The model organism *C. elegans*

Part II: Neurobiology

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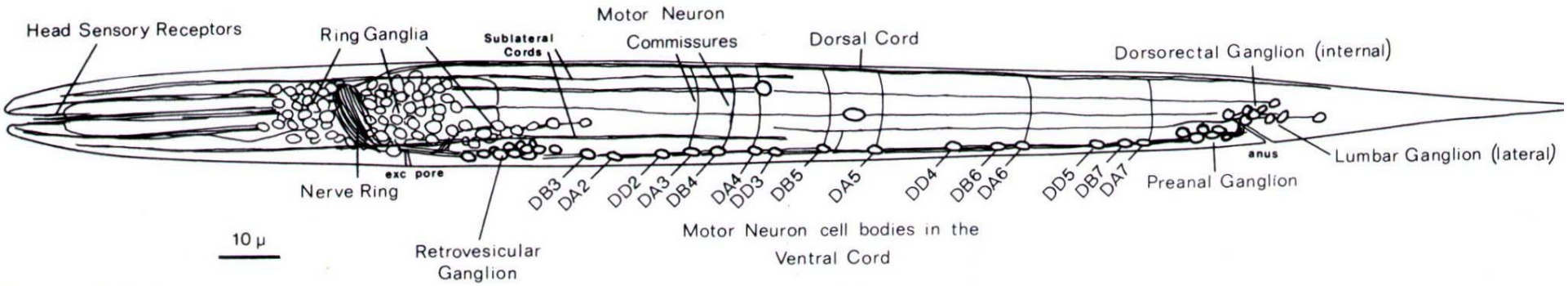
C. elegans neurobiology

- Anatomy of *C. elegans* nervous system
- Structure and function of sensory neurons
- Mechanosensing
- Chemotaxis and thermotaxis
- Male sensory neurons and mating behavior
- Motor circuits
- Synapses, NMJs and neurotransmitter
- Electrophysiological methods
- Habituation and learning

C. elegans neurobiology

- The *C. elegans* nervous system is simple and well described
- It consists of **302 neurons** interconnected by **chemical** and **electrical** (gap junctions) **synapses**
- The **position** and the characteristic of each neuron **does not vary** from animal to animal which makes it a very good model organism for studying neuronal processes
- Even though the neuronal system is simple, it regulates a wide variety of behaviors:
  - different **mechanosensory responses** (light, harsh, nose and texture touch)
  - **chemosensory responses** (e.g., can differentiate various types of alcohols)
  - **thermotaxis** (can detect < 0.1ºC)
  - complex responses to food with **habituation and learning**
  - **locomotion** (complex moving behavior)
  - **egg-laying** and **defecation**
  - complex **male mating behavior**



Compared to *Drosophila,* there are more neuronal protein coding genes in *C. elegans*

Protein Family	*Drosophila* Homologs	*C. elegans* Homologs
Voltage-gated sodium channels		
α subunit	2	0
β subunit	0	0
TipE	2	0
Voltage-gated calcium channels		
α subunit	4	5
β subunit	1	2
α2δ subunit	3	3
γ subunit	?1	0
Potassium channels		
K_v α subunit	5	10
K_v β subunit	1	0
KCNQ α subunit	1	3
MinK β subunit	0	0
EAG α subunit	3	2
MiRP1 β subunit	0	0
slo α subunit	1	2
slo β subunit	0	0
slack α subunit	1	2
SK α subunit	1	4
K_r α subunit	3	3
TWIK α subunit	11	50

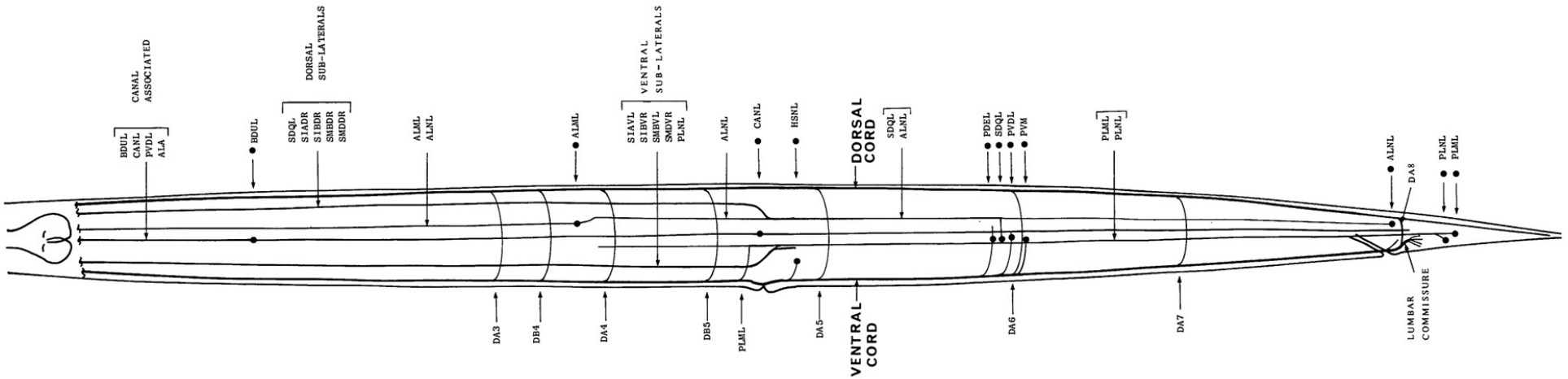
Protein Family	*Drosophila* Homologs	*C. elegans* Homologs
Chloride channels	3	6
CNG channels	4	6
Hyperpolarization-activated channels	1	0
Ionotropic glutamate receptors		
AMPA subtype	3	3
kainate subtype	15	4
NMDA subtype	2	2
δ subtype	4	4
divergent	6	2
nACh receptors	10	42
$GABA_A$/glycine receptors	10	37
Trp-like channels	13	11
Amiloride-sensitive sodium channels	24	22
Ryanodine receptor	1	1
IP_3 receptor	1	1
Innexins	8	24
Total	**145**	**251**

Littleton and Ganetzky, 2000, *Neuron*

Basic features of the nervous system

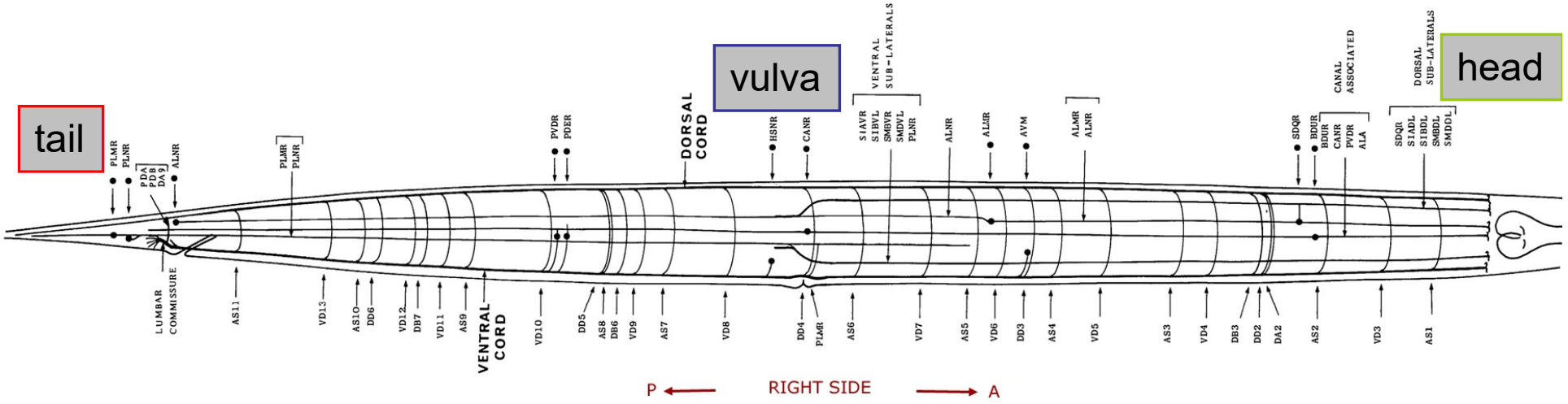
nerve ring

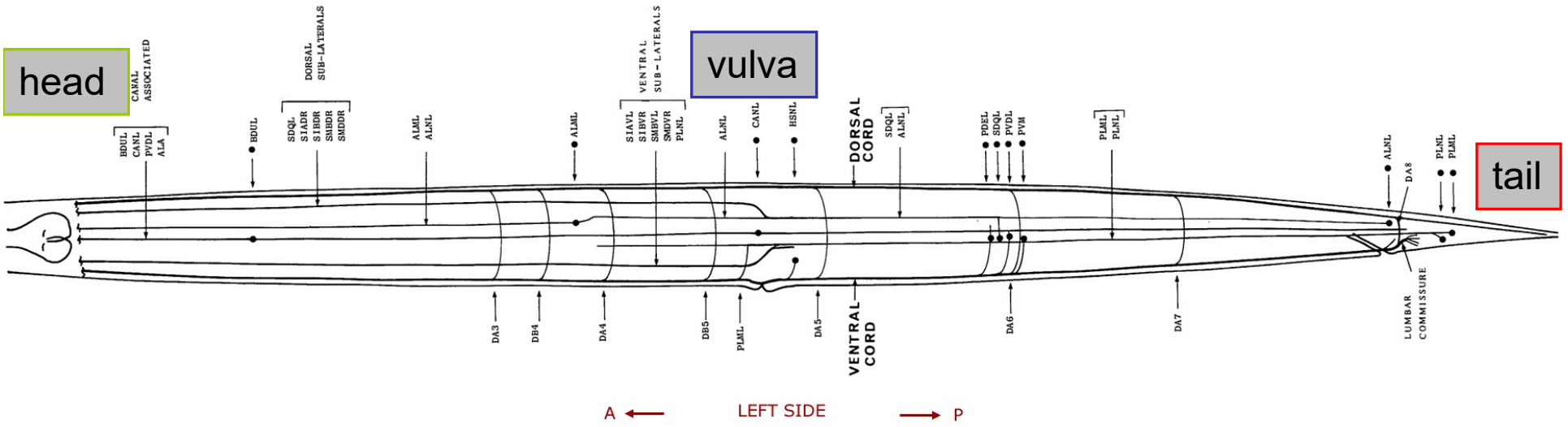
neuronal marker
(UNC-104::GFP)
expressed in *C. elegans*



Basic features of the nervous system

Neurons are paired





Basic features of the nervous system

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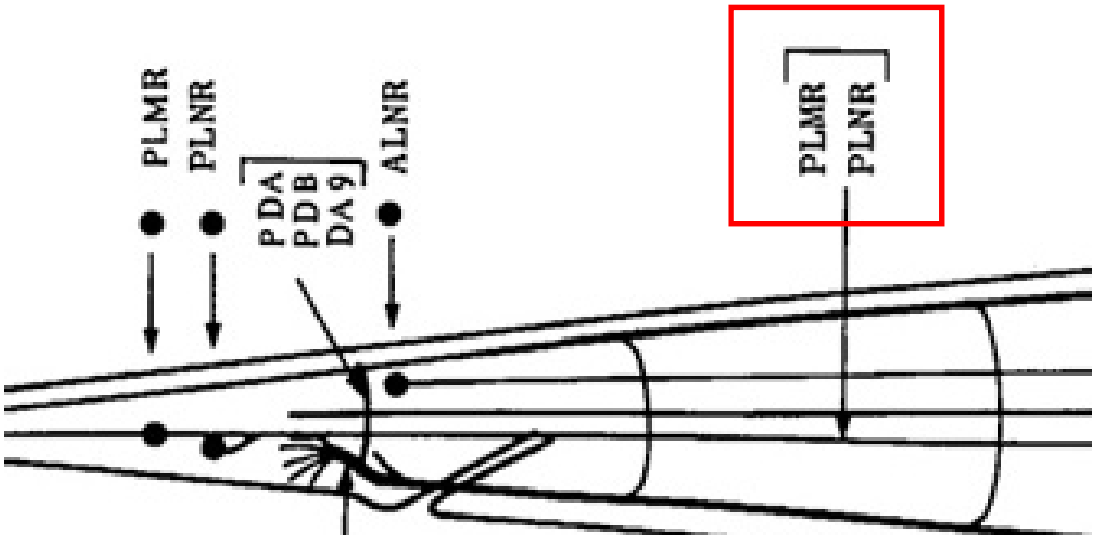
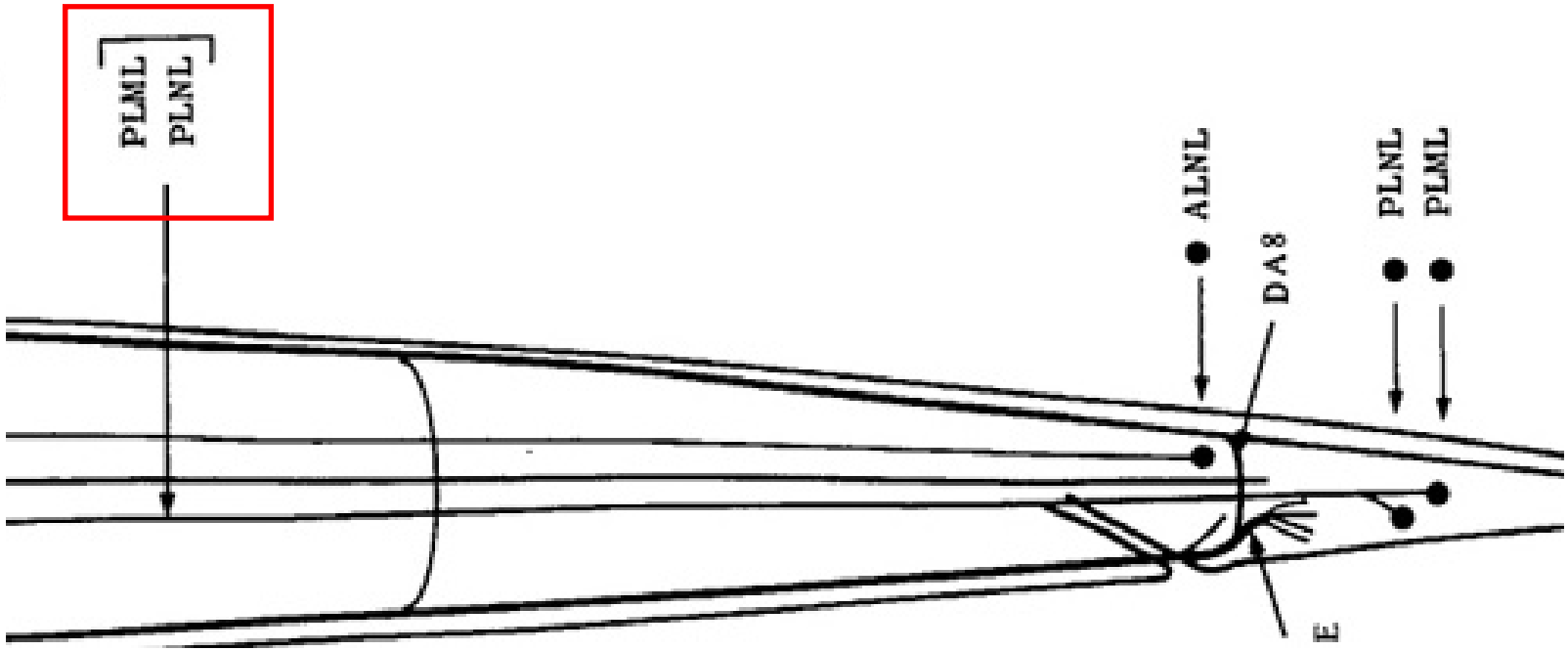
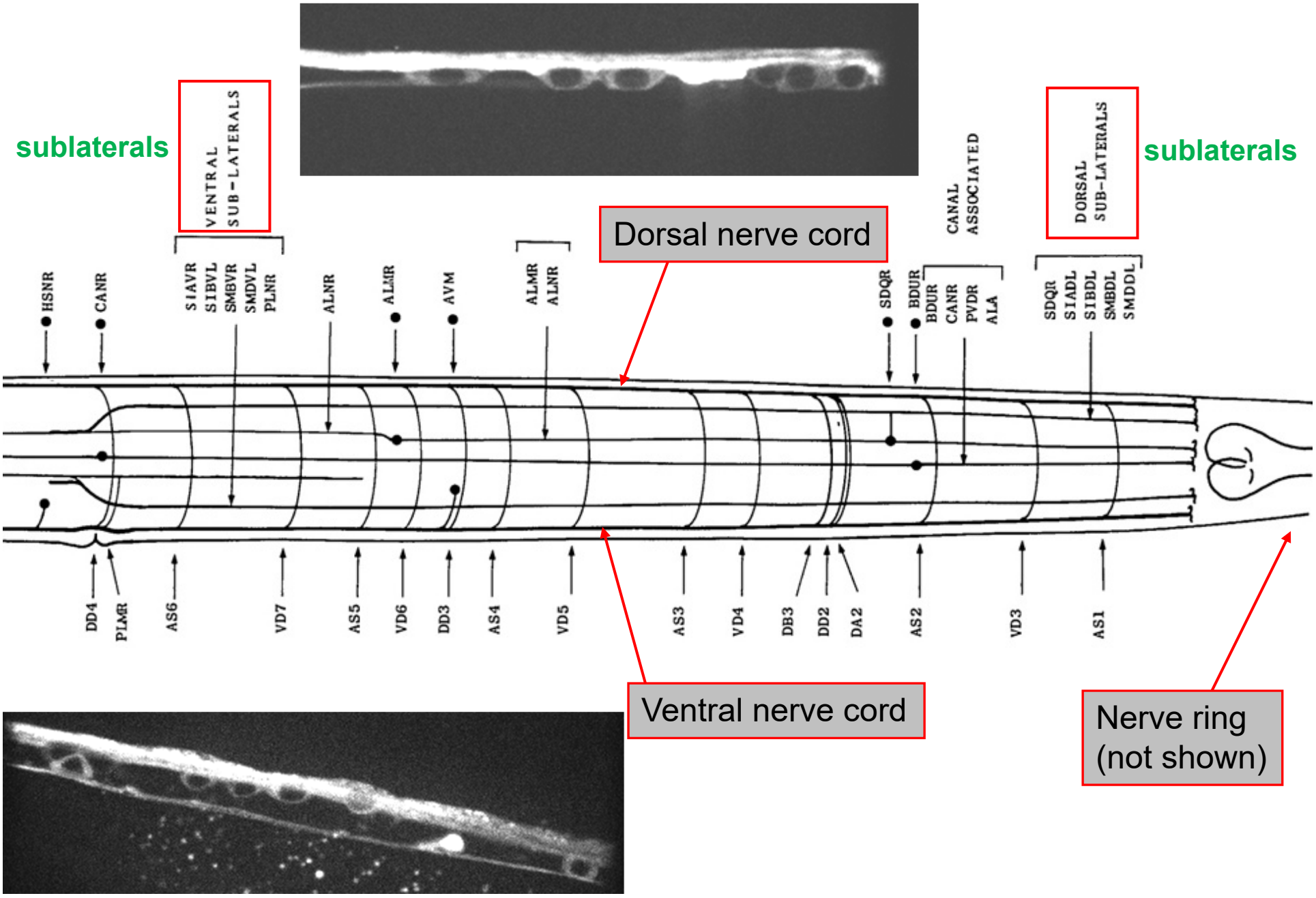


P = posterior
A = anterior
L = lateral
M = microtubule cell
N = interneuron
R/L = right/left

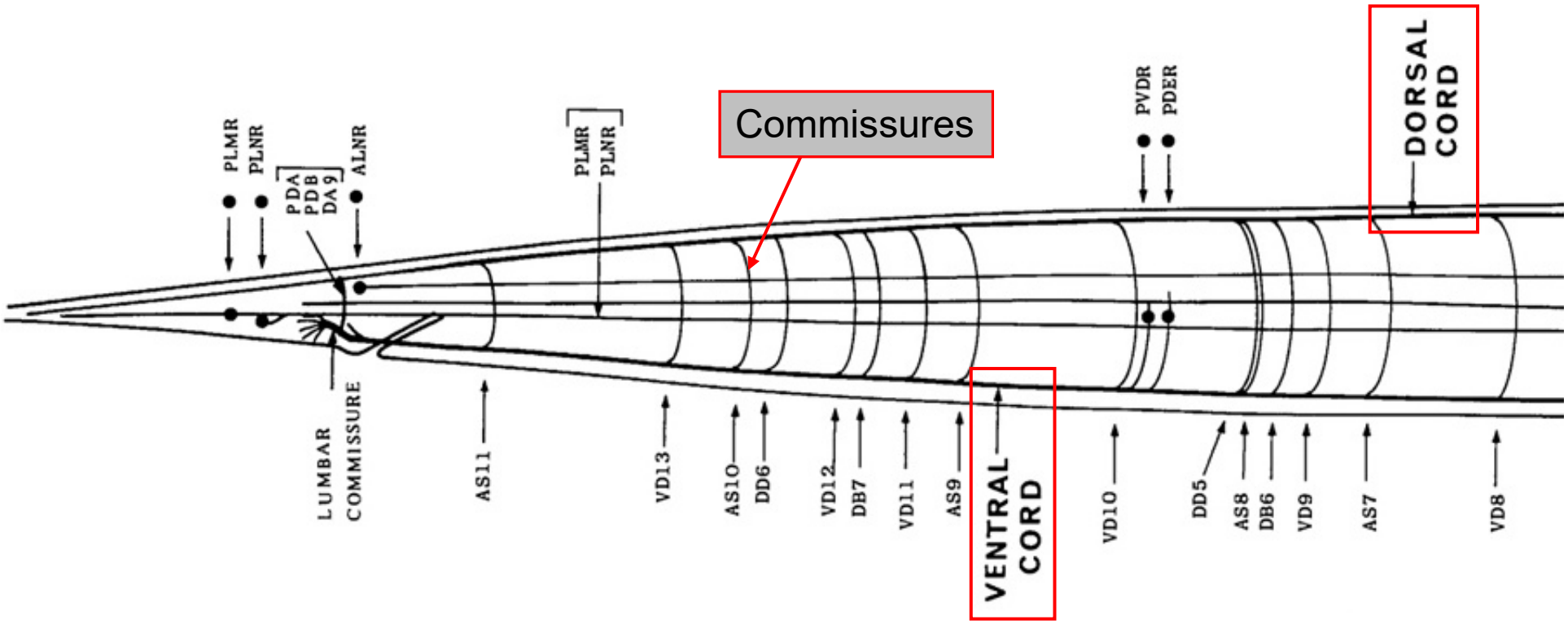


Basic features of the nervous system: Neuron bundles

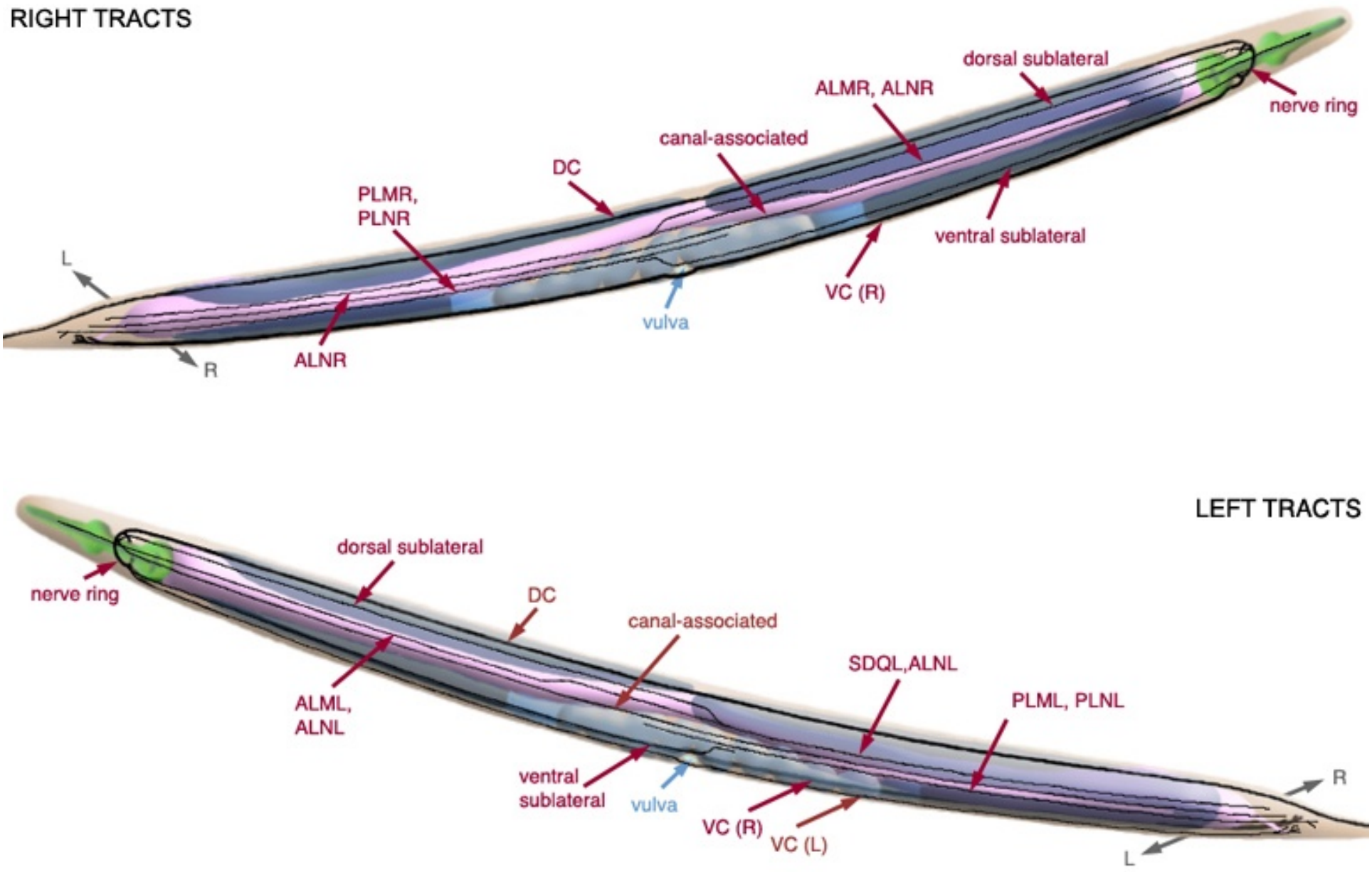


Basic features of the nervous system: Commissures

- Some ventrally located motor neurons make commissures to the dorsal nerve cord
- Interestingly, most **commissures** are located on the **right side** of the worm

