

Making Things Happen: Simple Motor Control

How Your Brain Works

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The Story So Far

- In the first few lectures we introduced you to some basic biophysical properties of neurons, which enable neurons to operate like little computing devices.
- We also looked at some basic brain anatomy.
- We then introduced you to the brain's sensory systems, which take in information from the environment and process this information to create our perceptions of the world we inhabit.
- We also looked at how neural networks can process information.
- Ultimately, all these functions serve to inform our actions and behavioural choices.
- It is time to start looking at how the brain “acts”.

Preview of this Lecture

- In this lecture we will trace neural control of movements, starting with very basic mechanisms of muscle structure and muscle control and then tracing our way up through the spinal cord to the brain's motor and prefrontal cortices.
- We will see that, as we climb up the pathway, motor control goes from the highly specific (individual motor units) to the increasingly abstract ("mirror neurons" which appear to encode specific action intentions irrespective of who performs the action).

“Efferents and Effectors”

- “Efferent” nerves carry impulses “away” from the central nervous system.
- Eventually they have to end either on **muscles** or on glands.
- Physiologists distinguish 3 types of muscle: “smooth”, “cardiac” and “striate” (or “skeletal”).
- In this lecture we are only interested in skeletal muscle which allows fast, voluntary movements.



Skeletal muscle

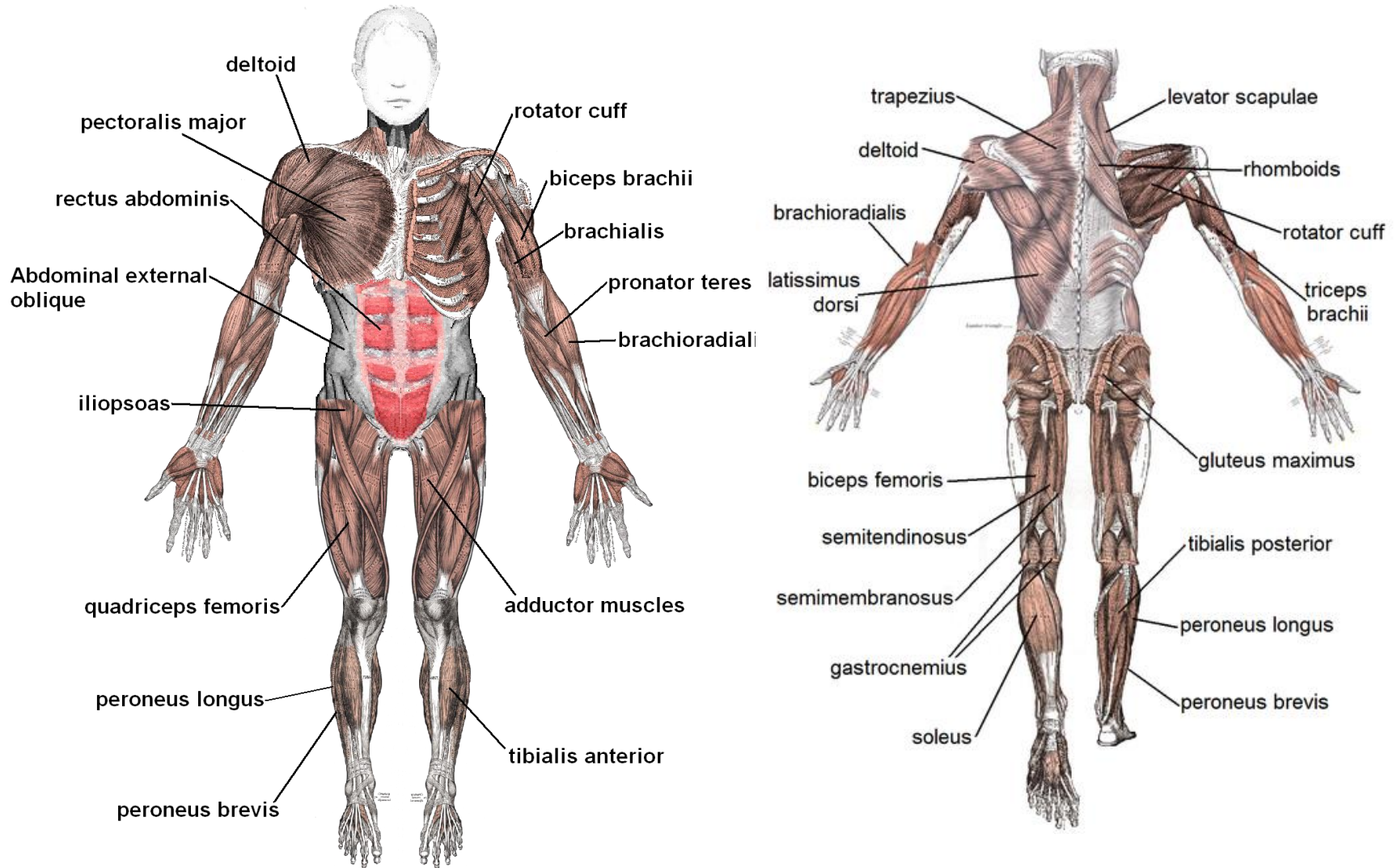


Smooth muscle



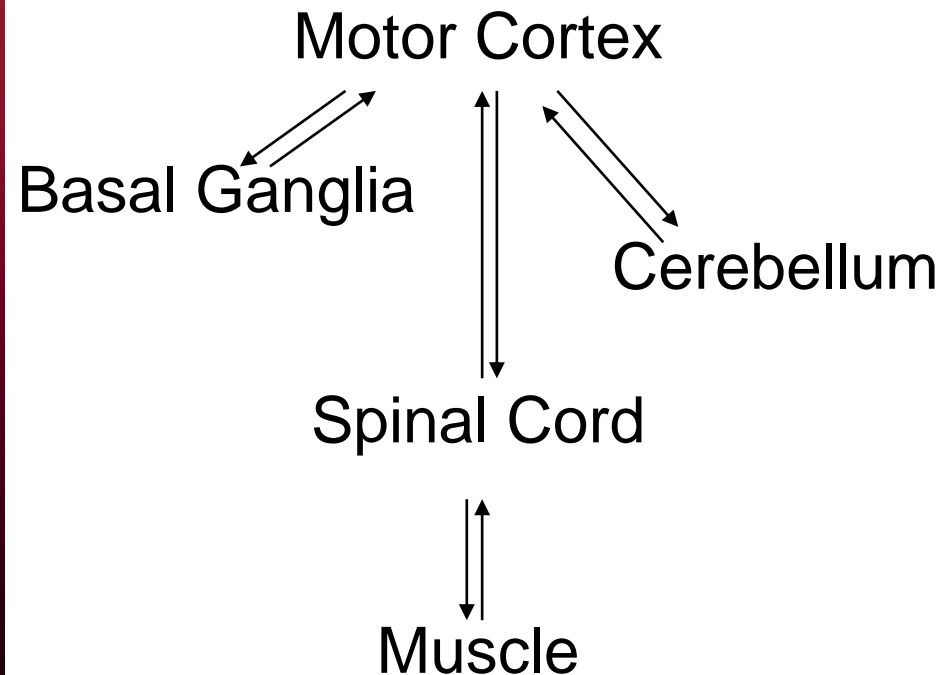
Cardiac muscle

Skeletal Muscle



- There are ~ 640 skeletal muscles in a human body

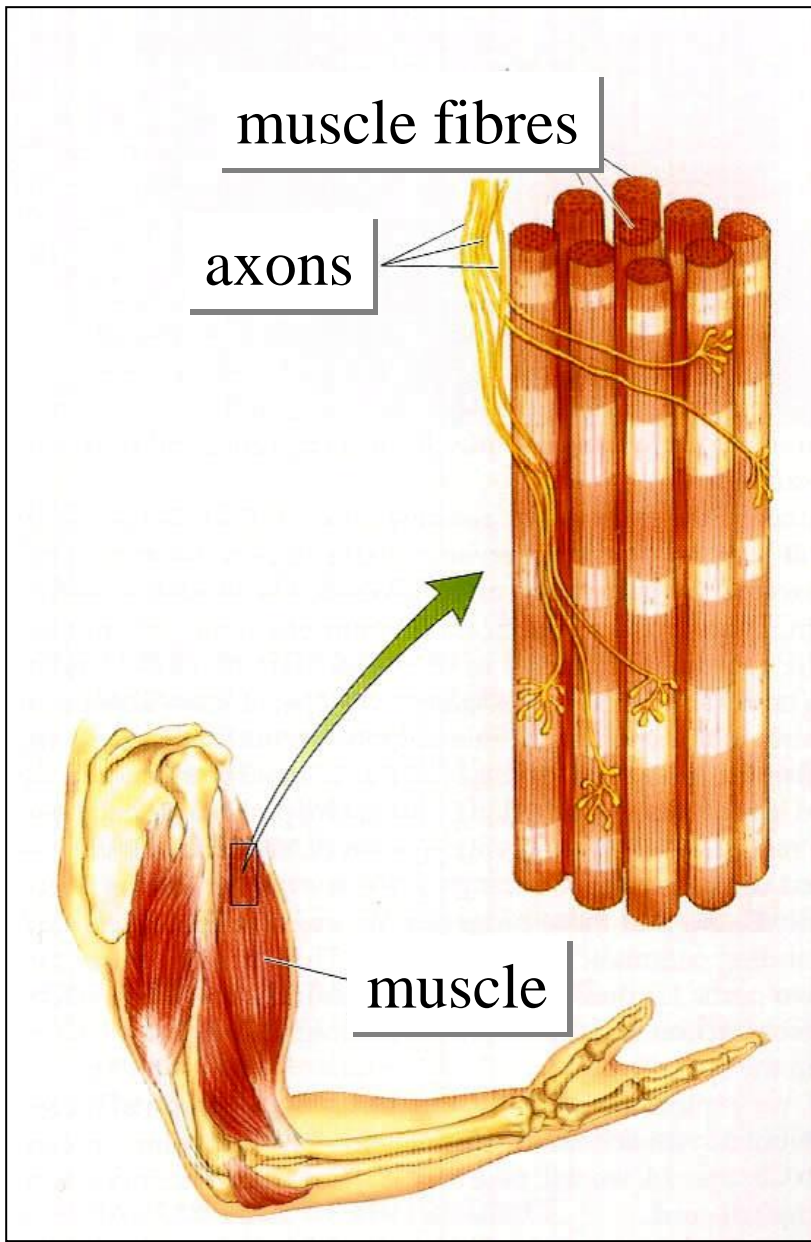
Nervous Control of Skeletal Muscle



Skeletal muscles sit at the end of a complex motor system with many feed-forward and feed-back connections.

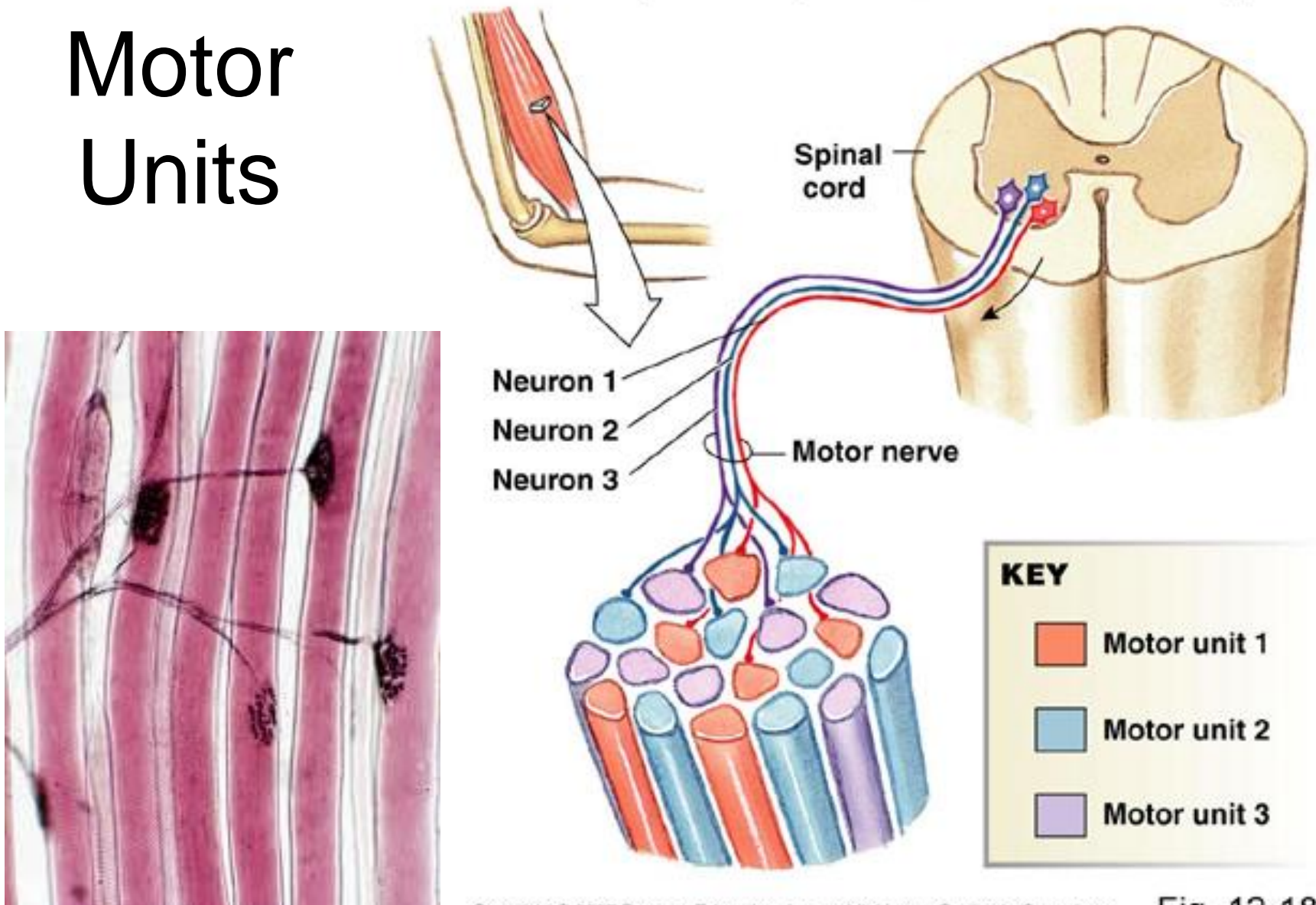
Muscle Fibre Structure

- Skeletal muscles are made of muscle fibers.
- Each muscle fiber receives input from a single spinal motor neuron.
- Spinal motor neuron cell bodies live in the ventral horn of the spinal cord.
- One spinal neuron may contact several fibers.
- All muscle fibers supplied by one motor neuron are called a motor unit.
- Each time the motor neuron fires an action potential, the fibers perform a short contraction (twitch).



