

Movement



Our brains evolved to move

Around 600 million years ago, first animals appeared in water.

Plants:

synthesize food
no digestive system
do not move

Animals:

consume organic material
have digestive system
move freely

Evolution of these new skills required new system for monitoring internal and external environment (sensory part) and response generation (motor part). These functions are carried out by the nervous system.

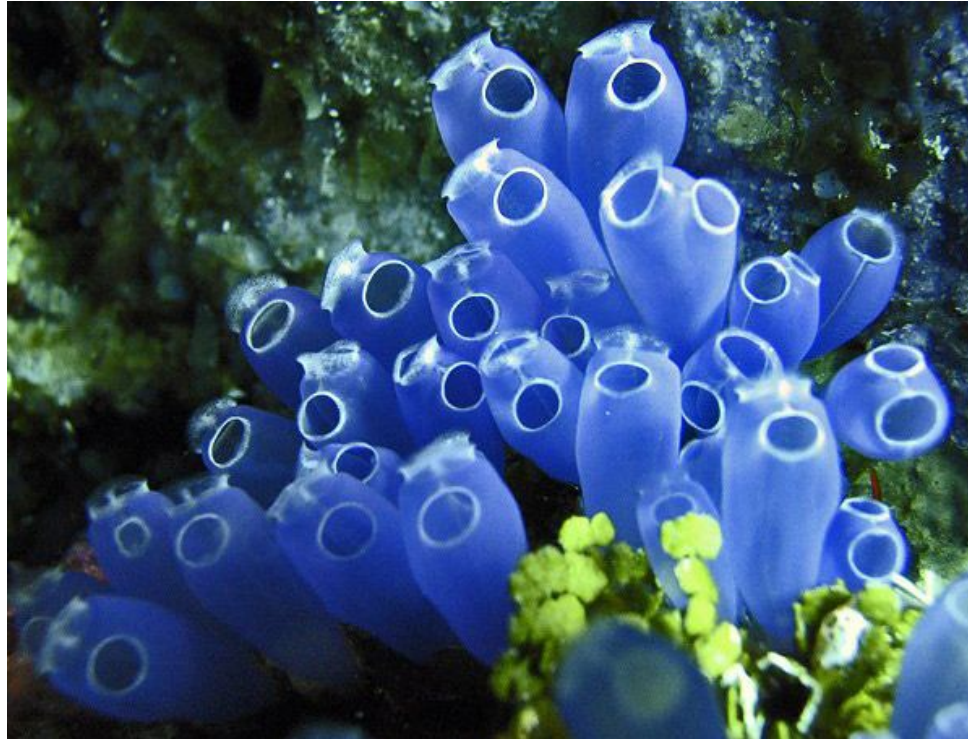


Sea sponge – animal without nervous system but with chemical communication between cells and propagation of electrical impulses through conductive tissue



Jellyfish– animal with a nervous system that transmit impulses (nerve net)

Sea squirt



The young sea squirt has a spinal cord connected to a simple eye and a tail for swimming. It also has a primitive brain that helps it move through the water. When it matures, it finds a suitable place to attach itself and digests its own brain for food.

Movement

The motor system generates:

- reflexes
- rhythmic activity
- voluntary movements



Reflexes

Reflexes are *involuntary* coordinated patterns of muscle contraction and relaxation elicited by peripheral stimuli.

Charles Sherrington introduced the concept of a reflex arc (neural pathway from receptor to effector). He also suggested that reflexes may be elementary units of behavior.

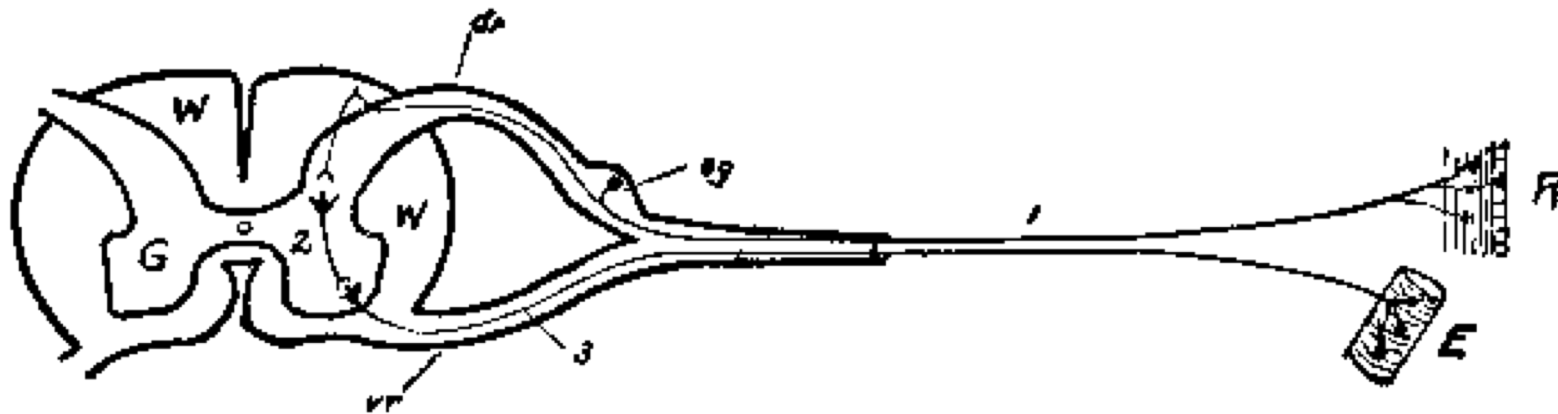
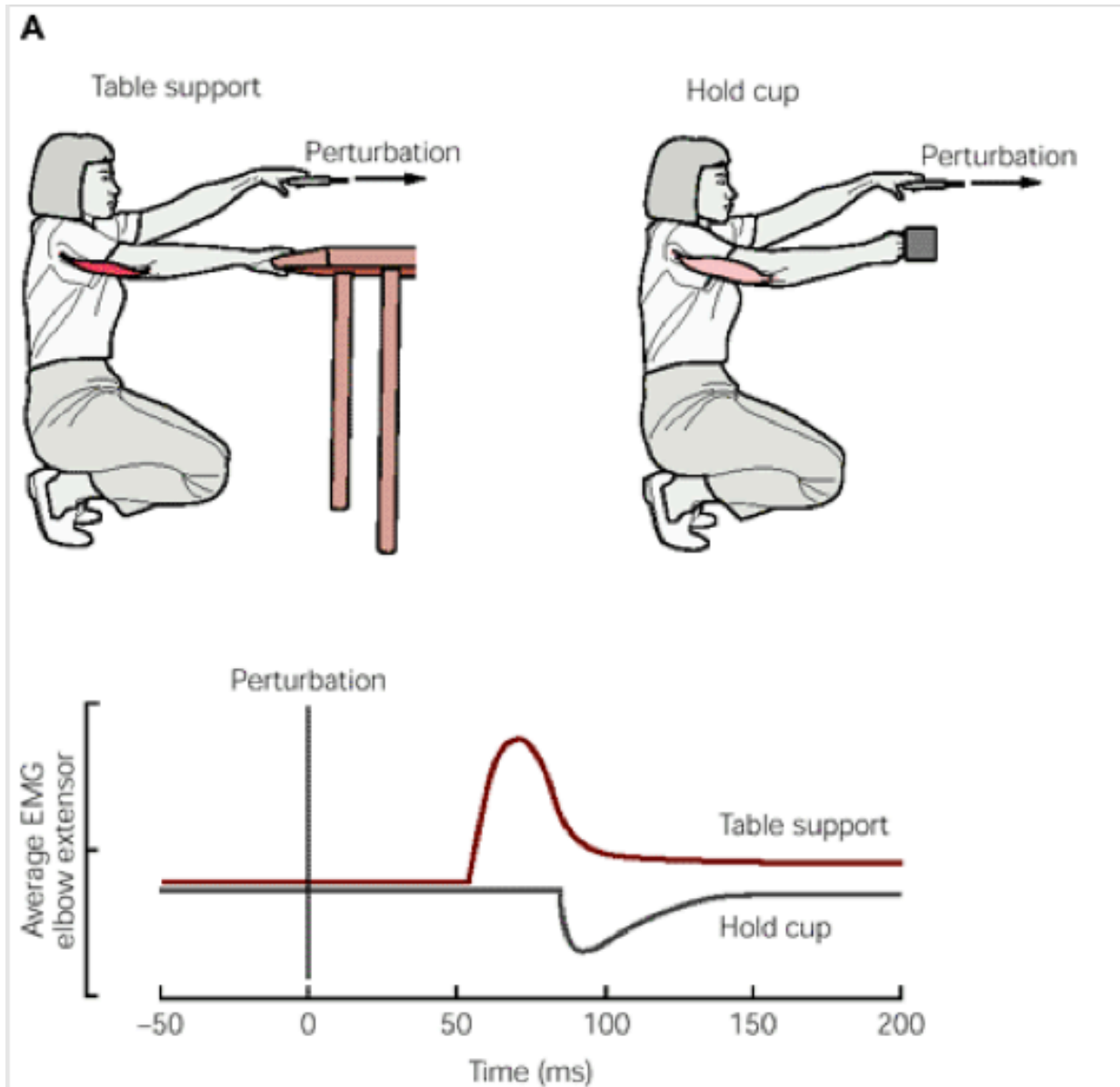


FIGURE 2. DIAGRAM OF A CROSS-SECTION THROUGH THE SPINAL CORD, SHOWING THE ELEMENTS OF A REFLEX ARC INVOLVED IN A SPINAL NERVE

(After Watson.) *W*, white matter; *G*, gray matter; *dr*, dorsal (posterior) root; *vr*, ventral (anterior) root; *1*, afferent neuron; *2*, central or association neuron; *3*, efferent neuron; *sg*, spinal ganglion of the dorsal root containing cell body of the afferent neuron; *R*, receptor — sense organs in the skin; *E*, effector — a striped muscle fiber.

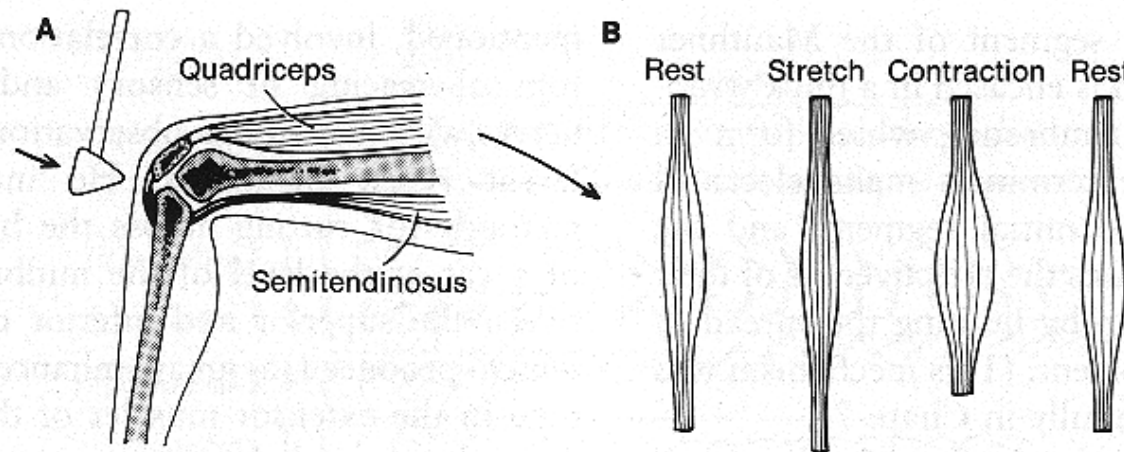
Reflexes can be complex



Reflex responses are often complex and can change depending on the task. Perturbation of one arm causes an excitatory reflex response in the contralateral elbow extensor muscle when the contralateral limb is used to prevent the body from moving forward, but the same stimulus produces an inhibitory response in the muscle (reduced EMG) when the contralateral hand holds a filled cup.