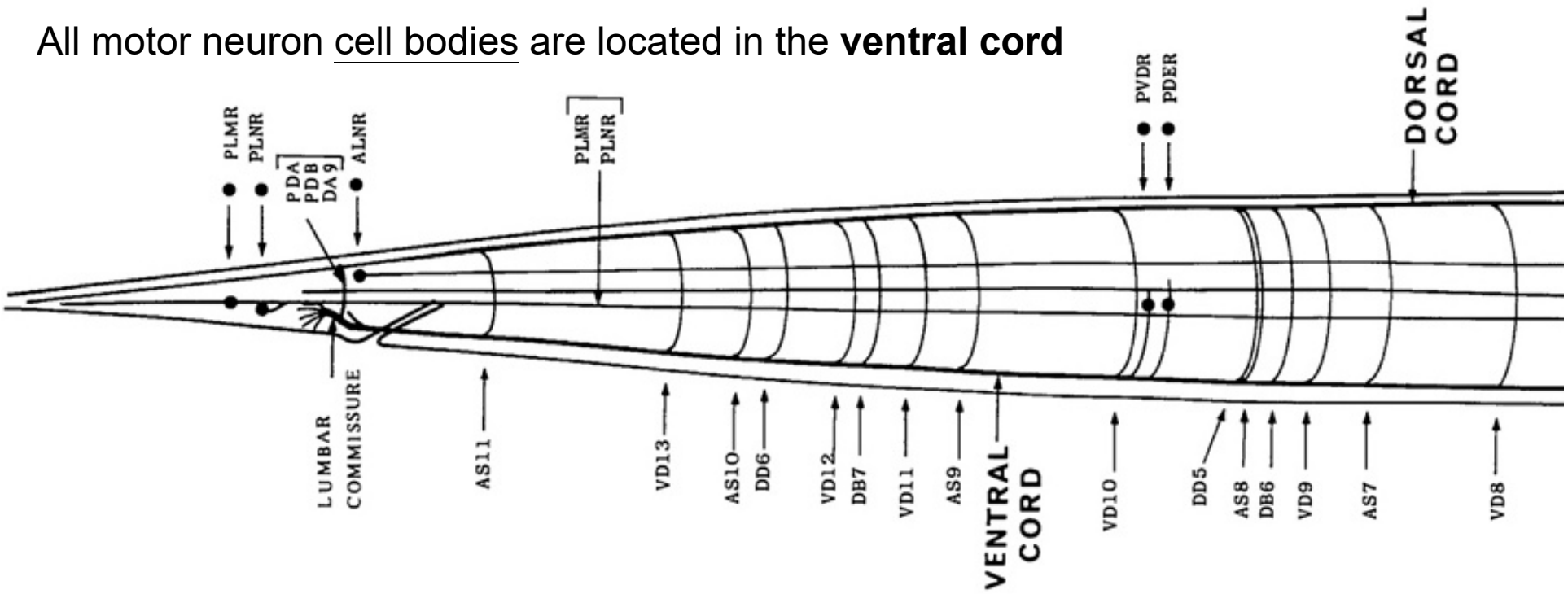


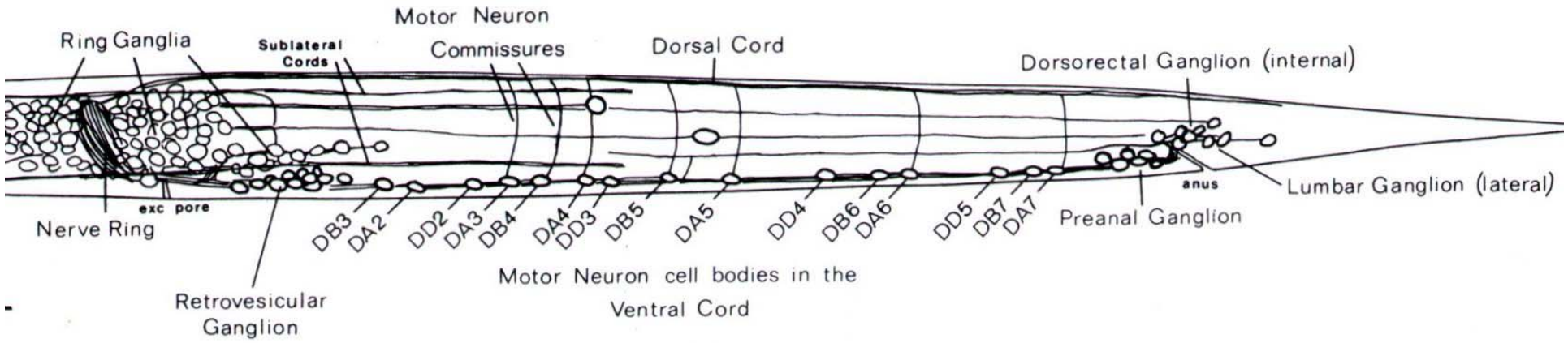
Basic features of the nervous system



Basic features of the nervous system

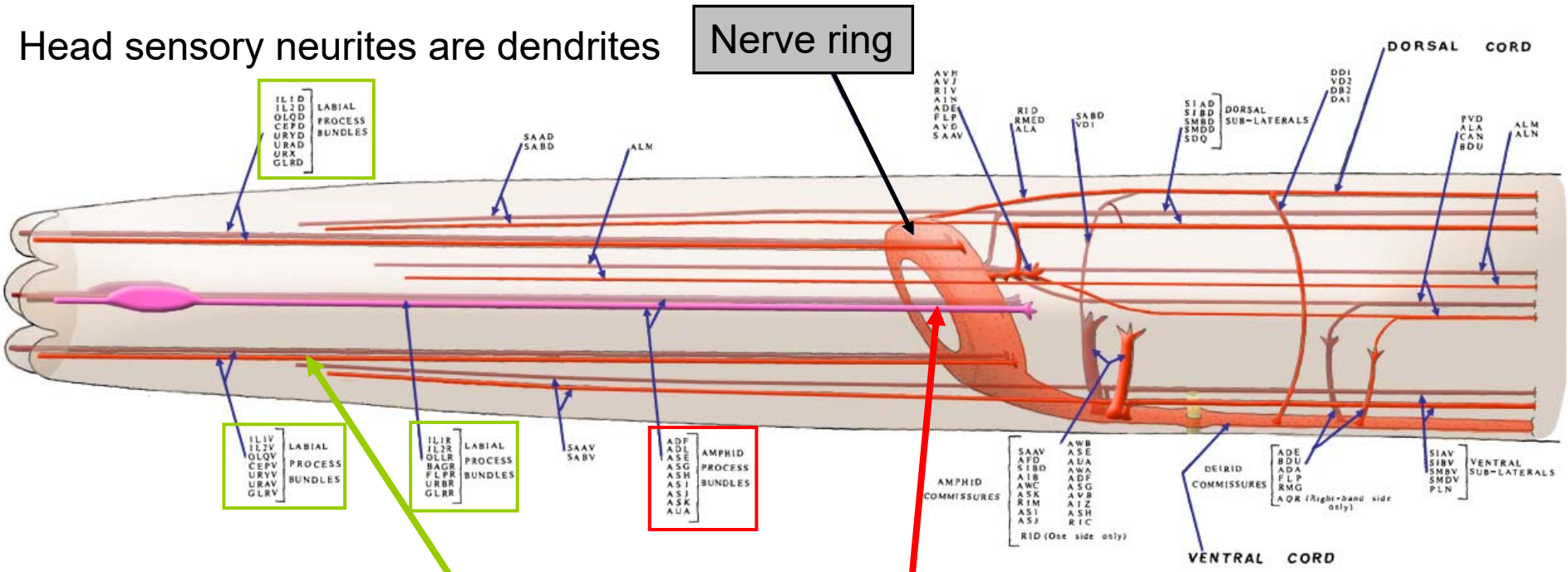
All motor neuron cell bodies are located in the **ventral cord**

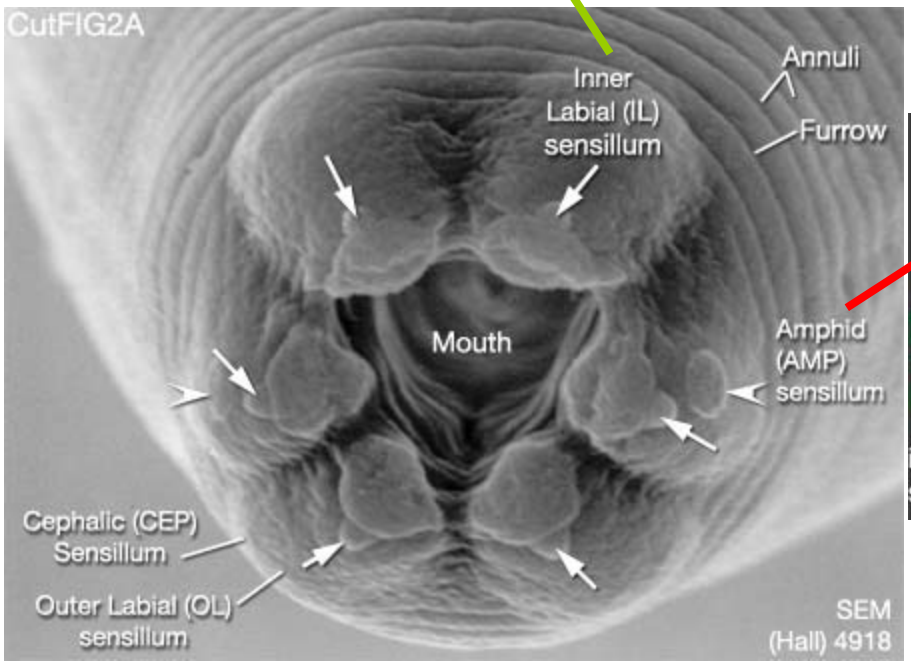




Head neurons

Head sensory neurites are dendrites





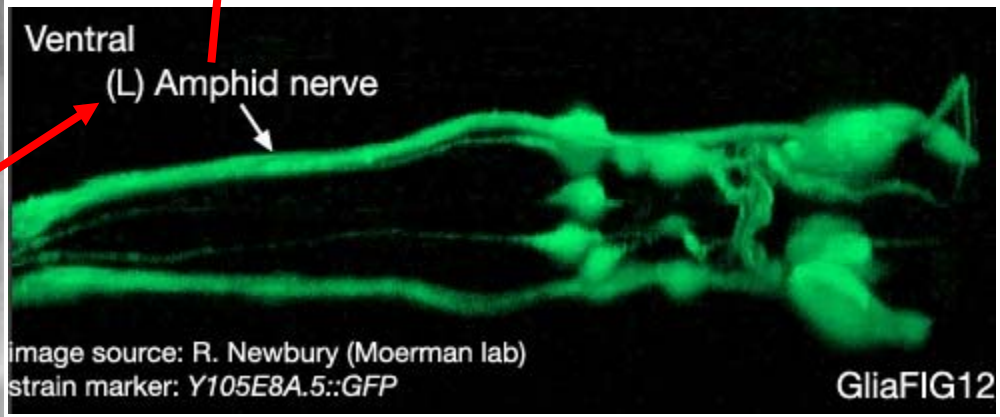
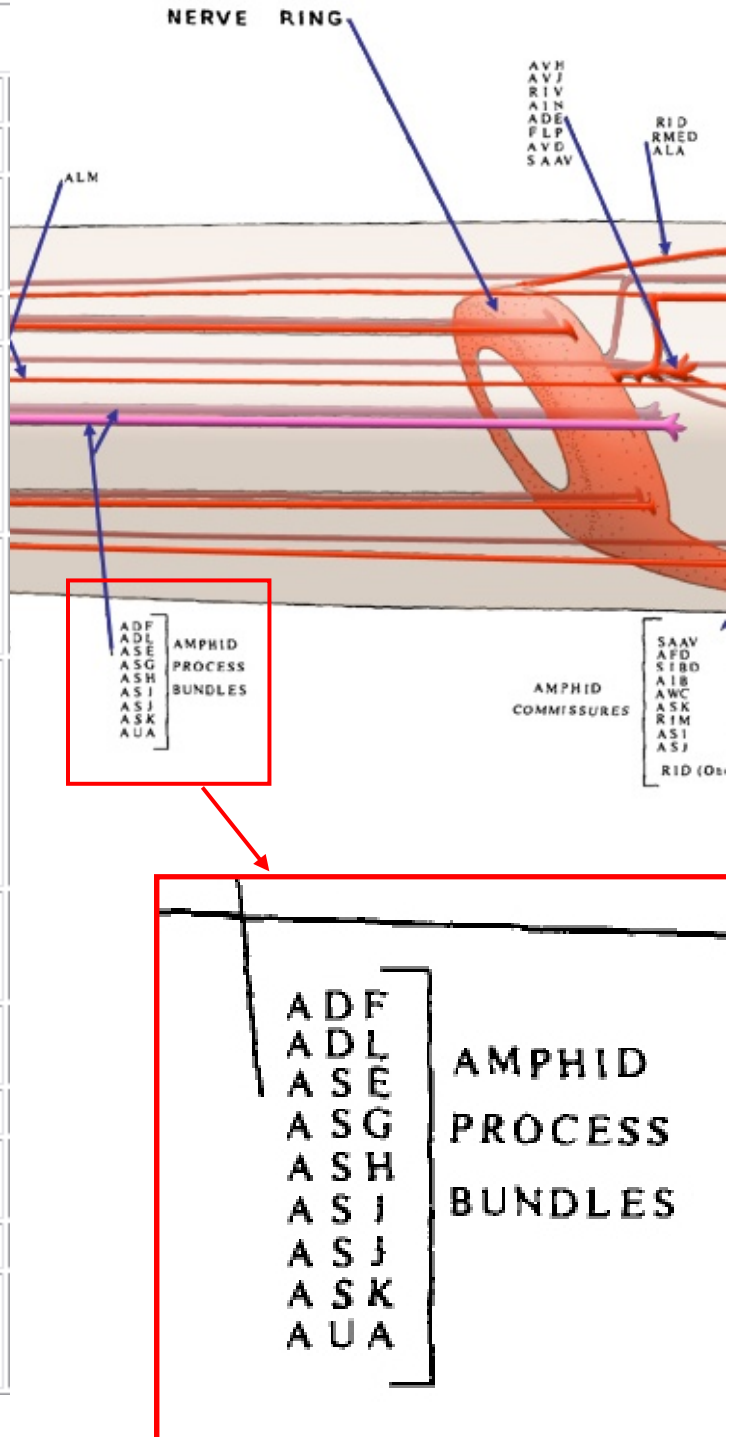


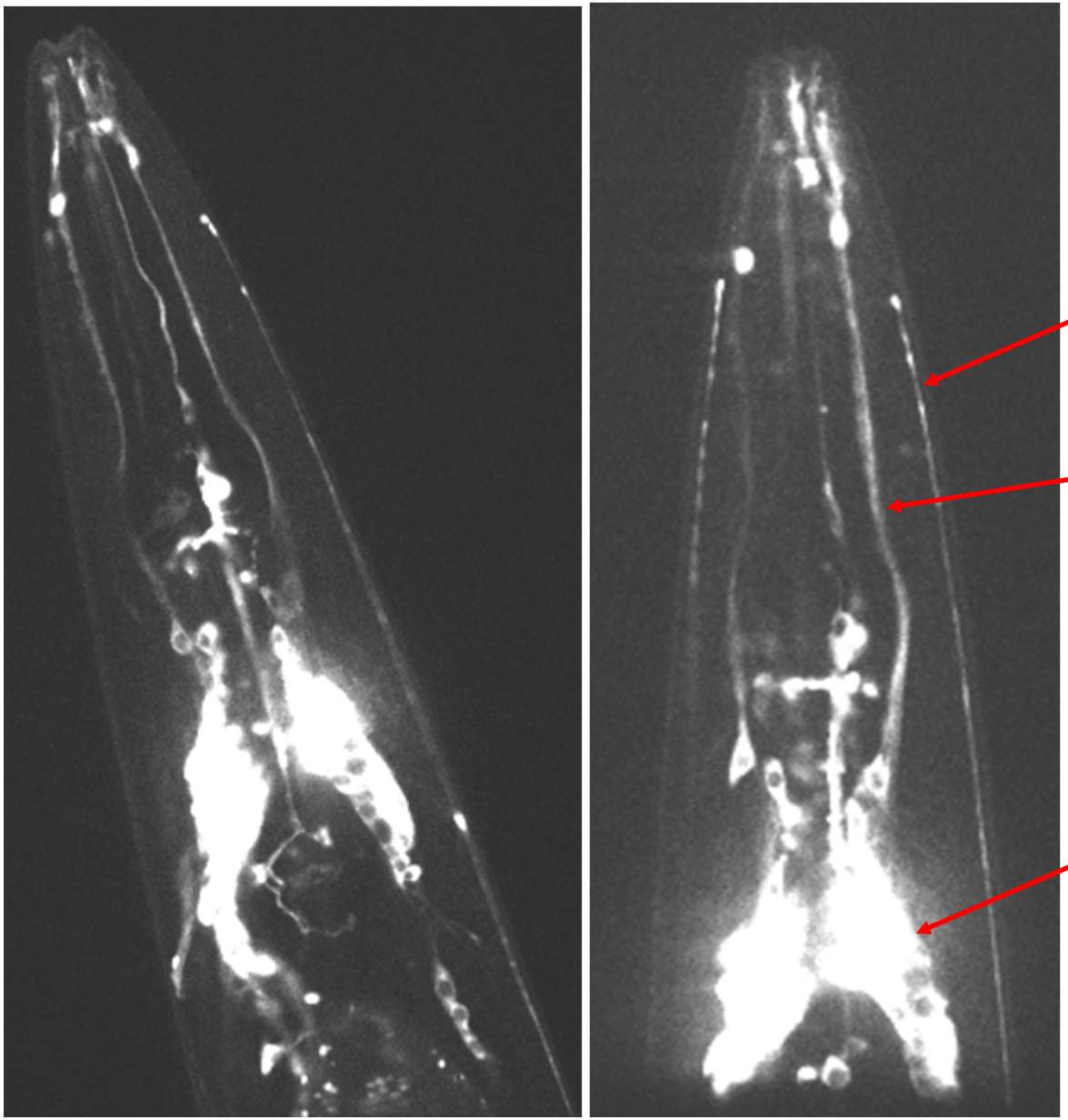
TABLE OF FUNCTIONS OF AMPHID NEURONS

NEURON	TYPE	FUNCTION
ADF	Chemosensory (taste)	Chemotaxis to Na+,Cl-,cAMP, biotin.
ADL	Chemosensory (taste) Odorsensory (olfaction)	Avoidance from Cd^{2+} and Cu^{2+} , and avoidance from volatile chemical, octanol.
AFD	Thermosensory	Thermosensory behavior.
ASE	Chemosensory (taste)	Chemotaxis to Na+(mainly ASEL), K+ (Mainly ASER), Cl- (Mainly ASER), cAMP, biotin and lysine.
ASG	Chemosensory (taste)	Chemotaxis to Na+, Cl-, cAMP, biotin and lysine. Dauer entry.
ASH	Chemosensory (taste) Osmosensory Mechanosensory	Avoidance from Cd2+ and Cu2+ and volatile repellent chemical, 1-octanol. Osmotic avoidance. Nose-touch response.
ASI	Chemosensory (taste)	Chemotaxis to Na+, Cl-, cAMP, biotin and lysine. Dauer entry.
ASJ	Probably chemosensory (taste)	Dauer recovery.
ASK	Chemosensory (taste)	Chemotaxis to lysine
AWA	Odorsensory (olfaction)	Chemotaxis to diacetyl, pyrazine, trimethylthiazole
AWB	Odorsensory (olfaction)	Avoidance from 2-nonanone, 1-octanol
AWC	Odorsensory (olfaction)	Chemotaxis to benzaldehyde,butanone, isoamylalcohol, 2,3 pentanedione and 2,4,5 trimethylthiazole



Head neurons

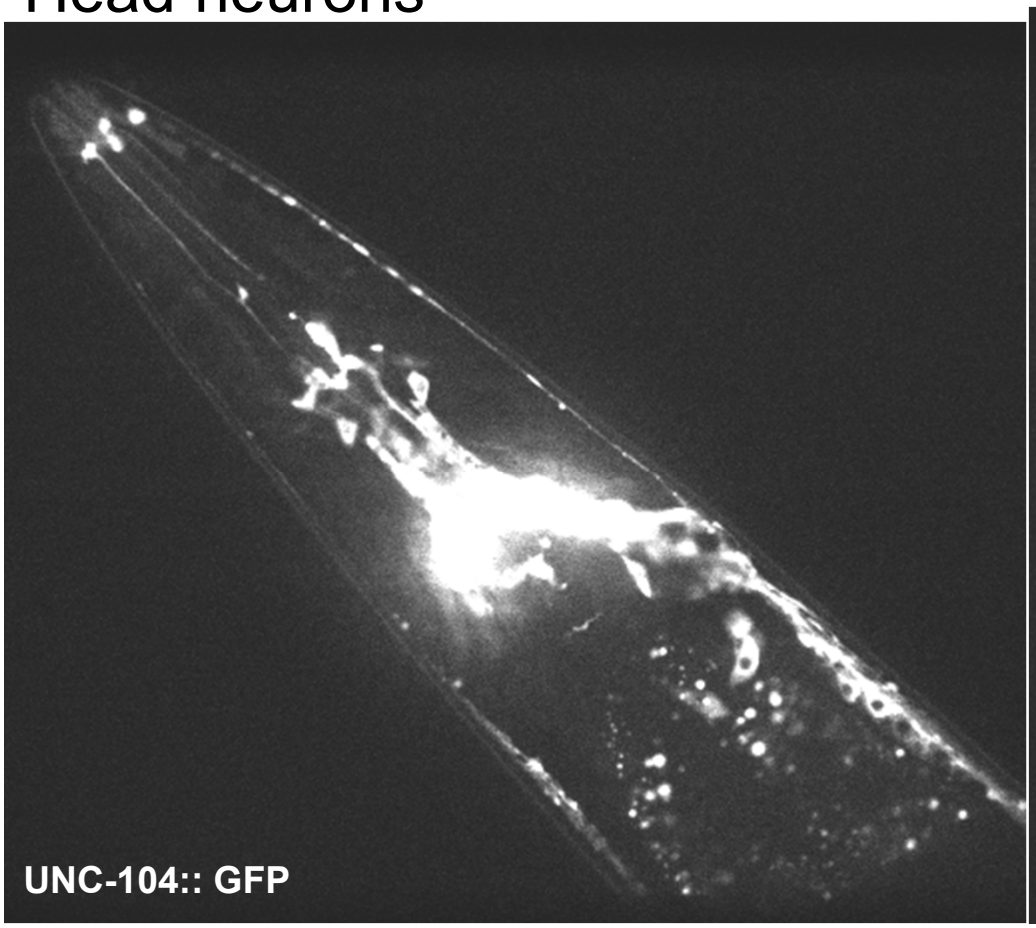
- The **nerve ring** contains mostly **sensory neurons** and almost all **interneurons**
- It is the “brain” of the worm

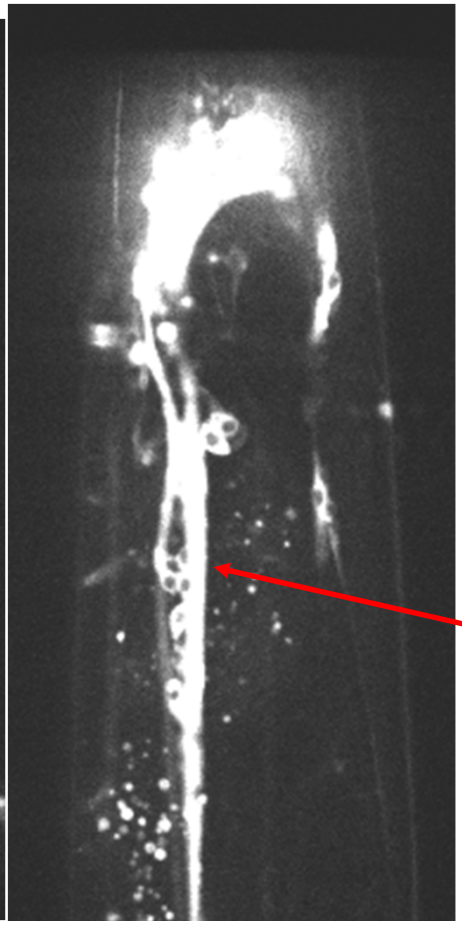


- **Dendrites** in *C. elegans* are usually unbranched
- They receive inputs along their length (without terminations)

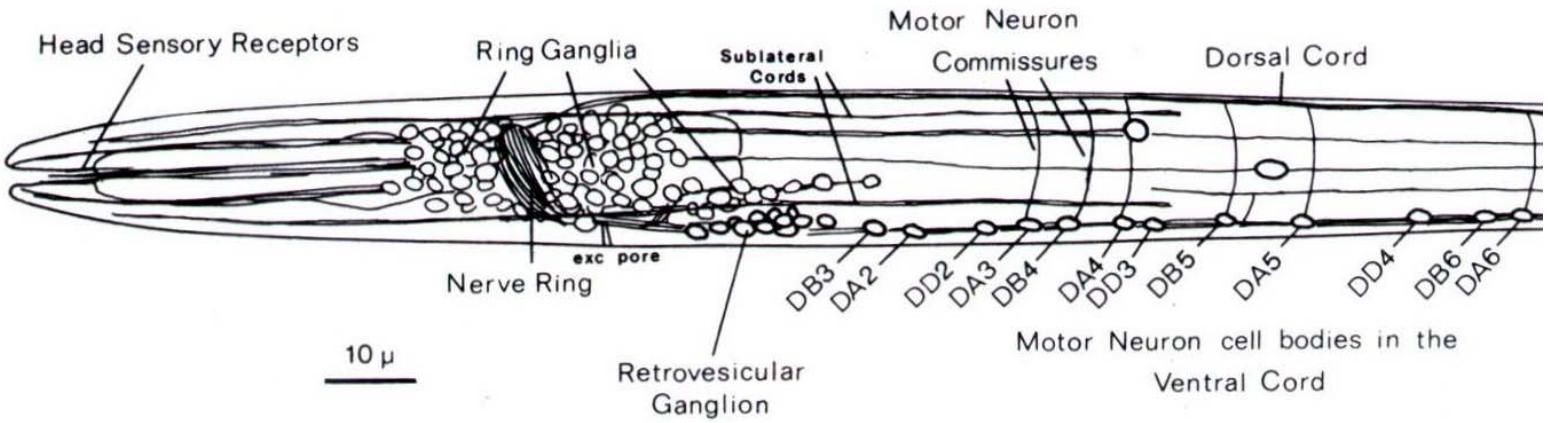
UNC-104:: GFP

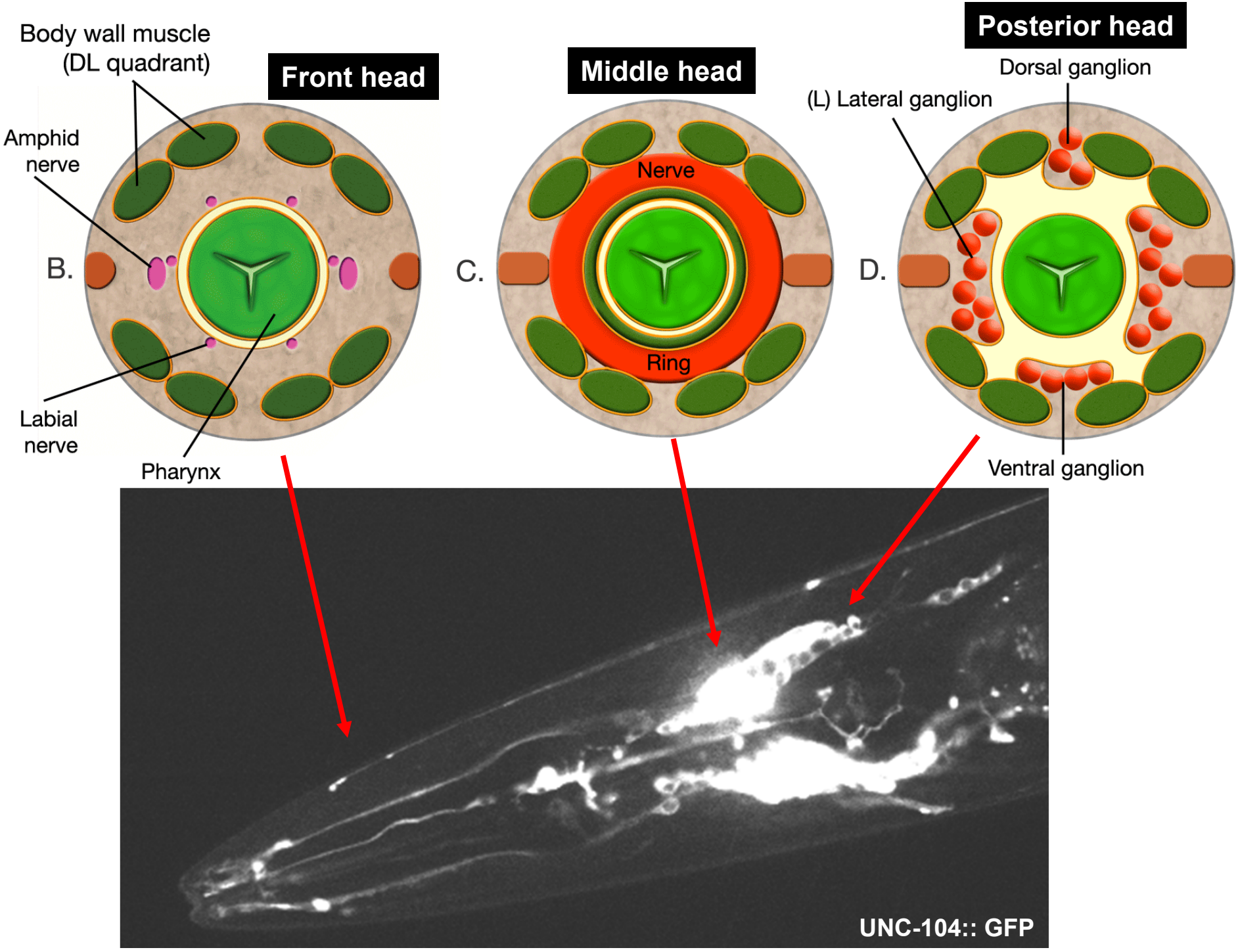
Head neurons





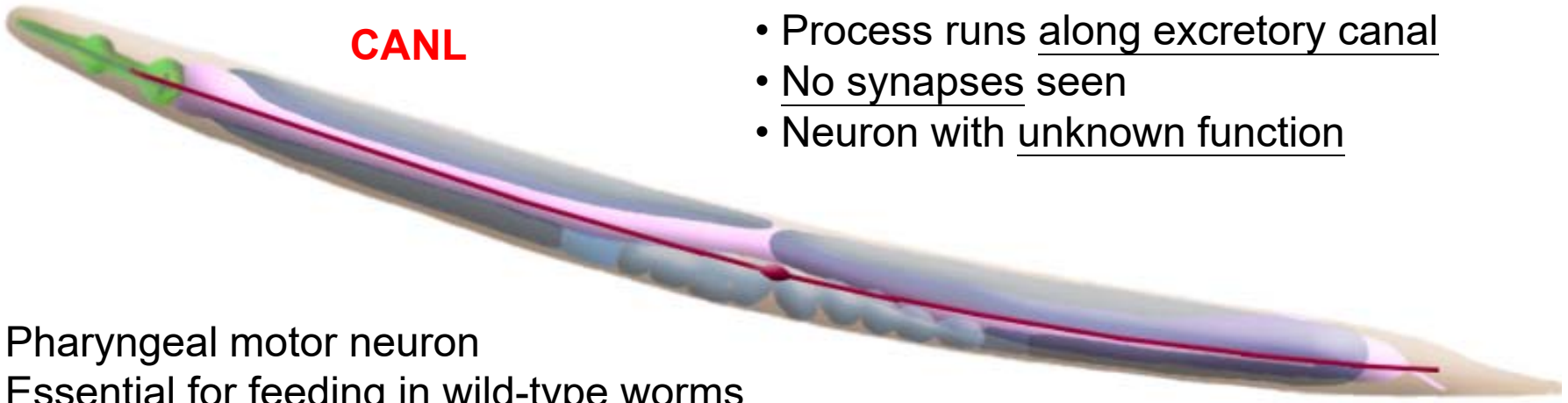
Retrovesicular ganglion




Body wall muscle
(DL quadrant)
Front head
Amphid
nerve
B.
Labial
nerve
Pharynx
Middle head
C.
Nerve
Ring
Posterior head
Dorsal ganglion
(L) Lateral ganglion
D.
Ventral ganglion
UNC-104:: GFP

