

## *Lawrence & Kuypers, 1968:*

- **Lesion #2: destruction of medial brainstem pathways** (added to pyramidotomy) *bilaterally*
  - Defective axial control:
    - Righting: only after 10-40 days
    - Falling: failure to elicit the usual corrective movements
    - Walking: only one monkey could take many steps because of disorientation; he veered from course, bumped into obstacles
  - Better distal control:
    - If monkey was strapped into a chair, it could grasp food objects with the whole hand

*Lawrence & Kuypers, 1968:*

- **Lesion #3: destruction of lateral brainstem pathways** (added to pyramidotomy)
  - Defective limb control: Hand flexion done only with total arm movements. Inability to grasp objects with the hand.
  - Good axial control
    - Hand used dramatically better in running & climbing (total body movements) \*

\*Thus, “paralysis” can be very specific if it is not due to loss of motor neurons.

# Conclusions

- These experiments made clear a fundamental *spatial* organization of brainstem pathways controlling movement in vertebrates
- It also made clear the quantitative dominance achieved by the pathways originating in the neocortex.

## Questions, chapter 15

- 5) What are the major symptoms of a lesion of most of the pathways from the brain to the spinal cord (sparing the pathways critical for breathing)?  
**below C4**

(A brief digression)

## Brief digression:

The brain disconnected from the motor output:

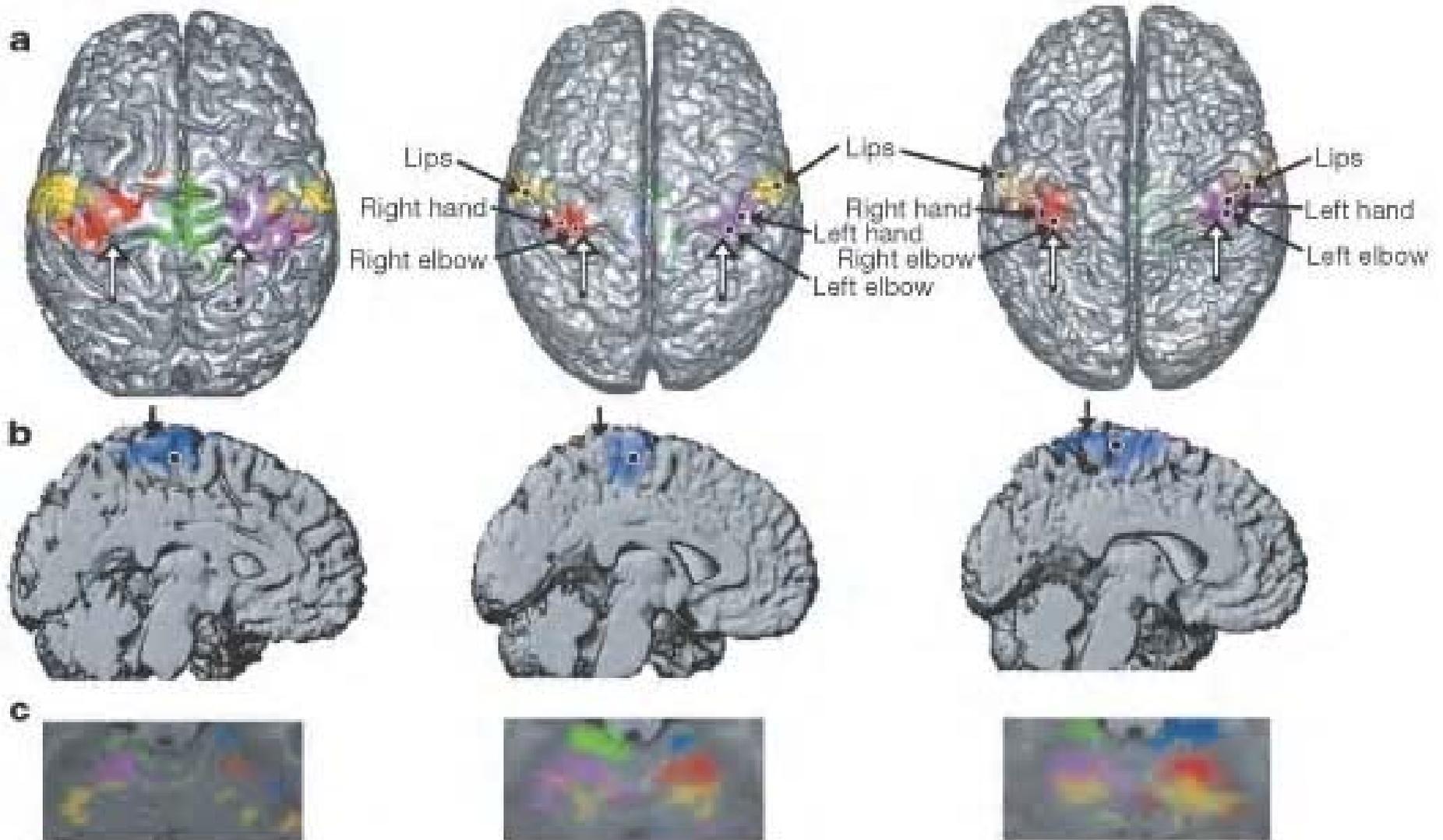
### **Motor cortical activity in human tetraplegics**