The stretch reflex

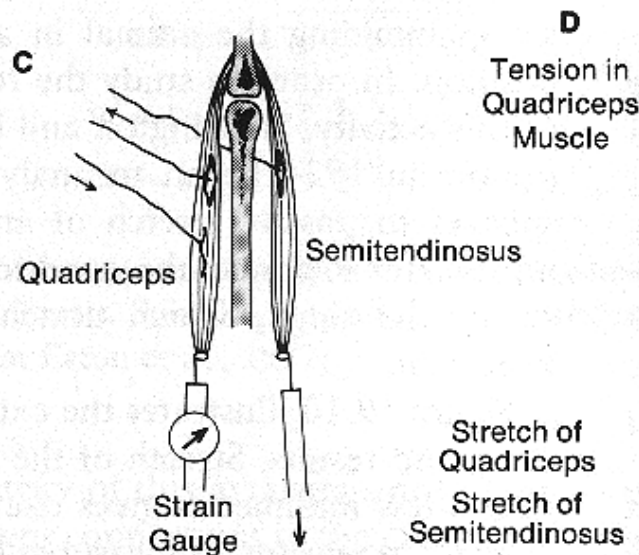
Early experiments on reflexes were performed by Sherrington (~1924) on extensor muscles of the cat.



A. Testing for the stretch reflex.

B. Different conditions of the muscle.

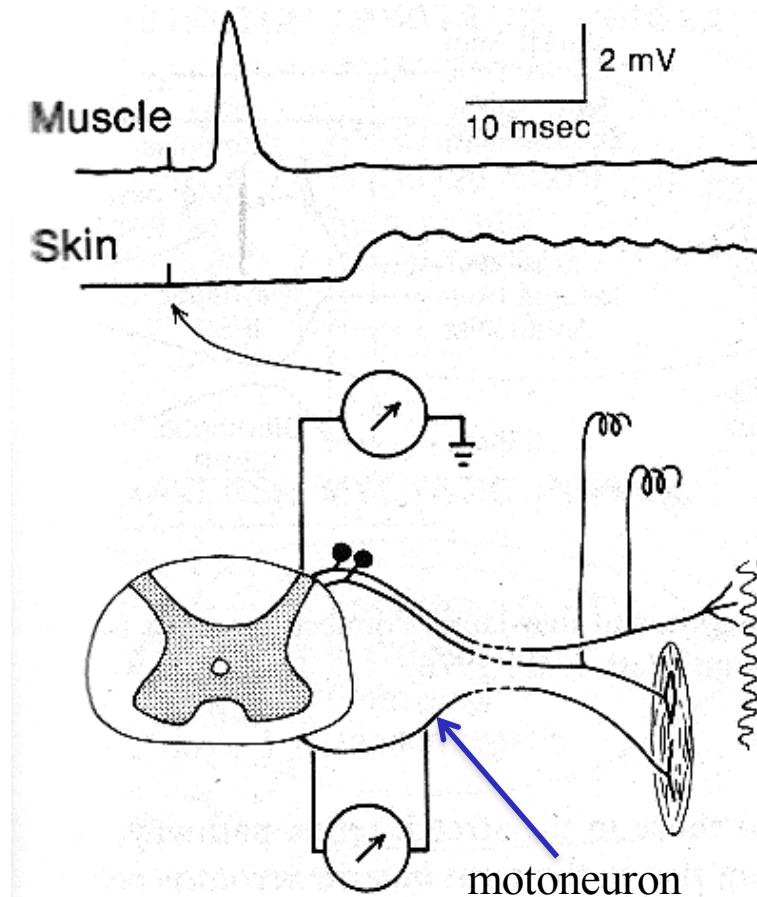
C. Experimental setup for analyzing the stretch reflex in the cat.



D. Stretch of a muscle results in large increase in tension, as measured by the strain gauge. If the muscle nerve is cut, the tension is small (passive tension). If it is intact, the tension is larger (active tension). This shows that the large tension depends on a reflex pathway but not on elastic properties of the muscle. The reflex activity produces contractions of the muscle that was stretched, hence the name 'stretch reflex'. Stretch of the antagonistic muscle has an inhibitory effect on the tension.

Muscle and skin reflexes

Analysis of nervous pathways involved in reflex activity begun in 1940 by David Lloyd.



Responses of the motoneuron axon in response to stimulation of the nerve from muscle and nerve from the skin. The input from muscles is carried over large, rapidly conducting axons and possibly monosynaptic pathway. The input from the skin is carried by slower conducting fibers and polysynaptic pathways.

Types of neural fibers (reminder)

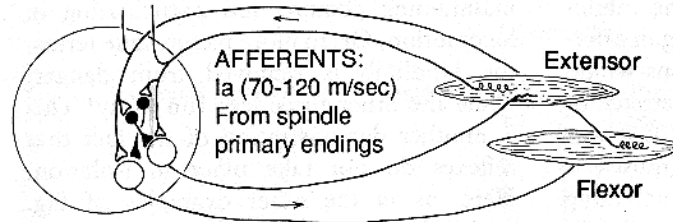
Table 13.2 The fiber spectrum of the peripheral nerves in the mammal

	Myelinated fibers				Unmyelinated		
A. Fiber diameter:	20	15	10	5	2.0	0.5	μm
B. Conduction velocity:	120	90	60	30	6	2.0	m/s
C. Sensory fiber class: (Gasser)	A α		A β	A γ	A δ	C	
D. Function: skin afferents	Vibration (Pacini)		Hair 'T'	Hair 'G'	Slowly adapting	High threshold pressure	Mechanical nociceptive
							'Slow' nociceptive
							'C' Touch fibers
							Temperature: cold
							Temperature: warm
E. Motor fibers:	α Motor		β	γ Motor			
F. Fiber class: muscle afferents (Lloyd)	Ia Primary spindle		II Secondary spindle	III Nociceptive fast		IV Nociceptive slow	
	Ib Golgi tendon organ						

After Somjen (1972)

Spinal reflexes - summary

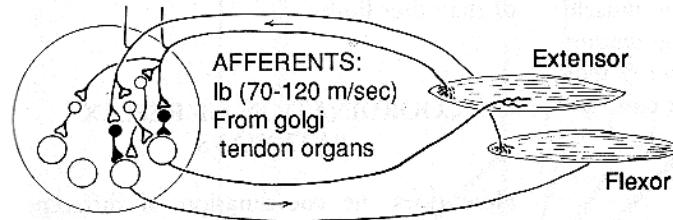
A. STRETCH (MYOTATIC) REFLEX



DETECTS: Phasic stretch
of muscle

FUNCTIONS:
Control of movement
? Antigravity

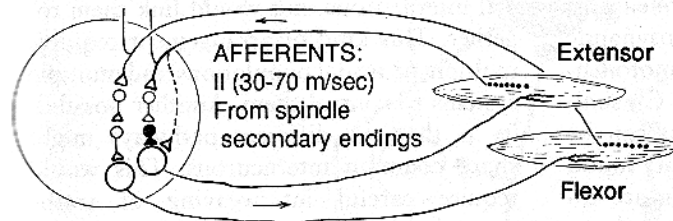
B. INVERSE MYOTATIC REFLEX



DETECTS: Active stretch
of tendon

FUNCTION:
Control of muscle force
Control of muscle
stiffness

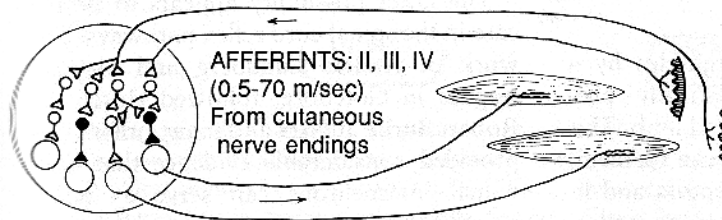
C. GROUP II REFLEX



DETECTS: Steady stretch
of muscle

FUNCTIONS:
Posture?