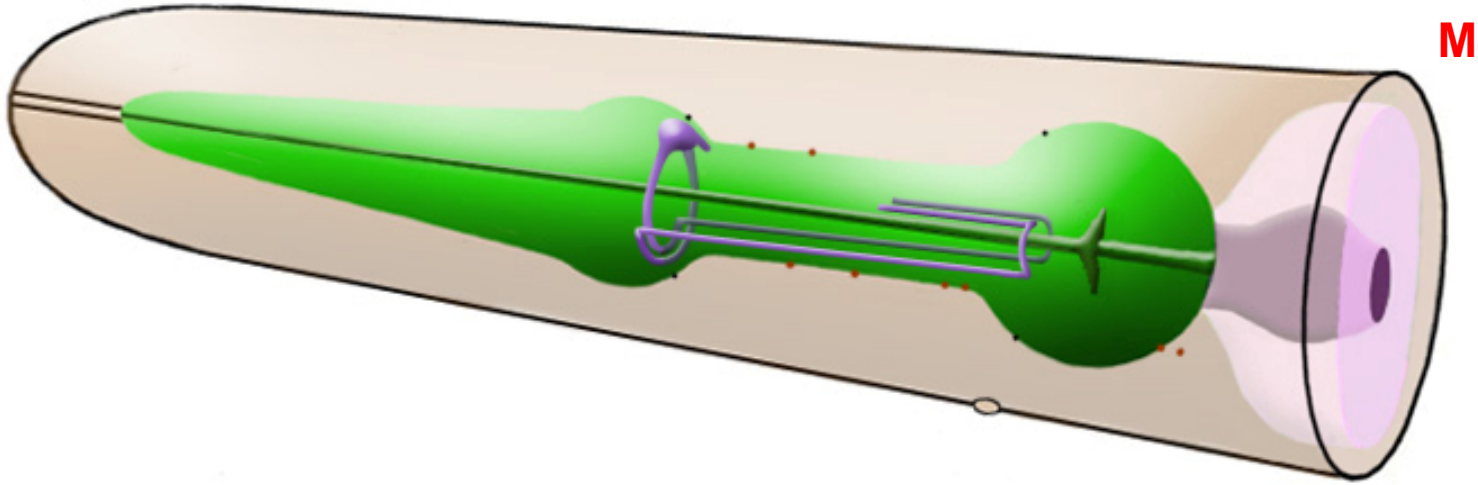
Only two neurons are essential

- Many neurons of the nervous system not essential to survive and reproduce
- Thus, even severe mutations affecting the nervous system can be used for research
- Only two neurons are essential for survival: **CAN** and **M4**



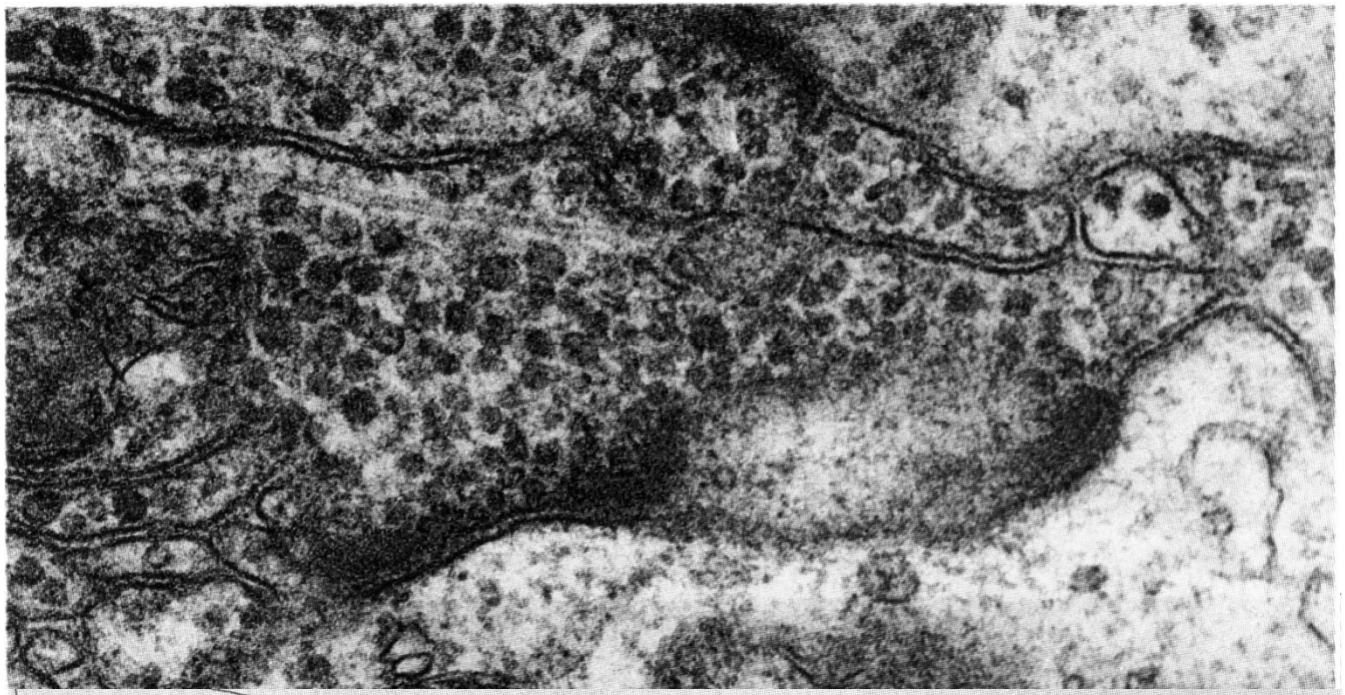
- Process runs along excretory canal
- No synapses seen
- Neuron with unknown function

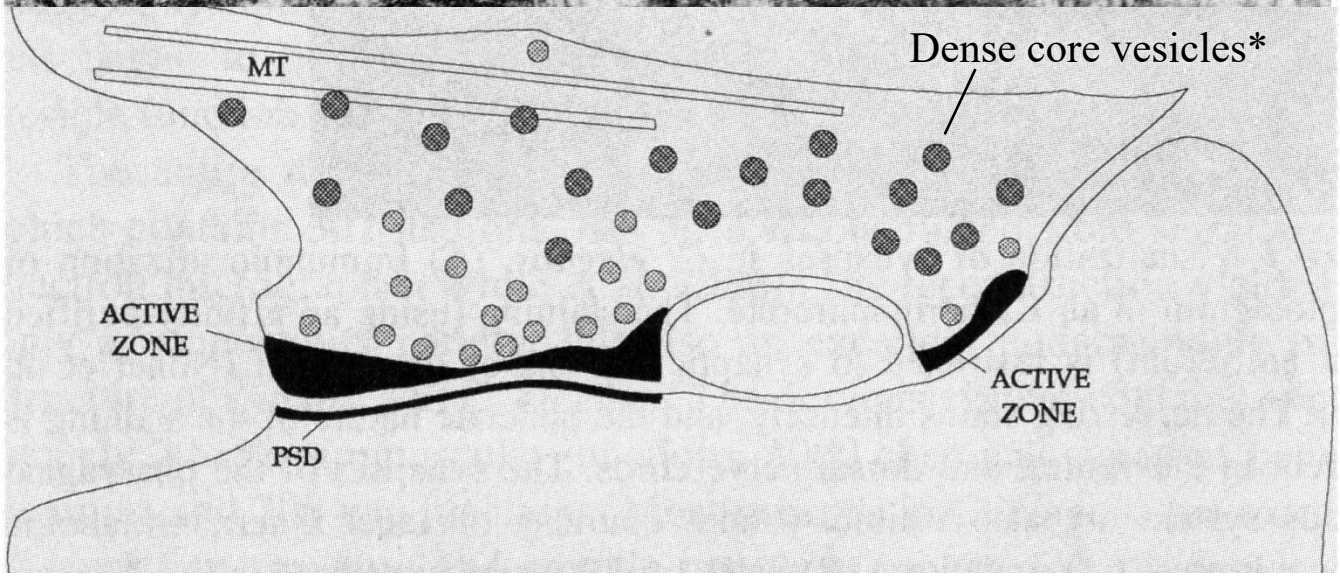
- Pharyngeal motor neuron
- Essential for feeding in wild-type worms
- Worms lacking M4 continue pumping, however, bacteria become trapped in the pre-bulb, therefore, worms fail to grow



Synapses

A synapse in most higher animals is composed of a pre-synapse (vesicle fusion), a synaptic cleft (neurotransmitter diffusion), and a post-synapse (containing receptors)



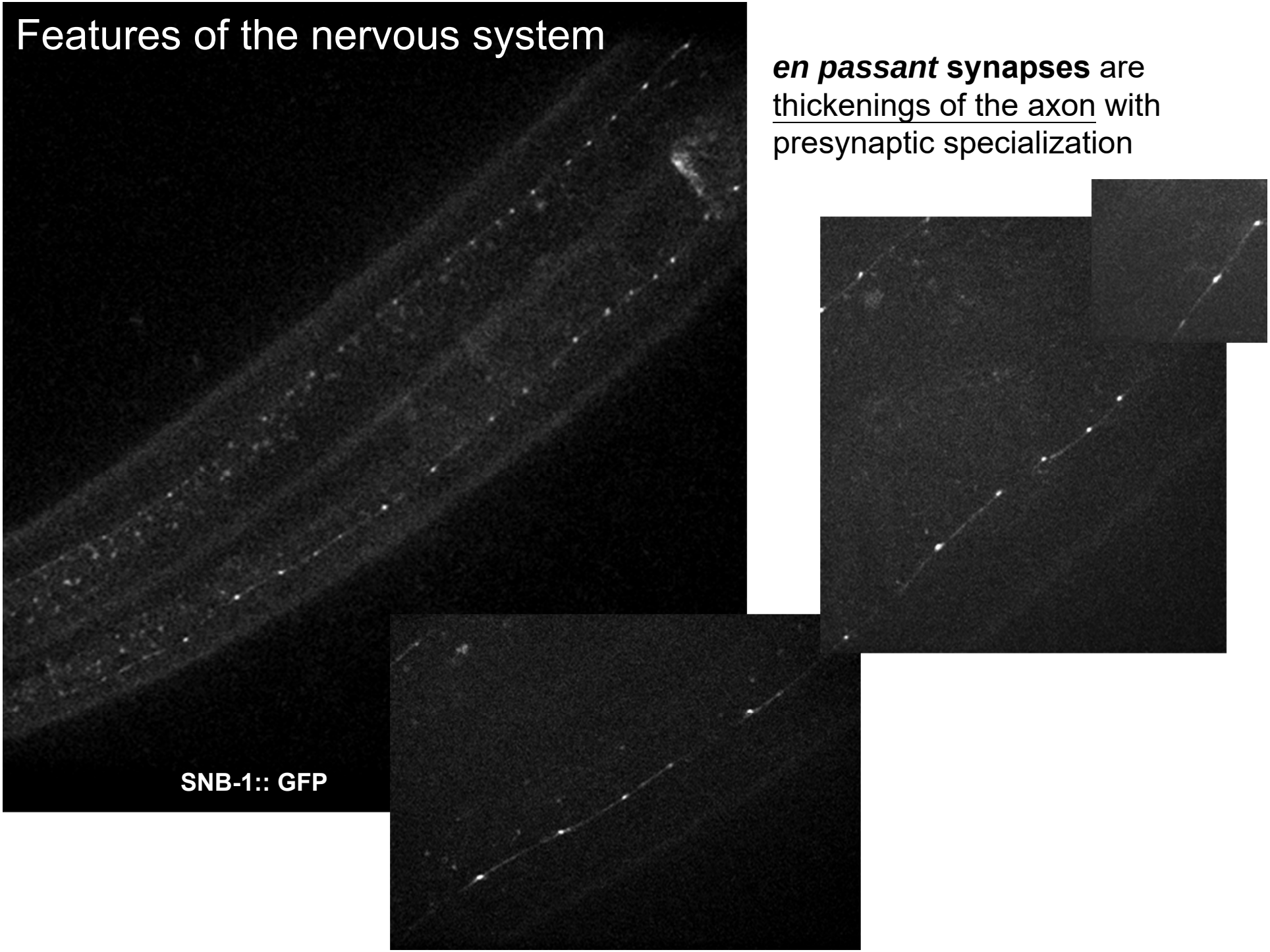


- **Active zone** is an electron-dense area where vesicle fusion and neurotransmitter release occurs
- In *C. elegans* EM micrographs reveal only weak **post**synaptic densities (difficult to study PSD proteins)
- **Pre**synaptic densities, however, are clearly visible

*contain neuropeptides

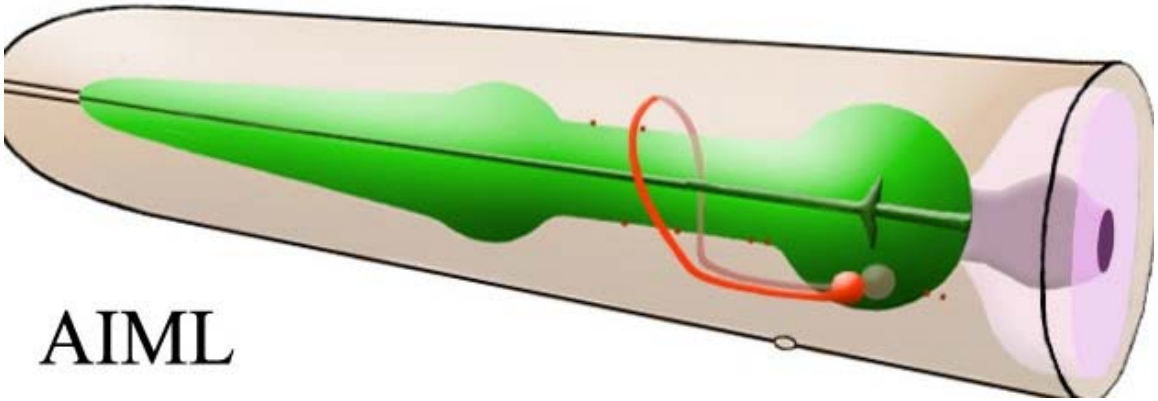
Features of the nervous system

***en passant* synapses** are thickenings of the axon with presynaptic specialization

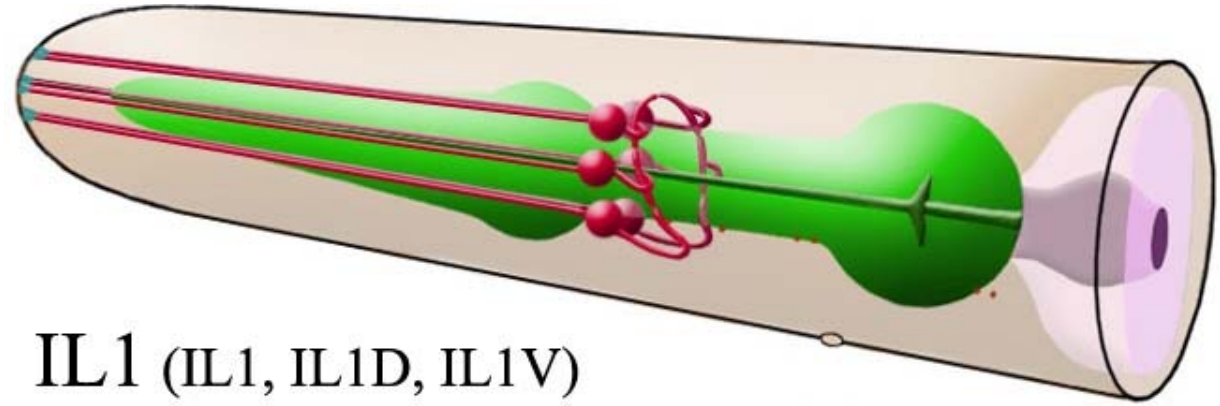


Features of the nervous system

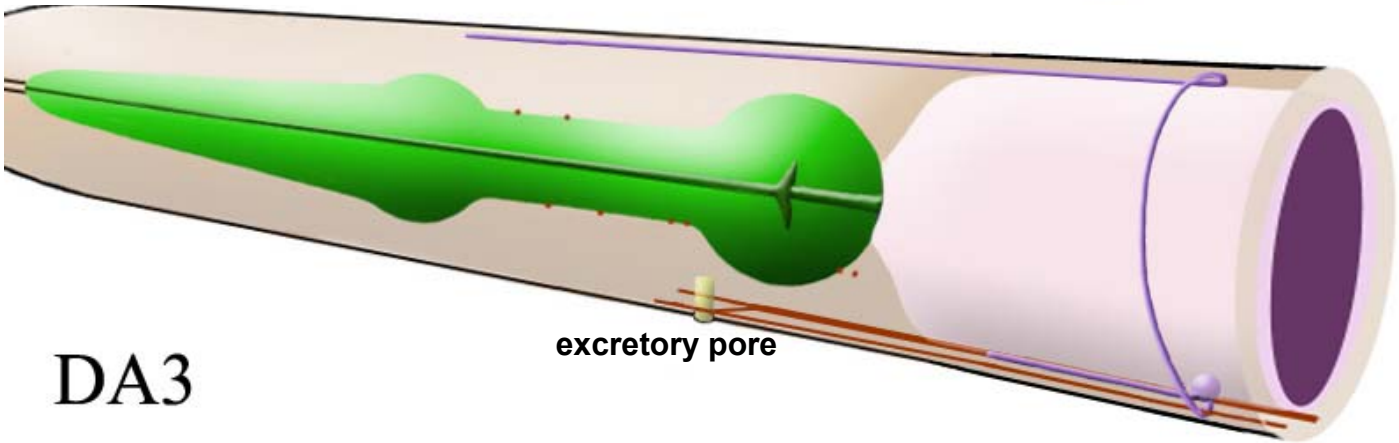
Neurons can be categorized in: **interneurons**, **sensory neurons** and **motorneurons**



interneuron



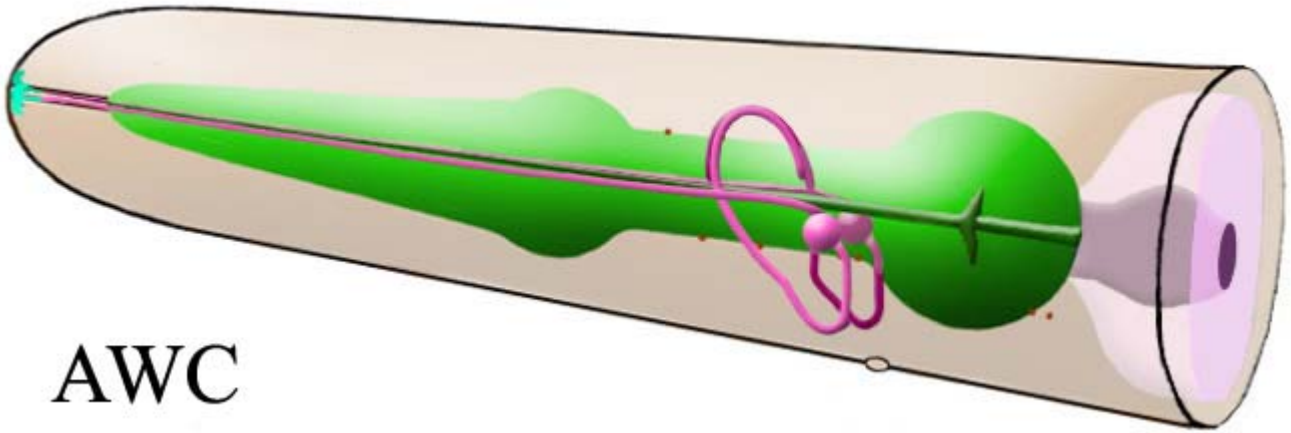
sensory neuron



motorneuron

Sensory neurons

- Located primarily in the head and sending **dendrites** to the tip of the nose
- Either **chemosensory** or **mechanosensory**
- 12 chemosensory neurons are bundled into each **amphid sensilla** at the nose
- Endings of mechanosensory neurons are scattered throughout the body
- One **thermosensory** neuron named AFD exist
- Some sensory neurons are still of speculative function: AQR and PQR send sensory neurons into the pseudocoelomic fluid (*C. elegans* "blood") probably **reporting the composition of the fluid** to the nervous system



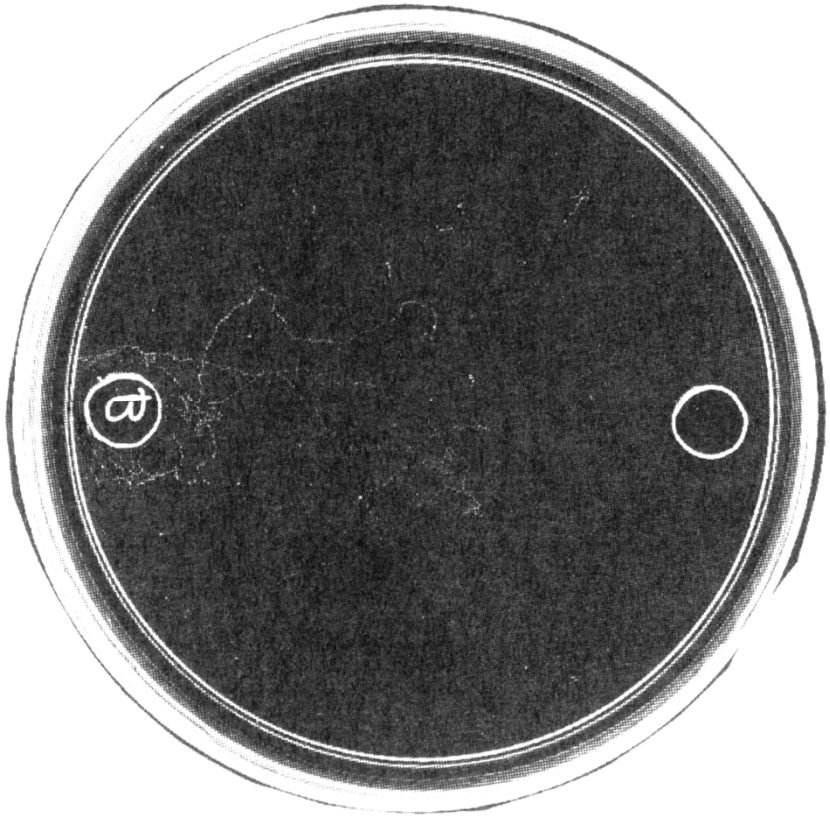
Amphid neuron

Odorsensory (olfactory)

C. elegans is now widely used to study "smell" and "taste"

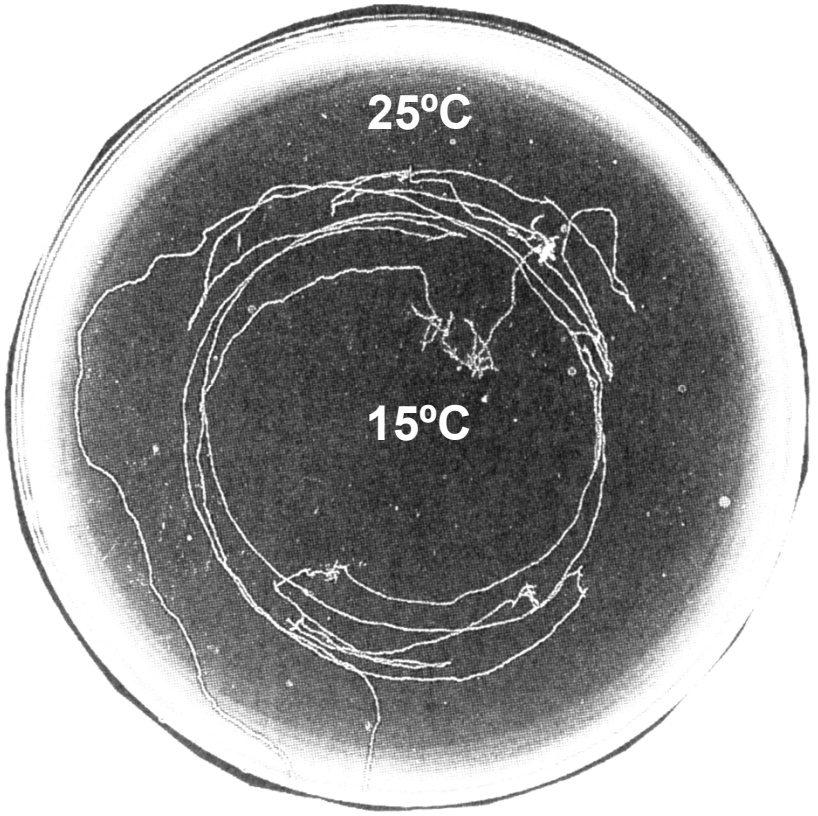
Sensory neurons

Chemotaxis behavior



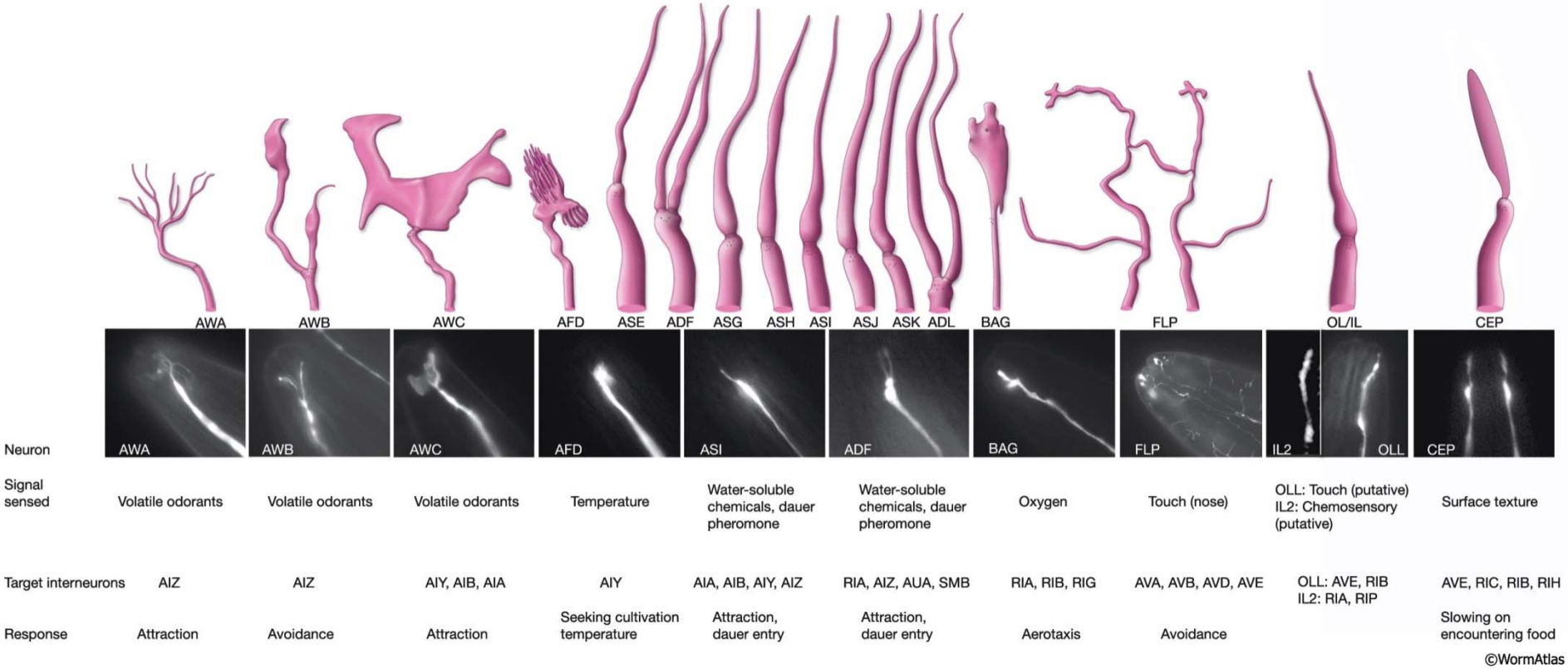
Traces of a worm which was allowed to freely move within one hour on a plate with an **attractant** (B = **biotin**) (right circle = buffer)