(all three descending pathways severed)

- Thinking without the ability to act: Activation of specific parts of the motor cortex
  - Without the connections to the spinal cord, the person moves only “phantom” limbs, using an intact motor cortex.
- Question: Can the long pathways be reconnected in people or animals with such injuries?

# Motor-cortical activity in tetraplegics

Nature 413, 25 Oct 2001



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# Motor cortex and corticospinal projections in phylogeny

## Three topics:

### 1) **The sensorimotor amalgam hypothesis**

- VL and VP projections (thalamic nuclei with projections to motor and to somatosensory cortex): Opossum and rat compared

### 2) **Corticospinal invasion and dexterity: comparative studies**

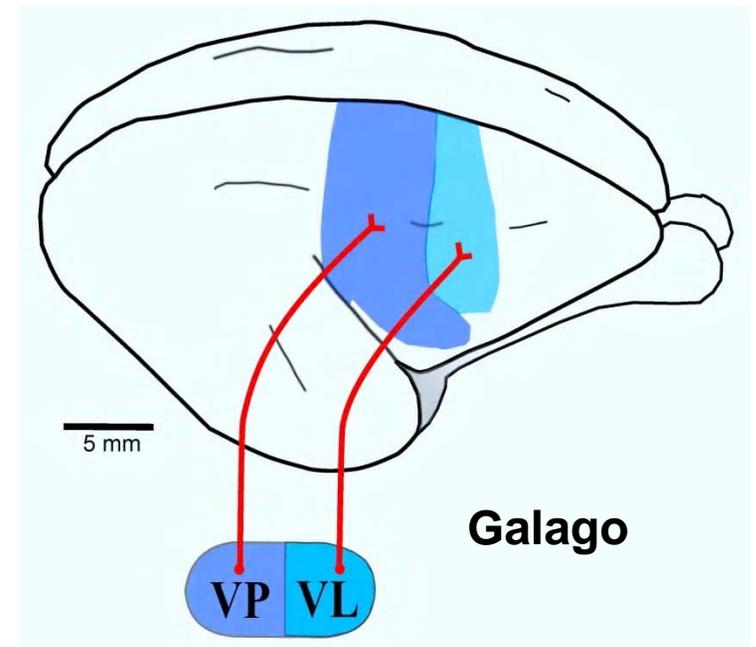
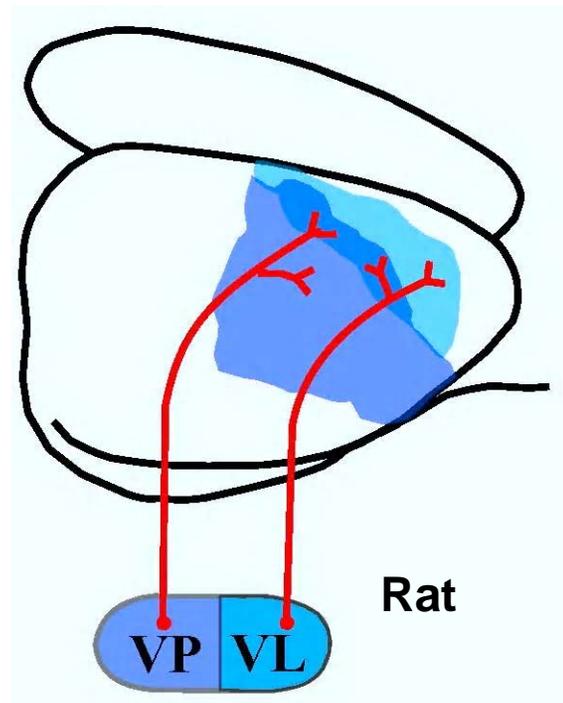
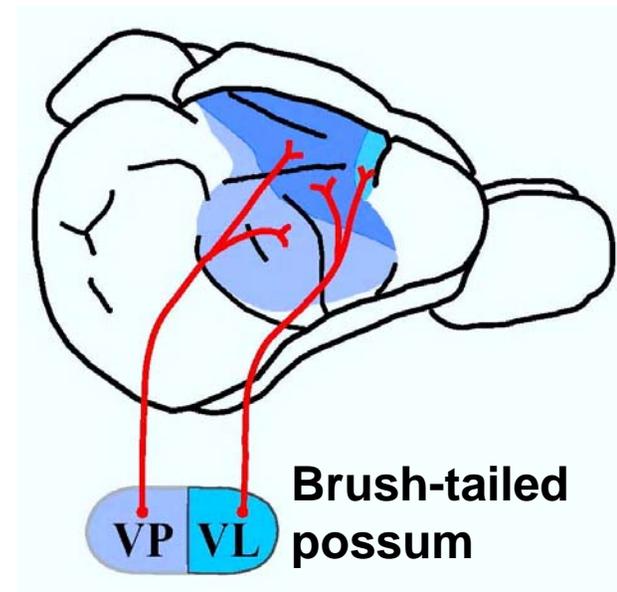
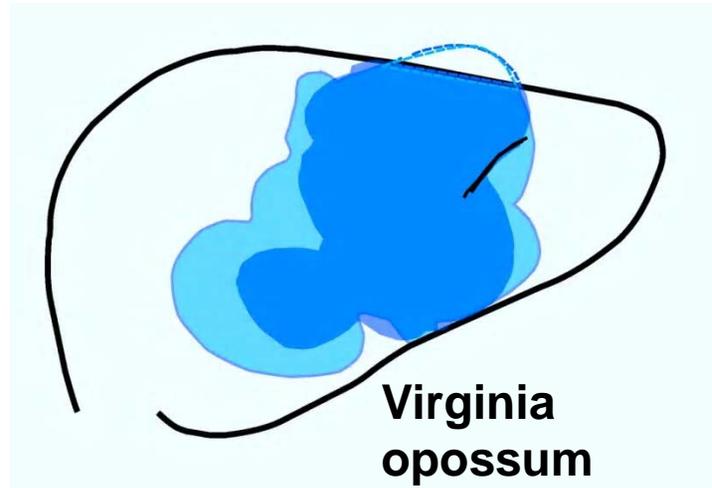
- Correlation between anatomy and behavior

### 3) **Comparative analysis of corticospinal neurons**

- More of these neurons when total size of neocortex is greater

## Questions, chapter 15

- 9) How can neuroanatomical experiments determine whether primary somatosensory neocortex overlaps fully or partially with primary motor cortex? Describe examples.