D. FLEXOR REFLEX

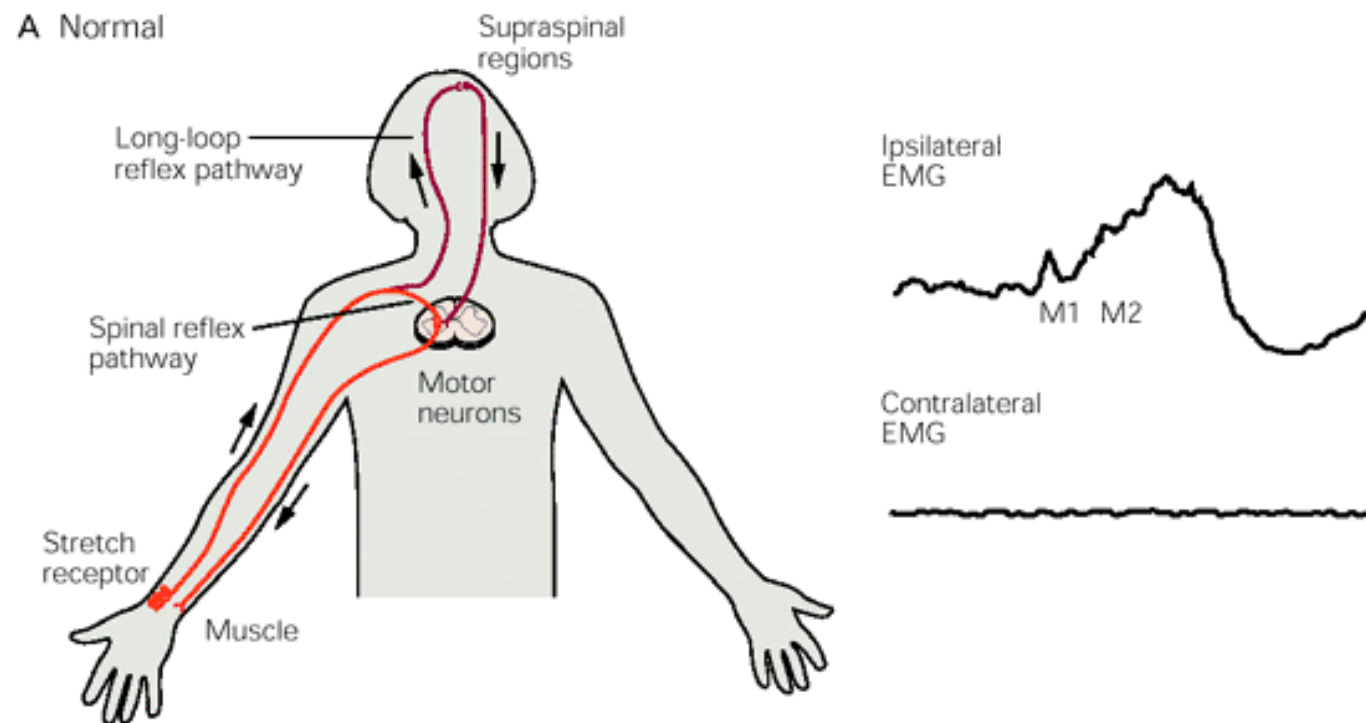


DETECTS: Harmful stimuli

FUNCTIONS:
Withdraw limb from harm

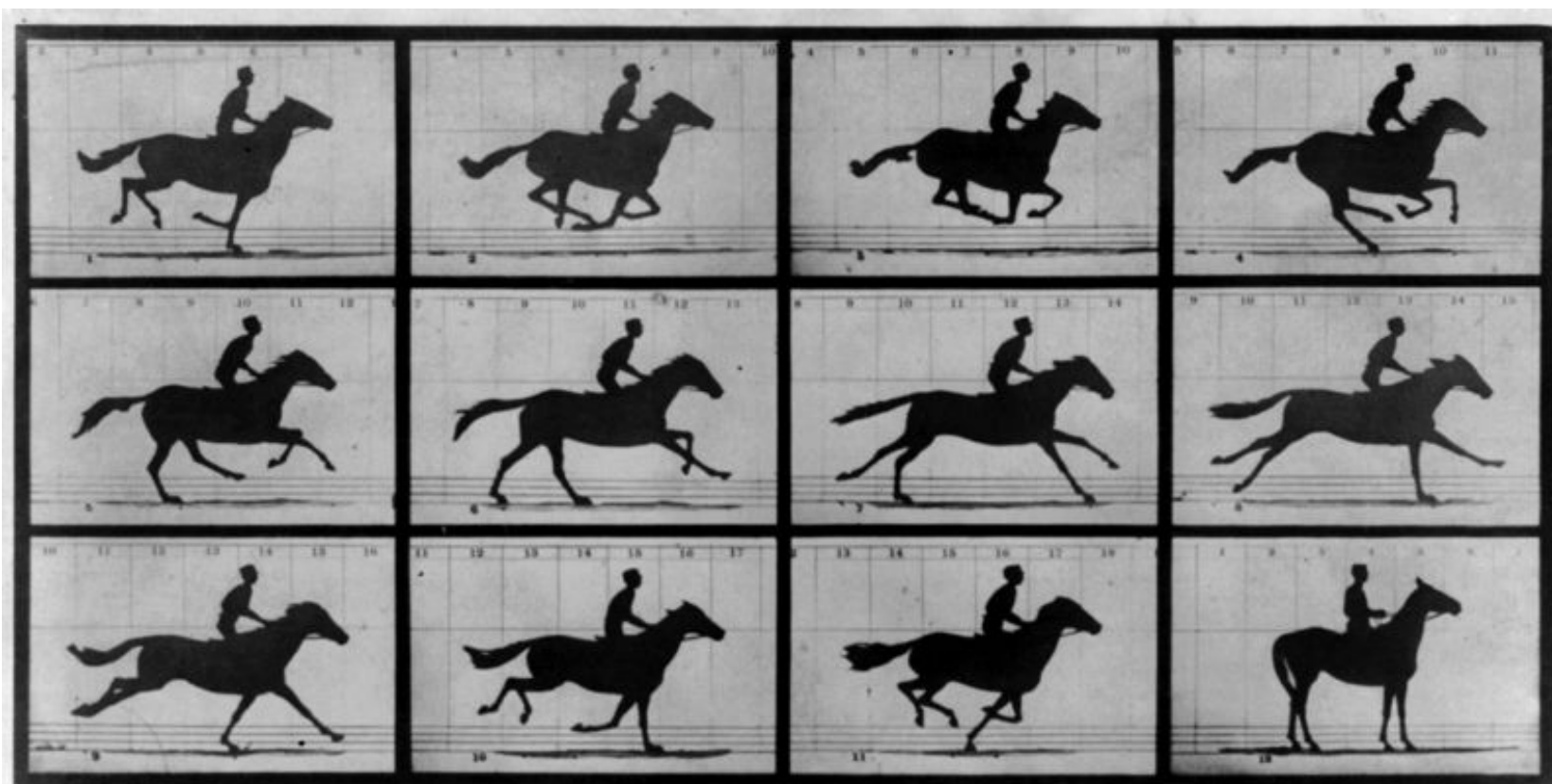
Spinal and supraspinal reflexes

Sensory signals produce reflex responses through spinal reflex pathways and long-loop reflex pathways that involve supraspinal regions.



A brief stretch of a thumb muscle produces a short-latency M1 response in the stretched muscle followed by a long-latency M2 response. The M2 response is the result of transmission of the sensory signal via the motor cortex.

Locomotion



Copyright, 1878, by MUYBRIDGE.

MORSE'S Gallery, 417 Montgomery St., San Francisco.

THE HORSE IN MOTION.

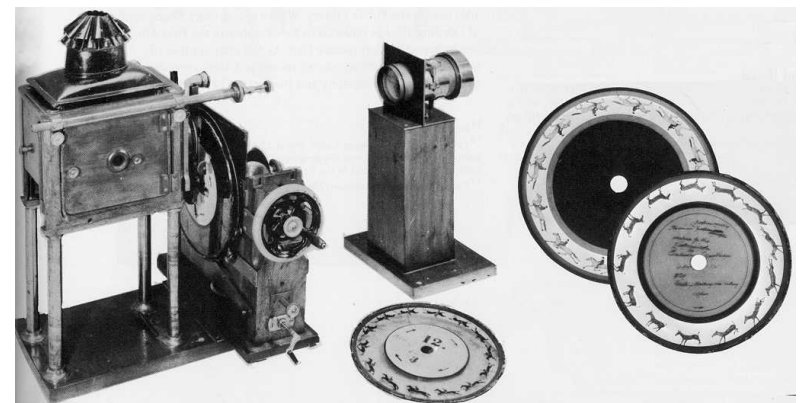
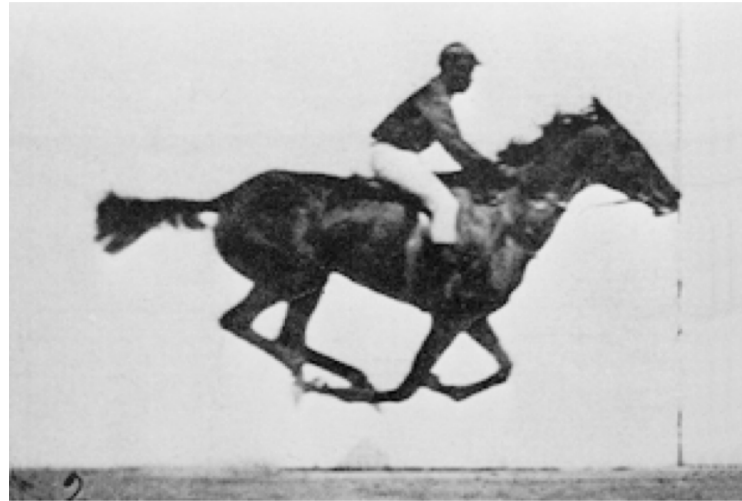
Illustrated by
MUYBRIDGE.

AUTOMATIC ELECTRO-PHOTOGRAPH.

"SALLIE GARDNER," owned by LELAND STANFORD; running at a 1.40 gait over the Palo Alto track, 19th June, 1878.

The negatives of these photographs were made at intervals of twenty-seven inches of distance, and about the twenty-fifth part of a second of time; they illustrate consecutive positions assumed in each twenty-seven inches of progress during a single stride of the mare. The vertical lines were twenty-seven inches apart; the horizontal lines represent elevations of four inches each. The exposure of each negative was less than the two-thousandth part of a second.

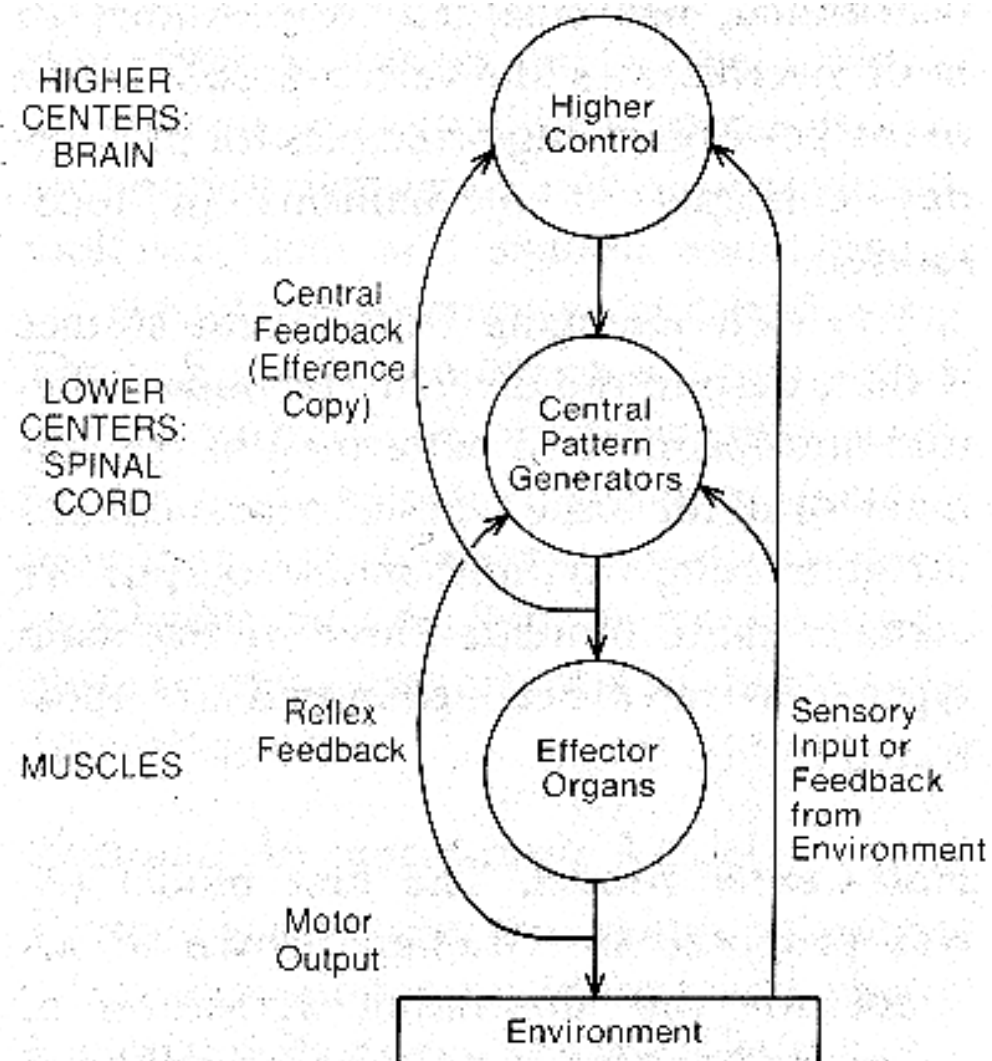
Eadweard Muybridge and his zoopraxiscope (1879)



Bullet-time effect – The Matrix (1999)



Components of motor systems

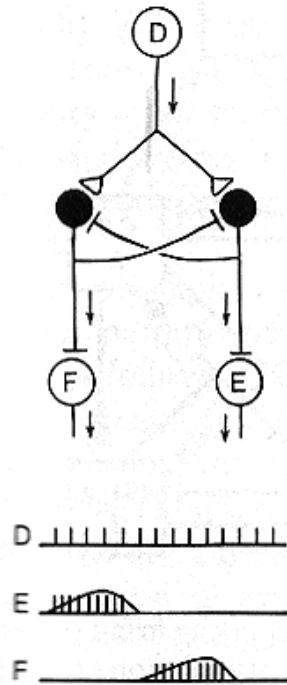


The main neural components common to most motor systems: muscles, generators of rhythmic activity and movement control centers.