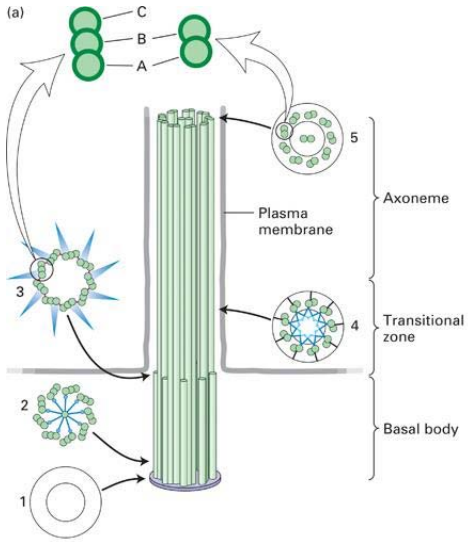
Thermotaxis behavior



- Traces of a worm in a **radial thermal gradient**
- Chooses an optimal temperature (similar to its cultivation temperature)
- **Circles in isotherms** at that temp.
- **Can detect thermal gradients < 0.1˚C**

Cilia morphology of the sensory neurons that terminate in the lips





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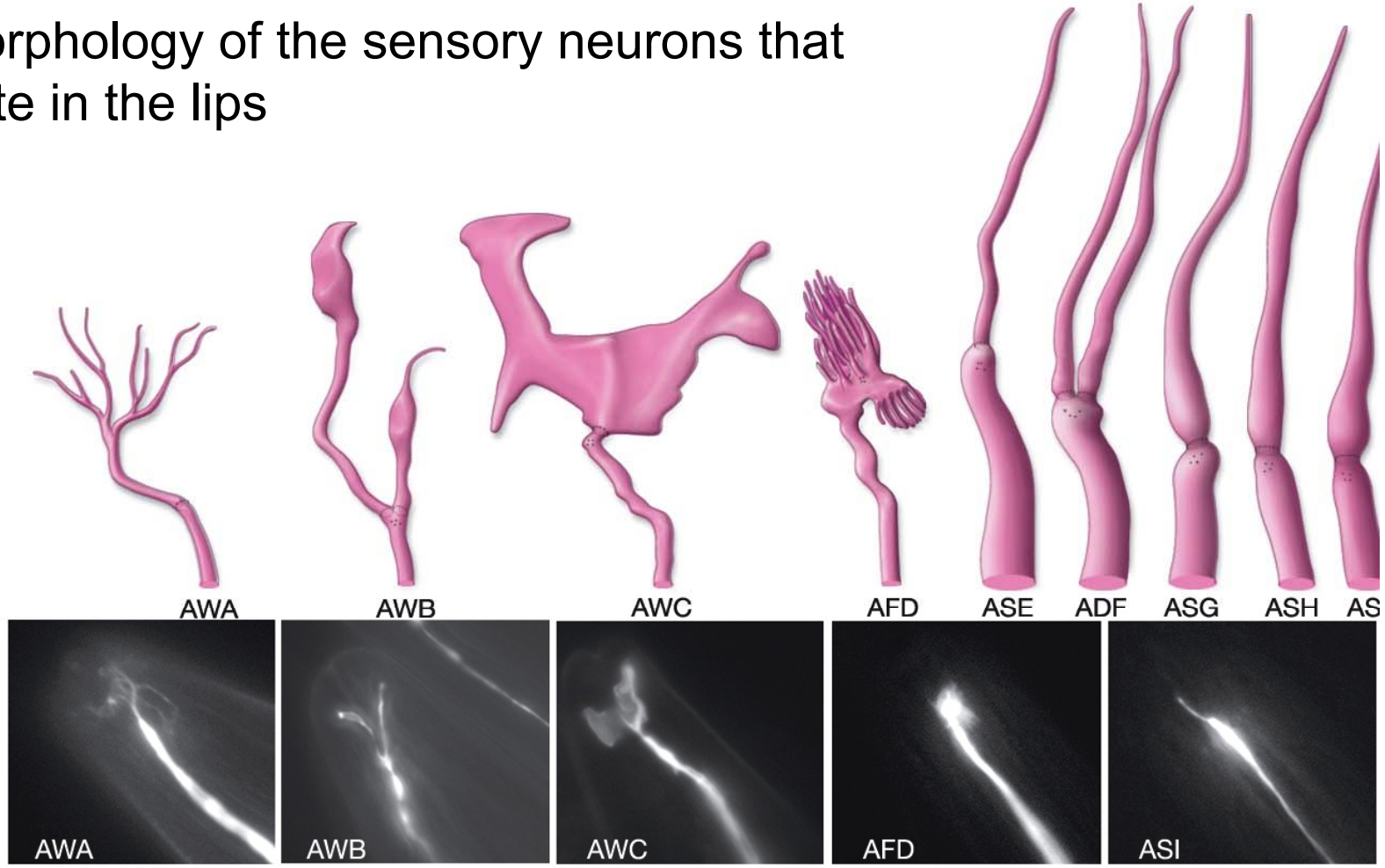
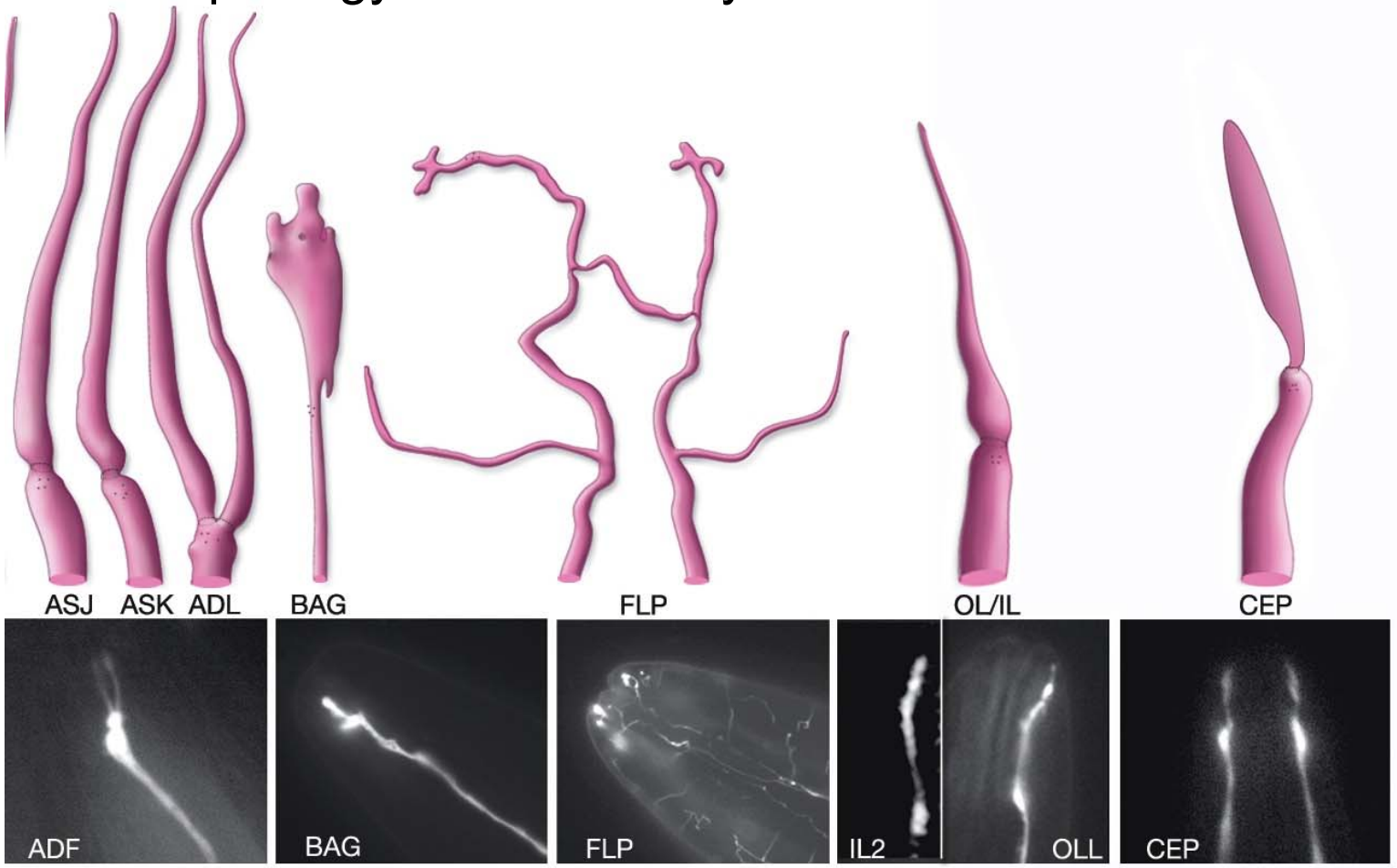


Neuron	AWA	AWB	AWC	AFD	ASI
Signal sensed	Volatile odorants	Volatile odorants	Volatile odorants	Temperature	Water-soluble chemicals, dauer pheromone
Target interneurons	AIZ	AIZ	AIY, AIB, AIA	AIY	AIA, AIB, AIY, AIZ
Response	Attraction	Avoidance	Attraction	Seeking cultivation temperature	Attraction, dauer entry

Cilia morphology of the sensory neurons that terminate in the lips

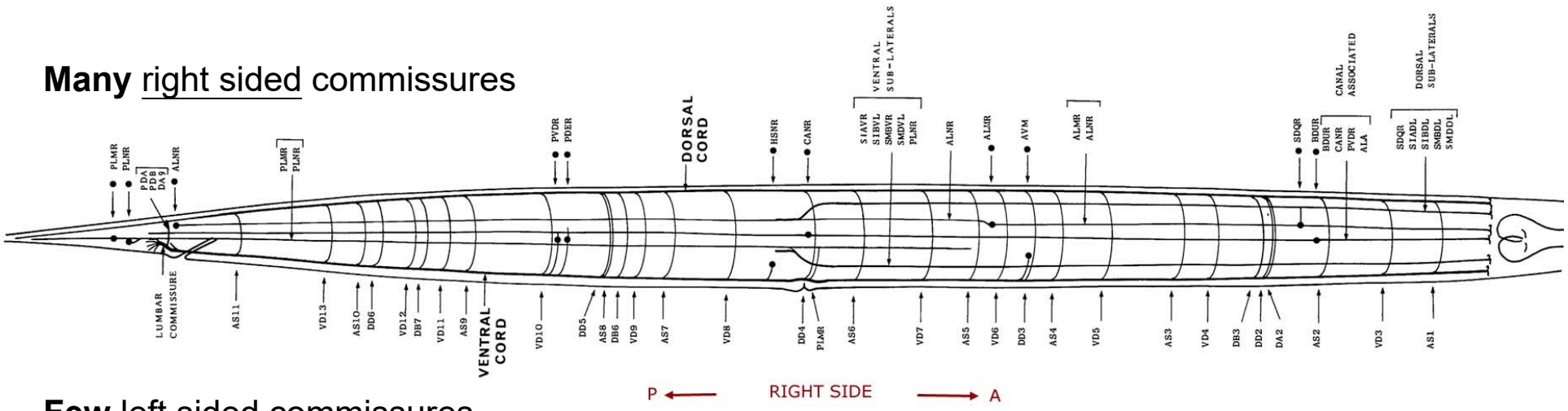


Water-soluble chemicals, dauer pheromone	Oxygen	Touch (nose)	OLL: Touch (putative) IL2: Chemosensory (putative)	Surface texture
RIA, AIZ, AUA, SMB	RIA, RIB, RIG	AVA, AVB, AVD, AVE	OLL: AVE, RIB IL2: RIA, RIP	AVE, RIC, RIB, RIH
Attraction, dauer entry	Aerotaxis	Avoidance		Slowing on encountering food

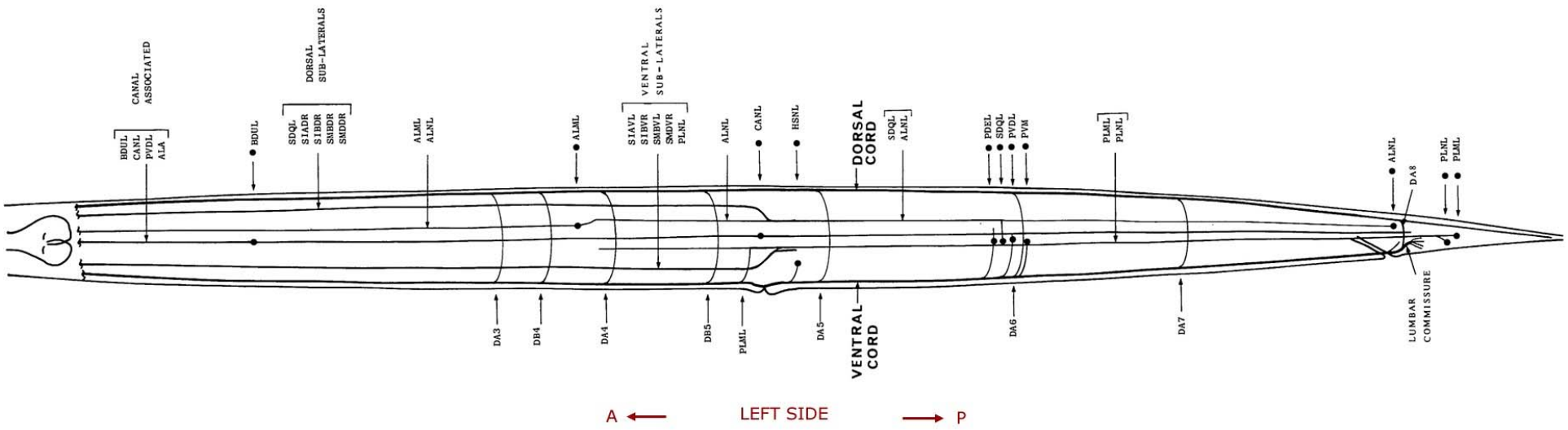
Motor neurons

- Innervate **body-wall**, **pharyngeal**, **egg-laying** and **defecation muscles**
- Some ventral motor neurons send processes to the dorsal cord via **commissures**
- Most of the commissures **travel along the right side** of the animal

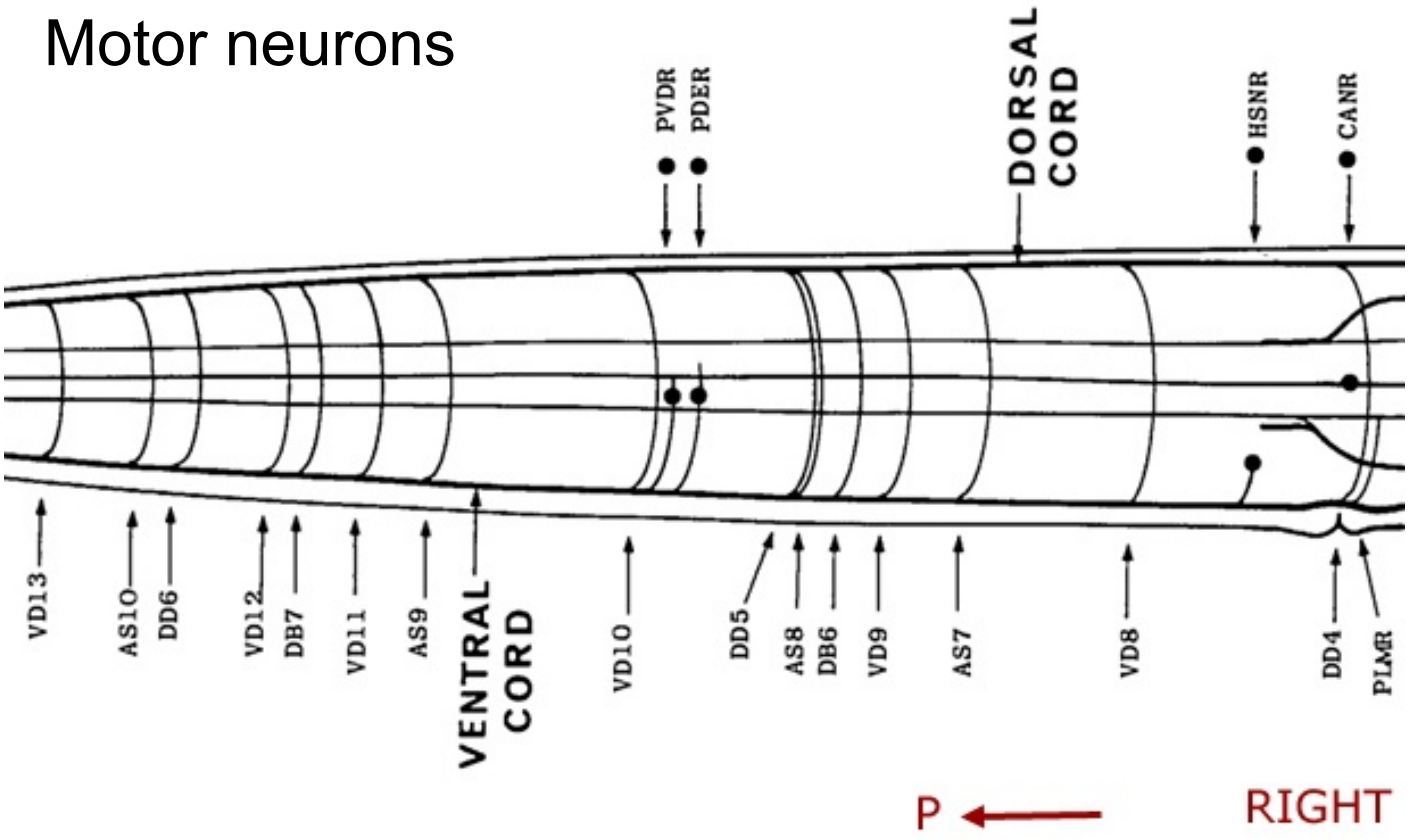
Many right sided commissures

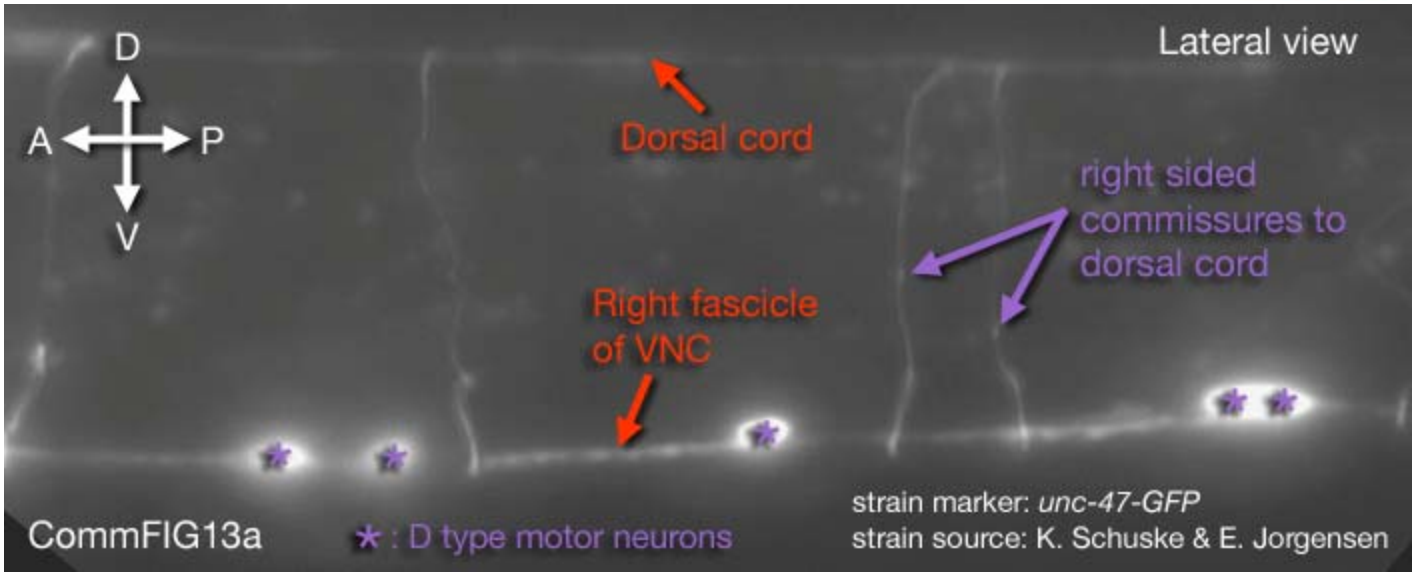


Few left sided commissures



Motor neurons

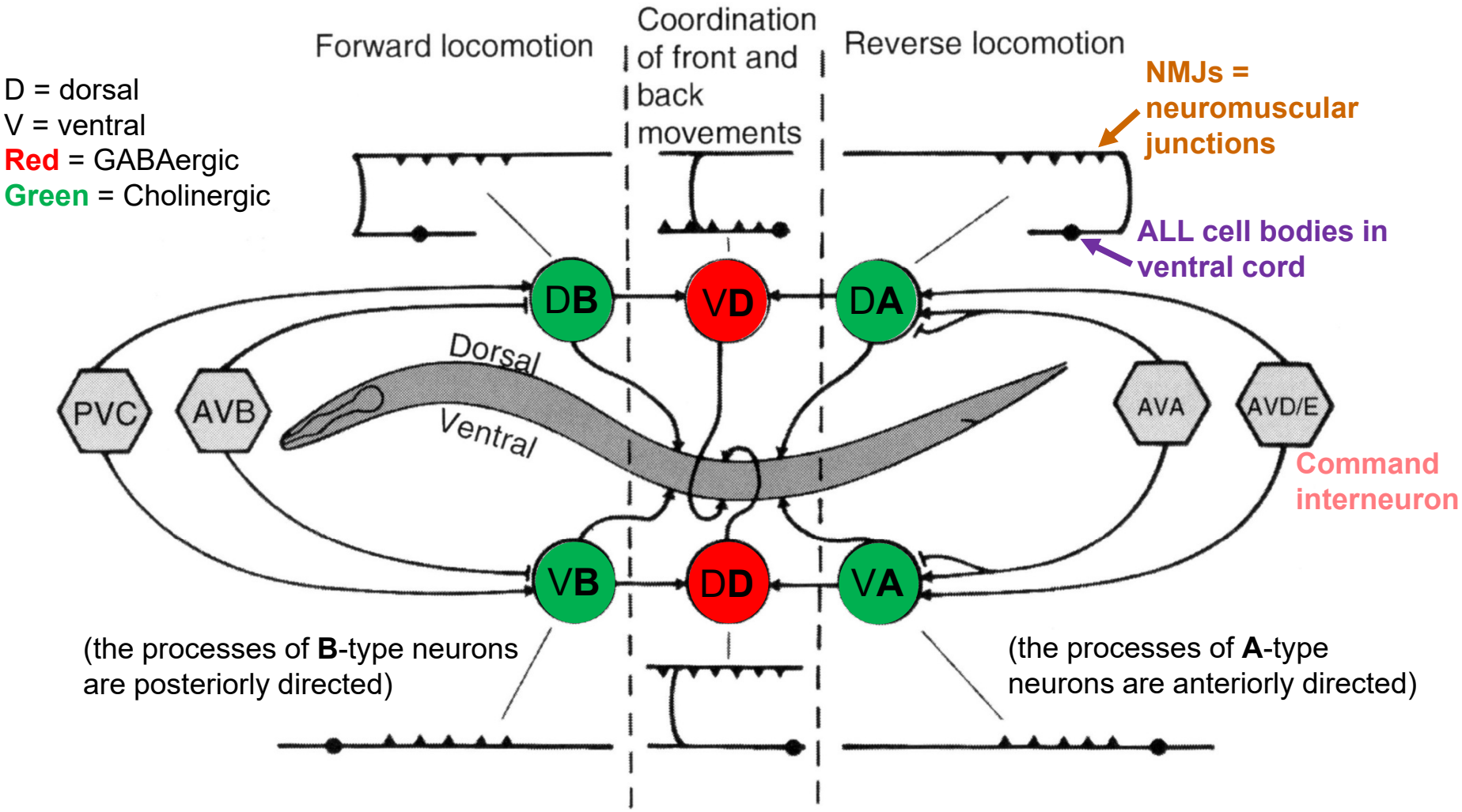




Most of the commissures travel alone, while few travel in pairs

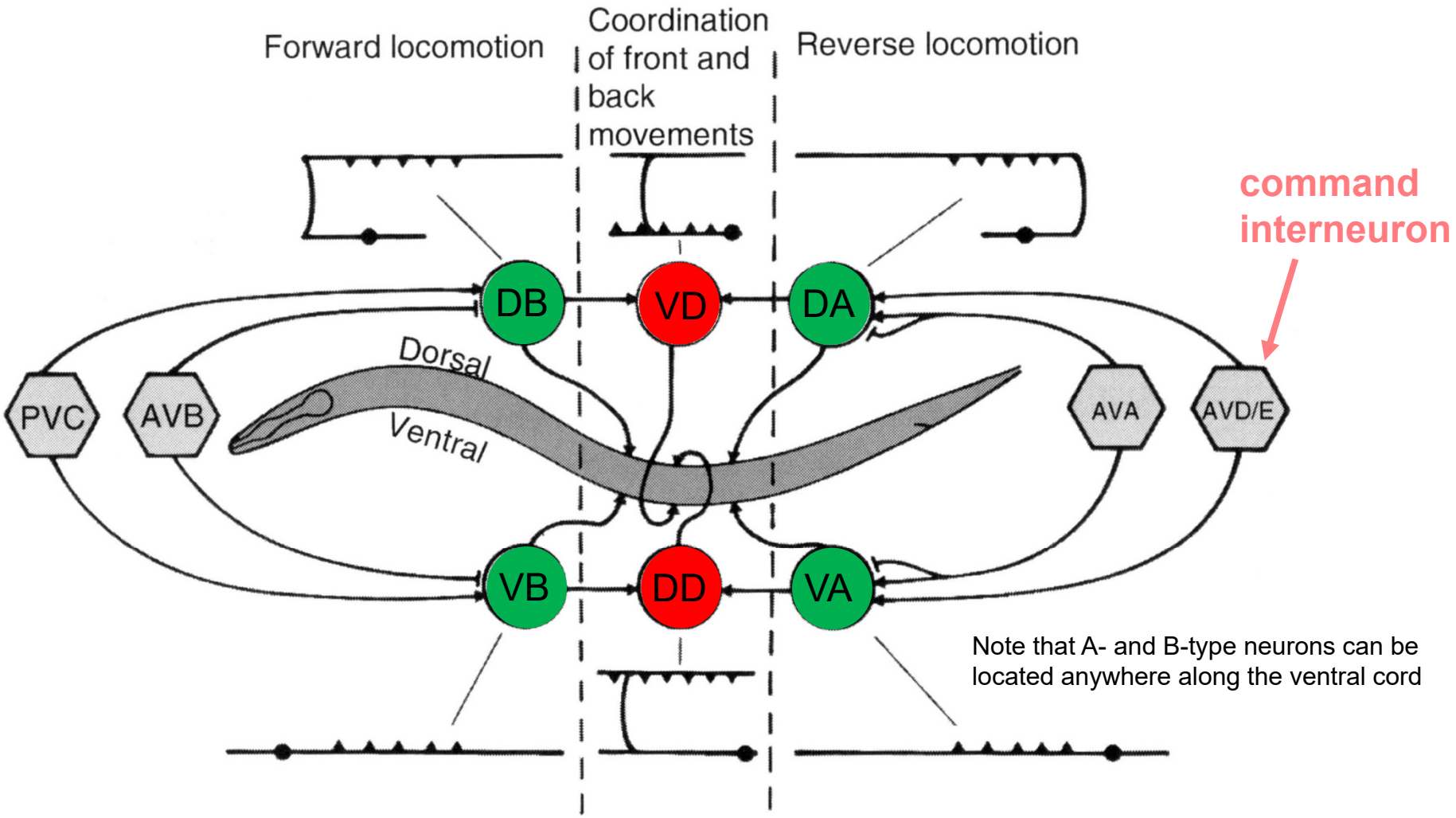
Motor circuits

- To complete the **sinusoidal locomotion**, body-wall muscles receive **excitatory *and* inhibitory** motor neuron input **at the same time** (cross inhibitory motor circuit)
- **Excitatory neurons** on one side ***also excite*** **inhibitory** motor **neurons** on the opposite side of the body (resulting in body bending)