VP = ventral posterior nucleus of thalamus (major inputs from medial lemniscus & spinothalamic tract)

VL = ventral lateral nucleus of thalamus (major inputs from cerebellum)

**Fig 15-6**

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**A parcellation of sensory and motor cortex has occurred in evolution.**

# **Penetration of corticospinal axons into ventral horn vs. neocortical volume**

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# Penetration of corticospinal axons down the spinal cord vs. neocortical volume

Figure removed due to copyright restrictions.

The greater invasion of spinal cord with increasing neocortical size fits  
“Deacon’s rule” which is summarized as “large equals well-connected”.

# Correlations with dexterity

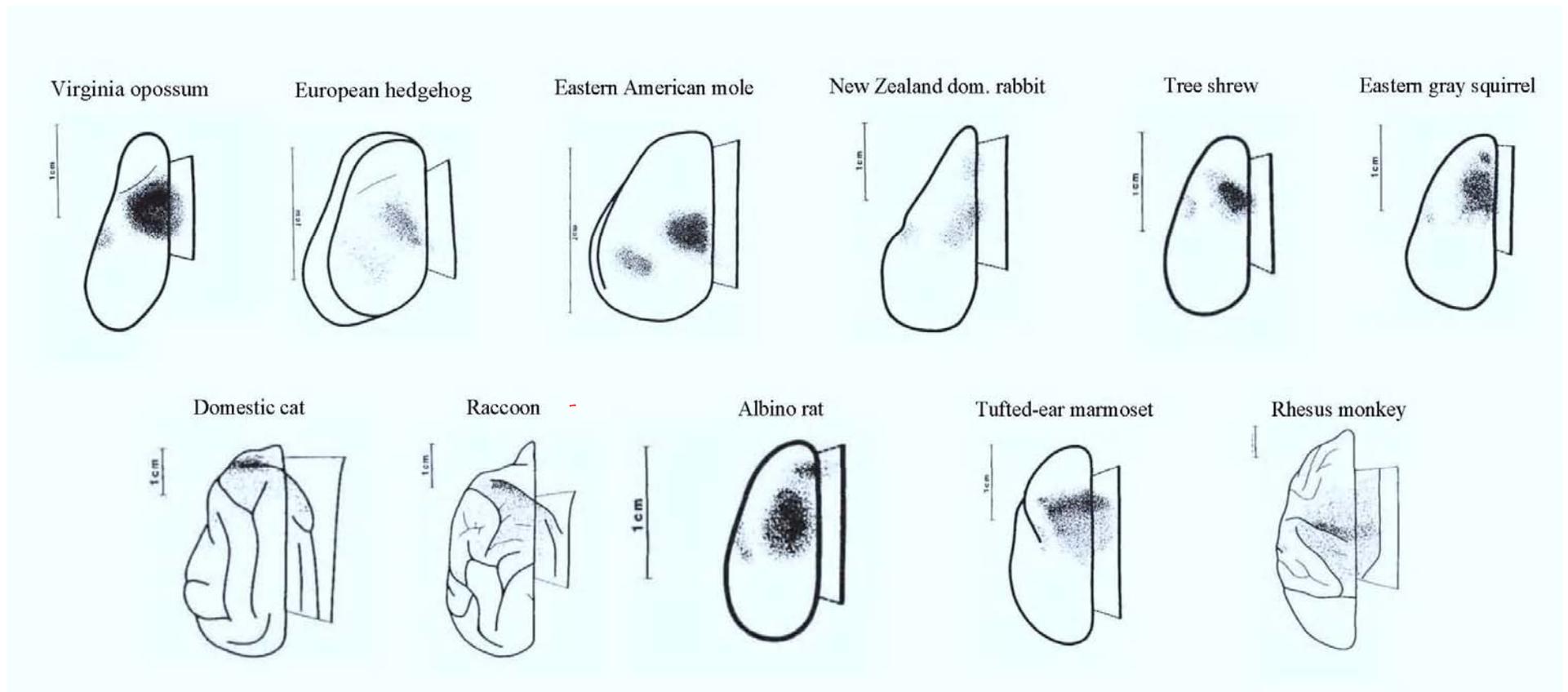
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## Dexterity Index