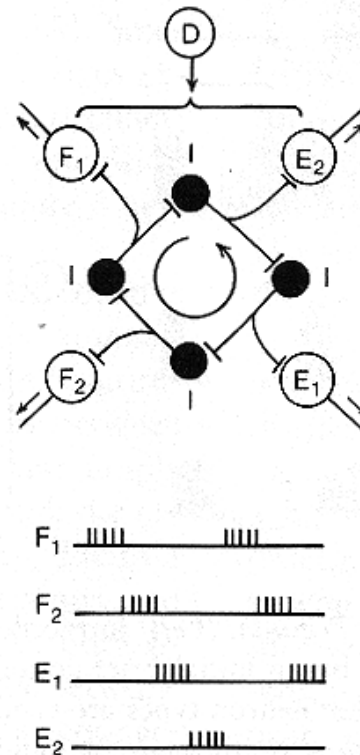
Central pattern generator

Central pattern generator (CPG) – neuronal mechanism capable of generating a rhythmic pattern of motor activity in the absence of phasic sensory input from peripheral receptors.

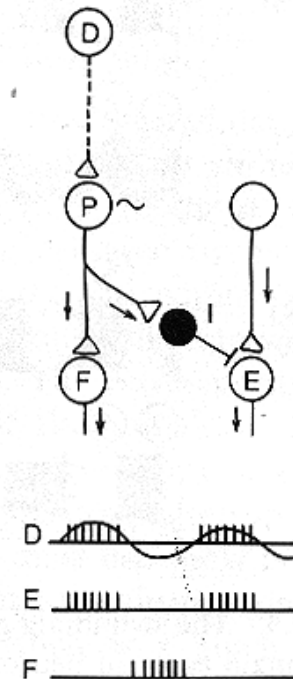
A. HALF-CENTER MODEL



B. CLOSED-LOOP MODEL



C. PACEMAKER MODEL



Basic types of rhythm generators. Abbreviations: D – driver, E – extensor motoneuron, F – flexor motoneuron, I – interneuron, P – pacemaker (rhythm generator). Excitatory neurons – open profiles, inhibitory neurons – filled profiles.

A. E and F motoneuron groups are activated by corresponding groups of interneurons. Inhibitory connections between interneurons ensure that when one group is active, the other is suppressed. Fatigue builds up in the inhibitory connections between the two half-centers allowing for switching activity between the centers.

B. Interneurons are organized in a ‘closed loop’. Corresponding motoneurons are activated or inhibited in sequence.

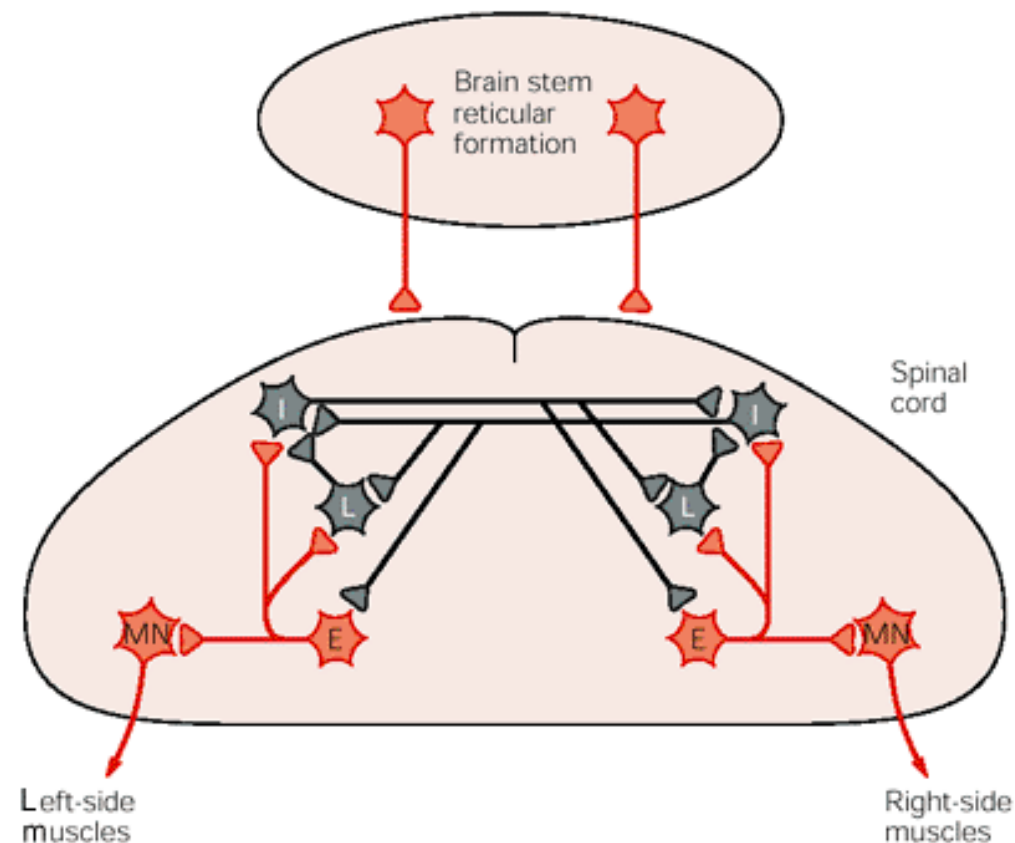
C. The rhythm arises from a pacemaker cell or group of cells. The pacemaker cell drives one group, and inhibits another group of motoneurons.

Swimming in Lamprey



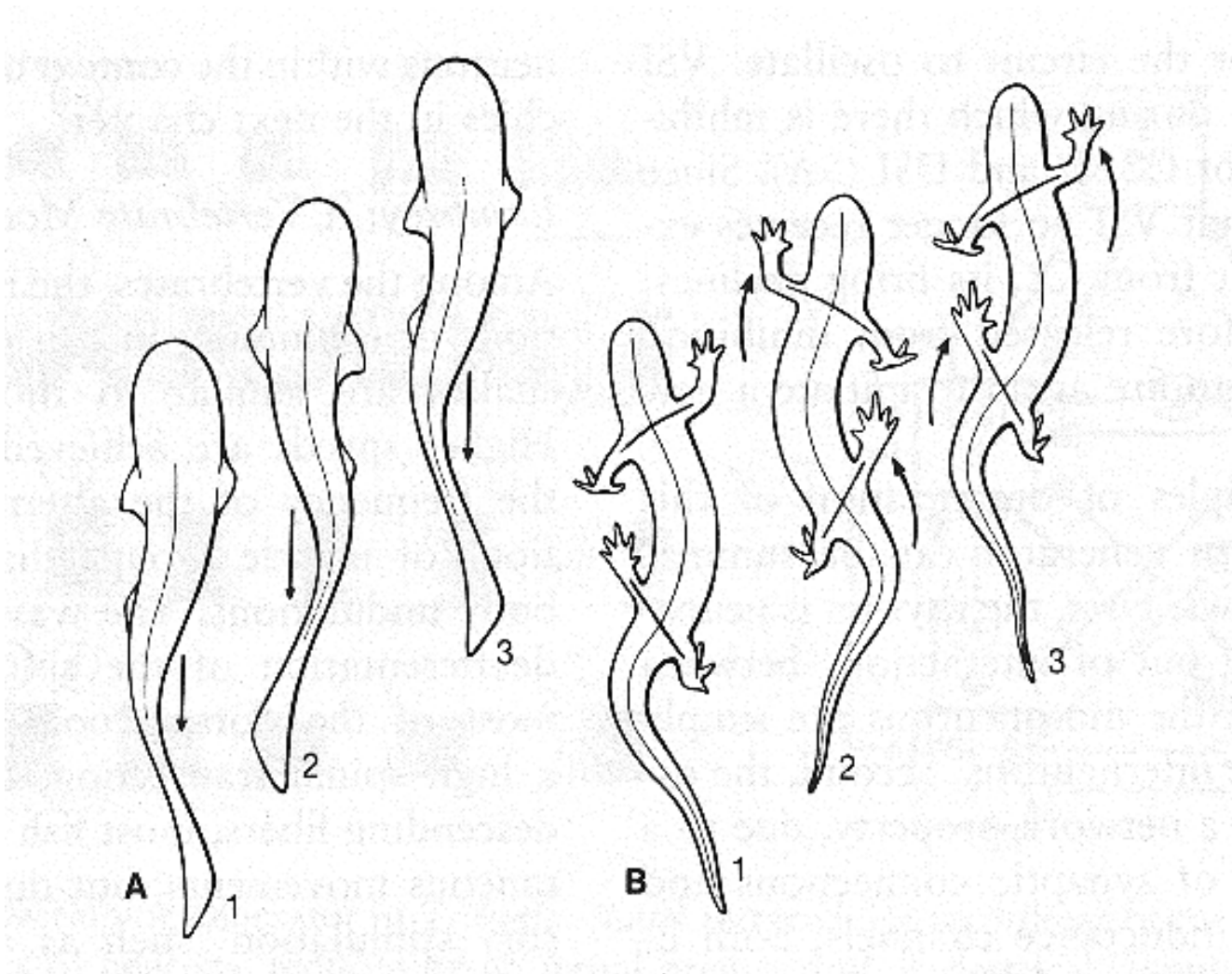
The lamprey swims by means of a wave of muscle contractions traveling down one side of the body 180° out-of-phase with a similar traveling wave on the opposite side. The wave amplitude increases towards the tail. Each of 100 body segments consists of CPG.