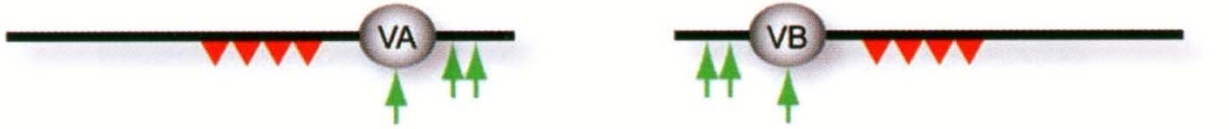
Motor circuits

- Cholinergic **excitatory B-type neurons** (VB and DB) control forward locomotion
- Cholinergic **excitatory A-type neurons** (VA and DA) control backward locomotion
- GABAergic **inhibitory D-type neurons** coordinate forward and backward motions
- A- and B-type neurons receive excitatory and inhibitory inputs from **command interneurons** (chemical and gap-junctions)

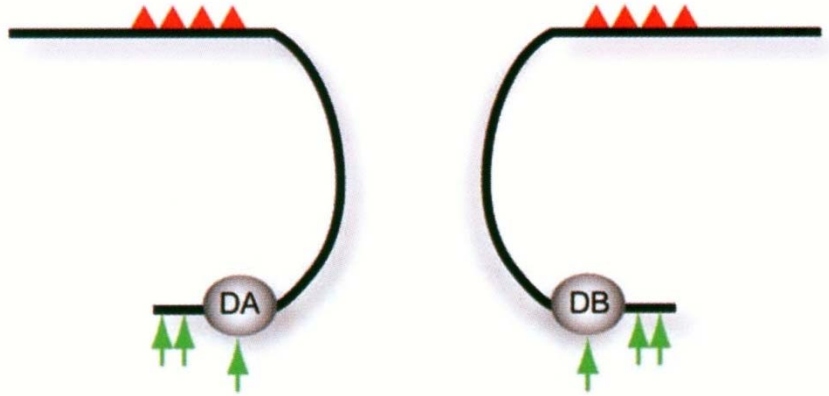


Organization of ventral cord motor neurons

Ventral A- and B-type: **NMJs** in the *ventral* nerve cord

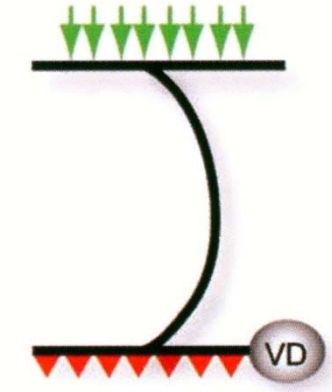


Dorsal A- and B-type: **NMJs** in the *dorsal* nerve cord (make commissures)

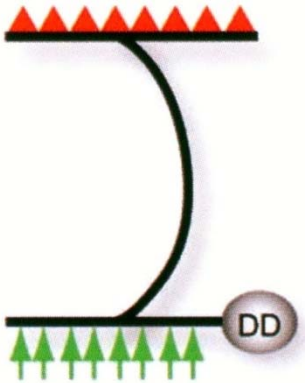


Cell bodies of motor neurons are ***always*** located in the ***ventral*** nerve cord

Ventral D-type (**inhibitory**): receives inputs dorsally



Dorsal D-type (**inhibitory**) looks similar to DA or DB



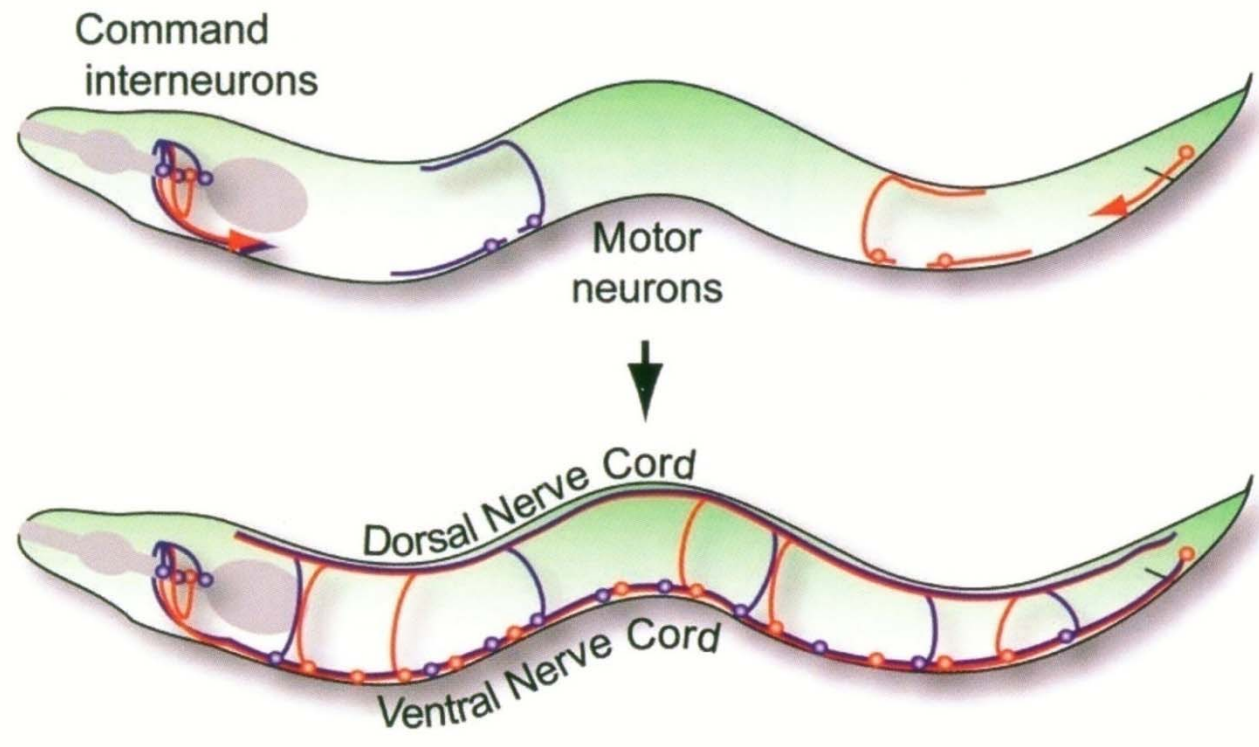
Motor circuits

C. elegans neurotransmitters and their neuronal distributions:

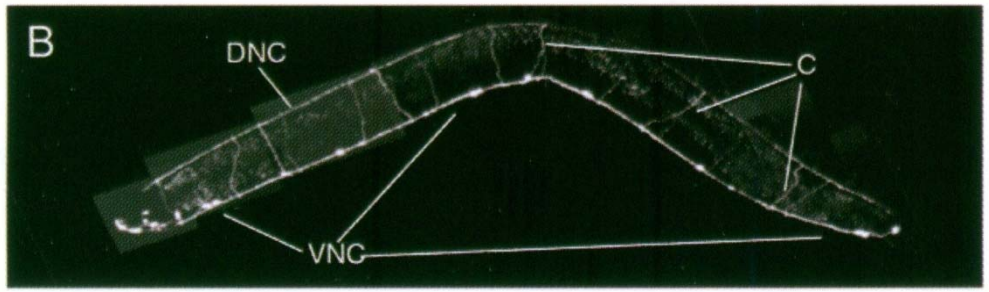
Transmitter	Cells
Acetylcholine (ACh)	ALN, AS, DA, DB, HSN, IL2, M1, M2, M4, M5, MC, PLN, RIM, RMD, SAA, SAB, SDQ, SIA, SIB, SMB, SMD, URA, URB, VA, VB, VC, CA (male)
Dopamine (DA)	ADE, CEP, PDE, plus male R5A, R7A, R9A
GABA	AVL, DD, DVB, RIS, RME, VD
Glutamate (GLU)	ALM, ASH, M3, PLM, probably many others
Octopamine	Unknown
Serotonin (5-HT)	ADF, HSN, NSM, RIG, RIH, VC4, VC5, plus male CA, CP, R1A/B, R3A/B, and R9A/B
FMRFamide-related	AIA, AIM or AIY, ALA, AVA or AVE, AVK, DVB, HSN, IL1, I4, M1, OLL, PQR, PVT, RID, RIG, RMG, URB, VC, uv1 (non-neuronal)[a]

FMRFamide-related = neuropetides (neuroendocrine peptides)
Glutamate receptors = AMPA and NMDA

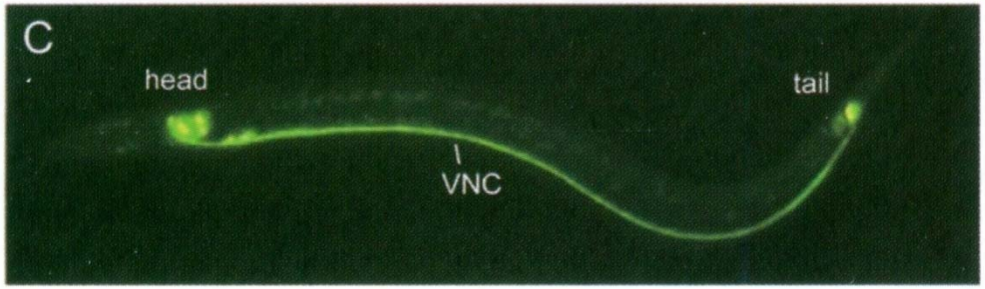
Motor circuits



- **Command interneurons** in the head and tail send processes into the ventral nerve cord
- They then make synapses to motor neurons (red and blue = two sets of command vs. motor neurons)



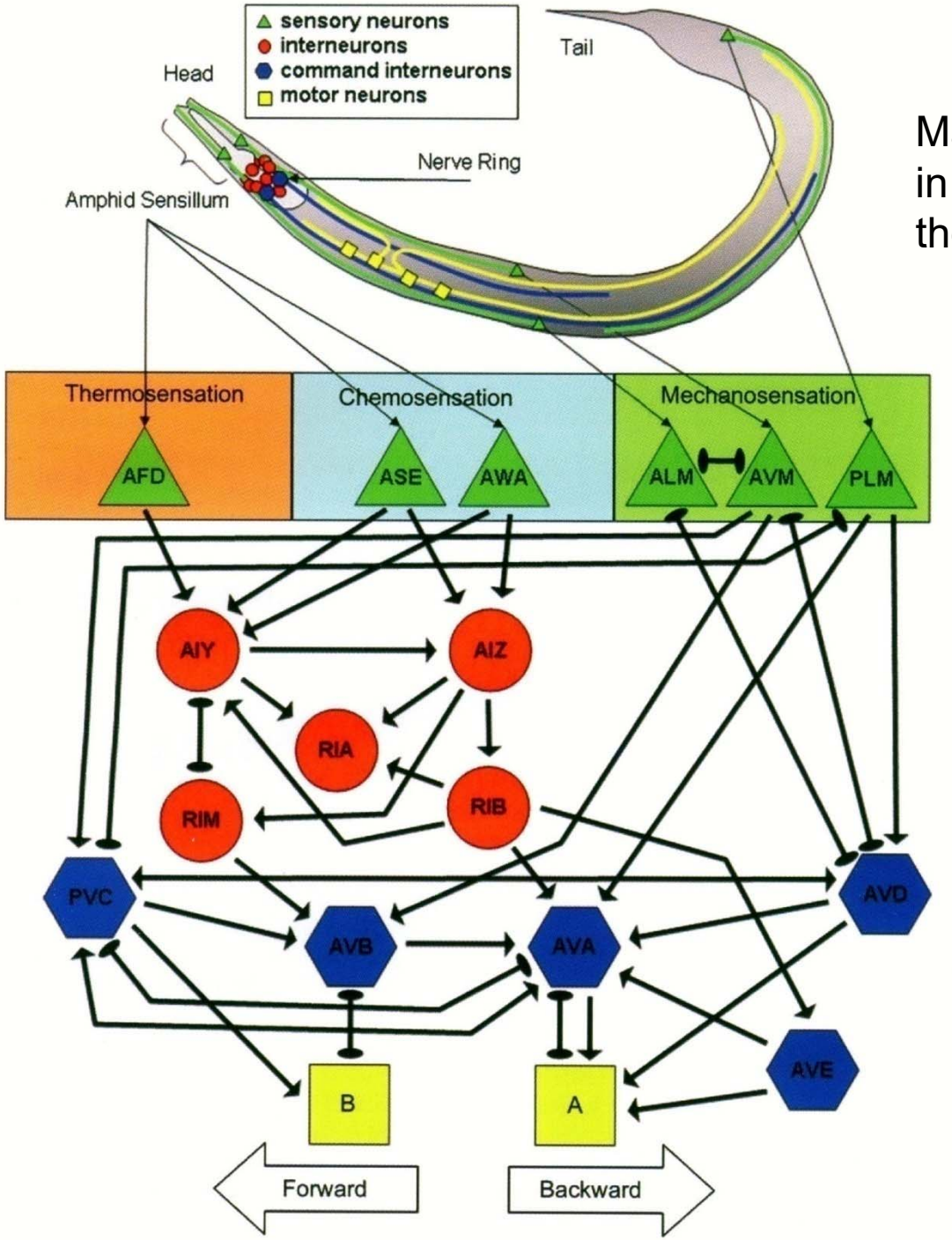
GFP driven by the *unc-47* promoter specifically labels the **GABA circuit** (VD, DD, AVB)



Some **command interneurons** marked with the *nmr-1*::GFP reporter

Motor circuit hierarchy

Major elements of the neuronal circuits in mechanosensory, chemosensory and thermosensory behaviors



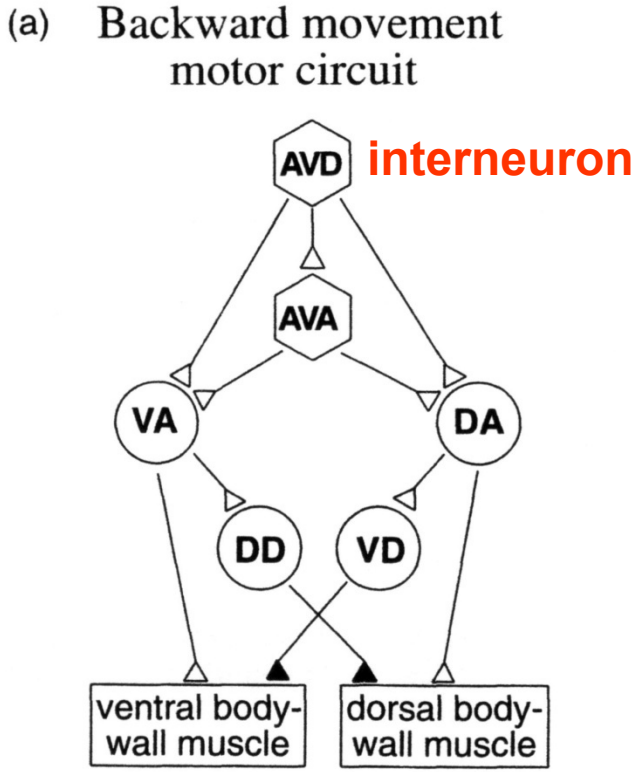
Sensory neurons
(environmental input)

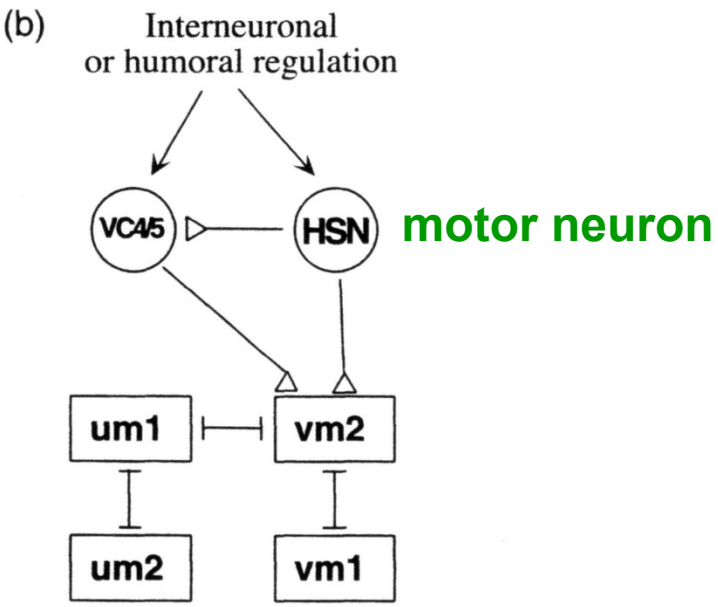
Head interneurons
(signal integration)

Command interneurons
(do excite or inhibit motor neurons)

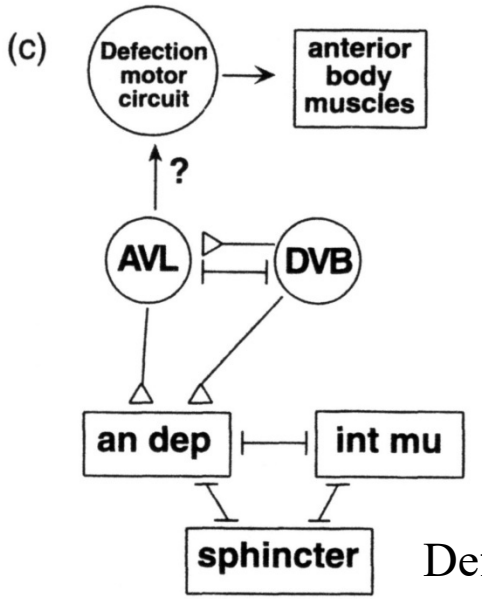
Pool of B- or A-type motor neurons
(do excite or inhibit muscles)

Motor circuits

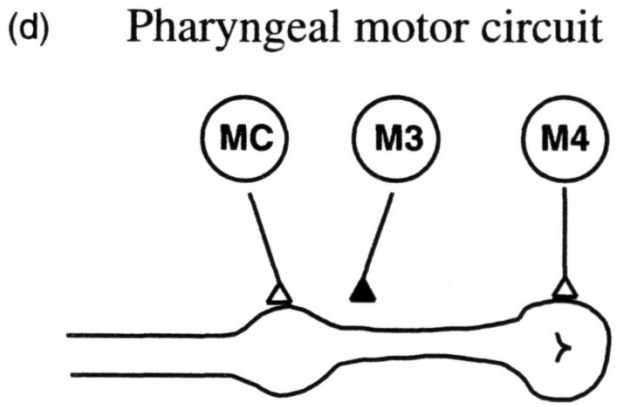




Egg-laying circuit

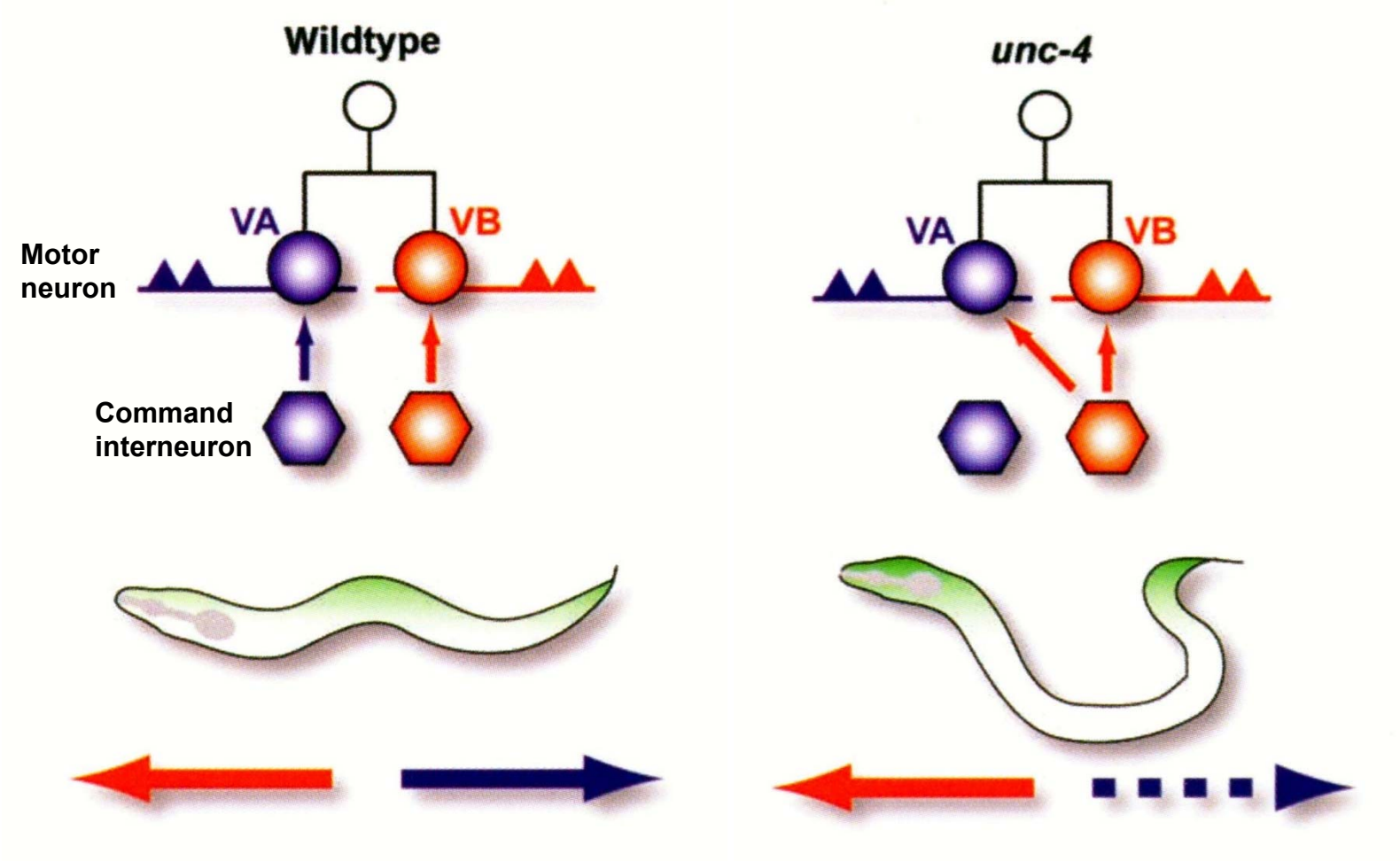


Defecation circuit



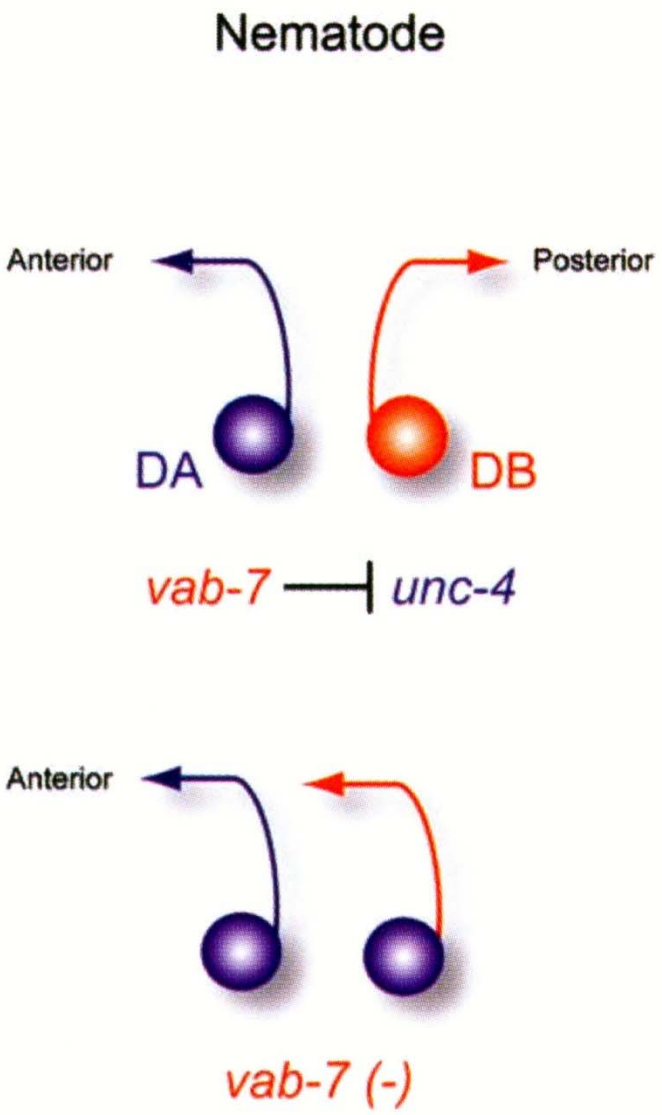
Neuronal plasticity

- **A-type** neurons control backward, **B-type** neurons control forward movements
- In ***unc-4* mutants** the **VA motor** neuron receives input from a **wrong command interneuron**
- As a result the **worm cannot move backward**

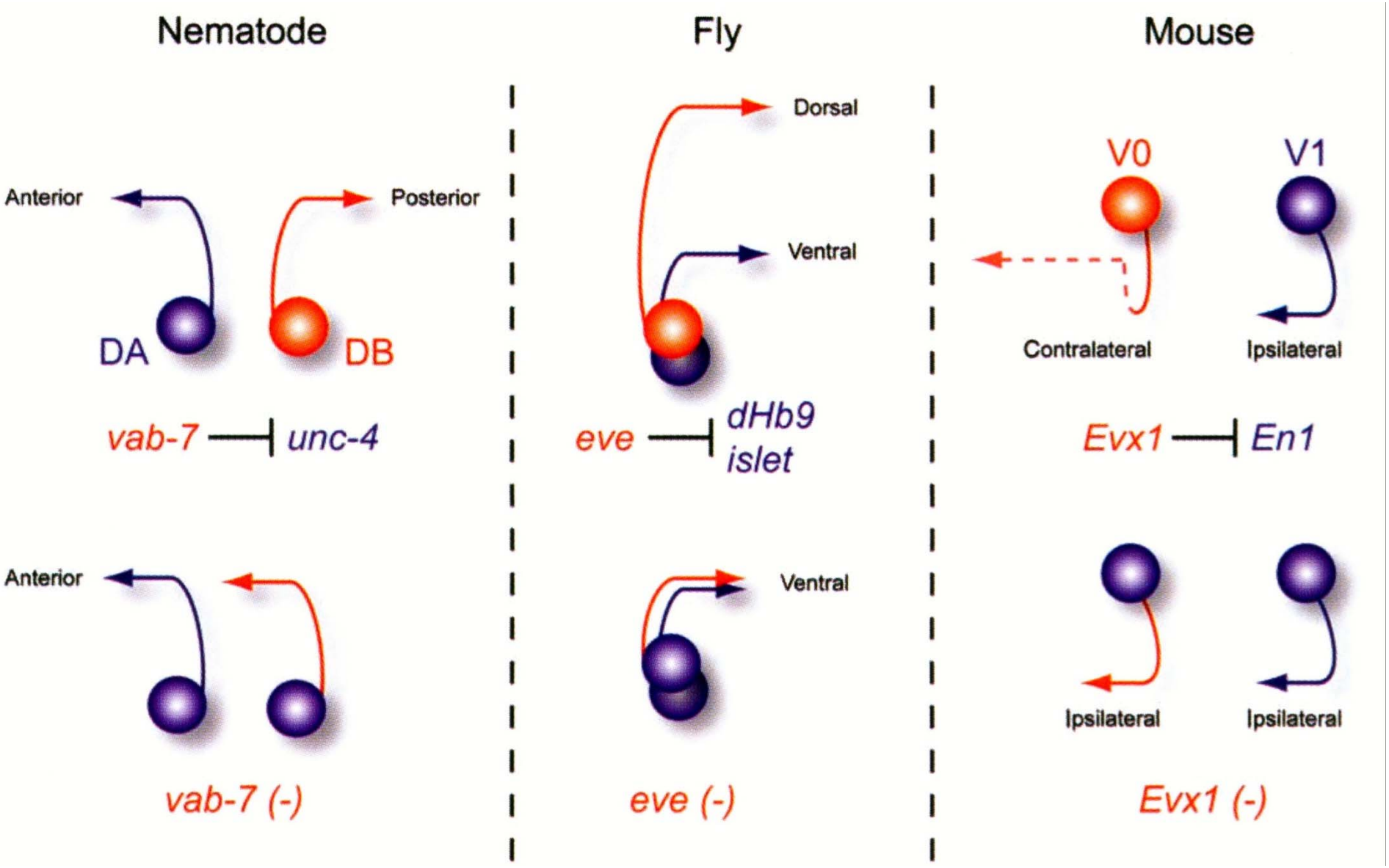


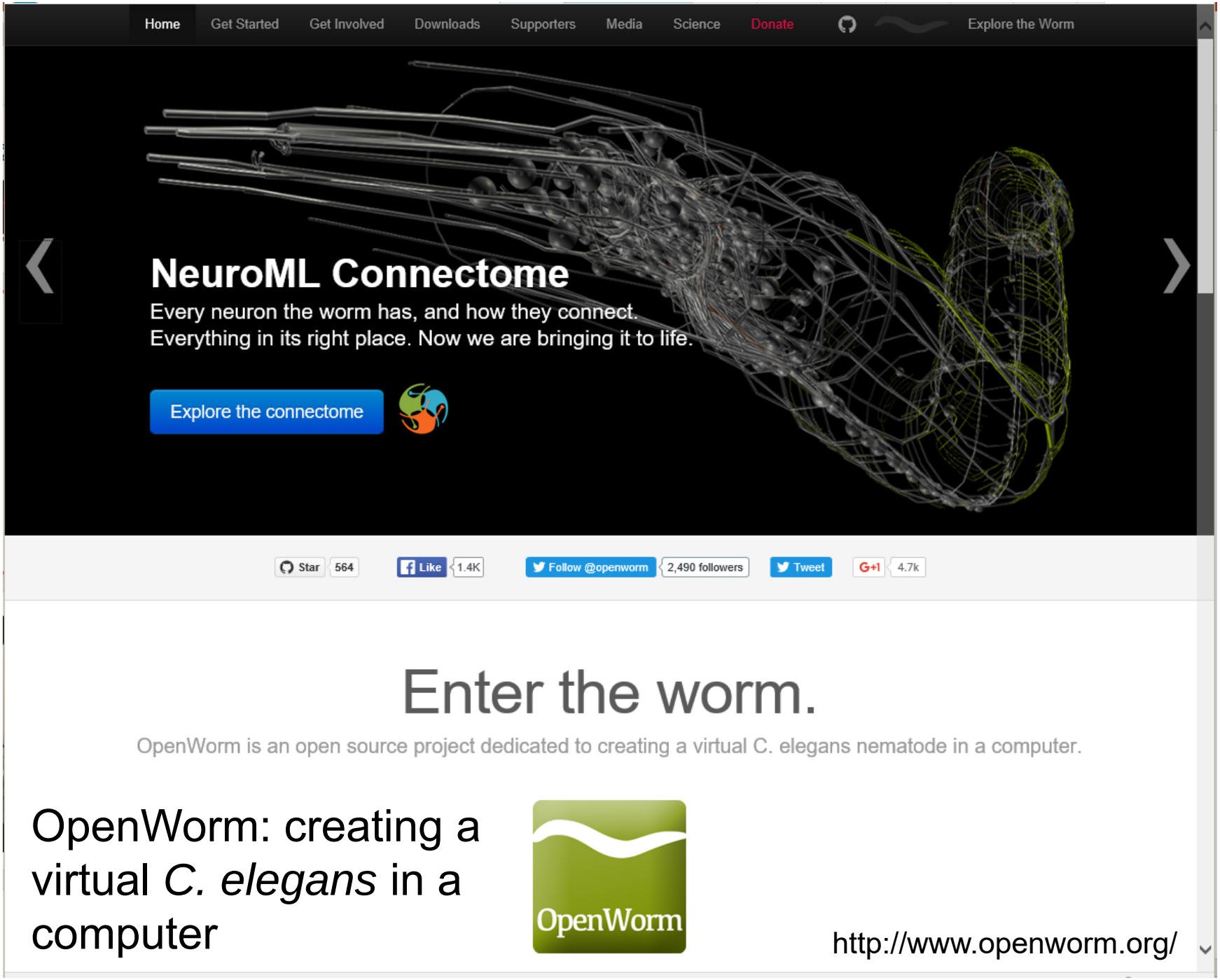
Neuronal plasticity

- **Transcriptional repressors** define neuron identity and axonal trajectory
- ***vab-7*** negatively regulates ***unc-4*** to prevent **DB motor neurons** from **projecting anterior**