Motor Units

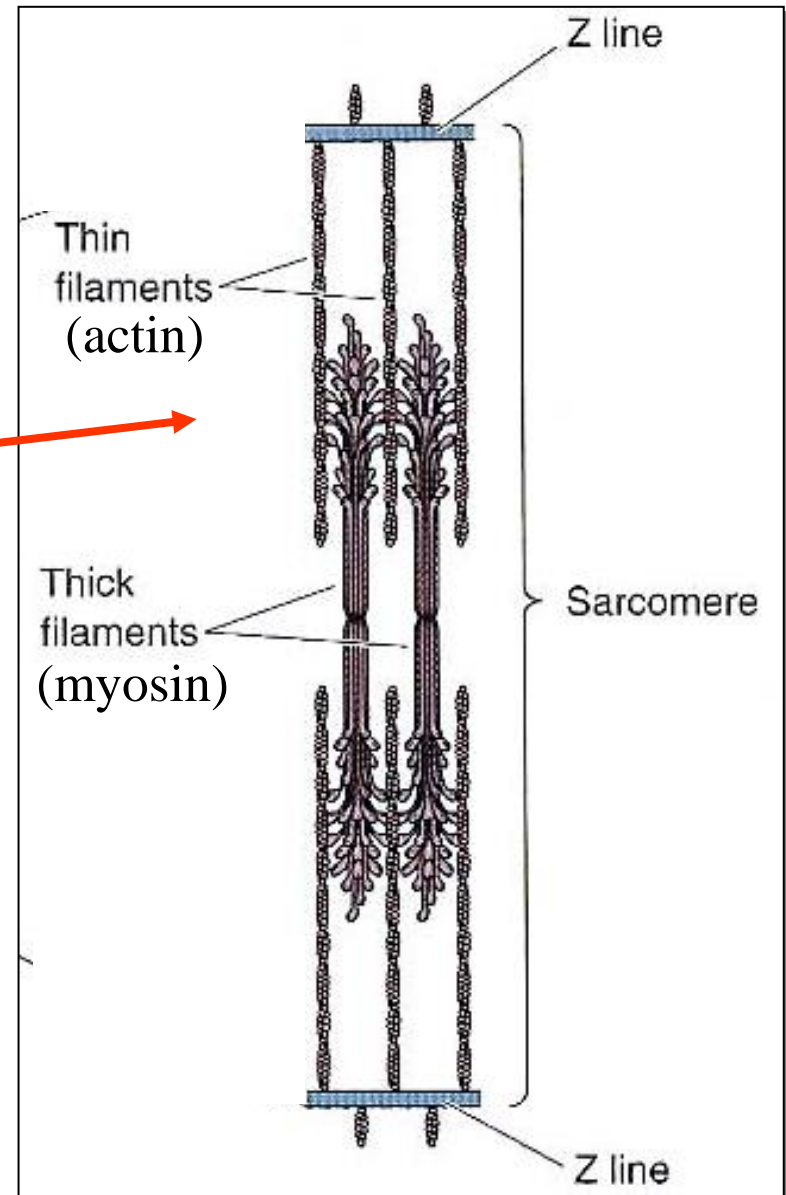
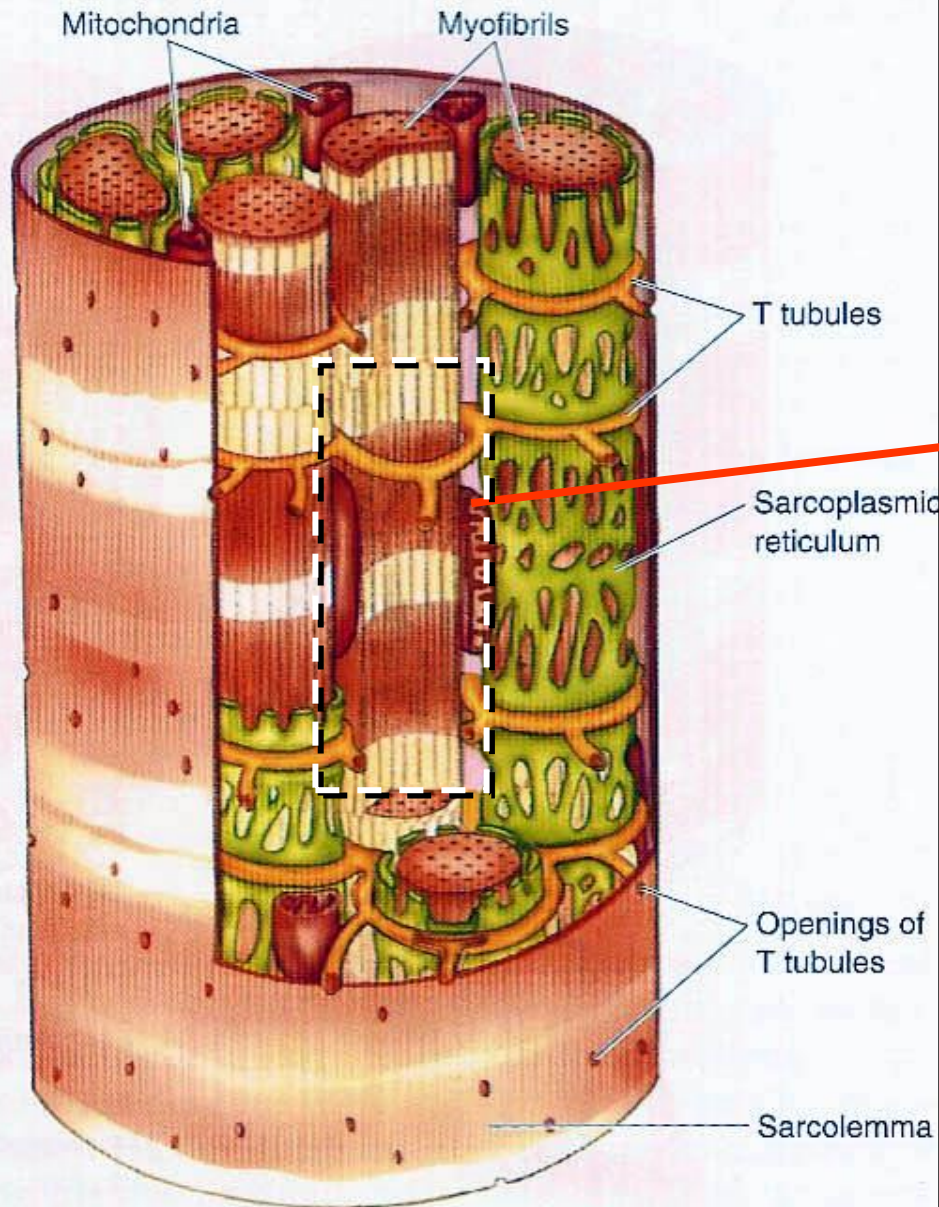
One muscle may have many motor units of different fiber types.



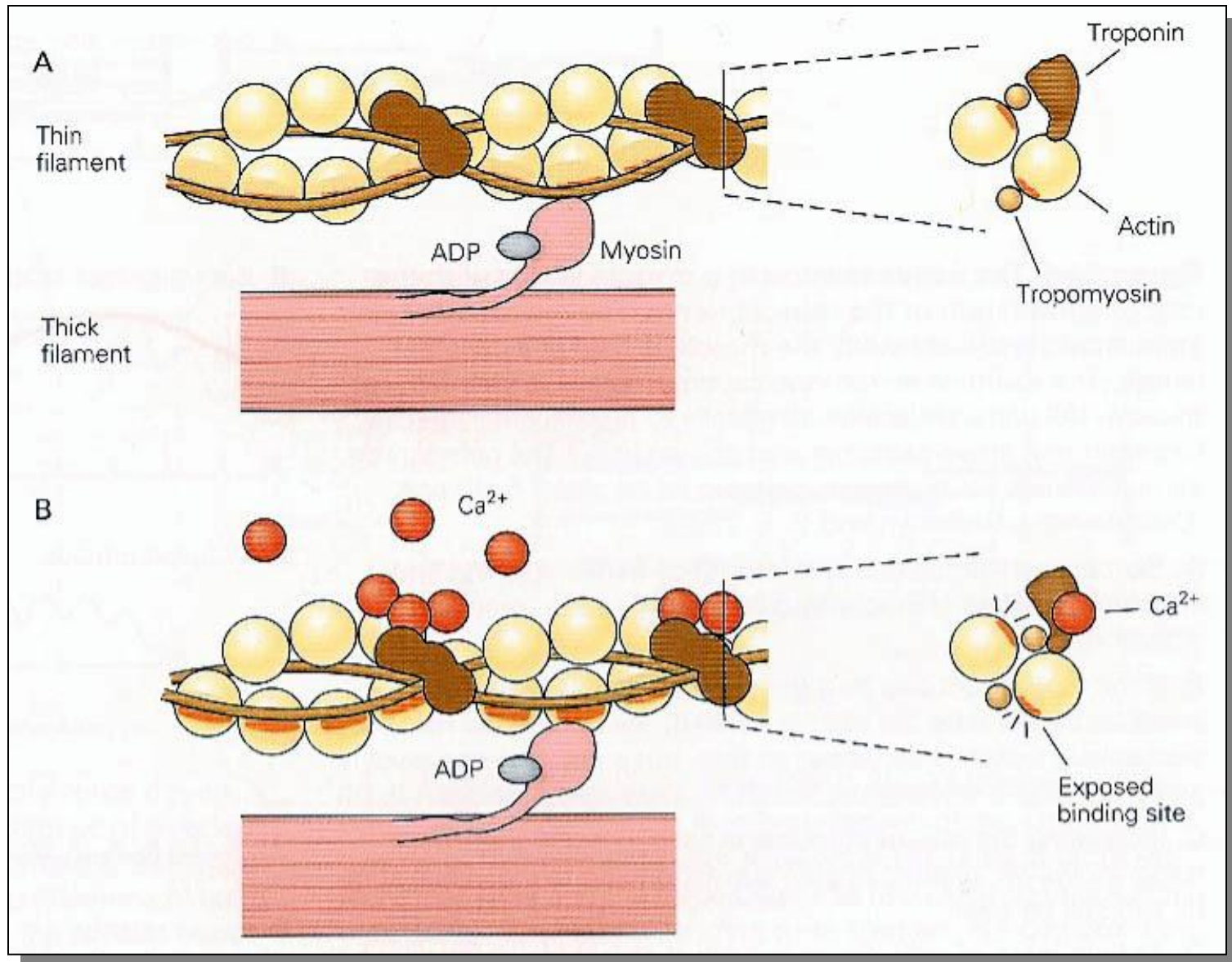
Muscle Fiber Organisation And Function

- Skeletal muscle is called striate because under the microscope it can be seen to contain alternating “stripes” or actin and myosin filaments.
- Nerve fiber activation causes action potentials along the muscle fiber membrane, which trigger Ca^{++} release. That, in turn allows myosin proteins to latch on to actin and to “ratchet” themselves along the actin fibers, leading to contraction.
- If there are no further inputs, Ca^{++} is reabsorbed, myosin lets go of the actin and the muscle relaxes.