# **Neocortex : Spinal Cord Ratio vs. Neocortical Volume**

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# Corticospinal neuron locations and densities



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**The number of corticospinal neurons is strongly correlated with total size of neocortex (not seen in this figure)**

**Fig 15-7** Note that the scale bar always represents 1 cm, and thus the larger brains are reduced in size much more than the smaller brains.

## Questions, chapter 15

- 10) What is Deacon's rule? What does it predict about the projections (outputs) of the optic tectum in birds, with a very large tectum, and in nocturnal mammals, with a much smaller tectum?
- 11) Neuroanatomical experiments indicate that the primary motor cortex of rhesus monkeys contains a rostral older part and a more caudal newer part. How are these two parts different? **See figure 15.8**
- 12) What is the "highest" level of motor control? This question can be answered in various ways. Try to answer it after defining what you assume to be highest.  
**(There is no single way to answer this question.)**

# A question about the motor system's higher levels

- Previously discussed: At highest level, we have neocortical sensory areas with projections to the striatum, resulting in outputs for learned habits.
- We also have motor cortex with direct projections to spinal cord, supporting fine control of extremities (as already discussed).
- **Question: Why has motor cortex become so dominant? in primates**

# Why has motor cortex become so dominant?

- It is not only because of its striatal connections or because of direct projections to motor neurons in cord.
- It is because of its close connections with a system for anticipation of, and planning for, the future:
  - The immediate future, e.g., frontal eye fields moving eyes to positions of expected stimuli
  - More distant future too: for achieving goals of motivational states
  - This is **role of the prefrontal\* cortex.**
    - Much of the prefrontal\* cortex – the lateral prefrontal region – is closely connected to anterior cingulate cortex, and thence to the hippocampal formation.
    - This lateral prefrontal cortex is not fully developed in humans until they are in their early 20s.

[\* Prefrontal = the frontal association cortex]

# **A sketch of the central nervous system and its origins**

G. E. Schneider 2014

**Part 6: A brief study of motor systems**

**MIT 9.14 Class 17**

- **Motor systems 3: Temporal patterns**
- **Brain state changes**

## Motor Systems 3: **Temporal patterns**

# **Rhythmic output and timing**

## *Topics*

- Temporal patterns in animal movements:  
Explanations
- Activity rhythms

# Temporal patterns in movements: types of explanations

- 1) S-R models: Straight-through processing concepts
- 2) Feedback circuitry
- 3) Endogenous CNS activity

## Questions, chapter 16

- 1) How can the concept of reflexes, or of stimulus-response (S-R) connections that underlie the fixed action patterns of innate behavior, be used to explain complex sequences of behavior that last much longer than any single reflex or S-R event?

# S-R models:

## Straight-through processing concepts

- *Topics*
  - Timing of movements in reflexes
    - Conduction time: temporal pattern in startle reflex
    - Chaining of reflexes or fixed action patterns
  - Lashley's 1917 paper: "The problem of serial order in behavior"

# Timing of movements in reflexes :

## Conduction times

- Temporal pattern in startle reflex in response to sudden, unexpected, loud sound, in order of occurrence:
  1. eye blink
  2. contraction of other facial muscles
  3. neck flexion
  4. arm flexion
  5. leg flexion (with very intense sound)
- Timing explained by:
  - fiber size
  - synaptic delays
  - temporal summation times

# Chaining of reflexes or fixed action patterns

- Tinbergen (1951): the courtship pattern of the three-spined stickleback fish is an S-R series
- Swallowing reflex (“Reflex deglutition”):  
Is the explanation the same?