• In **flies**, **dorsal motor neurons** adopt a **ventral trajectory** when ***dHB9/islet*** is **not repressed** in ***eve*** mutants
• In **mouse**, ***Evx1*** represses ***En1*** to maintain the **contralateral** axonal trajectory of **V0 interneurons** in the spinal cord



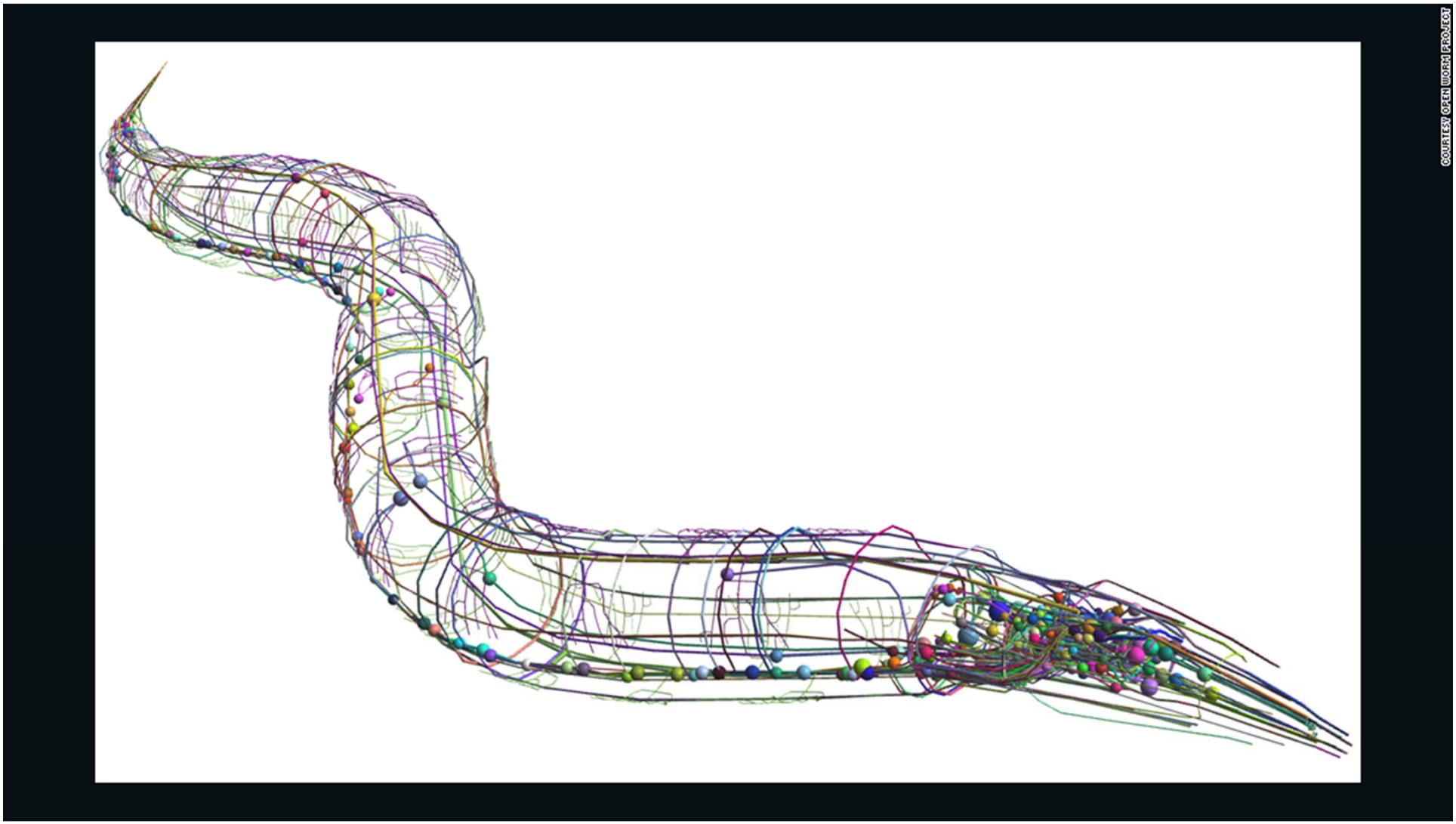


OpenWorm: creating a virtual *C. elegans* in a computer

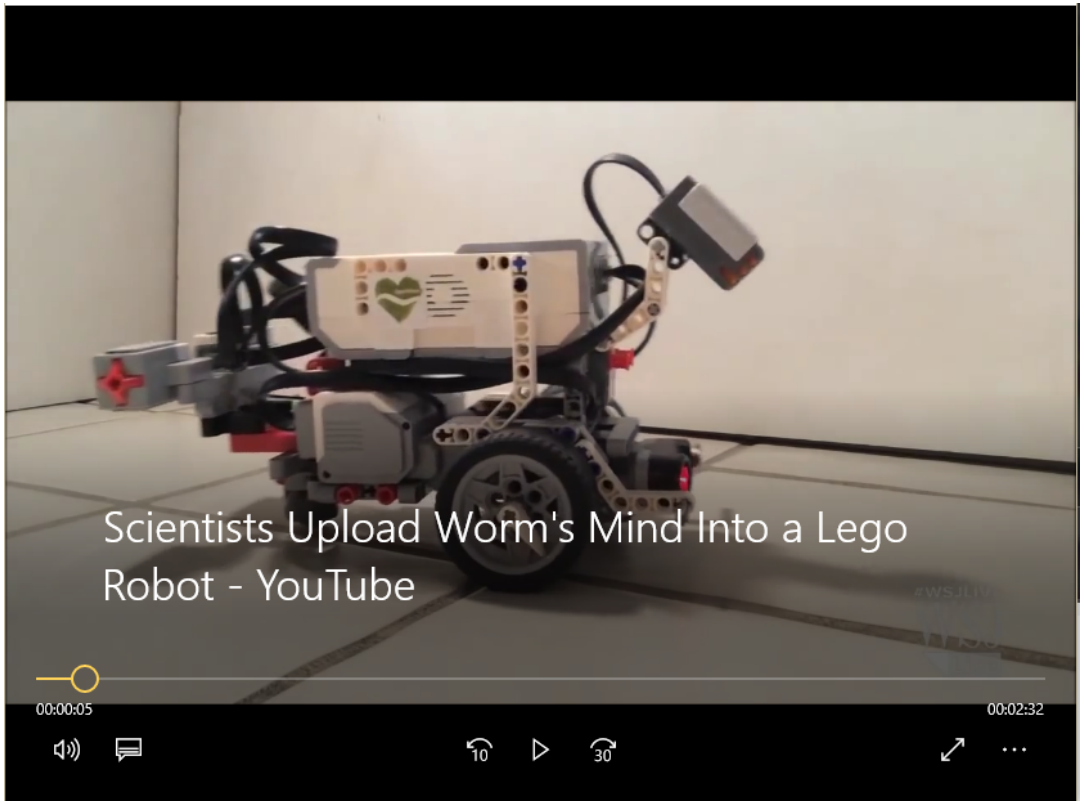
OpenWorm

http://www.openworm.org/

Everybody can do “online experiments” and tinker with the worm now



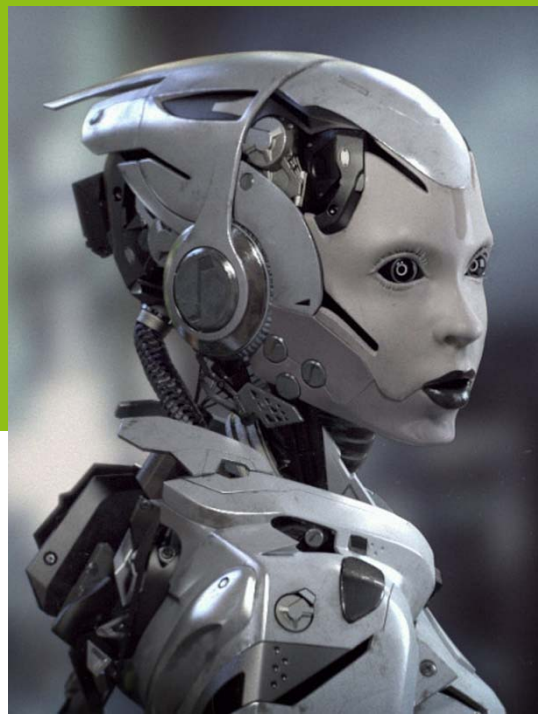
A LEGO robot emulates the worm's biological wiring



https://www.youtube.com/watch?v=2_i1NKPzbjM

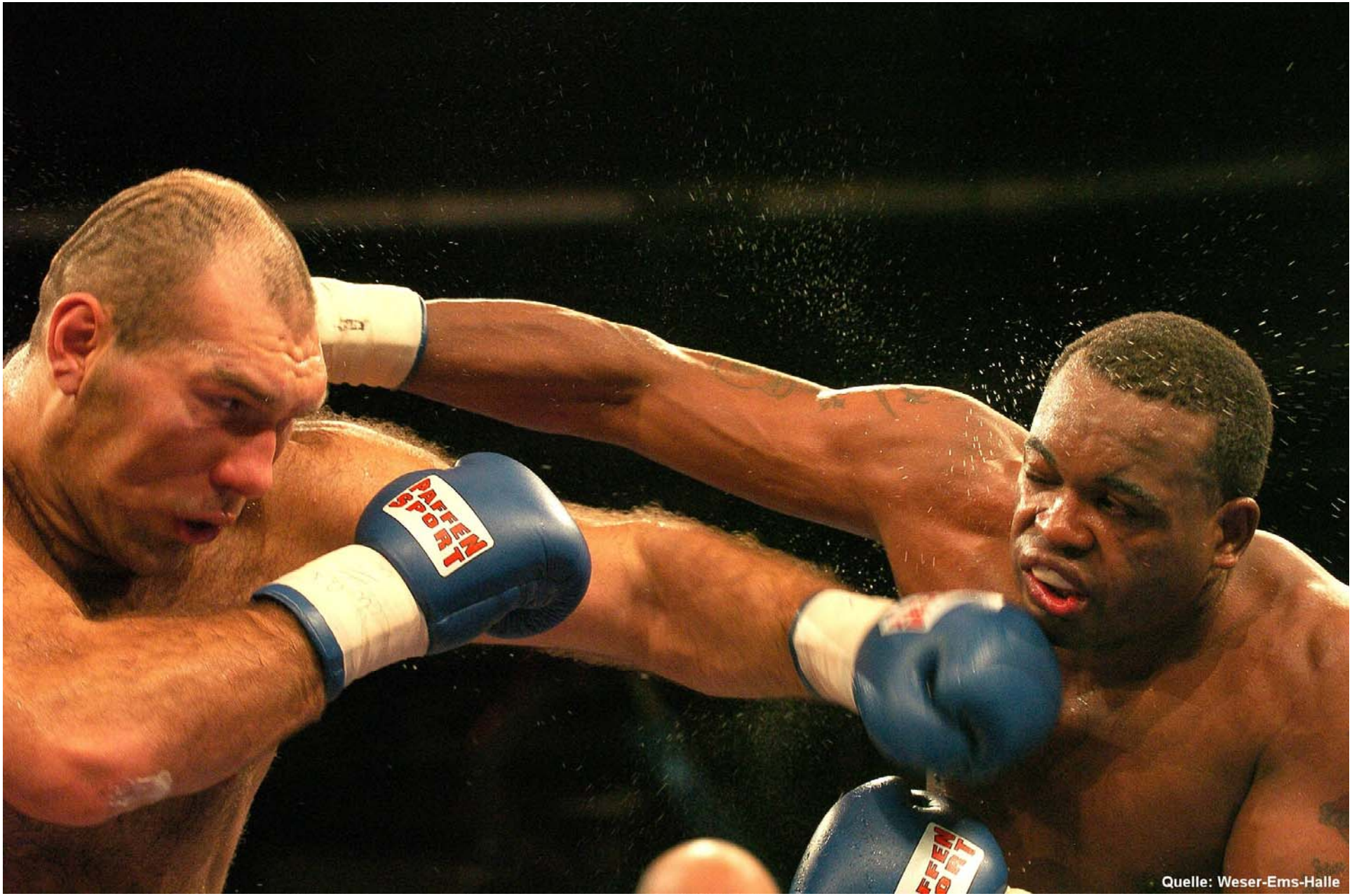
- The aim is to recreate the behavior of *C. elegans* in a machine.
- A **software** that is **modeled based** on the **worm's neuronal network controlled a Lego robot**
- The machine's sensors, **without any prior programming**, made the robot behave in a similar fashion to *C. elegans*, approaching and backing away from obstacles or stimulated by food.
- The worm's **nose neurons** are replaced by a **sonar sensor** and the **left and right motor neurons** control the **left and right motors** of the Lego bot

The OpenWorm project aims to digitally model the worm entirely in a virtual environment; creating a robot with an **elastic body** complete with **stretchy muscles**



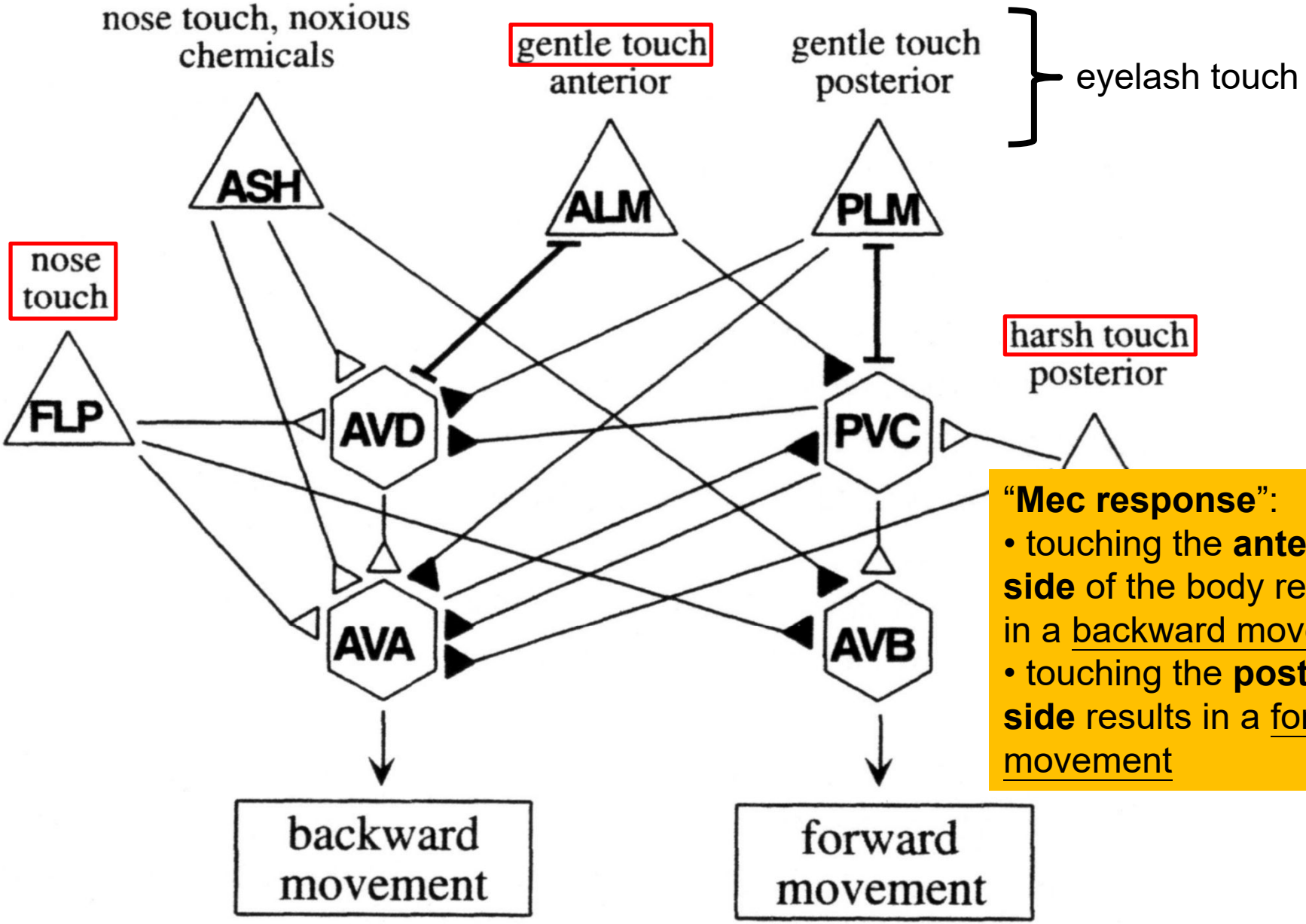
The project shows that artificial intelligence (AI) may become real soon modeling the human brain in a machine

Mechanosensing



Avoidance reflex circuits

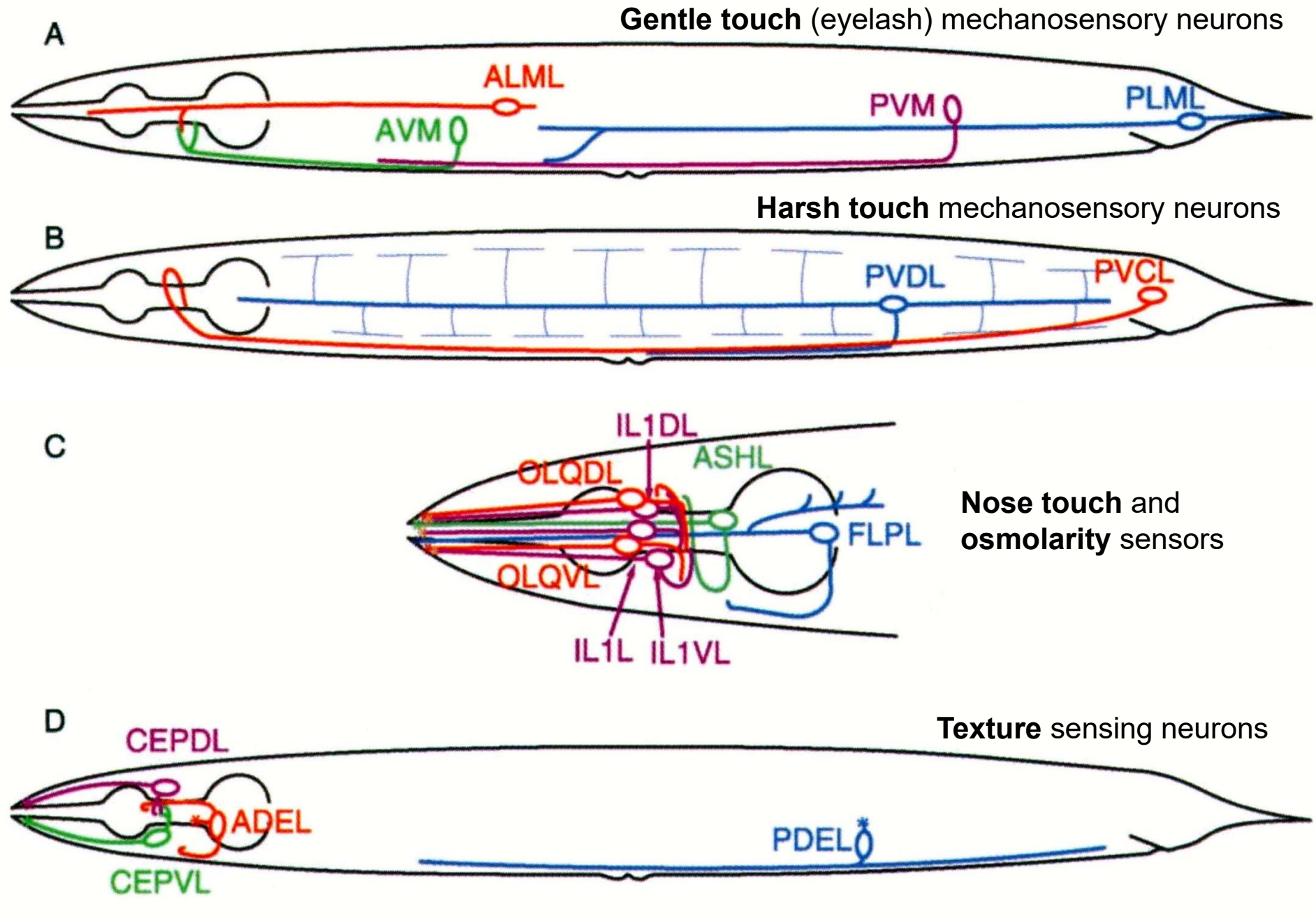
Mechanosensory neurons can sense different strength of touch:



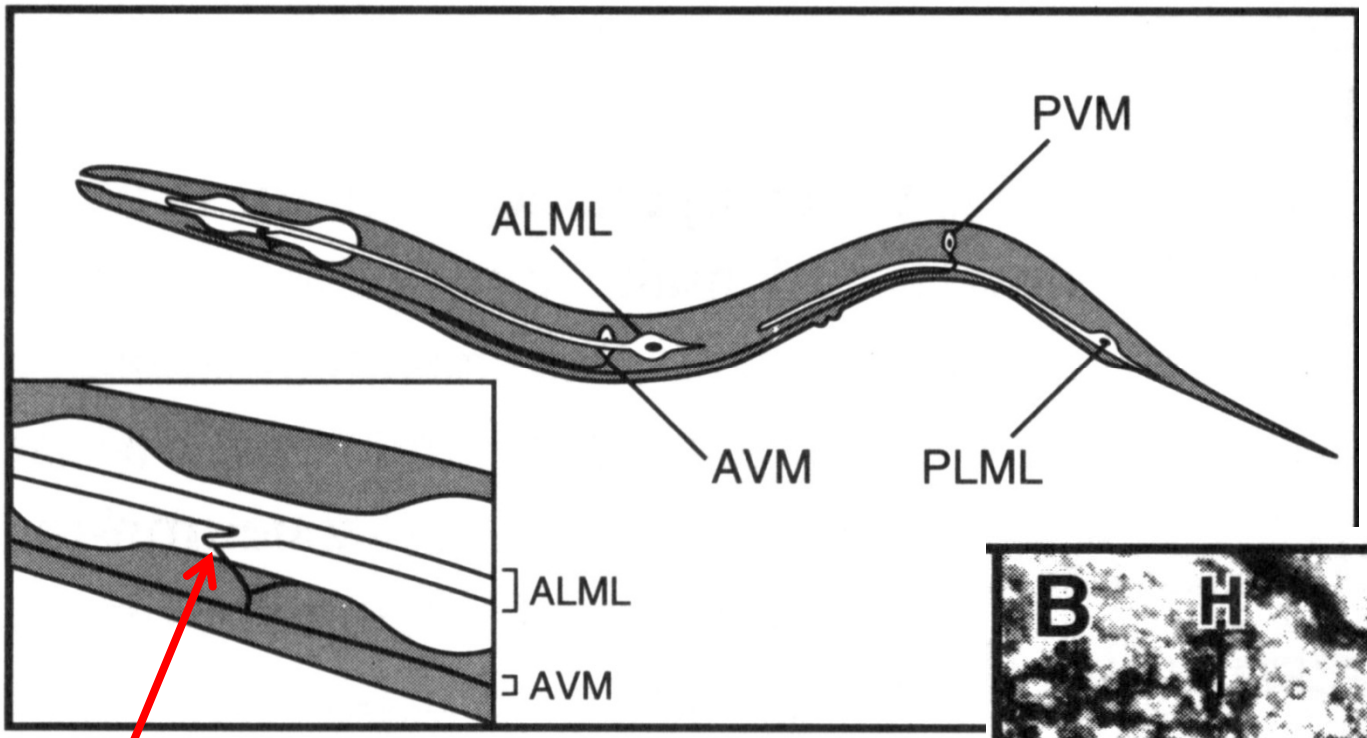
"**Mec response**":

- touching the **anterior side** of the body results in a backward movement
- touching the **posterior side** results in a forward movement

Neurons that sense the 4 different types of touches

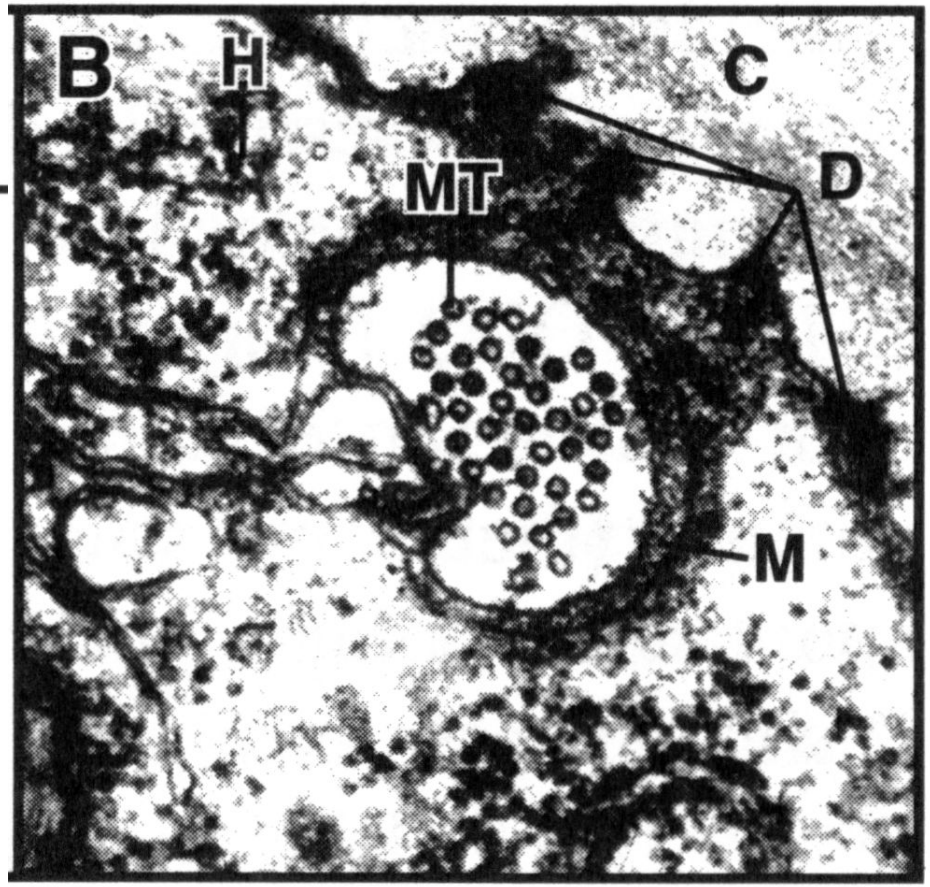


Touch receptors



synaptic branch

- Touch receptors are **unciliated**. They make **synaptic branches** to interneurons
- Touch is sensed through indentation of the cuticle