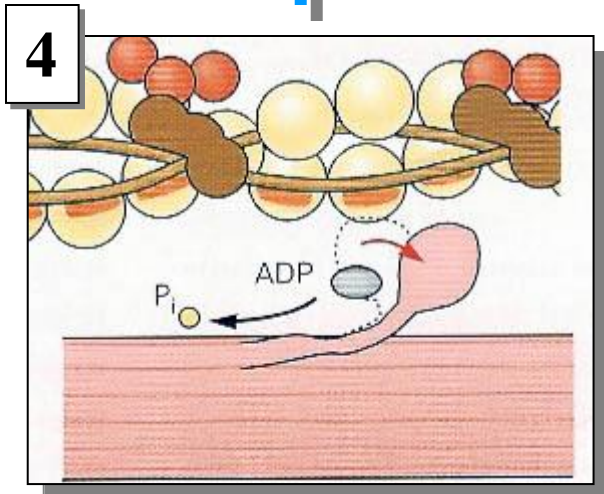
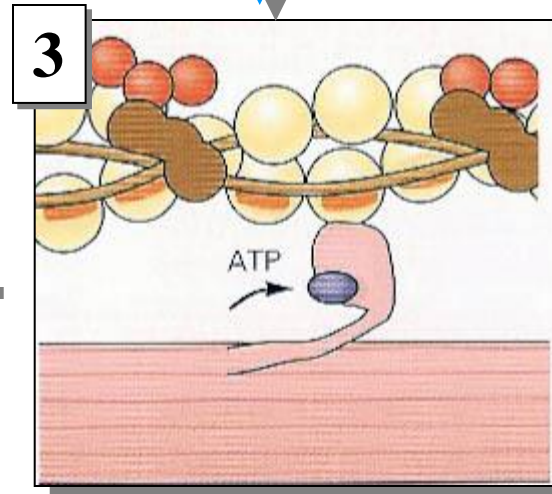
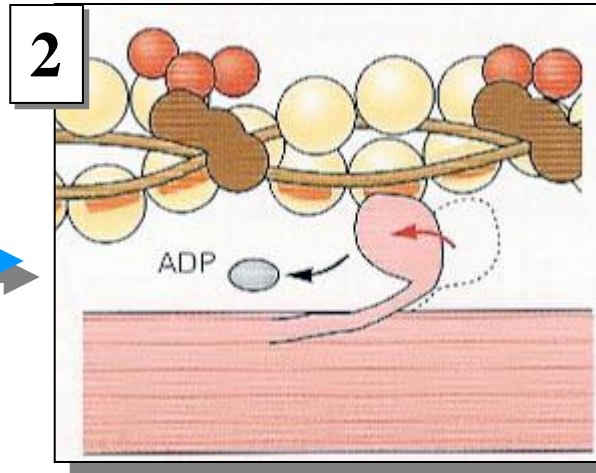
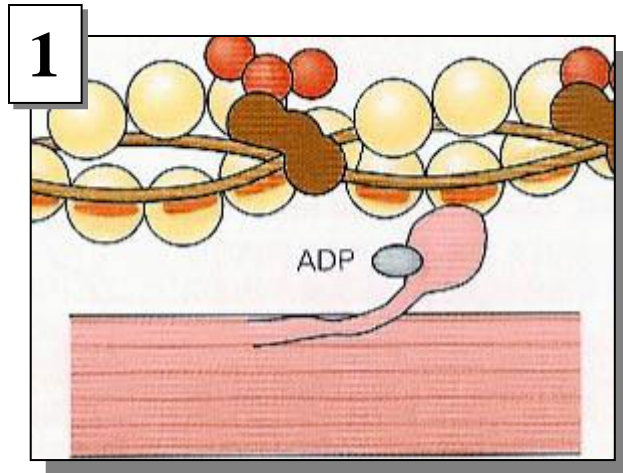
Organisation of Muscle Fibres



Ca^{++} exposes Myosin Binding Sites



The Myosin Cycle

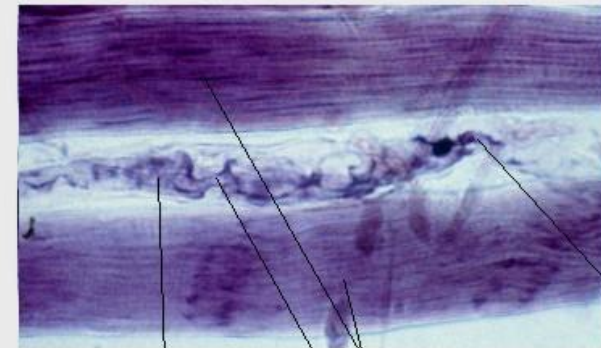
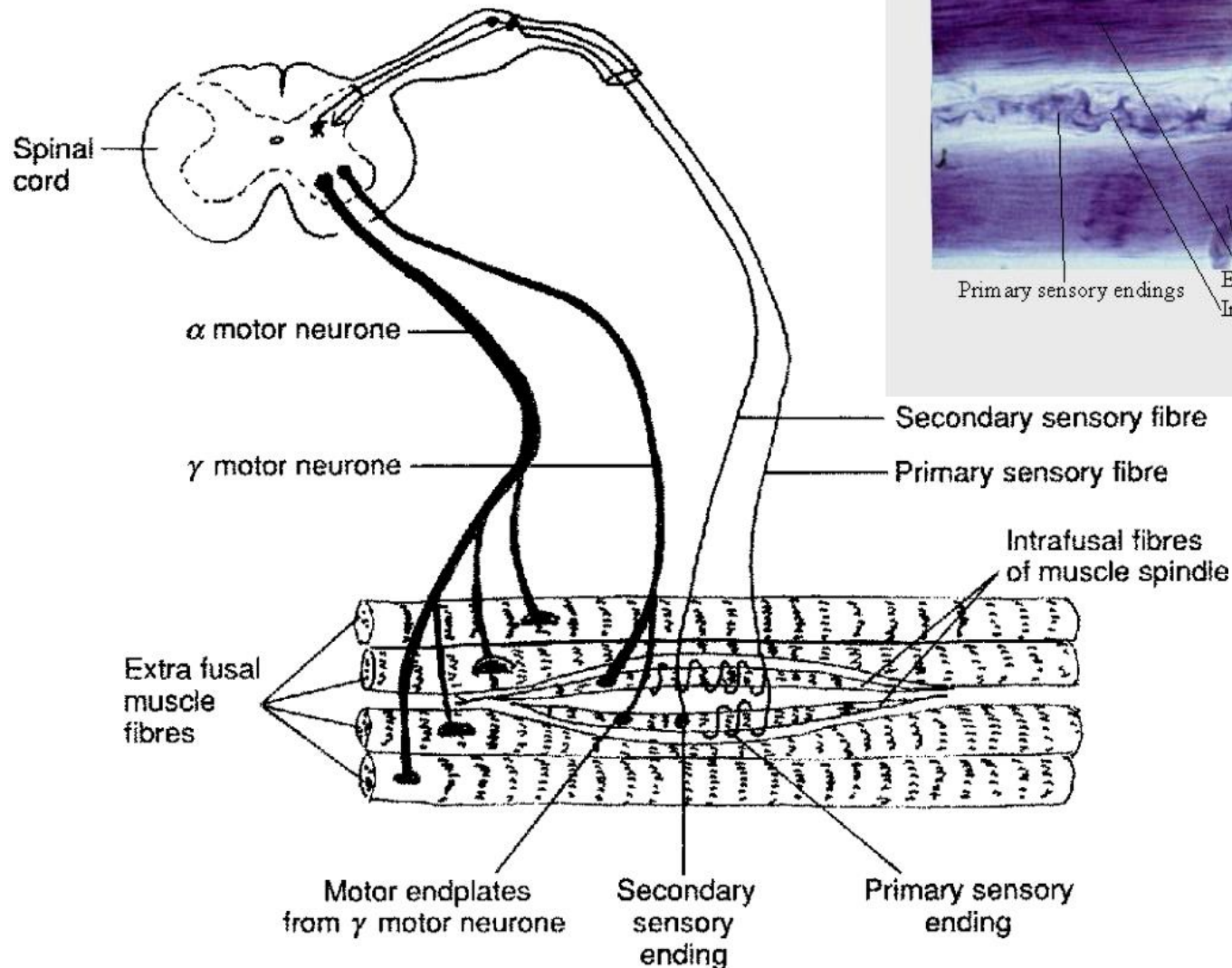


1. Myosin binds to actin.
2. Myosin head bends backward, releasing ADP and pulling itself forward.
3. ATP binds to myosin, causing release from actin.
4. Myosin uses energy from ATP hydrolysis to stretch itself, ready to undergo new binding and pulling cycle.

Feedback from Muscle and Reflexes

- In addition to normal muscle fibers, skeletal muscles contain specialised fibers called “spindles” which incorporate stretch receptors.
- Stretch receptors send signals through fast conducting A-beta fibers back to the spinal cord.
- Muscle spindles too can contract. Their contractions are controlled through so called “gamma” motor neurons. In contrast, the fibers controlling the contraction of ordinary muscle fibers are called “alpha” motor neurons.
- In the spinal cord, muscle spindle afferents can connect straight through to alpha motor neurons to form monosynaptic reflex arcs.

Muscle Spindles



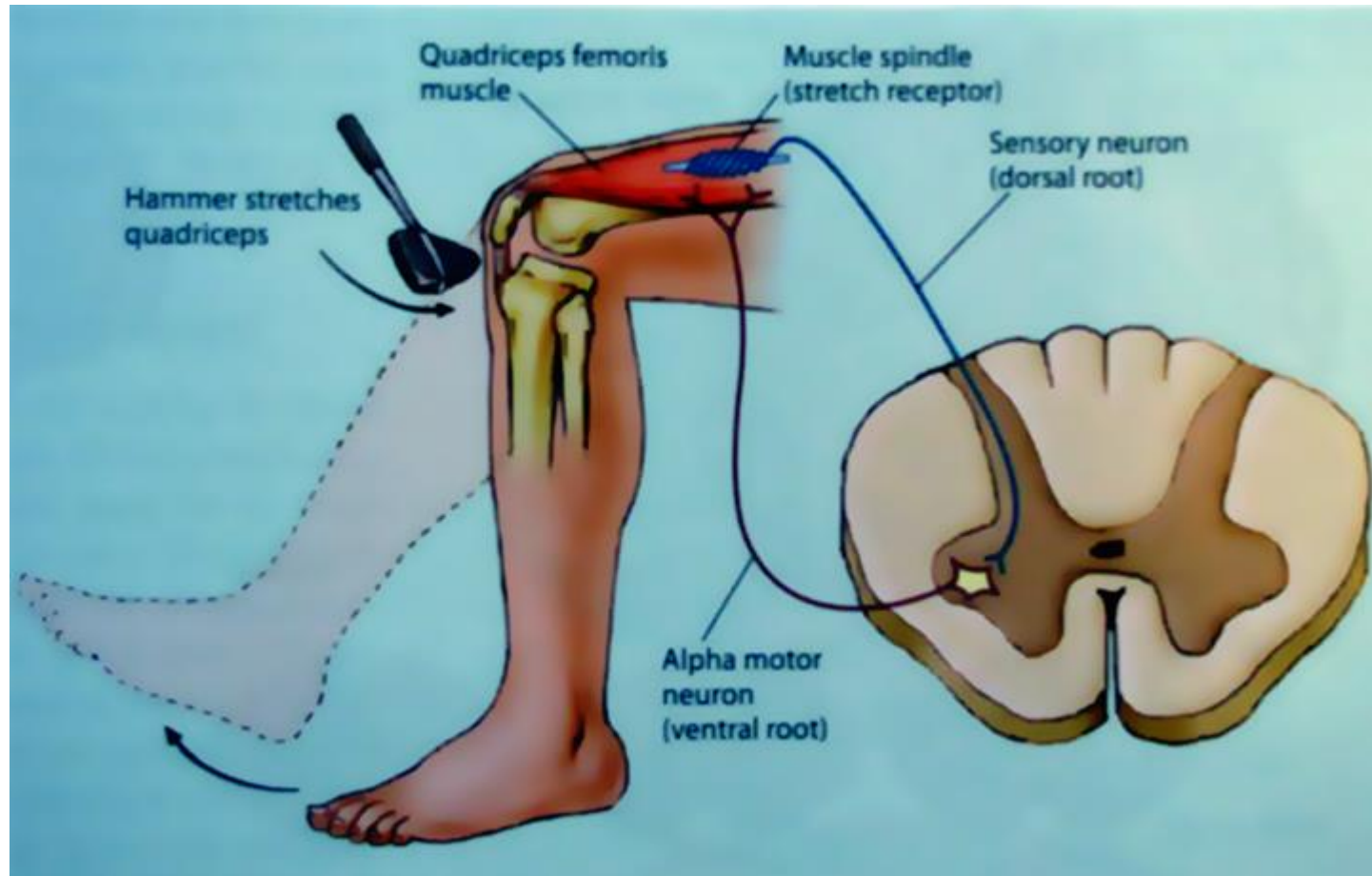
Muscle spindles are receptors for muscle stretch in the two-neuron stretch reflex.