# Tinbergen (1951): The courtship behavior of the three-spined stickleback fish

- Movements by a pair of animals rather than just one animal
- If a step is interrupted:
  - The sequence cannot proceed
  - Each step gives a necessary stimulus for triggering the next step.
- *This is presented in order to illustrate the chaining of S-R events, often called “reflex chaining”*

# The courtship behavior of the three-spined stickleback fish (Niko Tinbergen, 1951)

## Female actions

- Appears, swollen belly
- Courts (approaches)
- Follows
- Enters nest
- Spawns

## Male actions

- Zig-zag dance
- Leads to nest
- Special posture at entrance
- Trembles, snout to her tail
- Fertilizes

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Each step is a **necessary** stimulus for triggering the next step.  
In chapter 16, hamster foraging and food hoarding is described similarly, as a chain of fixed action patterns.

## Questions, chapter 16

- 3) Name a movement pattern in an animal or human that is largely under the control of hindbrain and spinal cord structures and is centrally generated, once it is triggered. How is it different from a reflex (even though it may be called a reflex by neurologists)? *swallowing*
- 3) Similarly, name a movement pattern that is largely under the control of the spinal cord, and completely so in many species. *walking and other gaits*

# “Reflex deglutition” (swallowing)

- Involves about 20 muscles controlled by neurons from midbrain to cervical spinal cord levels.
- In this case, experiments have shown that the pattern of contractions is **centrally programmed**:
  - Pattern is not changed by experimental elimination of proprioceptive feedback during any stage of the movement once it is triggered.
  - It is a “fixed action pattern” (FAP), inborn, and is executed rhythmically with a steady or varied stimulus *via* the superior laryngeal nerve.
  - It is normally triggered by stimulation of the tongue deep in the throat.
  - There is also an endogenous input that builds up over time and lowers the threshold for eliciting the response.

[*Study by Doty & Bosma, 1956*]

## Questions, chapter 16

- 2) What was the basic argument in Karl Lashley's paper in 1917 called "The problem of serial order in behavior"?

## Karl Lashley's 1917 paper: “The problem of serial order in behavior”

(Lashley is often considered to be the major pioneer of the field of “physiological psychology” or biopsychology, now called “behavioral neuroscience.”)

- Lashley argued against the adequacy of the reflex chaining hypothesis. Example:
  - “The finger strokes of a musician may reach 16/sec in passages which call for a definite and changing order of successive finger movements.”
  - “The succession of movements is too quick even for visual reaction time.”
- **Conclusion:** There must be **central generation** of patterns of movement.

## **Similarly, many fixed action patterns—inherited movement abilities—are centrally generated.**

- We have already mentioned one such pattern: swallowing.
- Others:
  - Grooming by mice (Fentriss' experiments): Movement patterns continue even without the usual feedback stimulation.
  - Egg rolling in gulls (Tinbergen): Movements can occur even after the stimulus has been removed.
  - Other examples of “*in vacuo*” movement patterns
  - Locomotor movements in fish: Central generation of rhythmic fin movements
  - Locomotor movements in mammals are similarly generated in the spinal cord, but they require activation from the periphery or from descending fiber systems (from the brain).

**How are these action patterns generated, if not by reflex circuitry?**

## Questions, chapter 16

- 5) How is central generation of a temporal pattern possible? What two types of mechanism other than S-R circuits are described in the chapter?