Segmental CPG in lamprey



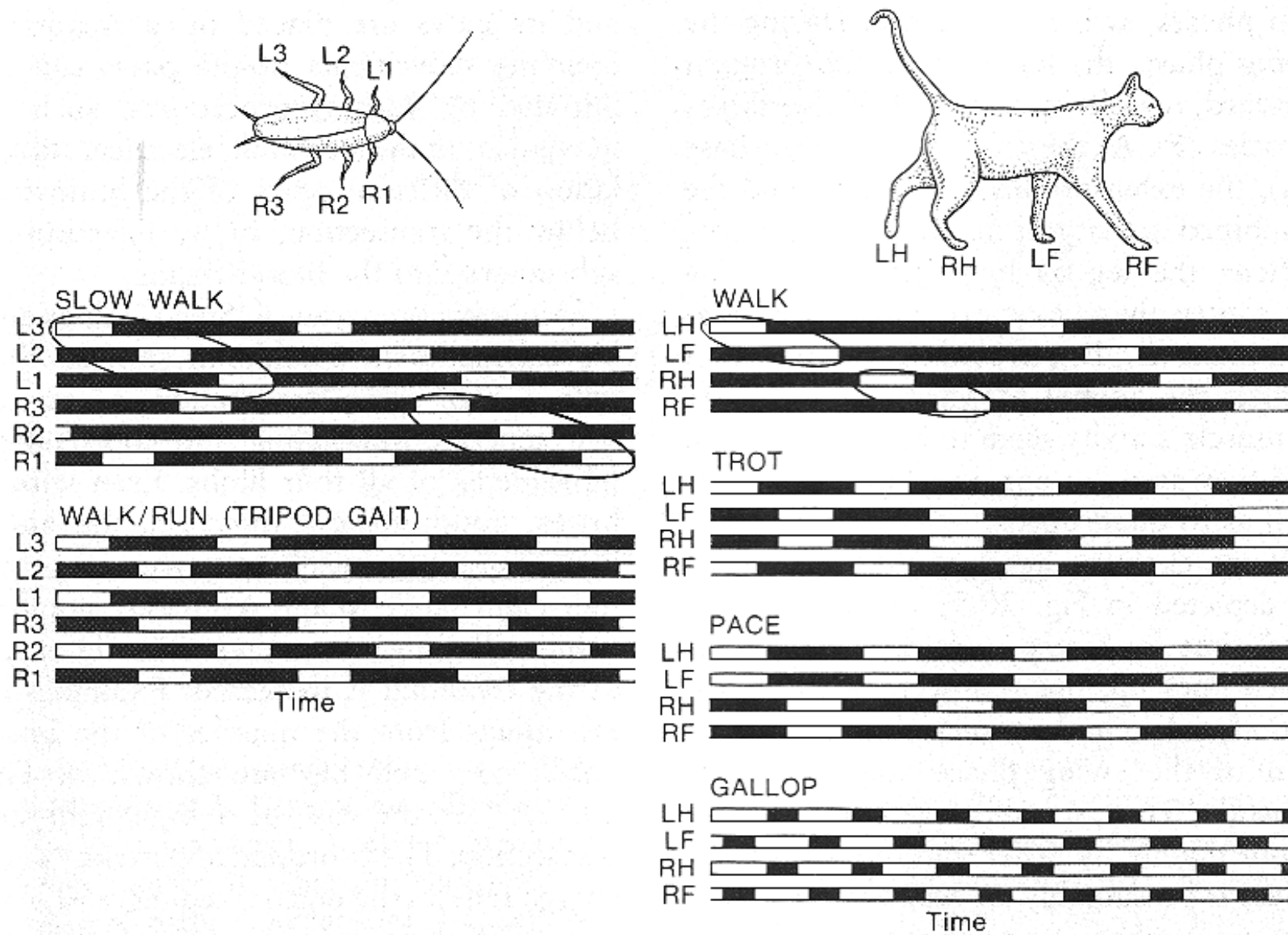
Some of the main features of the neuronal network in each body segment of the lamprey responsible for the rhythmic locomotor pattern for swimming. Activity in each segmental network is initiated by activity in glutaminergic axons descending from the reticular formation. On each side of the network excitatory interneurons (**E**) drive the motor neurons (**MN**) and two classes of inhibitory interneurons (**I** and **L**). The axons of the **I** interneurons cross the midline and inhibit all neurons in the contralateral half of the network, ensuring that when muscles on one side of the network are active, muscles on the other side are silent. The **L** interneurons inhibit the **I** interneurons on the same side.

From swimming to walking



Comparison between swimming movements of a fish and primitive walking movement of a salamander. Legs evolved from the fins to fulfill new functions. Forward movement is achieved by extension, placing and thrust of the limbs, in coordination with the swimming movements of the body.

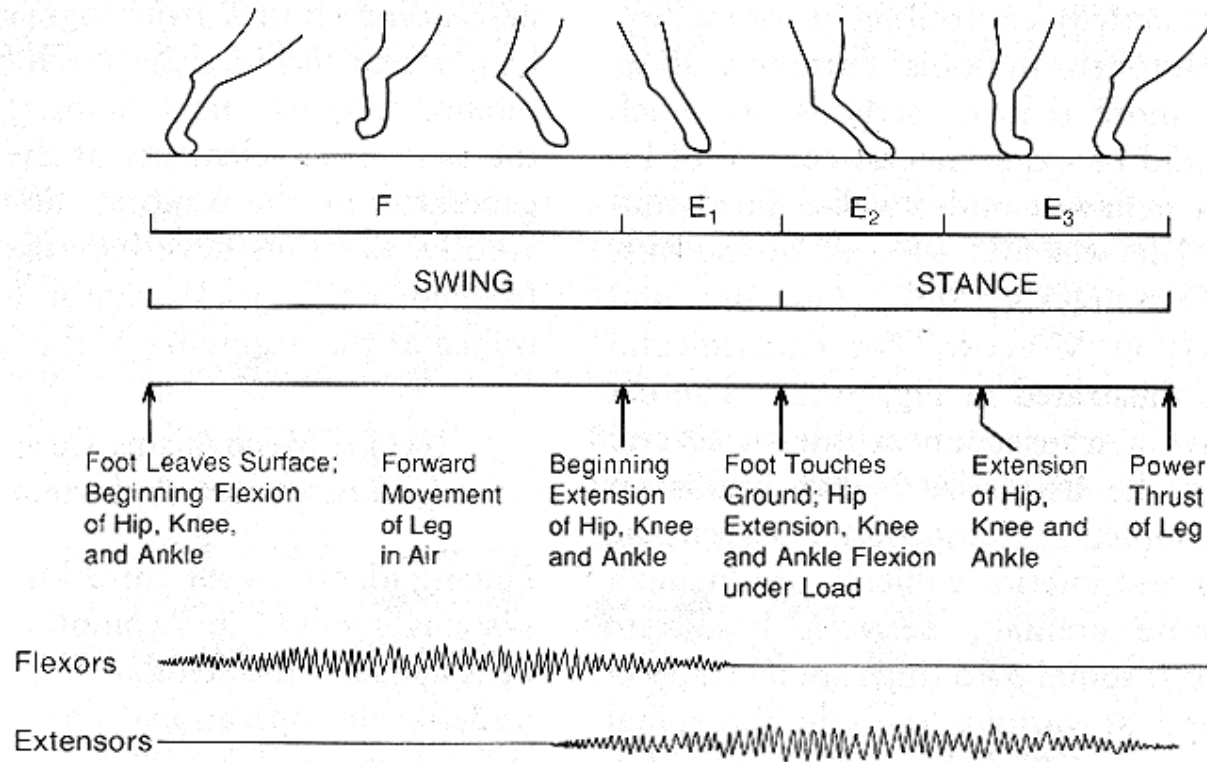
Gaits and step cycles



Comparison of the stepping movements of the cockroach and the cat for different gaits .

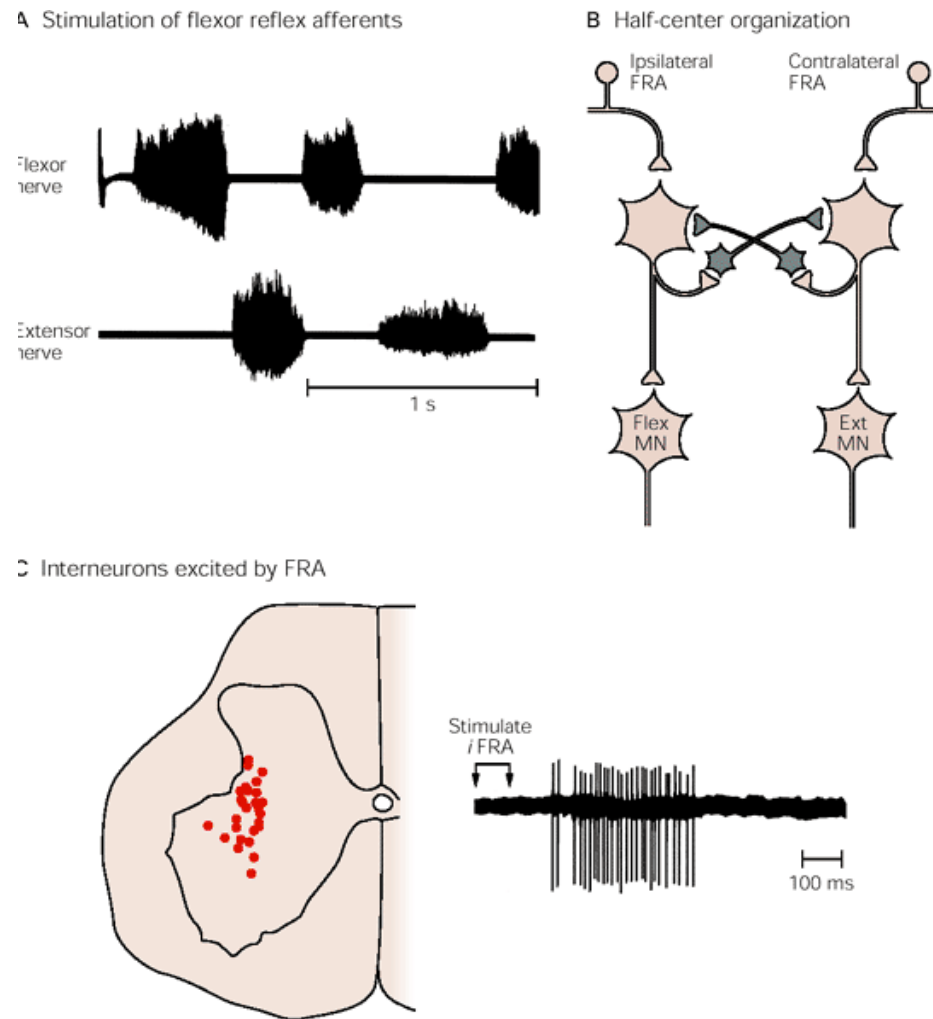
Foot lifted
 Foot planted

Step cycle



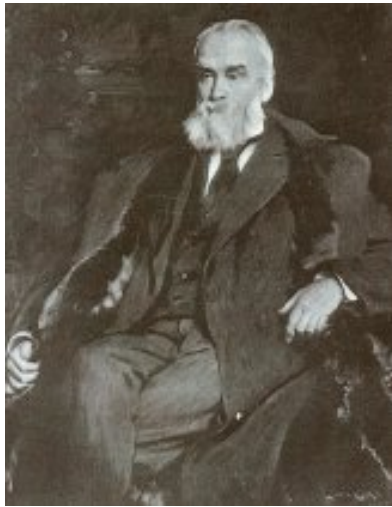
The step cycle consists of phases of leg flexion (F) and extension (E) which are seen in the electromyograph (EMG) recordings.

Spinal CPG



CPG in the cat is of 'half-center' type and is located in the spinal cord. A. Brief stimulation of ipsilateral FRA (flexor reflex afferents) evokes a short sequence of rhythmic activity in flexor and extensor motor neurons. B. The system of interneurons generating the flexor bursts was found to inhibit the system of interneurons generating the extensor bursts, and vice versa. C. Interneurons in the half-centers are located in the region of the gray matter in the spinal cord.