Intramuscular nerve trunk

Primary sensory endings

Extrafusal (contractile) fibers
Intrafusal (modulating) fibers

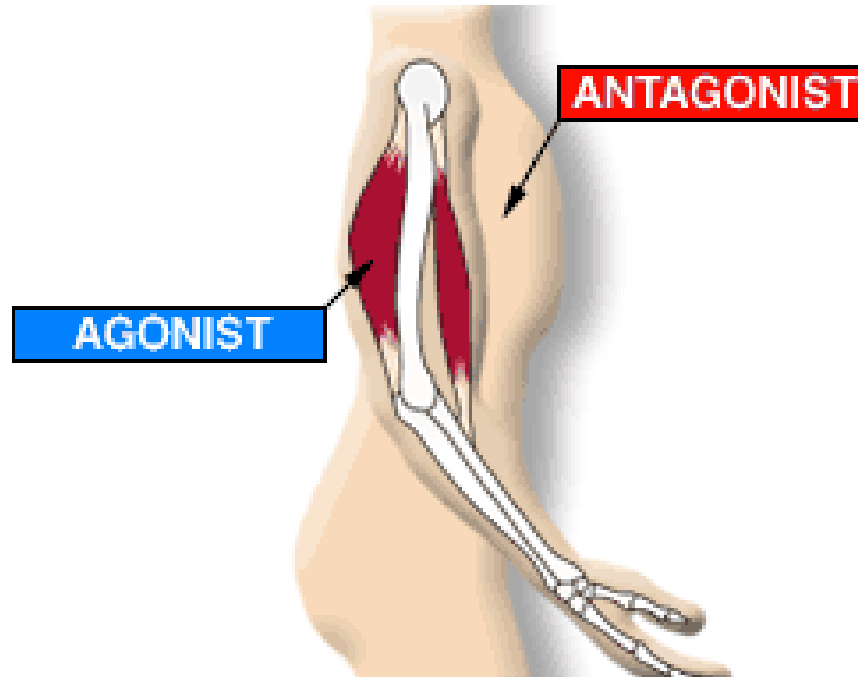
The Stretch Reflex



Increasingly Complex Reflex Circuits

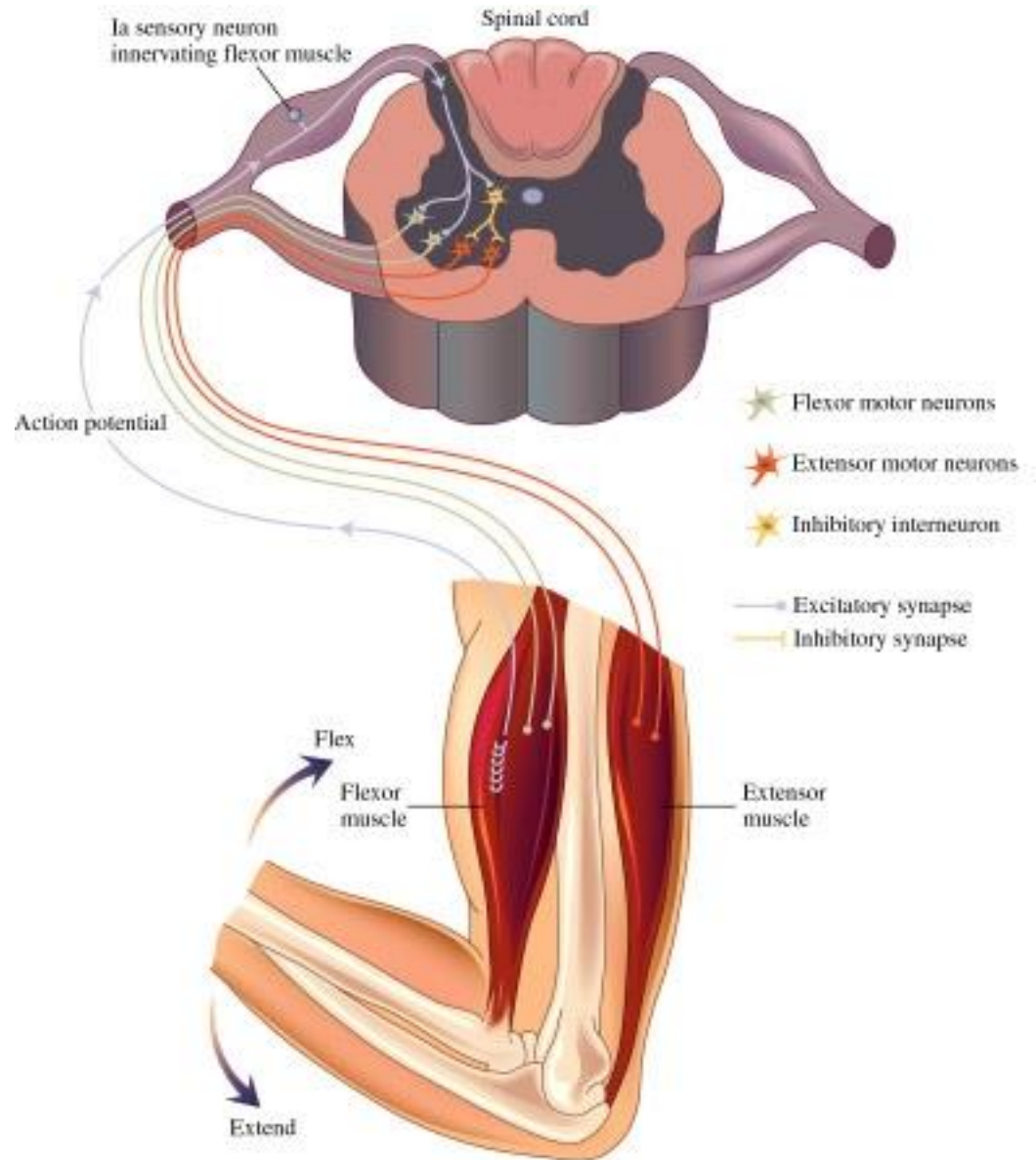
- The “monosynaptic” arc is just the tip of the iceberg. In addition to that simple, direct connection there are other, either synergistic or inhibitory connections which allow the reflex to serve functions for example for postural control.

Muscles tend to be arranged in pairs



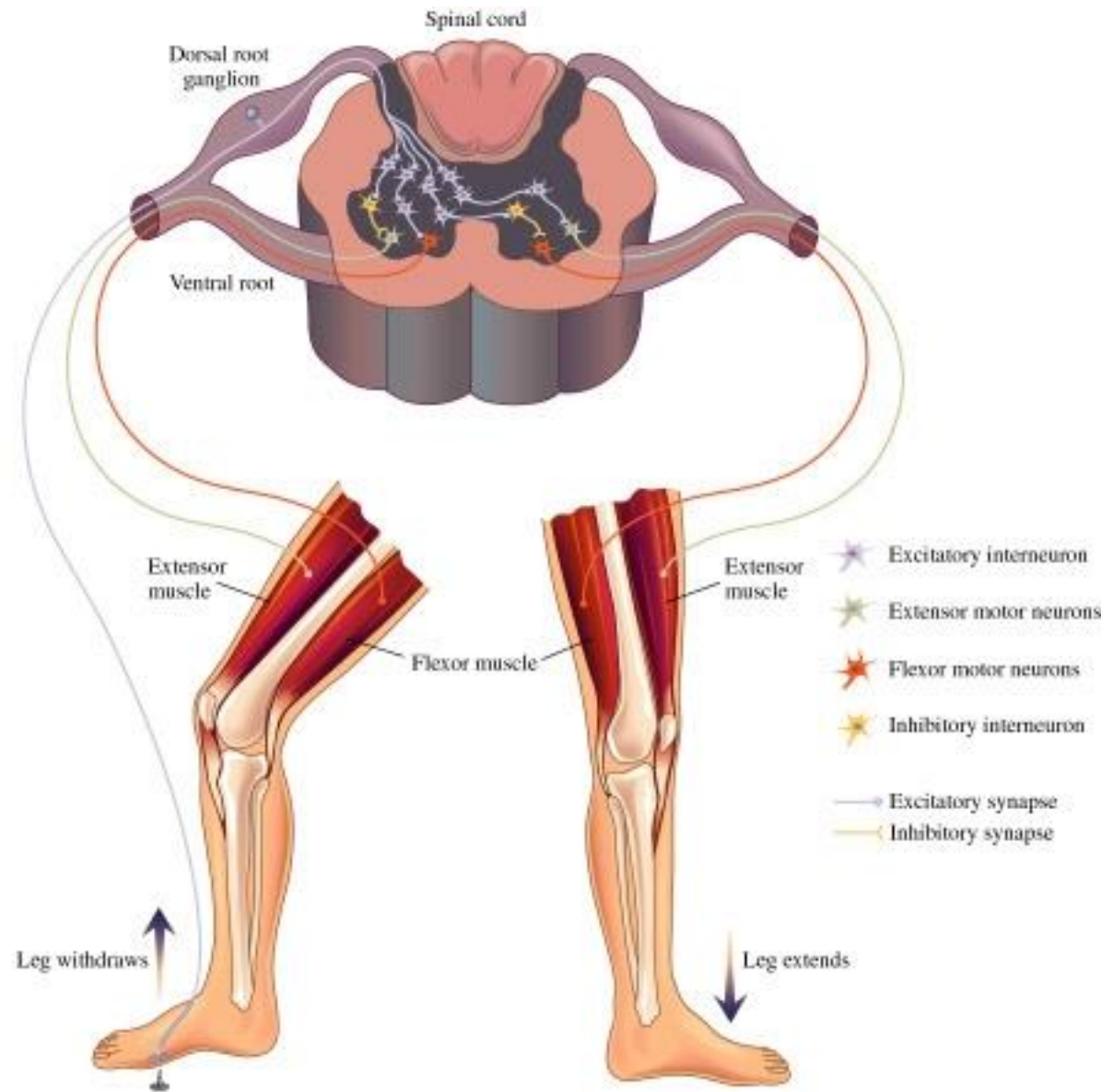
- Muscles can only contract.
- If one muscle bends a limb (the “flexor”) then there must be another muscle to stretch it (the “extensor”).
- Muscles are therefore typically arranged in agonist-antagonist pairs.

Spinal Cord Antagonist Circuits



Matthews “Neurobiology” Figure 8-3

Postural support through spinal reflexes



Increasingly Complex Reflex Circuits 2

- There are also many reflexes triggered by sensory afferents other than stretch receptors. (E.g. nociceptive withdrawal reflex, pupillary light reflex).
- Reflex arcs can also operate through multiple structures of the nervous system, not just sections of the spinal cord. They can, for example, go via somatosensory and motor cortex.
- Charles Sherrington thought that the brain might be understood in terms of increasingly complex reflex arcs, involving increasingly higher parts of the nervous system.