# Temporal patterns in movements:

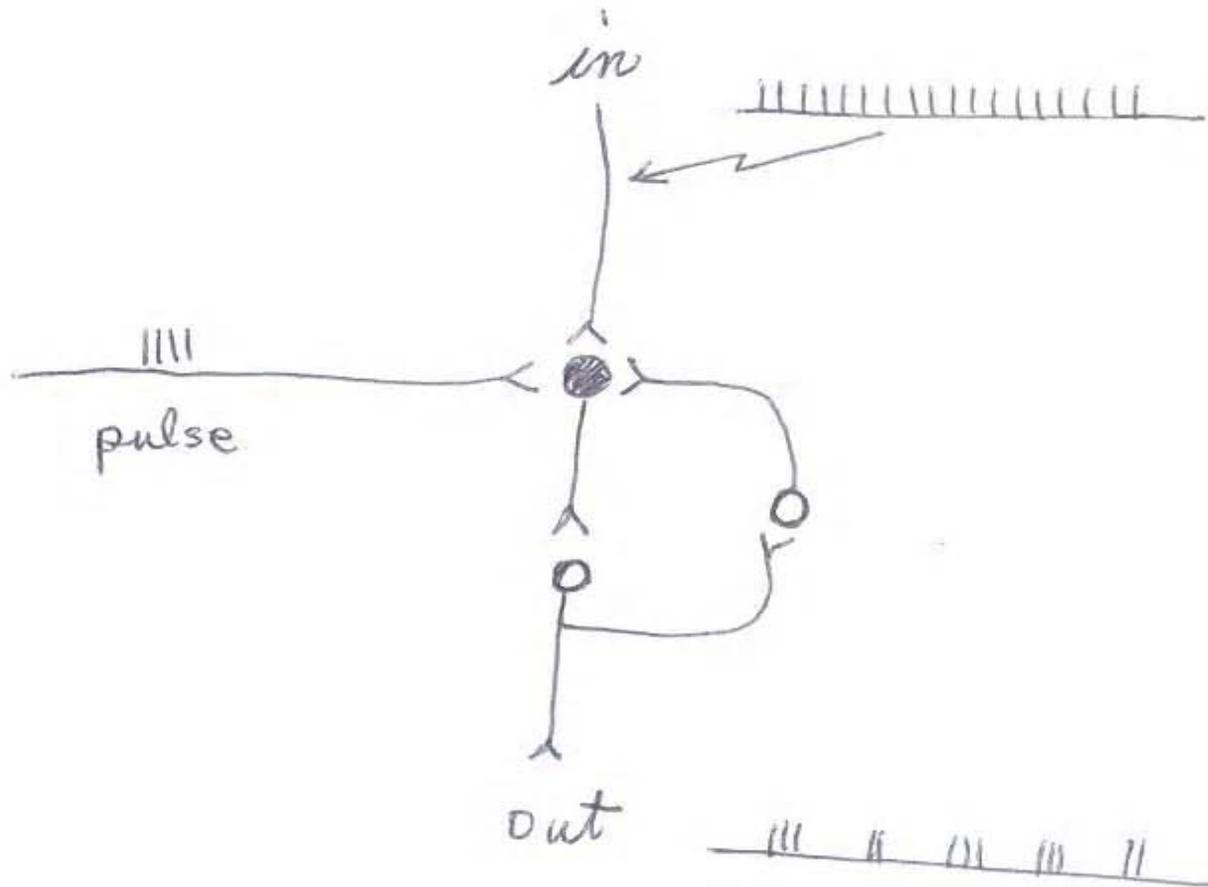
## types of explanations

- 1 • Straight-through processing concepts (S-R models)
- 2 • **Feedback circuitry**
- 3 • Endogenous CNS activity
- Combinations of these mechanisms

# Feedback circuitry: the “reverberating circuits” idea

- Self re-exciting loops
  - regular bursts of action potentials (a kind of central oscillator)
- Negative feedback in homeostatic mechanisms:
  - The response oscillates around a certain level of some input (the set point).

# Feedback circuit at its simplest level: patterned output from unpatterned input



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What assumptions are necessary for this simple circuit to work this way?

# Complexity and control

- To get more complex patterns, combine more than one such circuit. *(See slide 24)*
  - How stop the rhythm? *Fatigue or inhibitory input*
- Example: Breathing rhythms can be at least partially explained by such circuits.
- Neuroanatomical studies have revealed a great many examples of circuits that form loops involving few or many synapses.