Hierarchy of motor system – the beginnings

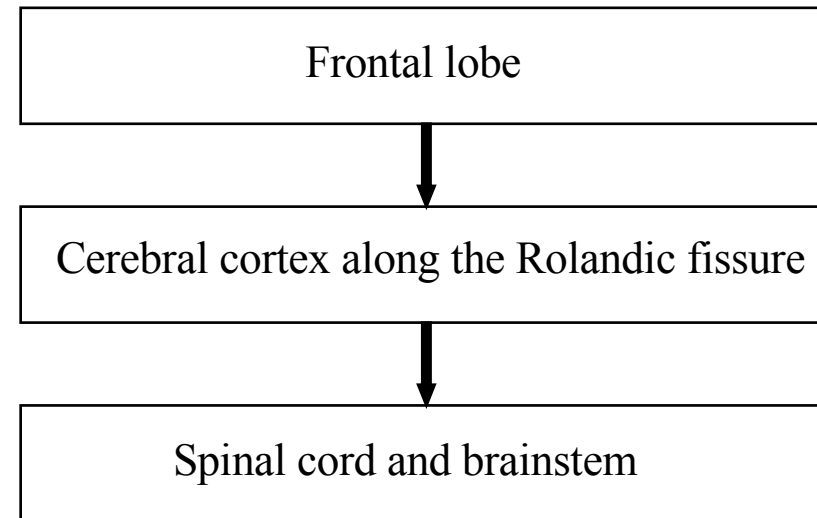


John Hughlings Jackson (1835 - 1911)

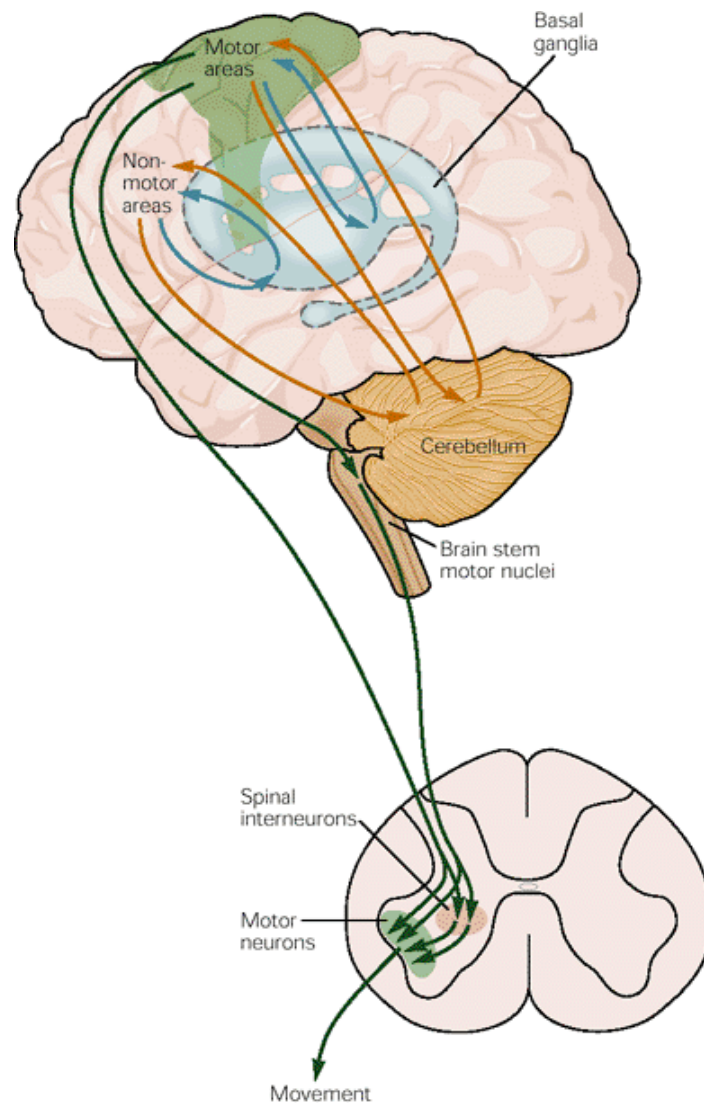
Based on observations of epileptic patients he came up with the idea that motor system is organized hierarchically. Higher levels exert control over the lower levels.

Automatic movements are controlled by lower levels, purposive movements by higher levels. When upper centers are destroyed by the disease, lower centers are released from higher control and the result may be hyperactivity.

The levels of motor control according to Jackson:

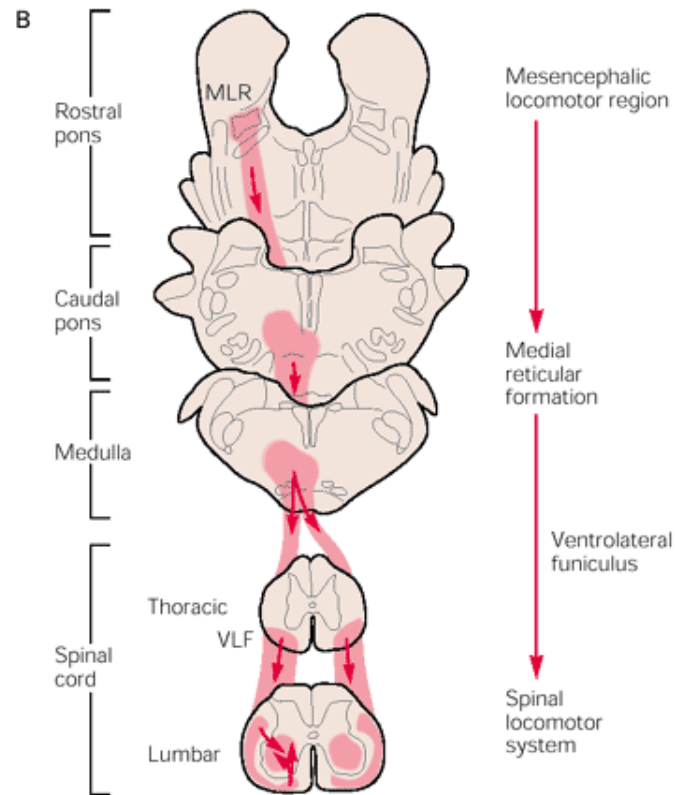
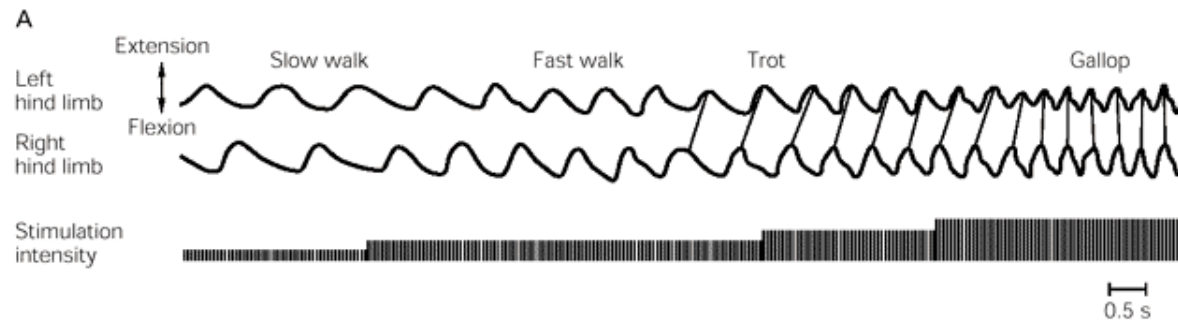


Hierarchy of motor system



The motor systems have three levels of control—the spinal cord, brain stem, and cortex. They are organized both serially and in parallel. The motor areas of the cerebral cortex can influence the spinal cord either directly or through the descending systems of the brain stem. All three levels of the motor systems receive sensory inputs and are also under the influence of two independent subcortical systems: the basal ganglia and the cerebellum. (The basal ganglia and cerebellum act on the cerebral cortex through relay nuclei in the thalamus, which are omitted from the diagram for clarity.)

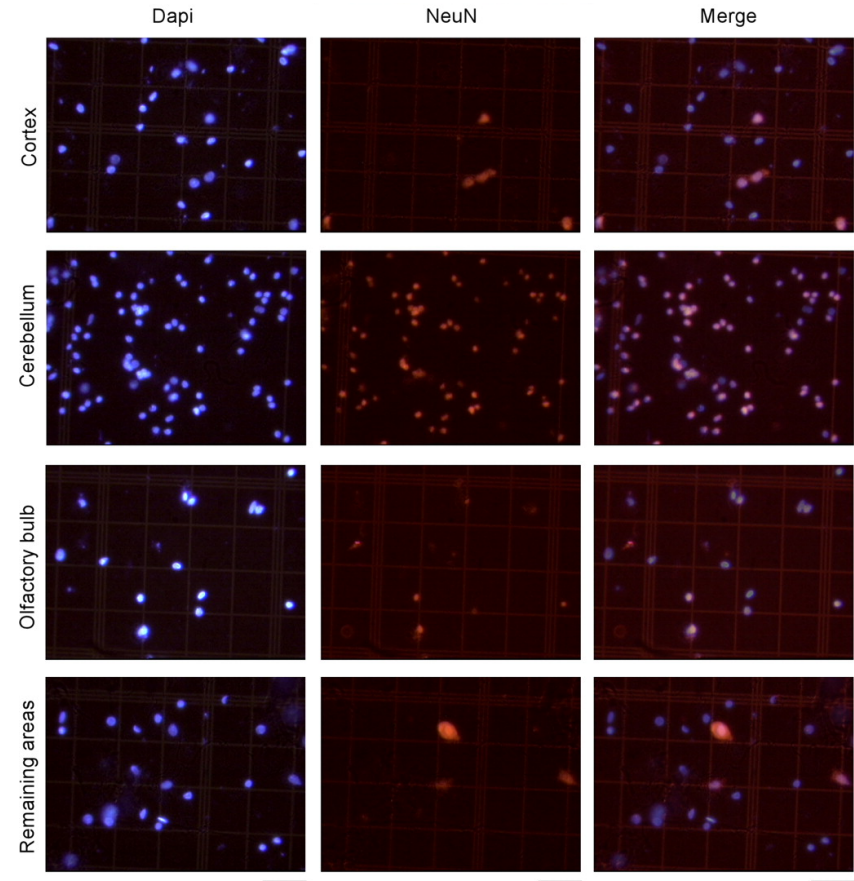
Locomotor responses to electrical stimulation of the mesencephalic locomotor region (part of the brainstem).



Increasing the strength of stimulation to the mesencephalic locomotor region (MLR) in a decerebrate cat walking on a treadmill progressively changes the gait and rate of stepping from slow walking to trotting and finally to galloping. As the cat progresses from trotting to galloping the hind limbs shift from alternating to simultaneous flexion and extension.

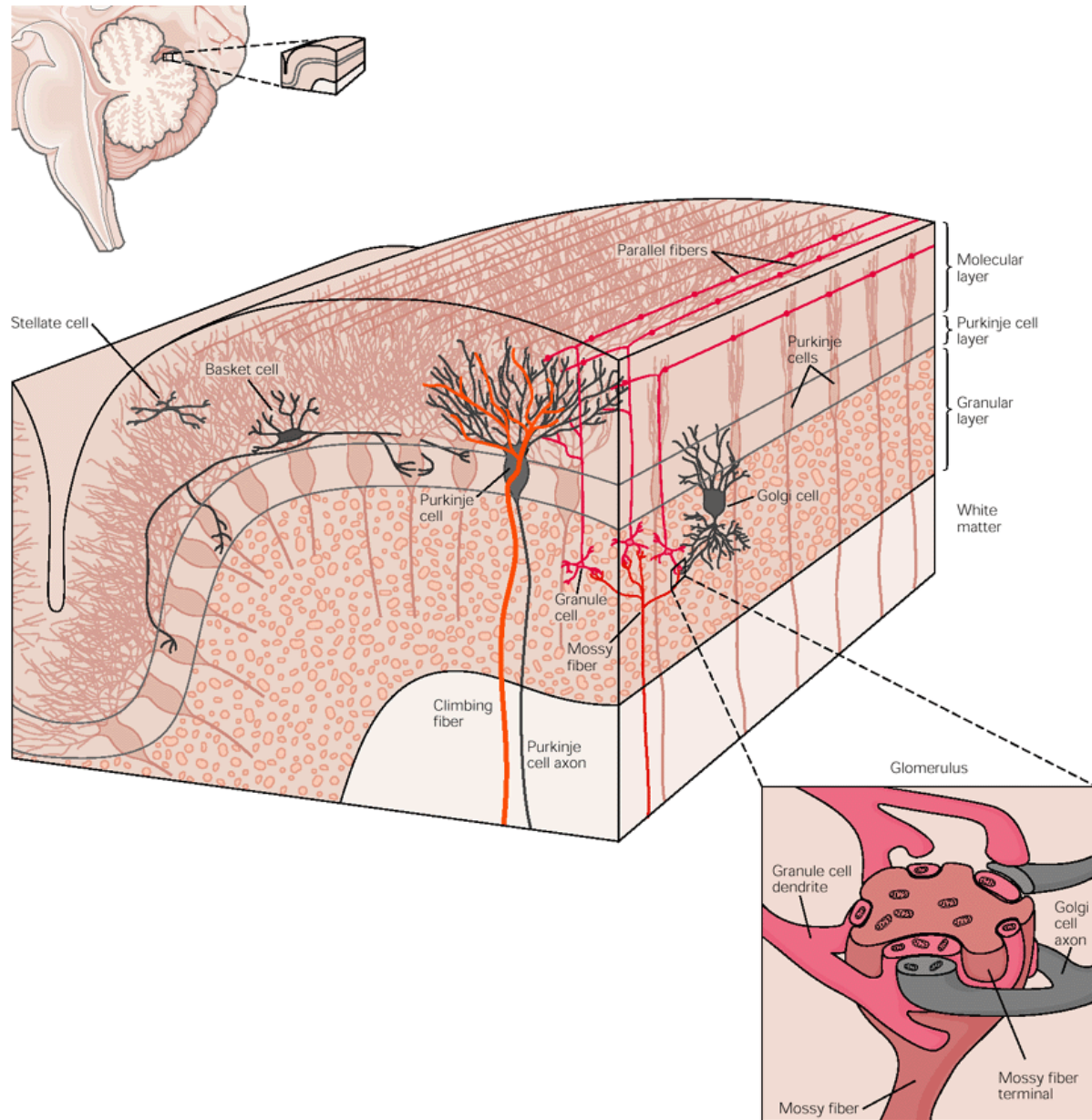
Cerebellum

- constitutes only 10% of the total volume of the brain but contains more than half of all its neurons
- dense connectivity with cerebral cortex - 40×10^6 (optic tract - 1×10^6) connections
- modular structure (performing the same operations on different inputs)