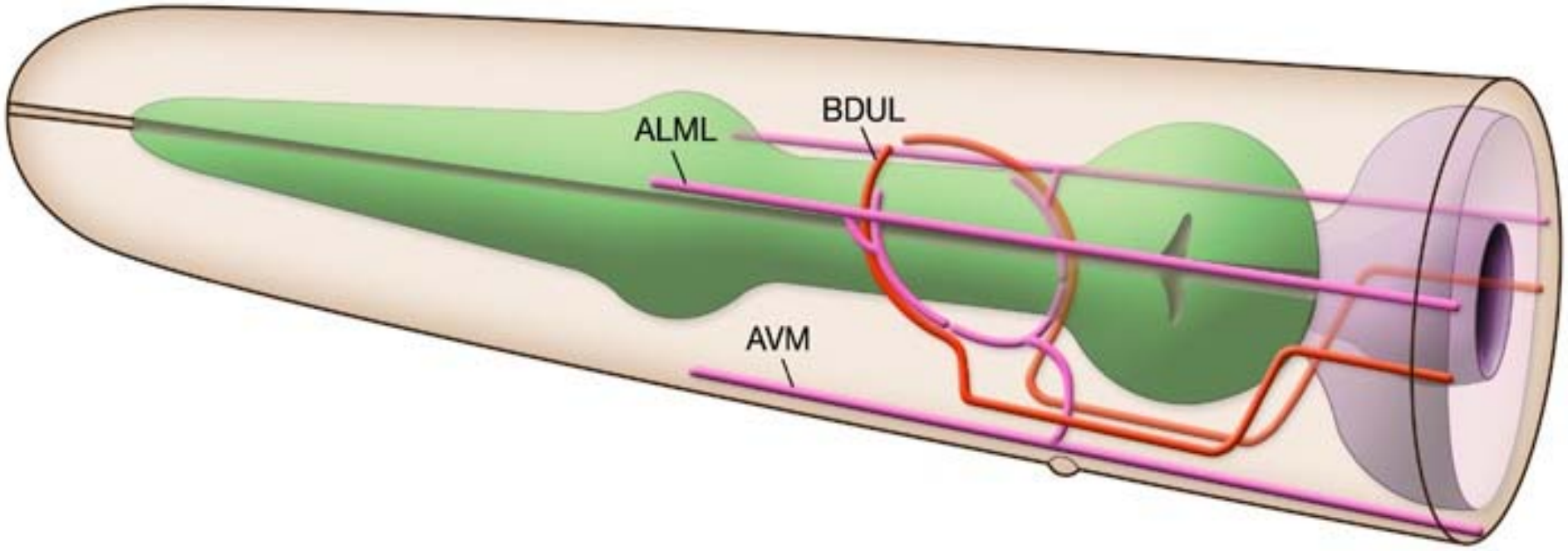


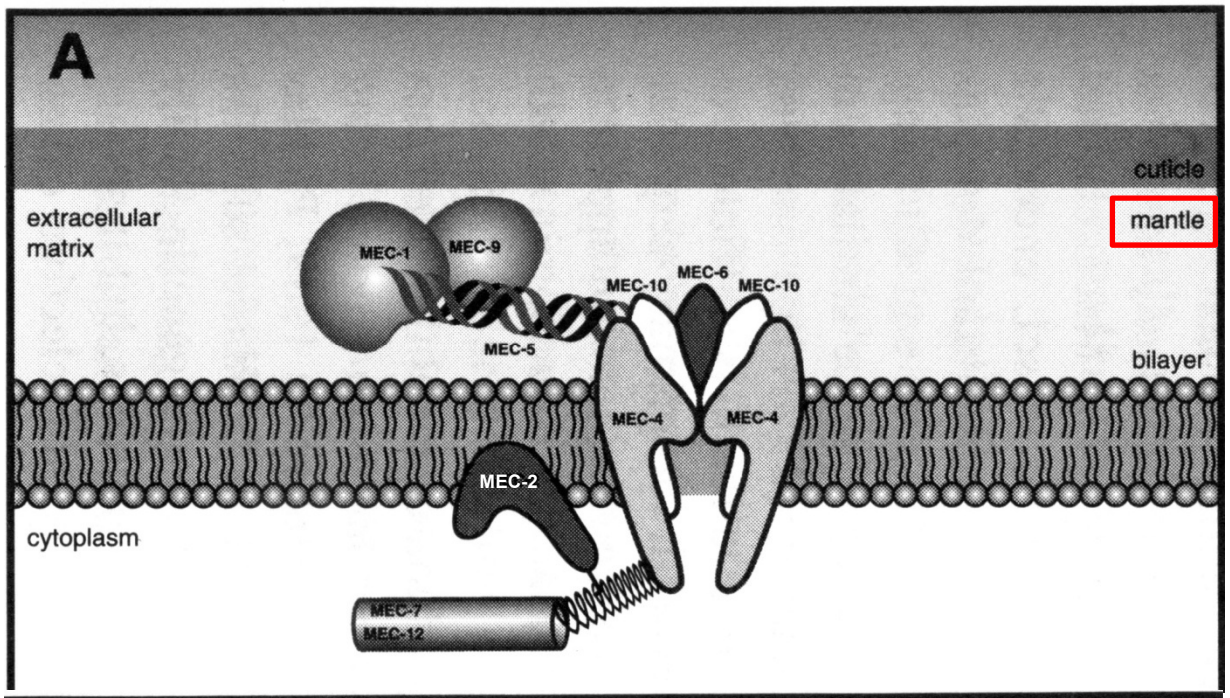
- Located just beneath the cuticle (**C**)
- Surrounded by a specialized extracellular matrix (**M**, mantel)
- Contain microtubules (**MT**) made up of **15 protofilaments** (“microtubule cells”)

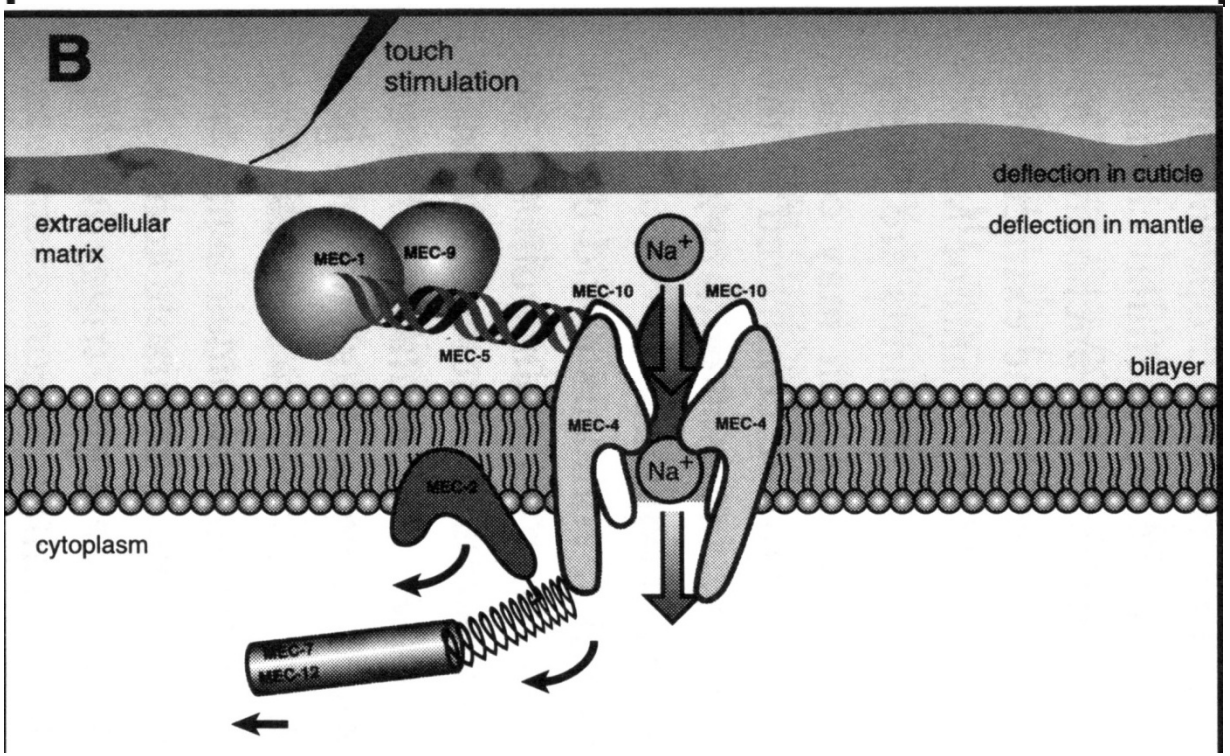
(C = cuticle, D = process anchors, H = hypodermis)

Touch receptors

Touch neurons connect to **interneurons** via a single synaptic branch





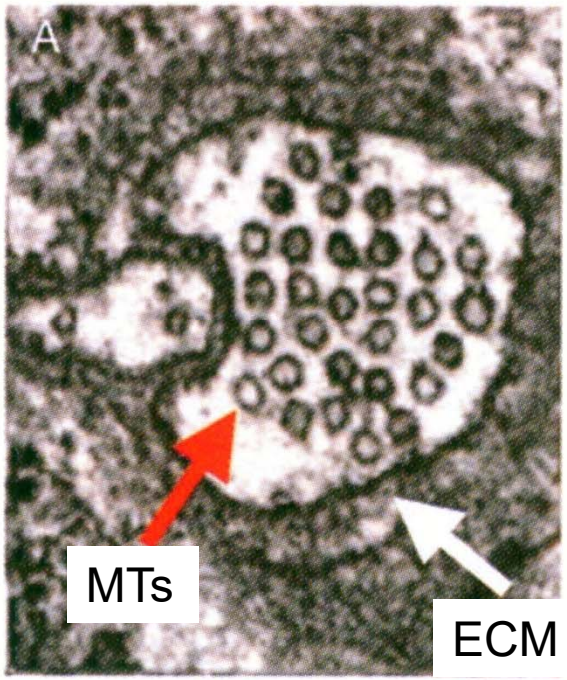


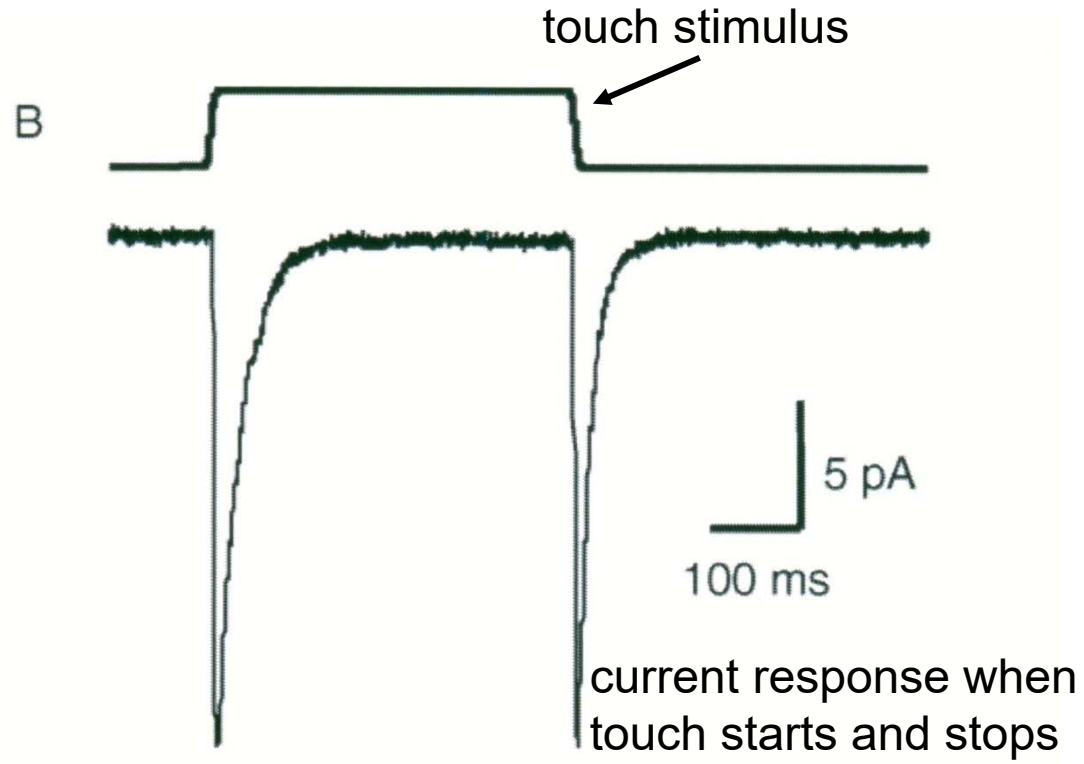
Model of mechano-reception

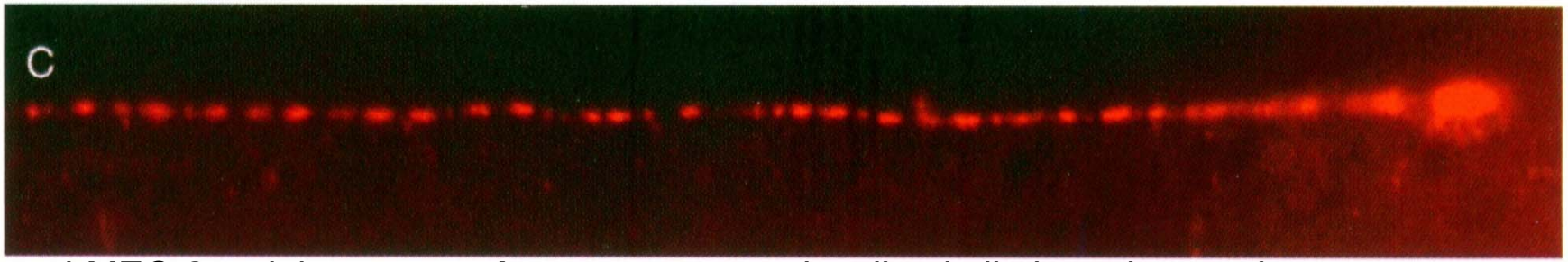
- **Mantle proteins** include the flexible MEC-5 collagen
- It also contains MEC-2 which tethers **15 protofilament** MTs via a spring-like element to the channel

- **Gentle touch** via an eyelash deflects the cuticle resulting in conformational changes that opens the channel
- Gating could be also initiated by a deflection of the microtubules (MEC-5 then serves to maintain tension)

Touch receptors

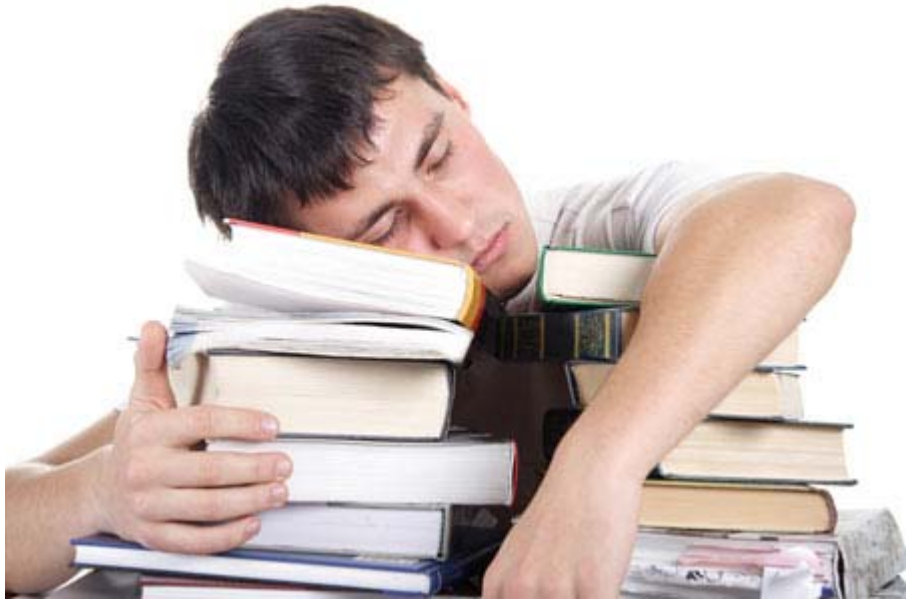




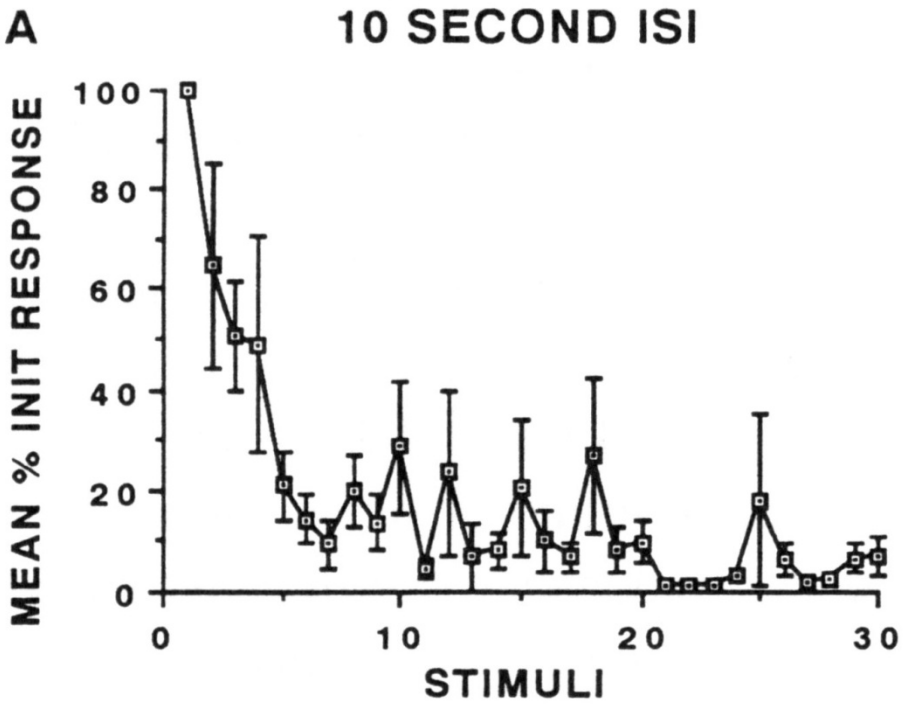


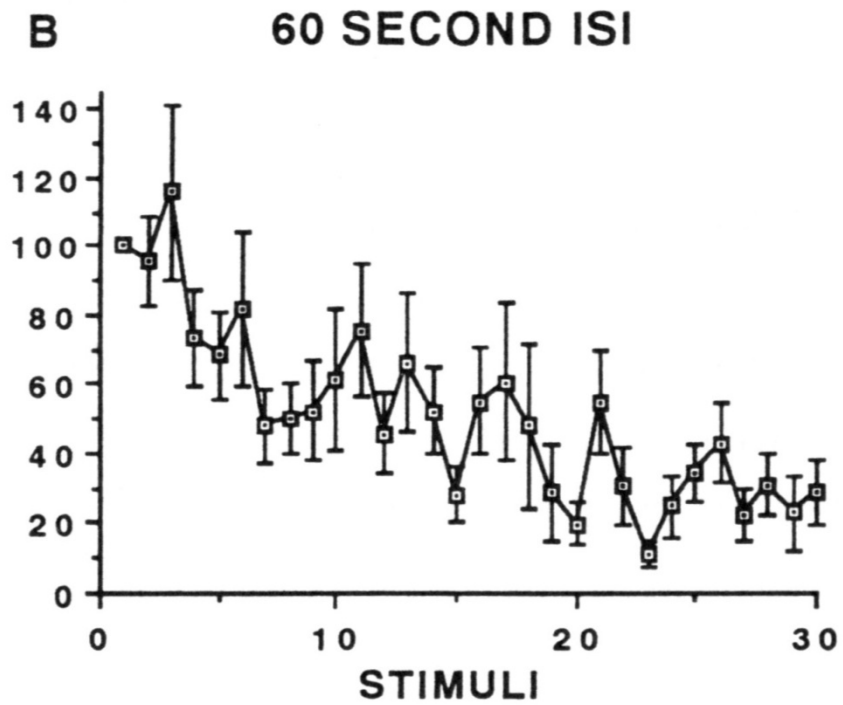
anti-MEC-2 staining => **touch receptors** are visualized all along the neurite

Learning and memory



Habituation (non-associative learning)





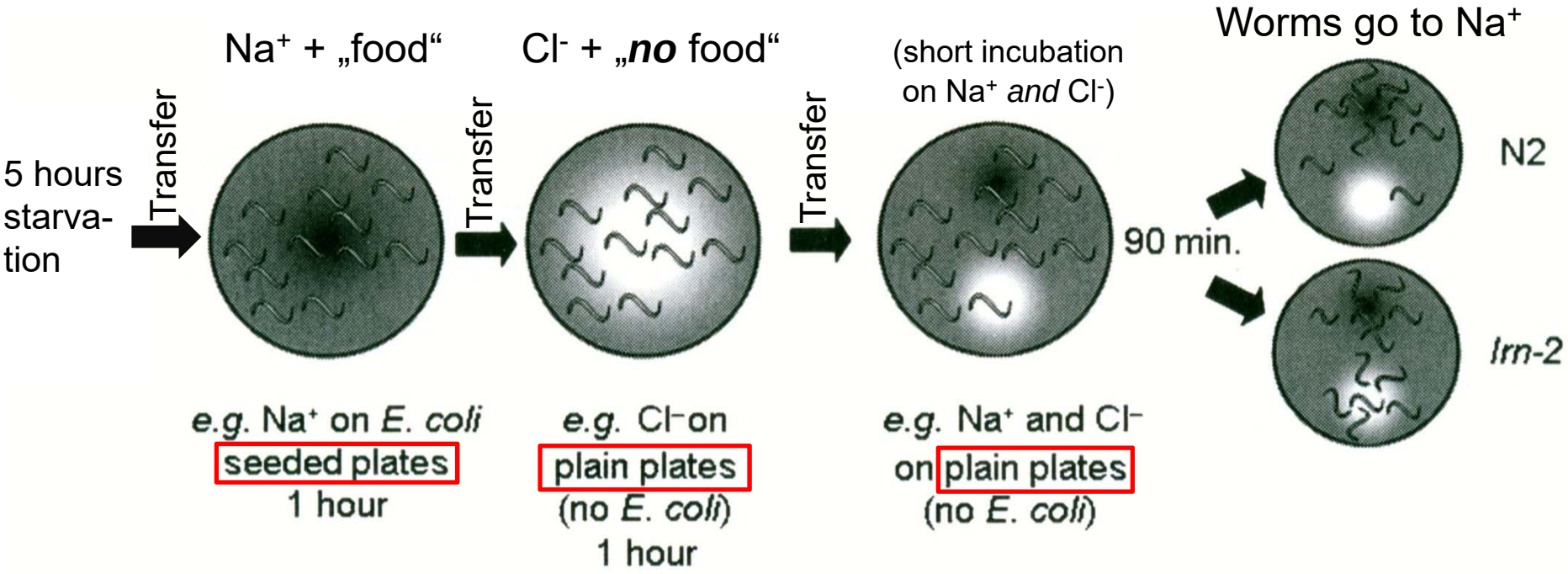
• Tapping at the side of the petri dish stimulates **backing response**
• Backing movement decreases if stimulus is continuously applied (every 10 seconds for total 30 minutes)

Habituation occurrence can be stored for more than 1 hour in the nervous system

• If stimulus is applied less often (every 60 seconds) decrease of backing response is less abrupt (indicating **habituation** and not worm fatigue)
• Also habituation can be rapidly abolished with an electroshock stimulus (**dishabituation**)
• Further, worms recover from short-interval habituation faster compared to long-interval habituation

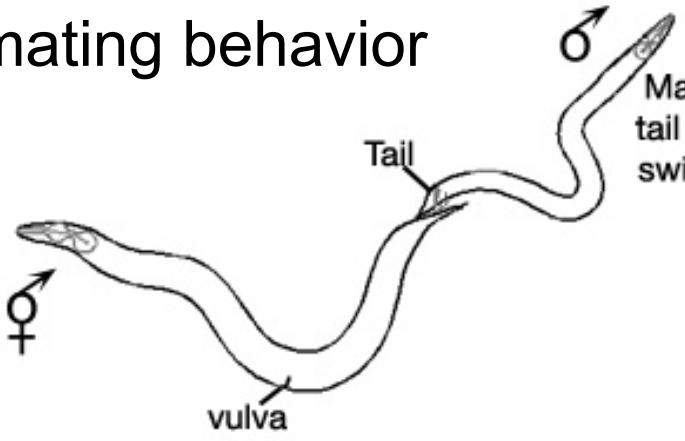
Classical conditioning (associative learning)

- Non-associative learning (habituation): an animal alters its behavior to a single stimulus
- **Associative learning**: an animal learns to use a previously **neutral stimulus** to predict a **second stimulus** (usually a more significant one)
- Example: after food deprivation, one ion is associated with food and the second ion is associated with the absence of food => a **conditioned animal** will move to the ion associated with food (even if no food is present)
- *lrn-1* and *lrn-2* (lrn = learn) are **genes involved in learning**



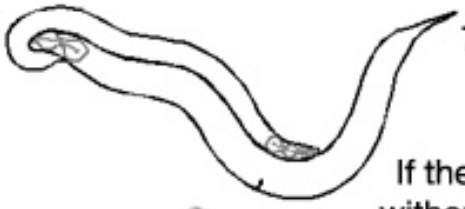
Male mating behavior

Male mating behavior



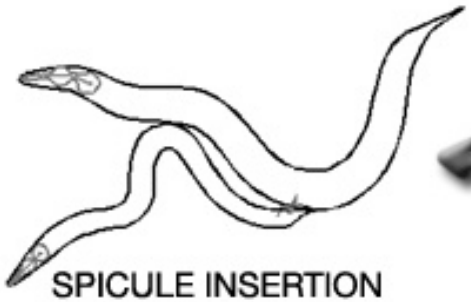
RESPONSE TO CONTACT (rays)
Male halts forward locomotion, presses tail (ventral side) against hermaphrodite, swims backwards in search of the vulva.

Repeated until vulva is detected



TURNING (rays)
If the male reaches the end without detecting the vulva, a tight turn is executed and searching continues along the other side.