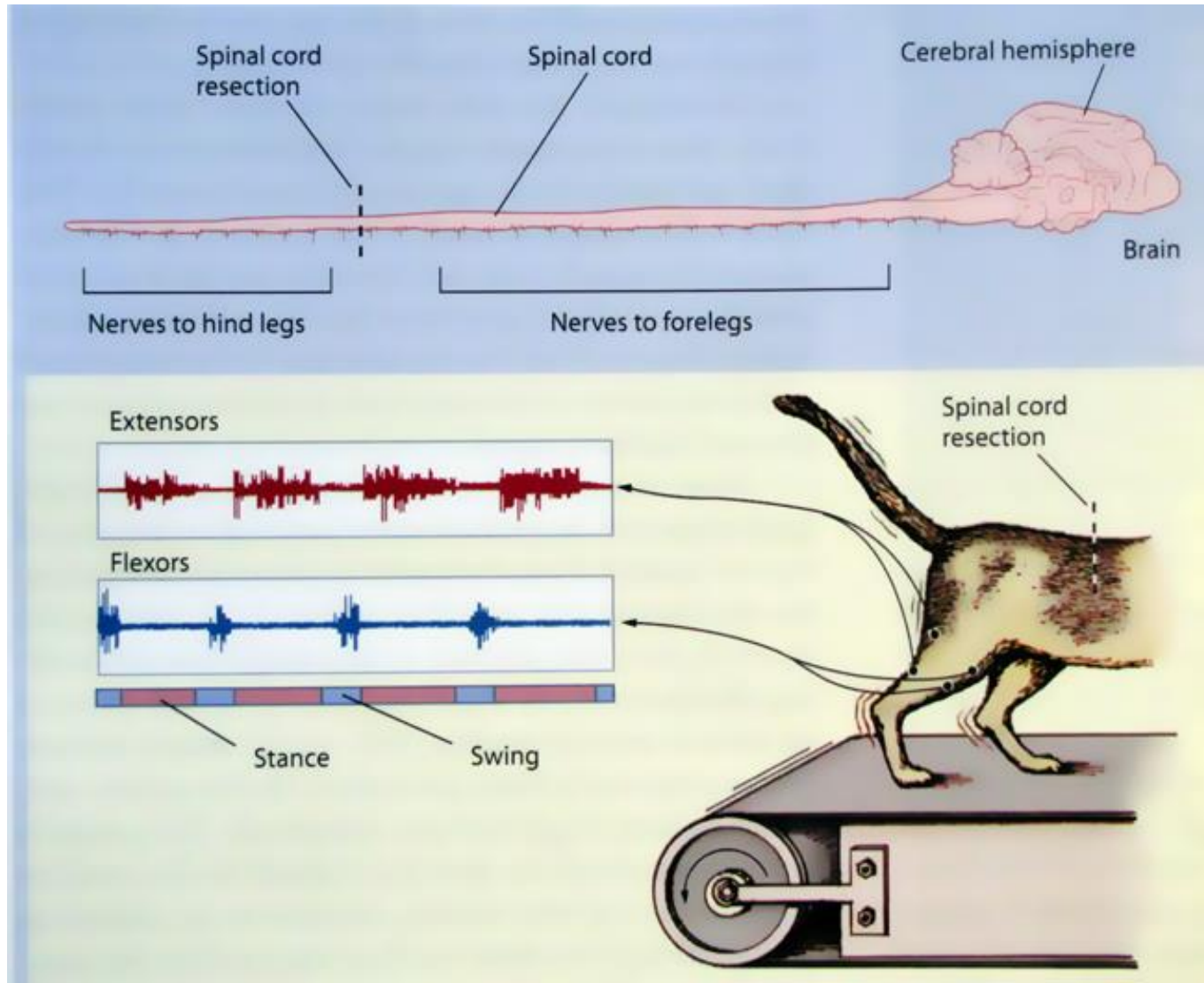
Withdrawal reflex in a headless frog



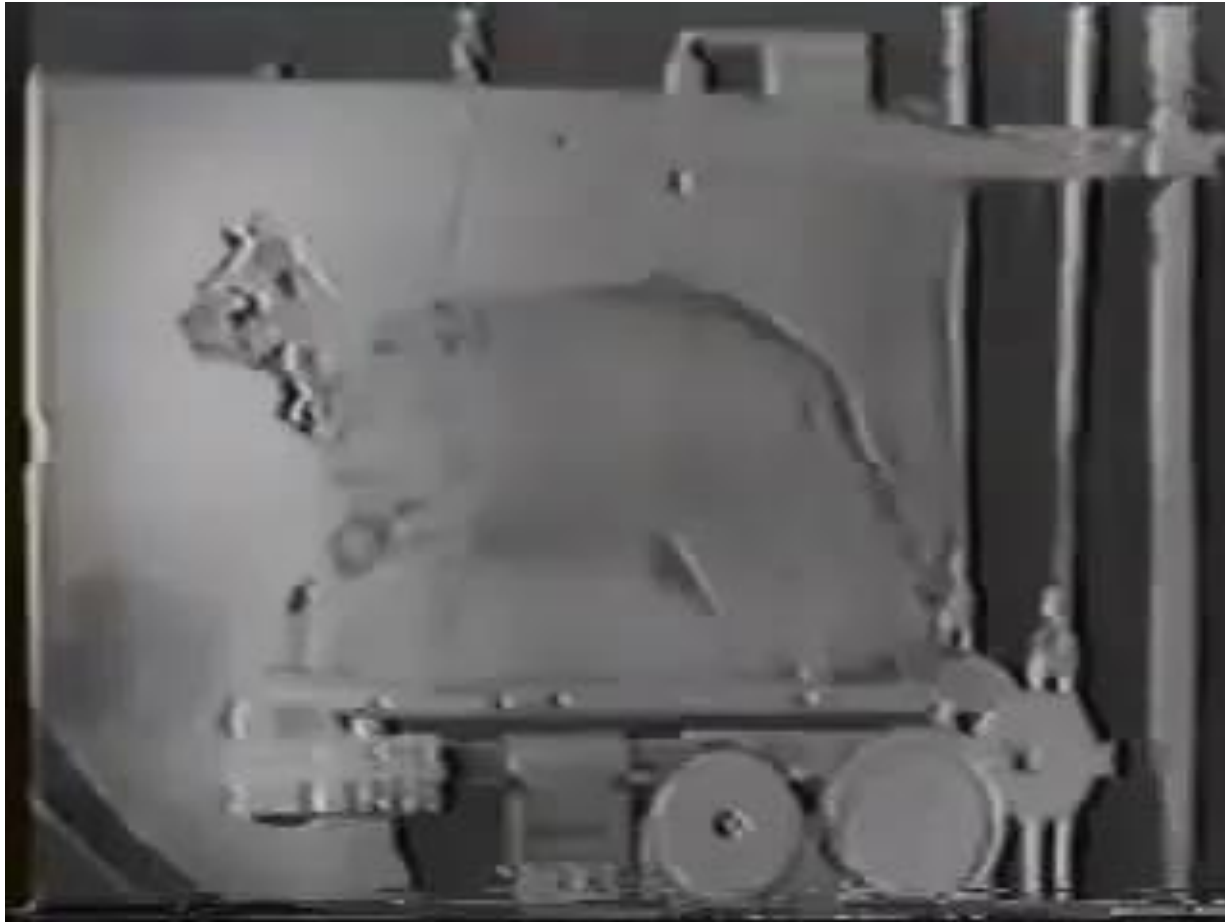
Beyond Sherrington and Reflexes

- “Reflex” theory of nervous system function makes the nervous system entirely reactive to external stimuli.
- However, even simple spinal motor circuits can sometimes exhibit spontaneous patterned activity (central pattern generators).
- Also, motor control is often predictive of, rather than reactive to, external stimuli. And it depends heavily on context (the “cognitive state” of the subject).
- Even just isolated spinal cords are sometimes capable of orchestrating astonishingly complex movements.

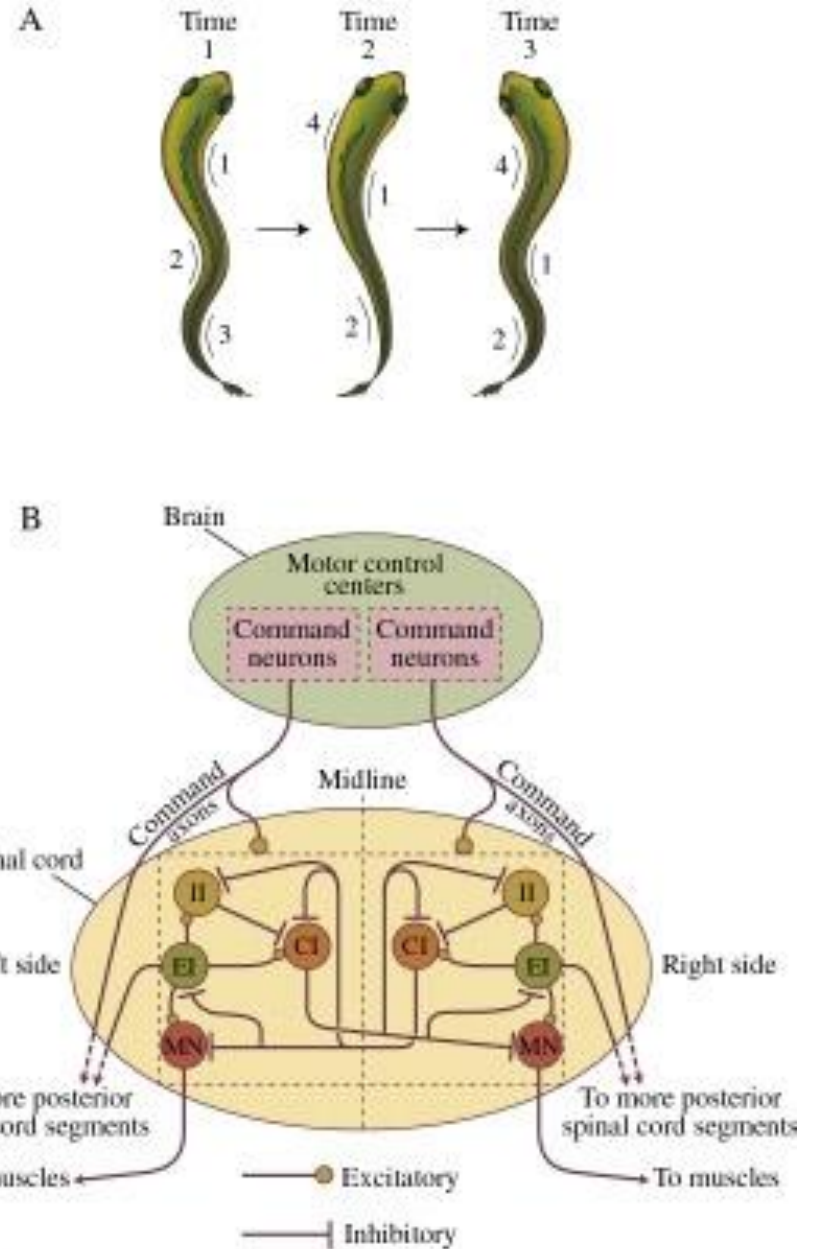
Spinal Pattern Generators



Decerebrate cat on a treadmill



Spinal cord pattern generators



Headless Chicken



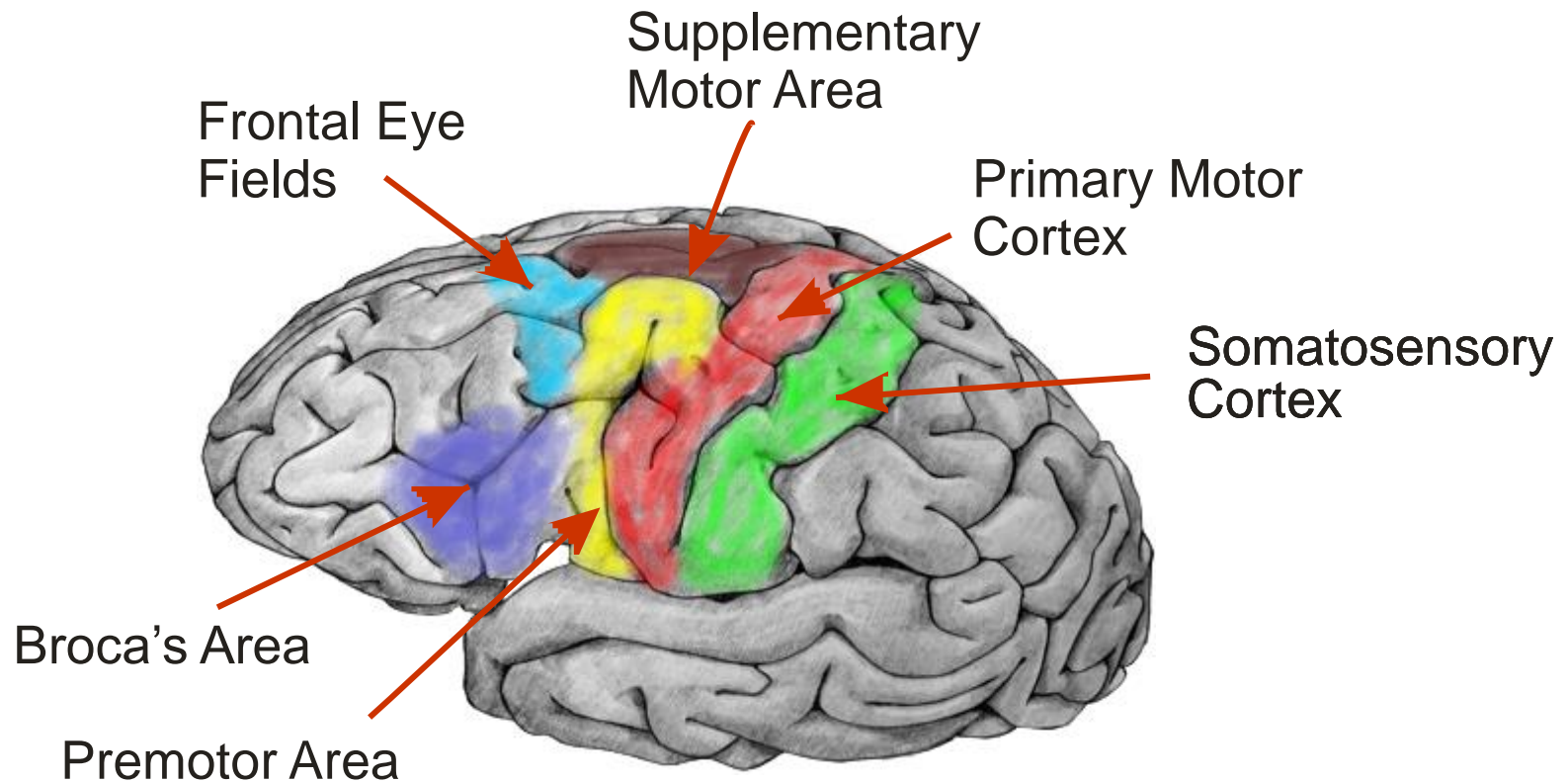
- **Warning:** some viewers may find the content of this video clip distressing.

