Lecture 24 -- Posture and Locomotion -- Krakauer

Posture

Introduction
- Postural control: taken for granted until you lose it! e.g., the most devastating and difficult symptom to treat in Parkinson’s disease.
- Postural system must maintain balance against gravity, must be able to anticipate changes in the center of gravity, and be adaptive.
- Static and dynamic equilibrium

Anticipation and Adaptation
- Postural adjustments require anticipatory motor actions, e.g., lifting leg sideways (Fig. 41.1)
- Context influences postural control: “postural set” (Fig. 41-2): interaction of feed-forward and feedback control.
- Learning the appropriate postural responses (Fig. 41.3). This adaptability requires the cerebellum (Fig. 41.4)
- Adaptive postural control is learned during locomotion (Fig. 41.5).

Locomotion

Introduction
- Anticipation and movement
- Adjustable rhythmicity
- Early research on spinal preparations revealed that stepping of the hindlegs could be initiated by lifting the leg or by non-rhythmic electrical stimulation of the cord. This led to the following conclusions:
  1. Supraspinal structures are not necessary for producing the basic motor pattern of stepping.
  2. The basic rhythmicity of stepping is produced by neuronal circuits contained entirely within the spinal cord.
  3. The spinal circuits can be activated by tonic descending signals from the brain.
  4. The spinal pattern-generating networks do not require sensory input but nevertheless are strongly regulated by input from limb proprioceptors.

- More recent research elicited walking on treadmill by spinalized animal by:
  1. application of adrenergic drugs
  2. stimulation of the brainstem.

The step cycle (Fig. 37.2)
- Swing phase: flexion (F) and first extension (E1).
- Stance phase: Second extension (E2) and third extension (E3).
The rhythmic movements of the legs during stepping are produced by contractions of a large number of muscles and the pattern is spatially and temporally complex: not just flexion during swing and extension during stance! The complex sequence is known as the **motor pattern for stepping**.

**The half-center model and flexor reflex afferents (Fig. 37.4)**

- In 1911 it was discovered that rhythmic extensor-flexor activity could occur in hindlimbs after transection of the spinal cord and of the dorsal roots. This led to the proposal of the **half-center model**. Note that in order to get rhythmicity there has to be switching between half-centers; proposed that this is due to decay in the inhibitory interneurons.
- Evidence for the half-center model came from spinal cats treated with L-DOPA, whose hindlimb small fiber cutaneous and spindle afferents were then stimulated. Note: non-rhythmic peripheral input generating the rhythmic locomotor behavior. What about generating the locomotor pattern intrinsically?
- A variety of motor patterns can be generated in the absence of phasic sensory input to the spinal cord. Please concentrate on Fig. 37.7D showing the arrangement of a locomotor pattern generator. Notice how this is similar to the organization of reflex circuits discussed in the previous lecture.

**Sensory input from the moving limb regulates stepping patterns.**

- Despite the existence of CPGs, it is clear that walking can be regulated and modulated by somatosensory afferents.
- Proprioceptors are responsible for regulating the duration of the stance phase and thus the rate of stepping: muscle spindles in hip flexors signal the hip angle at the end of the stance phase and trigger the swing phase.
- The GTO and muscle spindles in the hip extensors also are important but in this case activating them delays the onset of the swing phase (Fig. 37.9). Please note that the excitatory influence of the GTOs via the Ib afferent on extensor motor neurons during walking is the opposite of their inhibitory action when the animal is at rest. This **reflex reversal** is very useful because it means that the swing phase will not be initiated until the leg is unloaded as signaled by the decreased activity in the GTO.
- Sensory feedback contributes to the overall level of extensor motorneuron activity. This provides a way to adjust output at short latency in response to unexpected perturbations. There are at least three excitatory pathways that transmit information from extensor afferents to extensor motor neurons (Fig. 37-9B).
- The **stumbling-corrective reaction** in the spinalized cat. Note, corrective flexion only occurs if the paw is stimulated during the swing phase. The opposite occurs when the identical stimulus is applied during the stance phase. This is a **phase-dependent reflex reversal** (c.f. state-dependent reflex reversal above and in the previous lecture).
**Supraspinal Regulation of Stepping.**

Fine control of stepping involves numerous regions of the brain and brainstem (Fig. 37.10):

1. Brainstem descending pathways activate the spinal locomotor system (glutamatergic fibers from the medullary reticular formation [MRF]) and control the overall speed of locomotion. The intensity of stimulation of the mesencephalic locomotor region (MLR) determines the gait and rate of stepping. Note that a monotonically changing command signal can lead to time-varying effects on stepping. This is another example of how complexity in intrinsic spinal circuitry can simplify what is needed in descending commands (Fig. 37-11).

2. The cerebellum regulates the timing and intensity of descending signals. It does this by comparing the actual movements of the legs via proprioceptive signals in the dorsal spinocerebellar tract to intended movements via signals in the ventral spinocerebellar tract. The computed error signal is then sent to the brainstem nuclei.

3. The motor cortex is involved in the visually-guided control of walking.

**Relevant reading:** chapters 37 and 41 in “Principles”