The cerebellum influences the motor systems by evaluating disparities between intention and action and by adjusting the operation of motor centers in the cortex and brain stem while a movement is in progress as well as during repetitions of the same movement. Three aspects of the cerebellum's organization underlie this function. First, the cerebellum is provided with extensive information about the goals, commands, and feedback signals associated with movement. There are 40 times more axons project into the cerebellum than exit from it. Second, the output of the cerebellum is sent to the premotor and motor systems of the cerebral cortex and brain stem, systems that control spinal interneurons and motor neurons directly. Third, synaptic transmission in the circuit modules can be modified (plasticity).

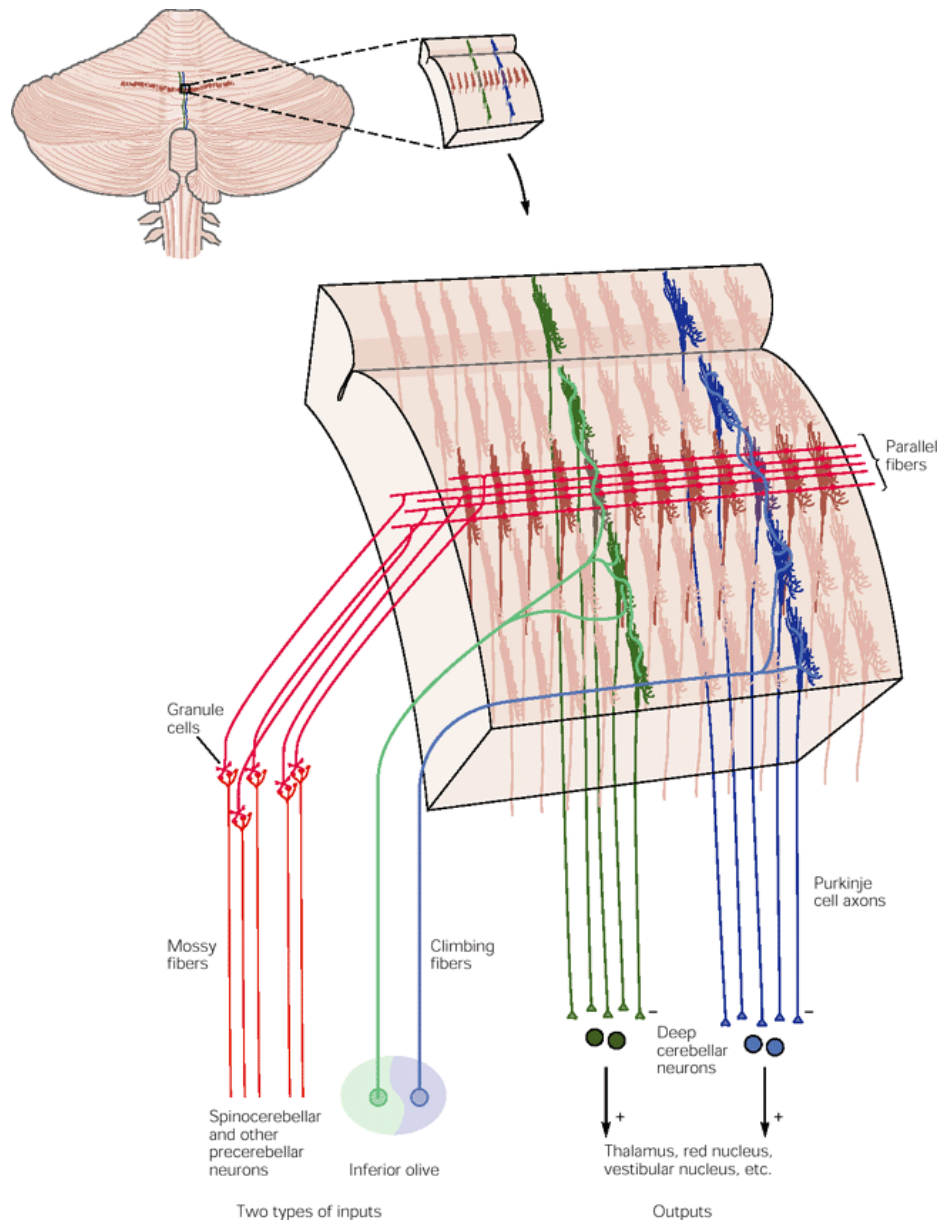
Cerebellar cortex



The cerebellar cortex is organized into three layers (molecular layer, Purkinje cell body layer, granule layer) and contains five types of neurons (Purkinje cells, granule cells, stellate cells, basket cells, Golgi cells).

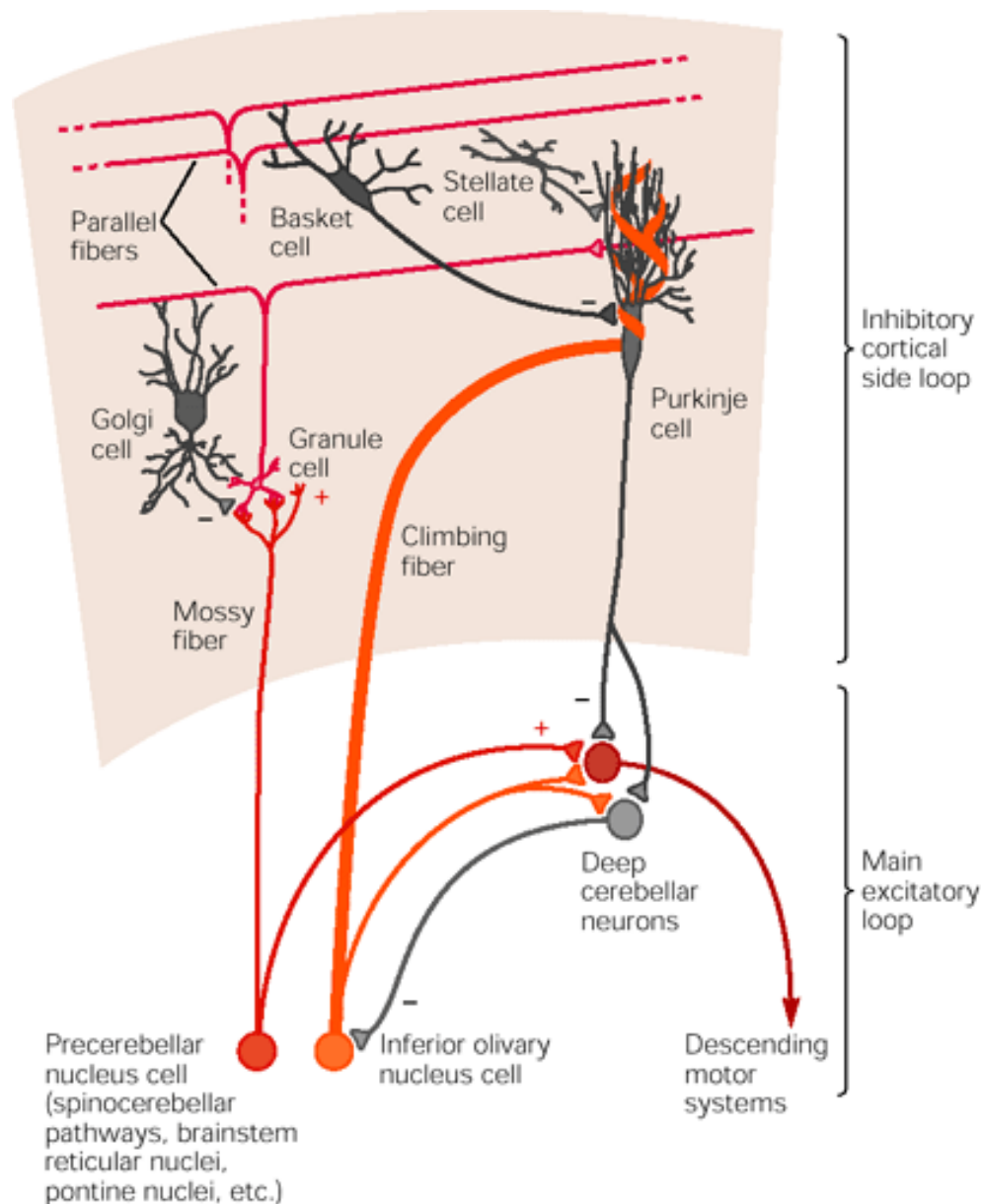
Cerebellum receives two types of inputs: mossy fibers and climbing fibers. Both types are excitatory but evoke different responses in Purkinje cells.

Cerebellar cortex – inputs and outputs



Mossy fibers excite granule cells whose parallel fibers branch transversely to excite hundreds of Purkinje cells. By contrast, climbing fibers excite 10 or so Purkinje cells anterior and posterior to the branch point. The connections of the parallel fibers and the connections of the climbing fibers thus form an orthogonal matrix. The output is conveyed by Purkinje cells axons through deep cerebellar nuclei.