Break

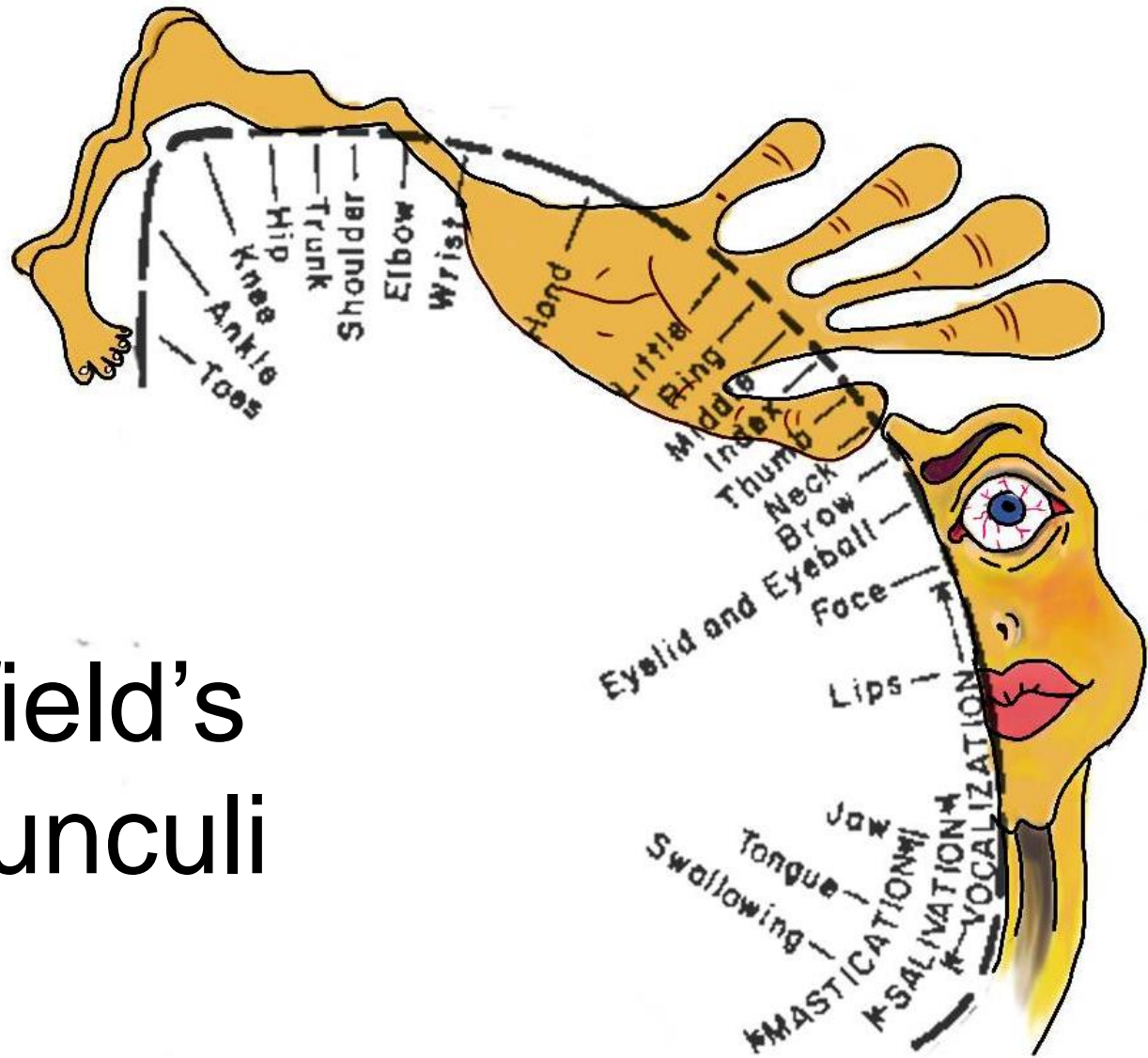
Cortical Control of Movement

- Although, as we have seen, the spinal cord is in principle capable of orchestrating quite complex and intricate movement patterns, in “higher” mammals motor control is increasingly controlled by the forebrain.
- This is particularly marked in monkeys and man. Just consider the essentially complete paralysis of humans with complete spinal cord lesions.
- Primary motor cortex (M1) connects directly to spinal motor neurons via the cortico-spinal tract.

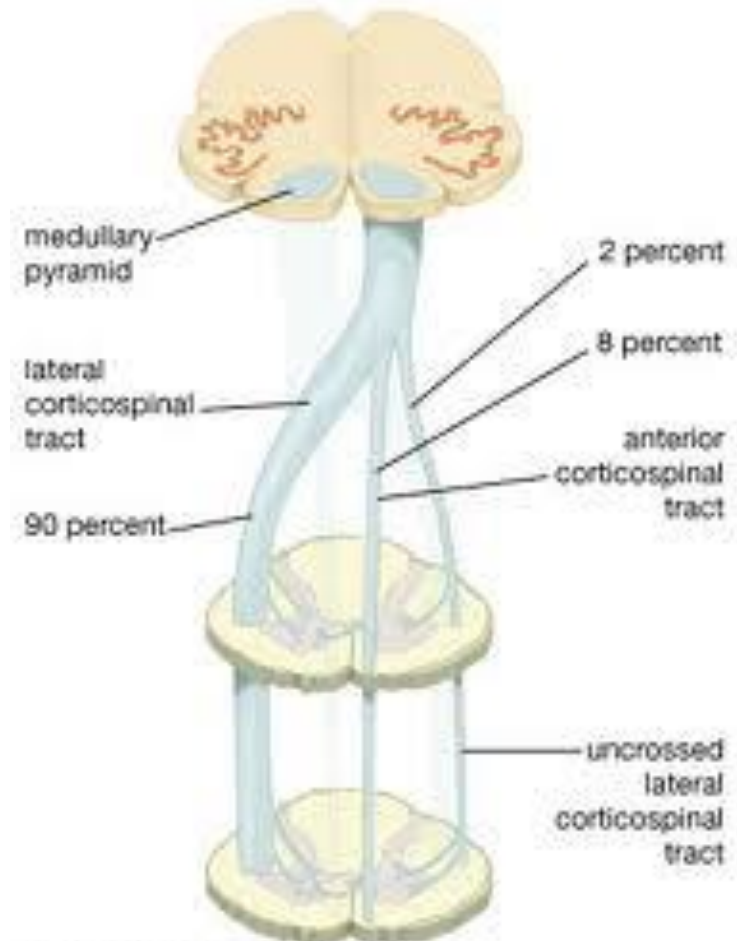
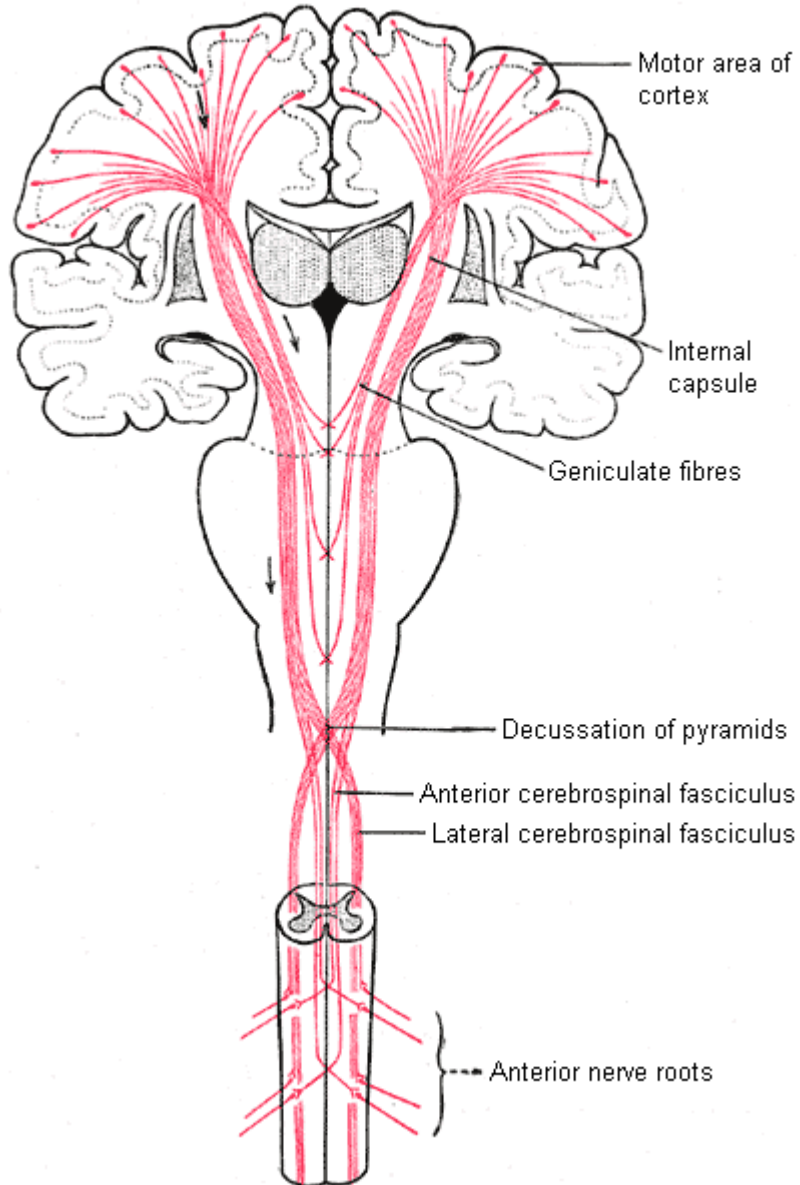
Motor Related Areas of Cortex



Penfield's Homunculi



The Cortico-spinal Tract

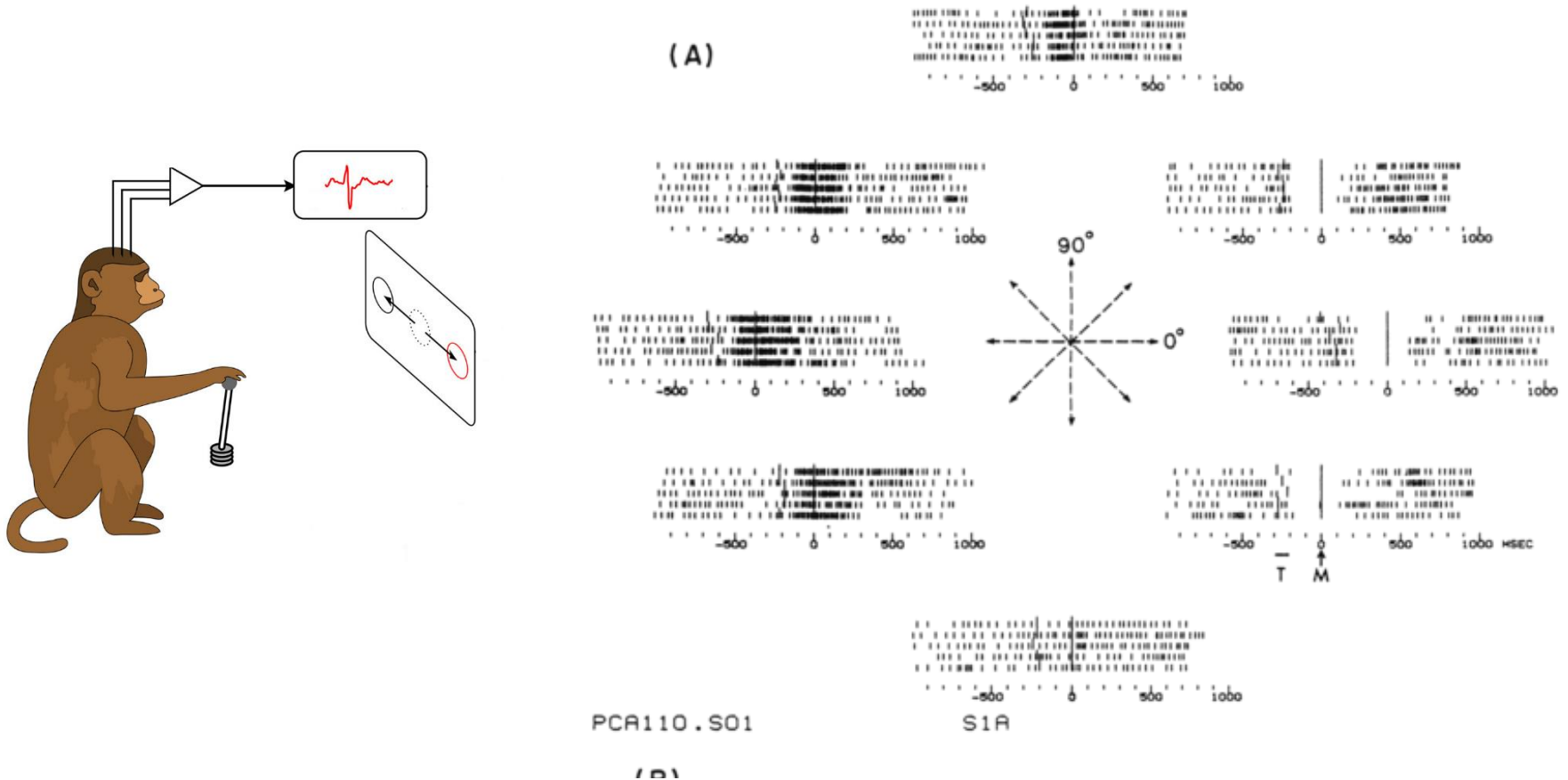


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Cortical Control of Movement