# Temporal patterns in movements:

## types of explanations

- Straight-through processing concepts (S-R models)
- Feedback circuitry
- **Endogenous CNS activity**

## Questions, chapter 16

- 5) How can a single neuron generate a temporal pattern of electrical activity? *slide 24*

# Endogenous CNS activity

- Endogenously generated rhythmic potentials can also cause bursting patterns of action potentials
  - Felix Strumwasser's *Aplysia* (sea slug) recordings, as illustrated earlier.
- Circadian rhythms in vertebrates

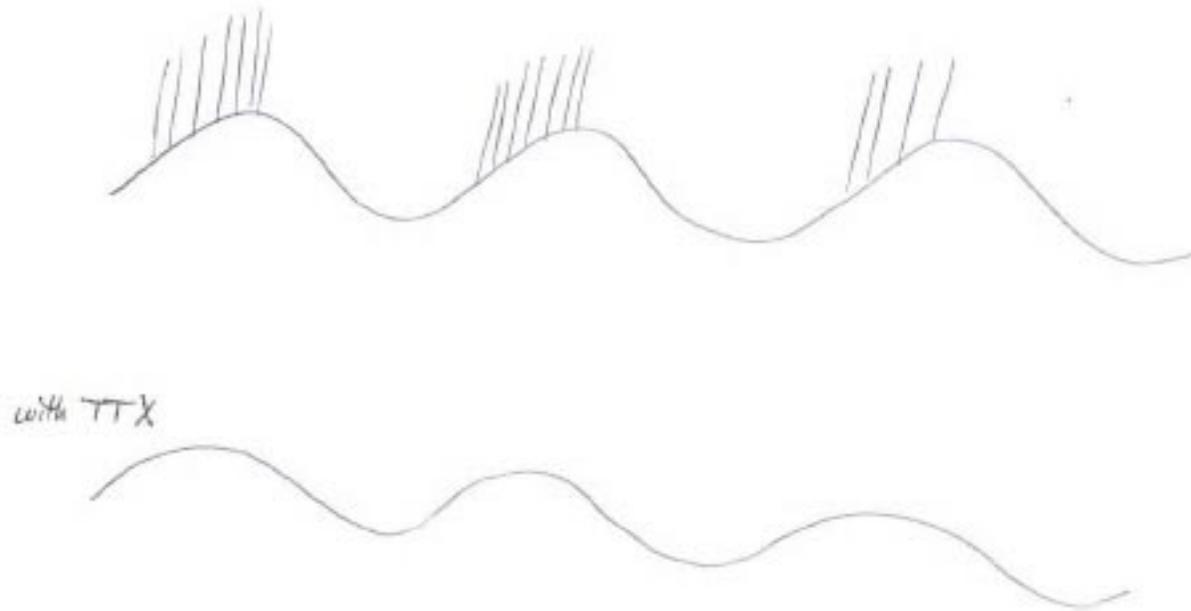
## REVIEW:

# Felix Strumwasser's Aplysia (sea slug) experiments

- Recordings from an identifiable large secretory neuron of the abdominal ganglion:
  - T=40 sec (rhythm persists if action potentials are blocked with TTX),
  - but not if sodium pump is blocked with Ouabain.
- This cell also showed a circadian rhythm that could be entrained by light.

## REVIEW:

# Endogenous oscillator



**A single neuron can generate rhythmic changes in membrane Potential because of “pacemaker loci” in the membrane. The oscillations are caused by specific molecules.**

**The potential for complex temporal pattern generation:  
Multiple oscillators added together could give any pattern,  
known from the mathematics of Fourier Analysis.**

**REVIEW:**

# Circadian rhythms in vertebrates

- Animals depend on such “biological clocks” for their daily schedule of activities.
  - Temporal schedules are important for animal survival.
  - The endogenous clock is circadian, with a period of approximately 24 hr
  - The biological clock is normally entrained by the day-night cycle.
  - The critical input for this entrainment comes from the retina, *via* a projection to the hypothalamus.

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## 9.14 Brain Structure and Its Origins

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