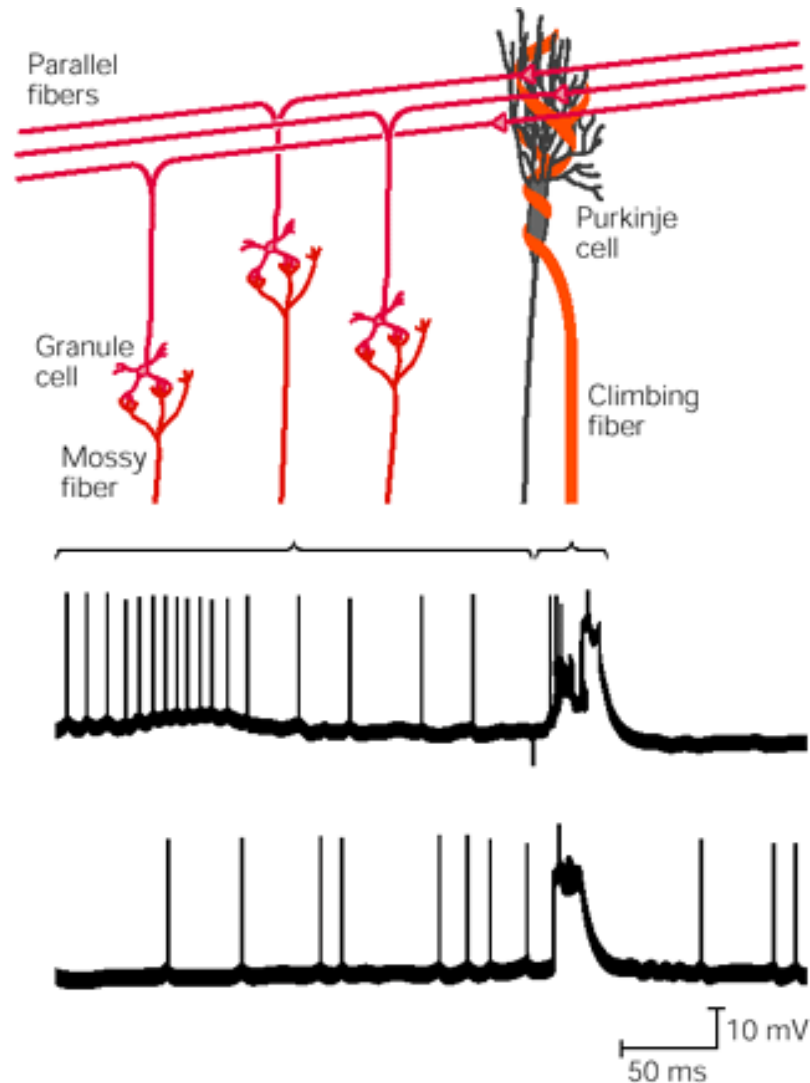
Cerebellar circuits



Synaptic organization of the basic cerebellar circuit module.

1. Both inputs (climbing fibers CF and mossy fibers MF) are excitatory.
2. Deep nuclei also receive inputs from CF and MF.
3. All other connections are inhibitory.
4. The excitatory output loop through the deep nuclei is modulated by inhibitory loop passing through cerebellar cortex (real time control).

Firing patterns of Purkinje cells

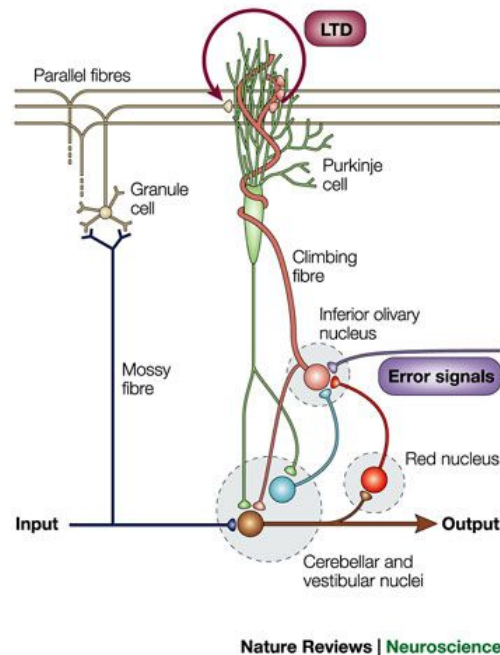


Simple and complex spikes recorded intracellularly from cerebellar Purkinje cells. Complex spikes (right bracket) are evoked by climbing fiber synapses, while simple spikes (left bracket) are produced by mossy fiber input.

Mossy and climbing fibers code differently sensory inputs. Spike frequency in Purkinje cells depends on sensory fibers activity and motor activity. Spike frequency thus codes movement duration and intensity. Complex spikes are rare and therefore code timing relations between input signals and may be a 'trigger' for activity.

Plasticity in the cerebellum

A possible basis for learning in the cerebellum is a long-term depression (LTD) at parallel fibers synapses following repeated stimulation of Purkinje cells by climbing fibers.

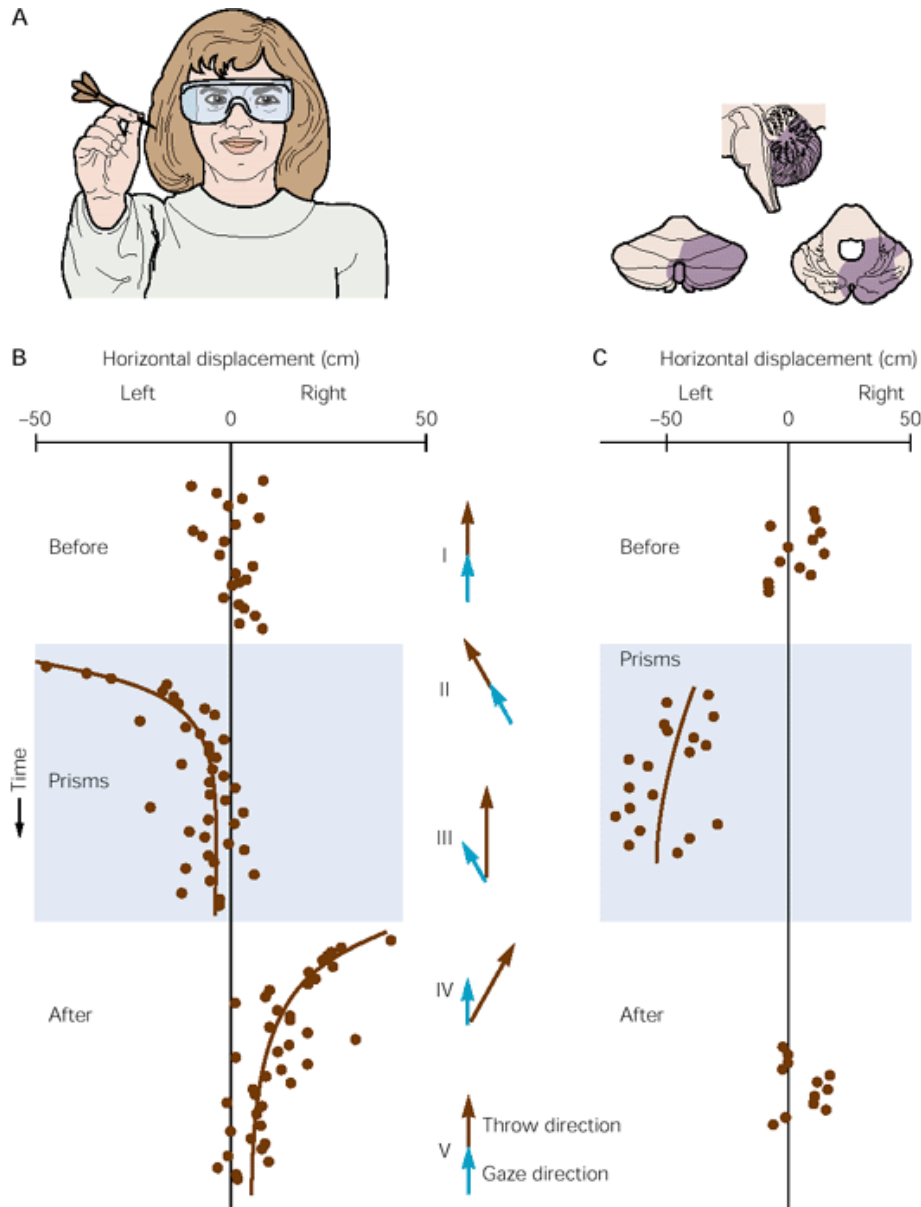


Mechanism: repeated climbing fibers activation by error signals induces increased intracellular Ca^{2+} in Purkinje cells. Ca^{2+} activates second messenger mechanism leading to desensitization of AMPA receptor for glutamate at parallel fibers synapses onto Purkinje cell spines.

Motor learning

Climbing fibers receive error signal corresponding to differences between expected and actual sensory inputs. Repetitive stimulation of the climbing fibers leads to suppression (LTD) of Purkinje cell activation by parallel fibers. Successive trials of task execution modify Purkinje cell output such that performance improves. Once the behavior becomes adapted as learned, it is performed automatically.

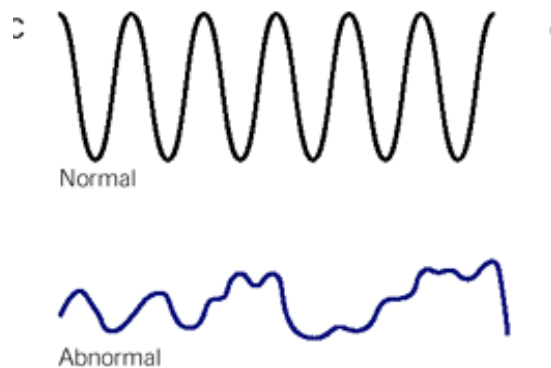
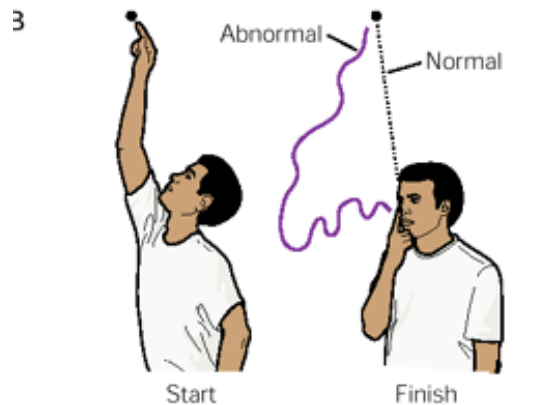
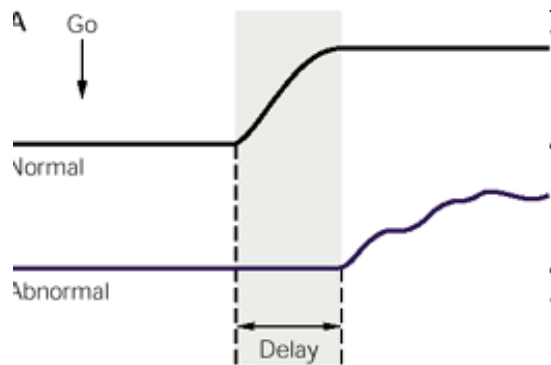
Eye-hand coordination



A, B. When people wear prisms, which bend the light path sideways, the initial throw in the direction of gaze misses the target to the side. With repeated throws aimed at the perceived target, subjects gradually increase the angle between the direction of gaze and the direction of throw, so that the darts land on target within 10-30 throws.

C. Adaptation fails in a patient with unilateral lesions of the cerebellar cortex.

Typical defects observed in cerebellar diseases



Cerebellar diseases have distinctive symptoms and signs.

- A.** A lesion in the right cerebellar hemisphere delays the initiation of movement. The patient is told to clench both hands at the same time on a “go” signal. The left hand is clenched later than the right, as evident in the recordings from a pressure bulb transducer squeezed by the patient.
- B.** A patient moving his arm from a raised position to touch the tip of his nose exhibits dysmetria (inaccuracy in range and direction) and decomposition of movement (moves shoulder first and elbow second). Tremor increases on approaching the nose.
- C.** Dysdiadochokinesia, an irregular pattern of alternating movements, can be seen in the abnormal position trace of the hand and forearm as cerebellar subjects attempt alternately to turn around the forearm while flexing and extending at the elbow as rapidly as possible.

Damage of the cerebellum also leads to deficits in cognitive domains – decision making, spatial cognition, language and affect. It challenges the traditional view of the cerebellum being responsible solely for regulation of motor functions.