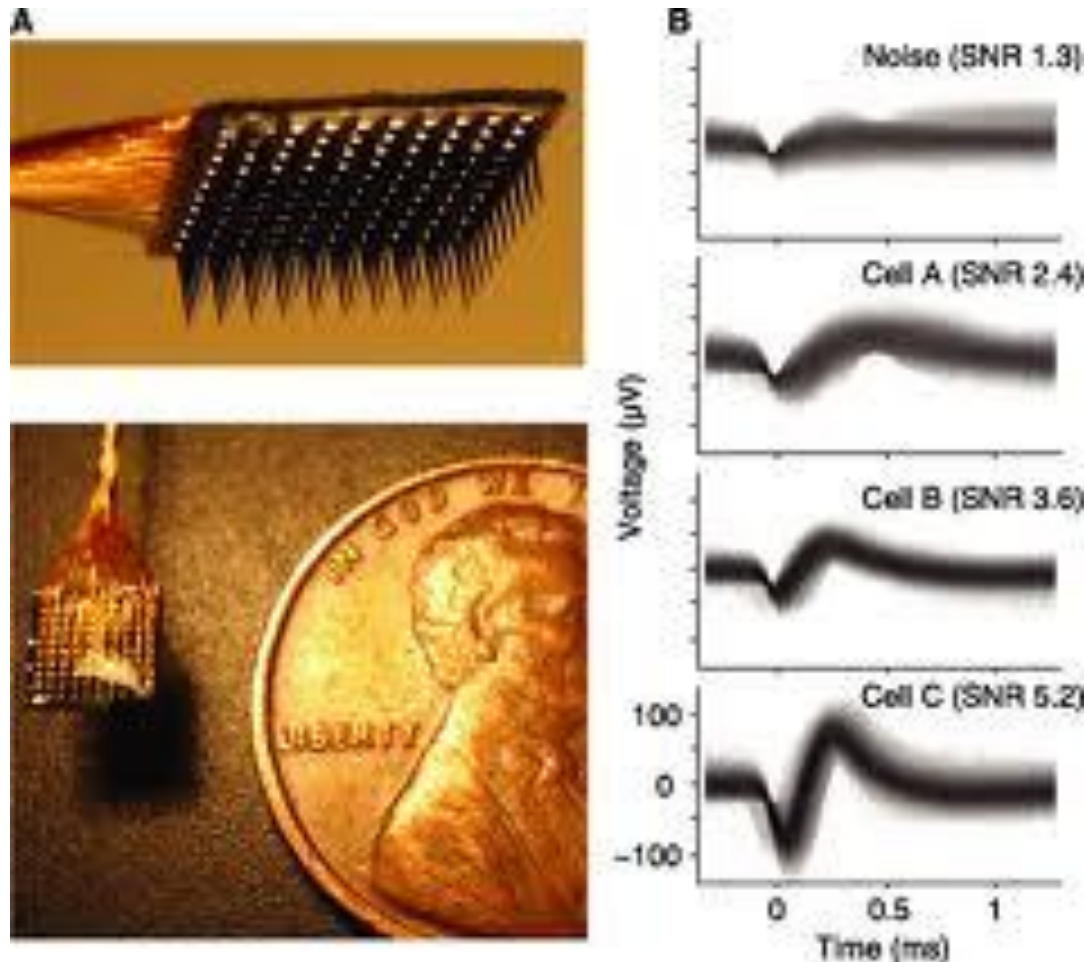
- Primary, supplementary and premotor cortex all have a somatotopic organisation.
- They compute movement intentions in collaboration with the basal ganglia and the spinal cord. We will be looking much more at the basal ganglia in the next lecture.
- Neurons in these cortical areas tend to be movement direction tuned. The overall movement direction is specified by a “population vector”, which weights preferred direction of each neuron by how strongly it is activated.

Motion Direction Sensitivity in Monkey Primary Motor Cortex



- Georgopoulos et al, Science 1986

Silicon Array Electrodes



- Population vectors can be “read out” in real time with multi-electrode arrays.

Primate moving robot arm



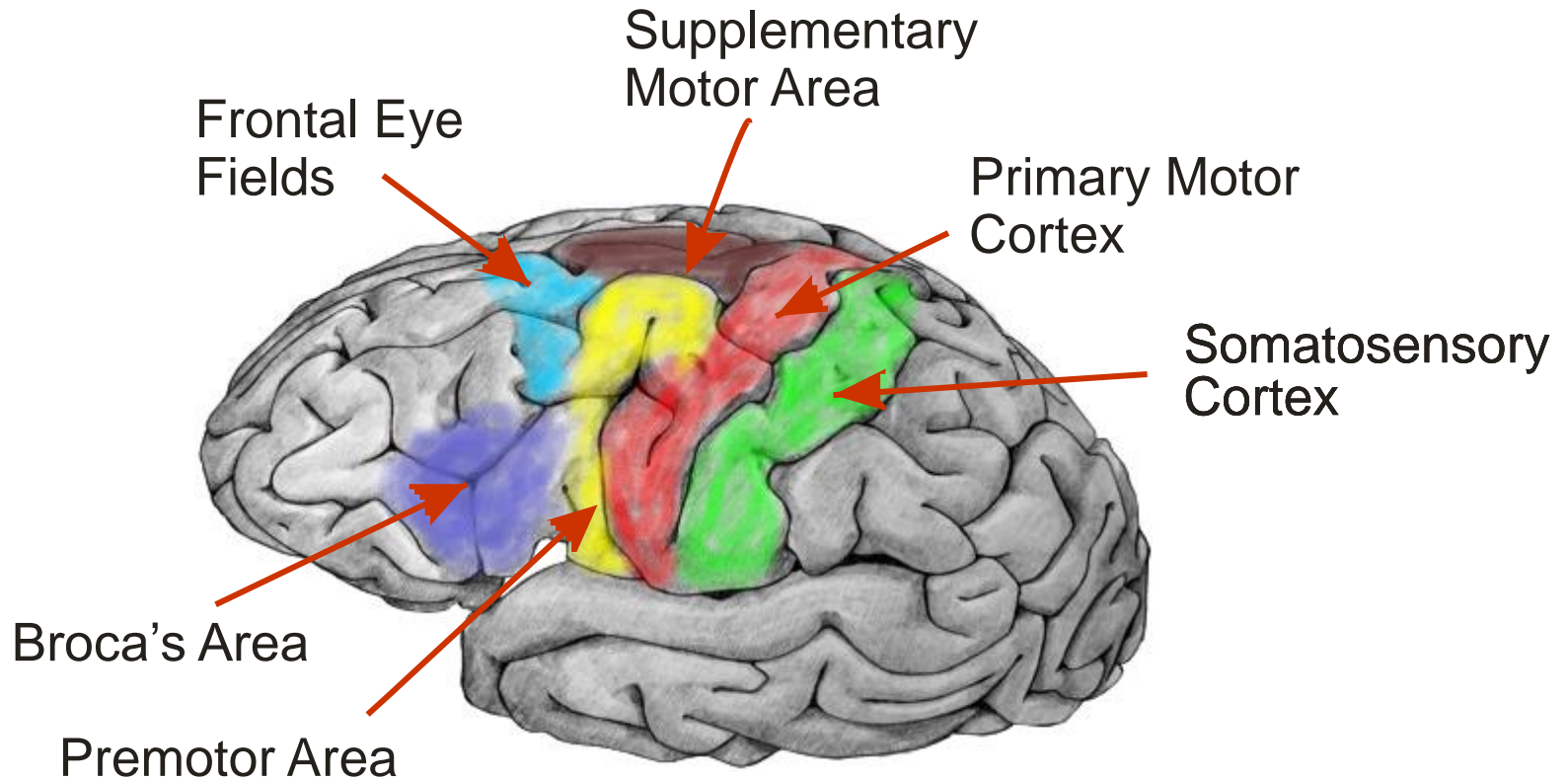
- Reading out population encoding of motor intention makes brain-machine interfaces possible. At least in theory.

Human Primate Matthew Nagel



- In practice brain-machine interfaces have a long way to go before they really have much to offer to paralysed patients.

What about “Higher Order” Motor Cortex?



Cortical Control of Movement

- As we move away from the deep layers of M1 (where the cortico-spinal tract originates), movement encoding becomes more abstract.
- Instead of specifying which motor unit to contract, neurons may encode which direction to move a limb in, irrespective of which precise muscles are needed to achieve that.
- Supplementary and pre-motor areas may specify co-ordinated movements involving more than one muscle or even more than one limb.
- Pre-frontal cortex also contains mirror neurons which appear to encode “actions” irrespective of who the action is performed by.

Mirror Neurons

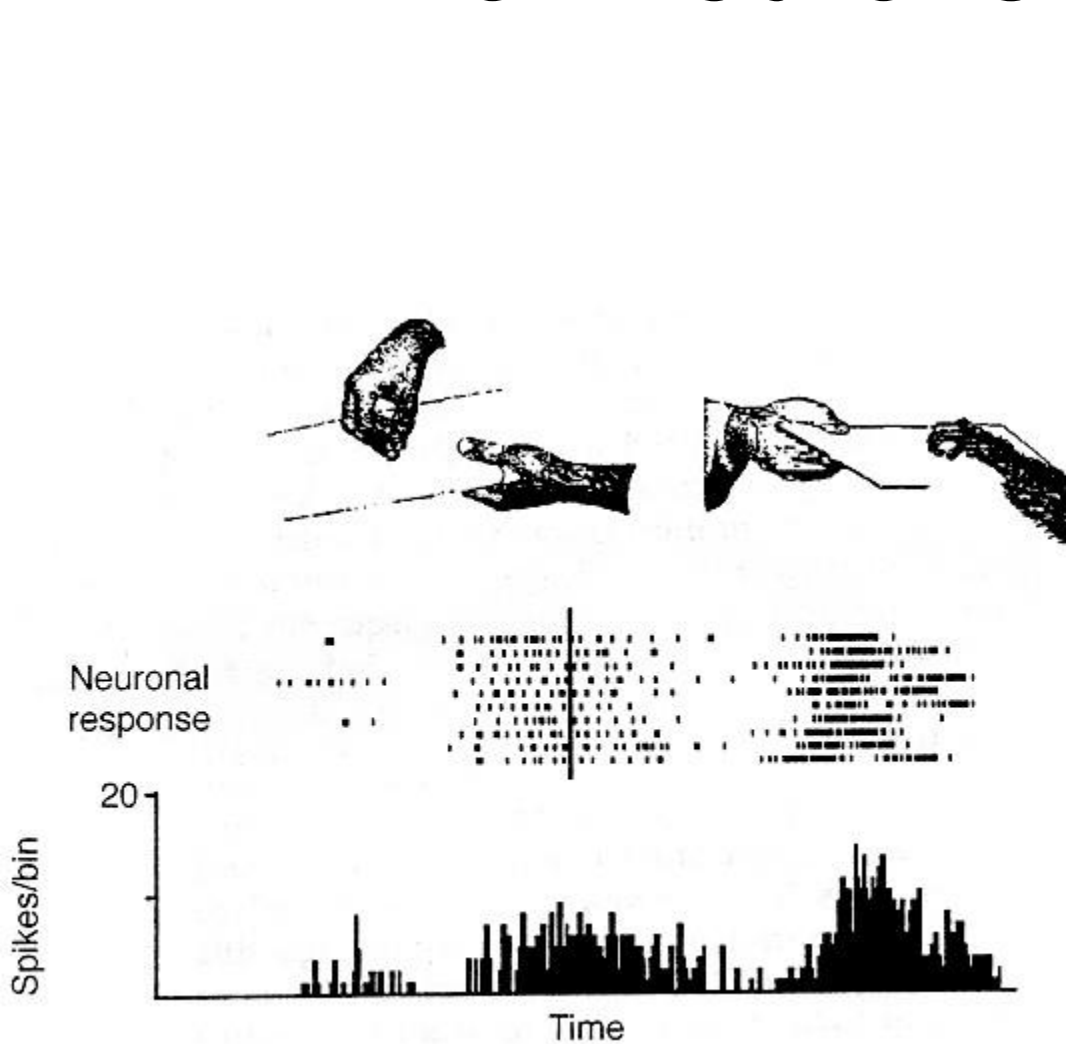
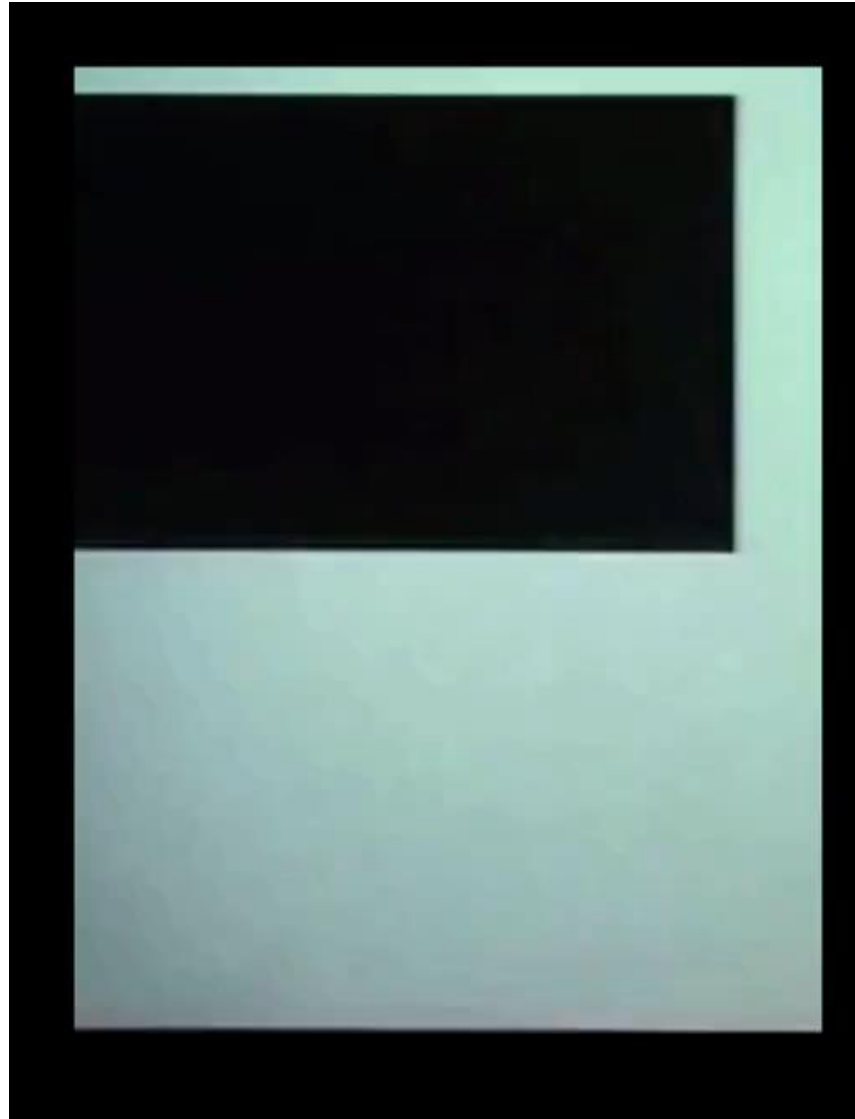


FIG. 1. Examples of transitive and intransitive actions performed by the experimenter in front of the recorded monkey (right column); same gestures made by the monkey (left column). Intransitive monkey actions, although rarely evoked during recording sessions, are shown here to outline their similarity with the same actions performed by the experimenter. From top to bottom: grasping of a piece of food; sucking juice from a syringe; lips protruded face.

