, ablation of particular sense organ no or only weak effect
- Effect only in the moving not/barely in standing animal

Sense organs on insect legs

- Chordotonal organs (stretch receptor, velocity, acceleration, position)
- Hair plates (position between two joints)
- Campaniform sensilla (single receptor neuron per sensillum, compression of cuticle perpendicular to long axis)
- Tension receptors (signals the force generated by the muscle)
- Strand receptors (cell bodies in CNS, axons strung across joints or attached to apodemes of muscles)
- Muscle receptor organs
- Subgenual organ

There are a lot of receptor and they can act in parallel.
They can possibly influence each other.

Central pattern generator (CPG)

A neural circuit capable of producing repetitive activity in the absence of any sensory input

Although a CPG doesn’t need sensory input in order to produce oscillatory output, its activity can be affected by sensory input.
simple pattern generators:

- spontaneous bursting cell (can be started by neuromodulators)
- network of cells: cellular properties, synaptic properties, connections
  - neuromodulators can change cellular and synaptic properties -> changed motor pattern
- needed: time dependent changes in activity: postinhibitory rebound, synaptic depression, delayed excitation, different time in synaptic action ("delay line")

post-inhibitory rebound

- After release from inhibition neurons tend to fire a burst of action potentials.
- Not in all neurons.
  - Hypermotivation reduces the number of inactivated sodium channels this decreases the neuron's firing threshold.
  - If the neuron repolarizes abruptly (as when it is disinhibited), then the membrane potential crosses the threshold and the cell fires action potentials.

Examples for Central Pattern Generators

- flying (locust)
- walking (cockroaches, walking stick, locust, cat)
- breathing (mice, rat)
- stomatogastric ganglion (lobster, crab)
- swimming (leech)
- chirping (crickets)
Simple CPG model - a two neuron CPG model can be constructed using post-inhibitory rebound.

Two reciprocally inhibitory neurons that fatigue and show post-inhibitory rebound will oscillate.

Input sets cycle off by release of inhibition, here from neuron A. The neurons oscillate until inhibition of A is turned on again.

The most famous Central Pattern Generator: Stomatogastric Ganglion (about 30 cells)

- esophagus
- cardiac-sac region of the stomach
- gastric region/gastric mill teeth
- pylorus

* 2 commissural ganglia (each several 100 neurons)
* esophageal ganglion (about 12 neurons)
* stomatogastric ganglion (about 30 neurons)

stomatogastric ganglion

gastric muscle sequence  pyloric muscle sequence
Neuromodulators change CPG rhythms