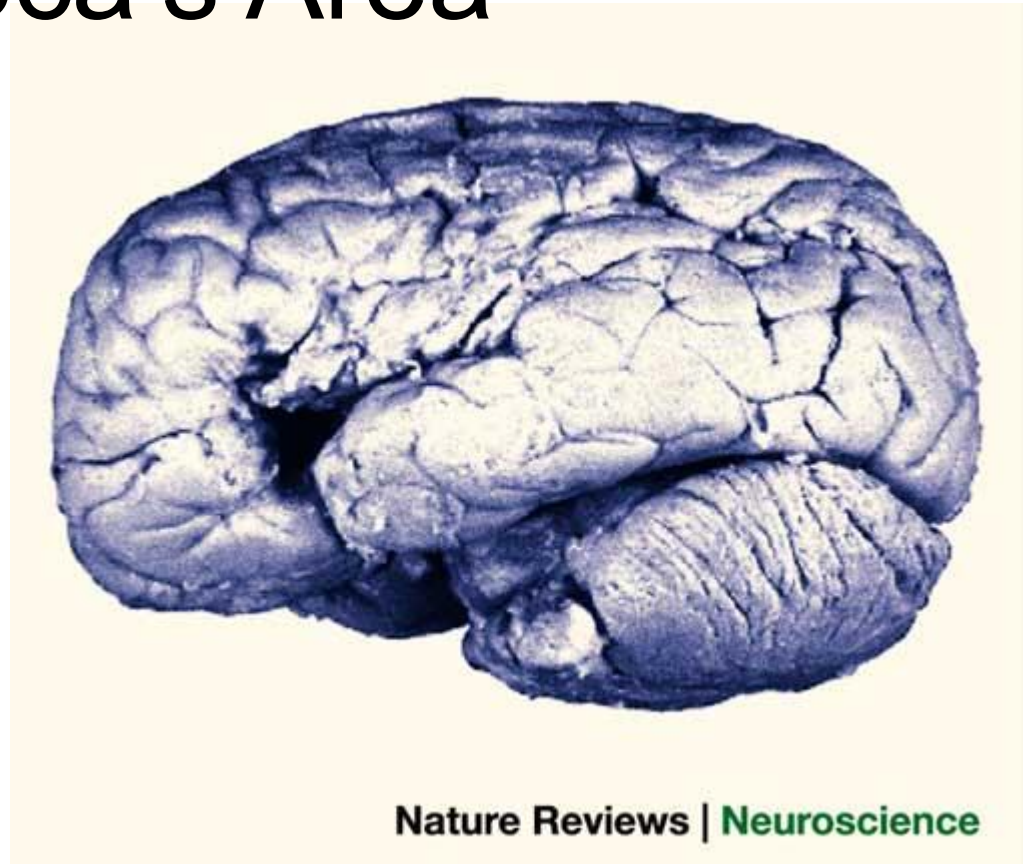
Firing of Mirror Neurons



Highly specialized “higher order motor areas”

- Broca's area can be thought of as a higher order motor area.
- It is lateralized to the left in almost everyone, and very important for the production of grammatical speech.
- Speech is like a highly rule-based, “fast dance of the vocal tract”.
- Damage to Broca's area leads to motor aphasia while leaving the ability to understand speech intact.
- Speech understanding is more based around Wernicke's area, which is a not very well defined region involving mostly superior temporal and parietal areas.
- Broca's and Wernicke's areas are tightly coupled.

Broca's Area

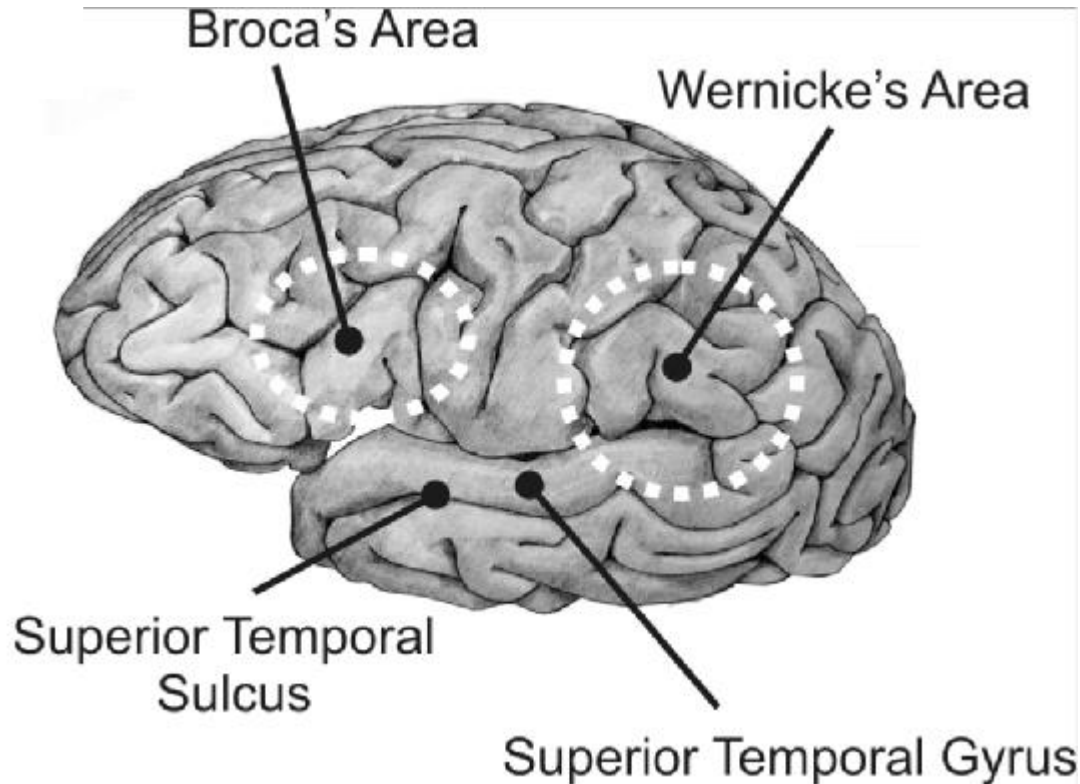


- Broca's aphasia is usually associated with lesion to the left frontal cortex.
- See here the brain of Broca's Patient, Mr Leborgne ("TanTan") features a large lesion in Broca's area.

Motor Aphasia



Wernicke's Area



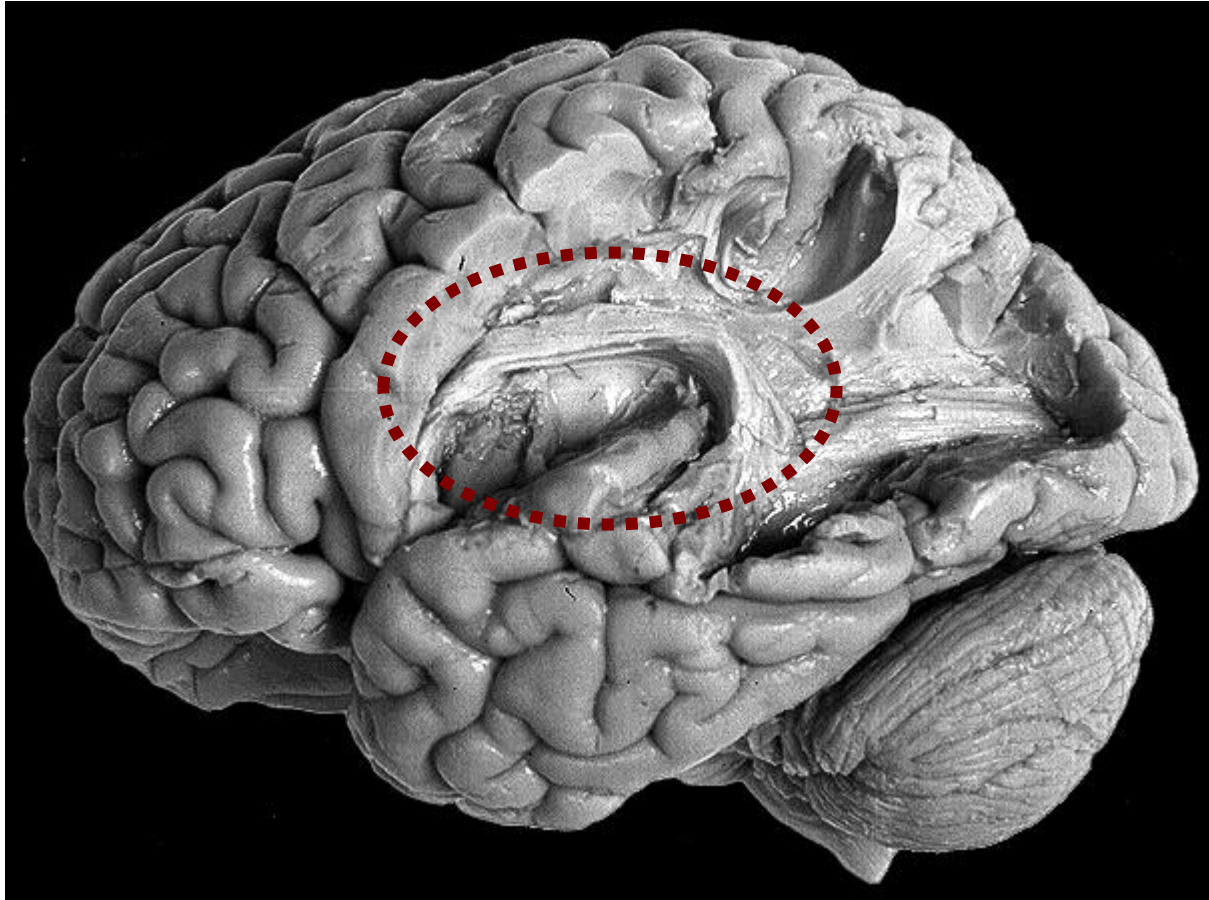
- Wernicke's aphasia is often associated with lesions at the boundary of the superior temporal and parietal lobes on the left hemisphere.

A Patient with Wernicke's Aphasia



- From the archives of the University of Wisconsin

The Arcuate Fasciculus

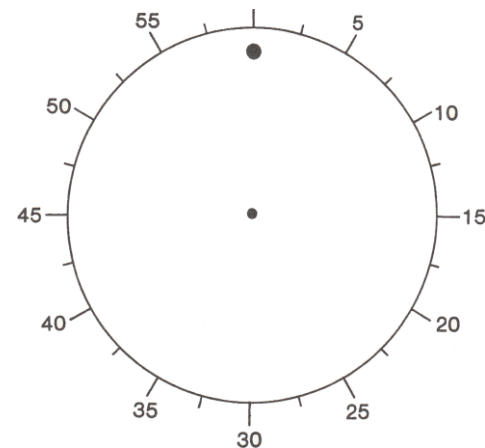
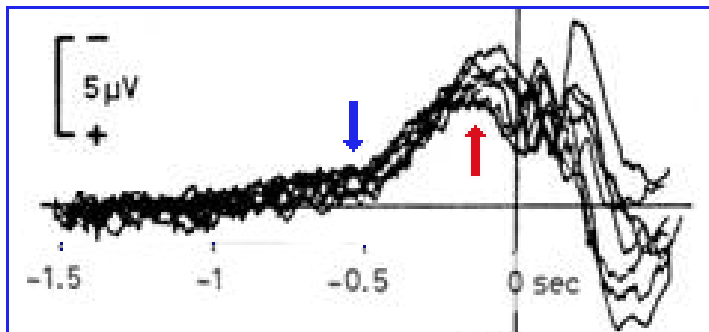


Big fibre bundle connecting Broca's and Wernicke's Areas
<http://www.biocfarm.unibo.it/aunsnc/pictef14.html>

Cortical Control of Movement and “Free Will”

- The further up you go the motor hierarchy, the more activity will precede the actual movement initiation.
- Already in the supplementary motor area you can get electrical activity as much as half a second prior to a spontaneous, self-timed movement.
(“Bereitschaftspotential” BP or “readiness potential”).
- Libet showed that the BP commences before a person is aware that they would like to move.

http://www.informationphilosopher.com/freedom/libet_experiments.html



Cortical Control of Movement and “Free Will”

(2)

- If you electrically stimulate M1, people feel their limbs are being moved. If you stimulate supplementary motor areas, they feel they want to move.
- If you judge a person by their action then your motor cortices make you who you are. But they don't do that all by themselves. They work closely, for example, with the basal ganglia, about which we will learn in the next lecture.