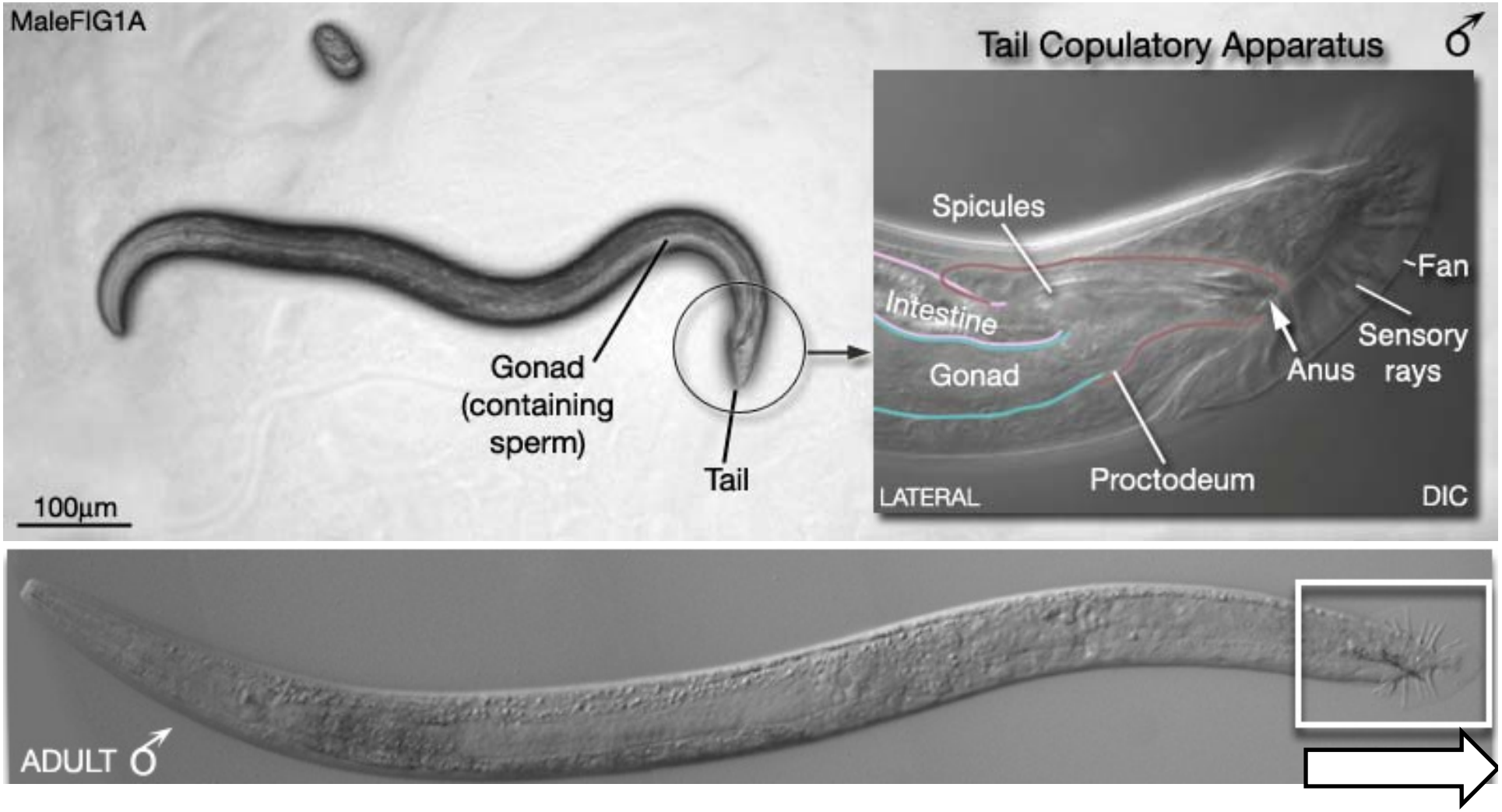
VULVAL LOCATION
If the male detects the vulva (hook, PCS), he commences a slow search of the area, prodding for the slit with his spicules.



SPICULE INSERTION
SPERM TRANSFER
The male inserts spicules fully into the vulva, locking himself to the hermaphrodite and ejaculates

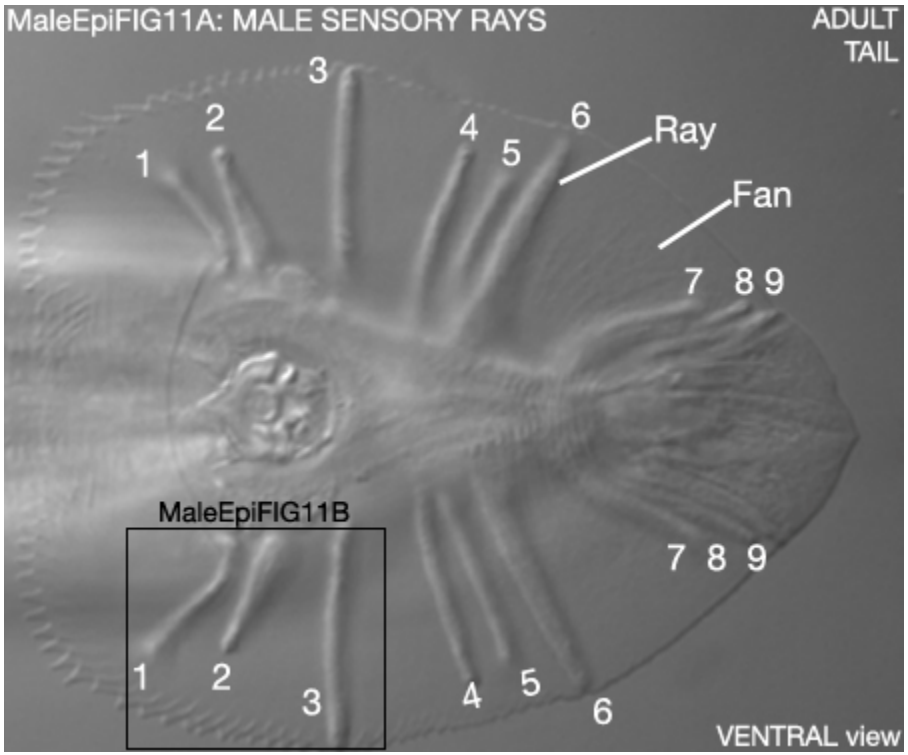
Male specific sensory neurons

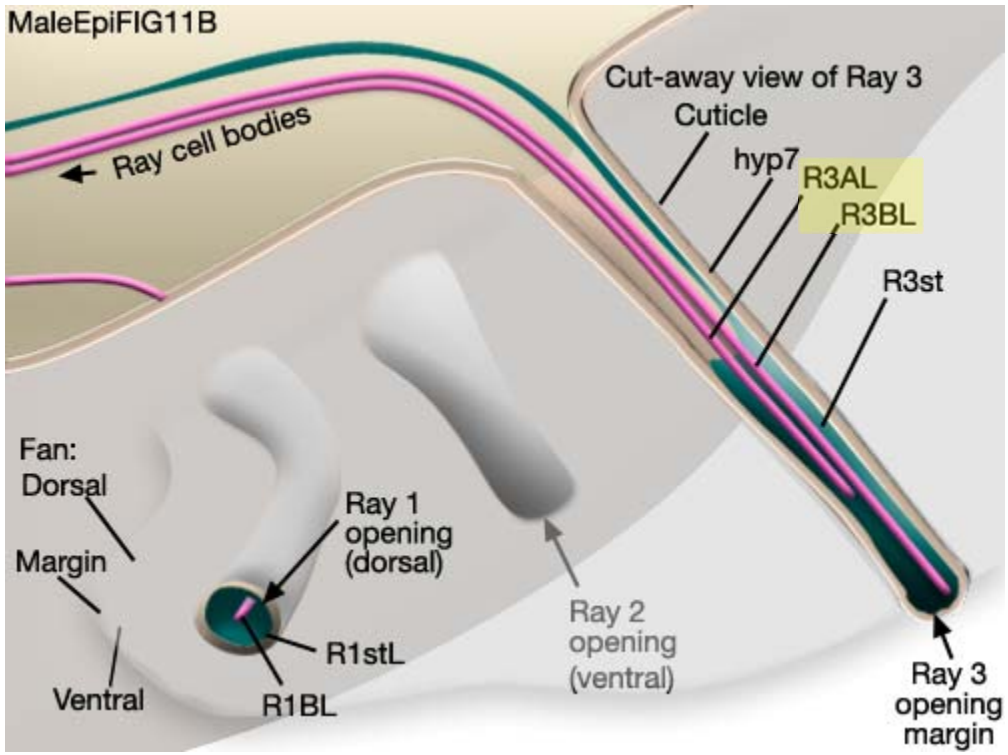
- The copulatory apparatus at the mail tail is composed of a **fan**, **sensory rays** and **spicules**
- The **fan** at the male-tail is a lateral extension of the cuticle
- The fan holds **nine** bilateral pairs of **sensory rays**



Male specific sensory neurons

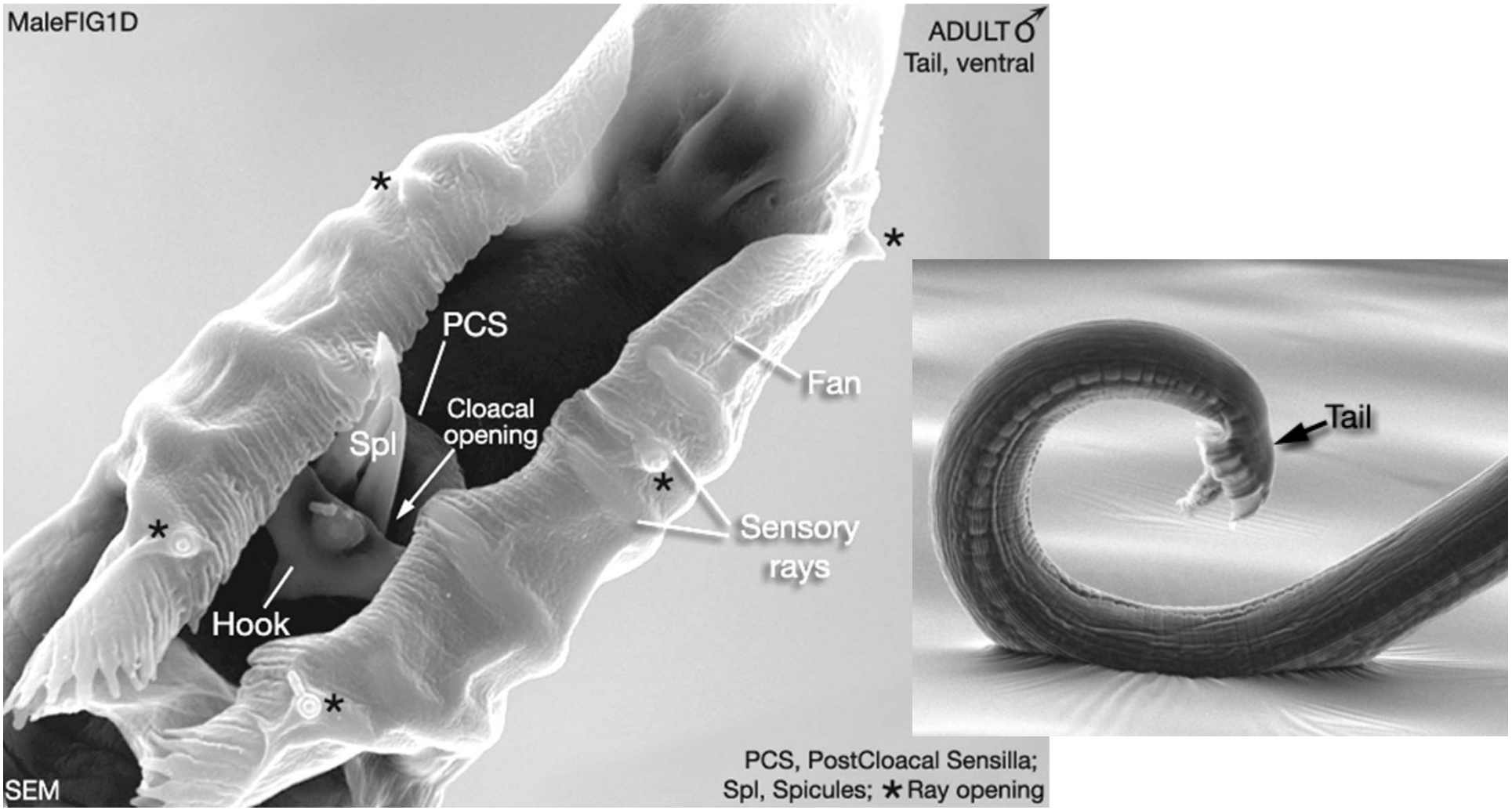
- **Rays** are required for the male mating behavior:
  - rays 1, 5 and 7 are required for **initial contact response** upon encountering the hermaphrodite
  - rays 7-9 are required for **turning**
- Each **ray** contains **two sensory neurons** (**RnA**, **RnB**) which are surrounded by a single tube-like cell (**Rnst** = ray **structural cell**)
- All rays (except ray 6) are opened to the environment at their tip

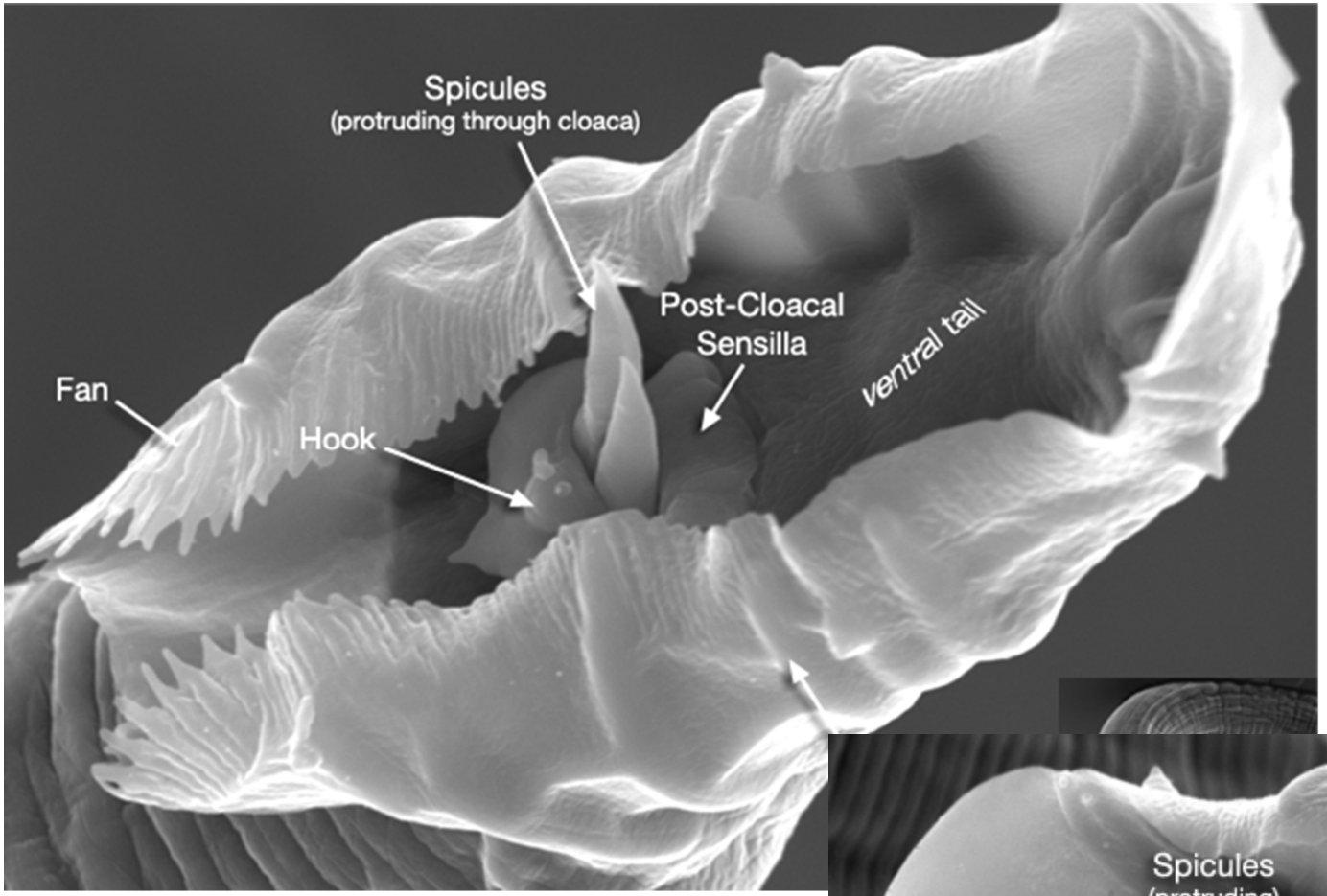




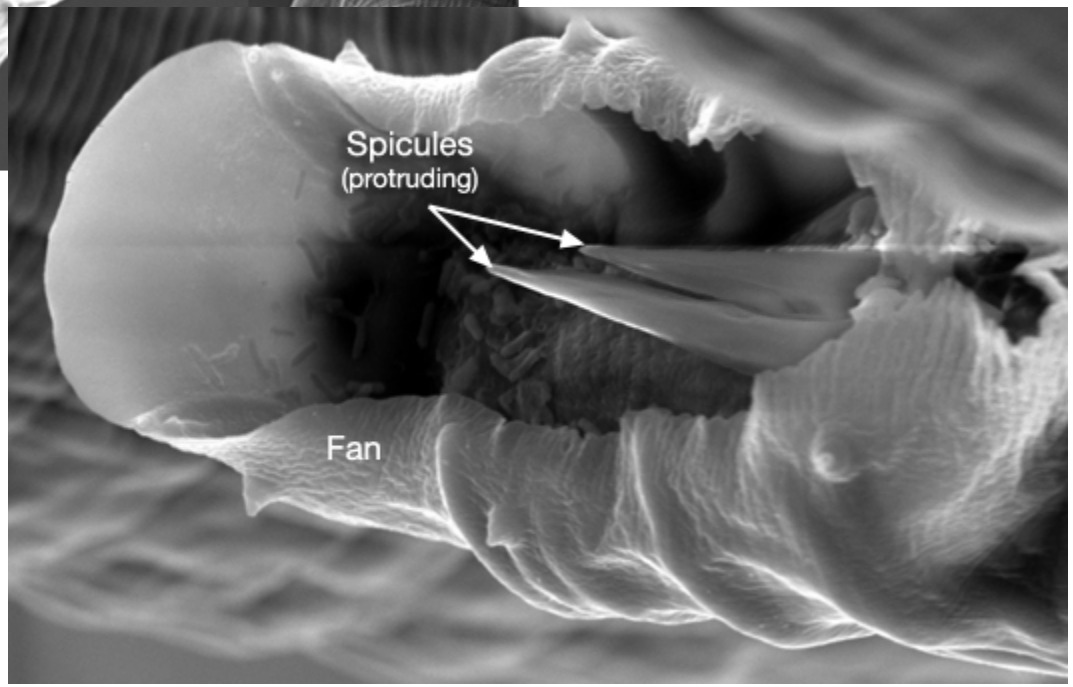
Male specific sensory neurons

- On the ventral surface of the tail are the **hook** and the **p**ost**c**loacal **s**ensilla (PCS)
- Hook and PCS are located on either side of the **cloaca** (male anus)
- A chamber sits in front of the cloaca named **proctodeum** (the male rectum) housing spike-like **spicules** (Spl)
- Spicules are sensilla covered in a hard, sclerotic cuticle





Each spicules contain two <u>sensory neurons</u>



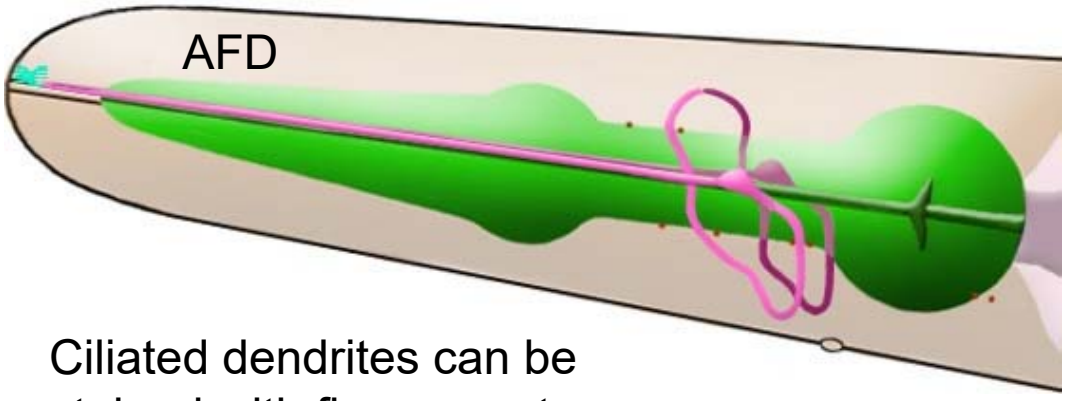
Thermosensory neurons

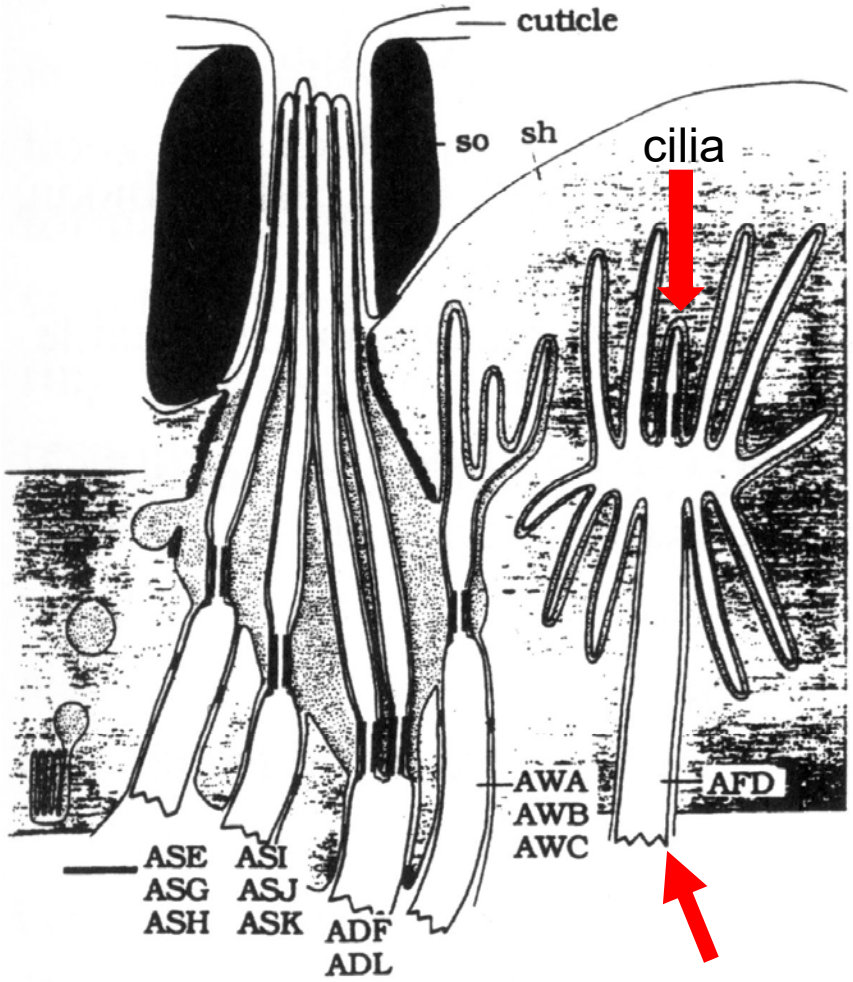
Hawaiian strain CB4856
(lots of single nucleotide polymorphisms)

Thermosensory neurons

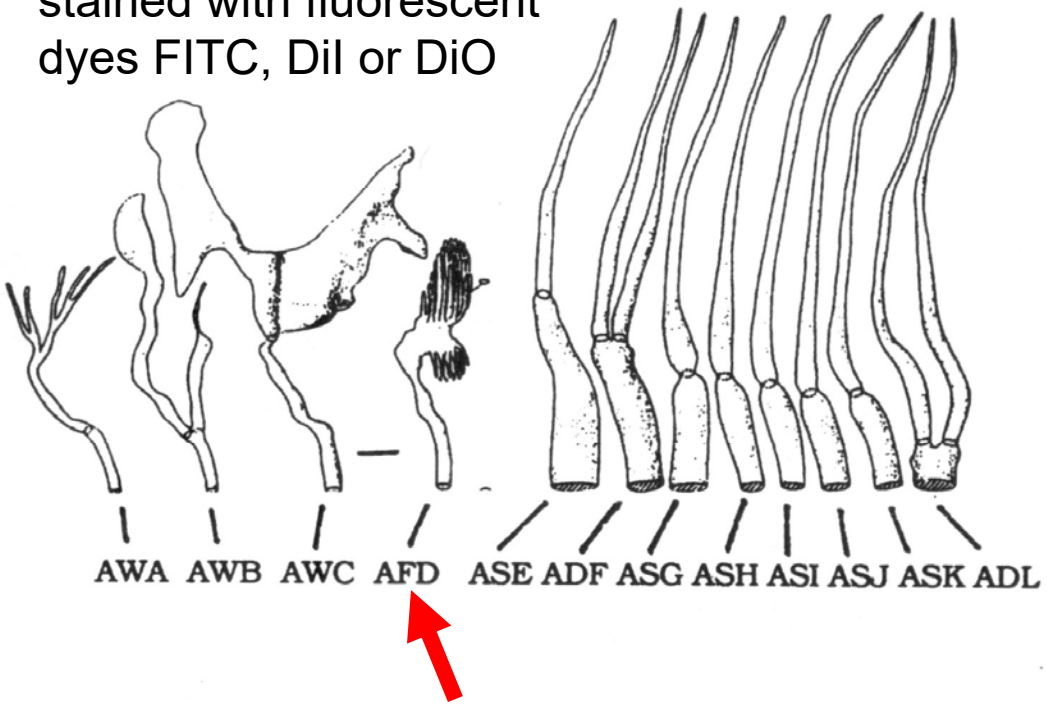
• A single amphid sensory neuron, **AFD** is required for isothermal tracking and normal temperature preference

• The AFD neuron is NOT opened to the environment and has 40 finger-like microvilli and ONE cilia



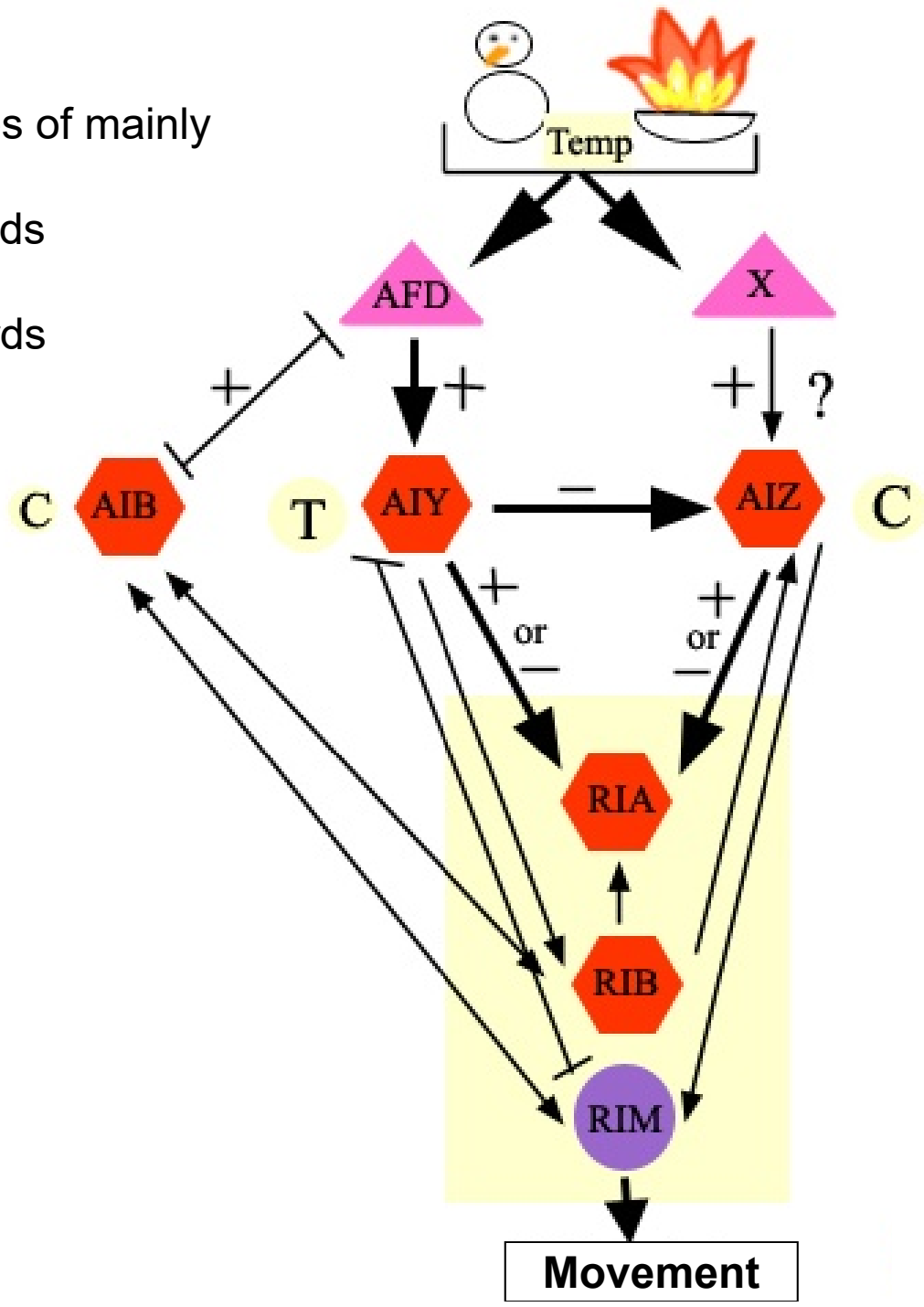


Ciliated dendrites can be stained with fluorescent dyes FITC, DiI or DiO



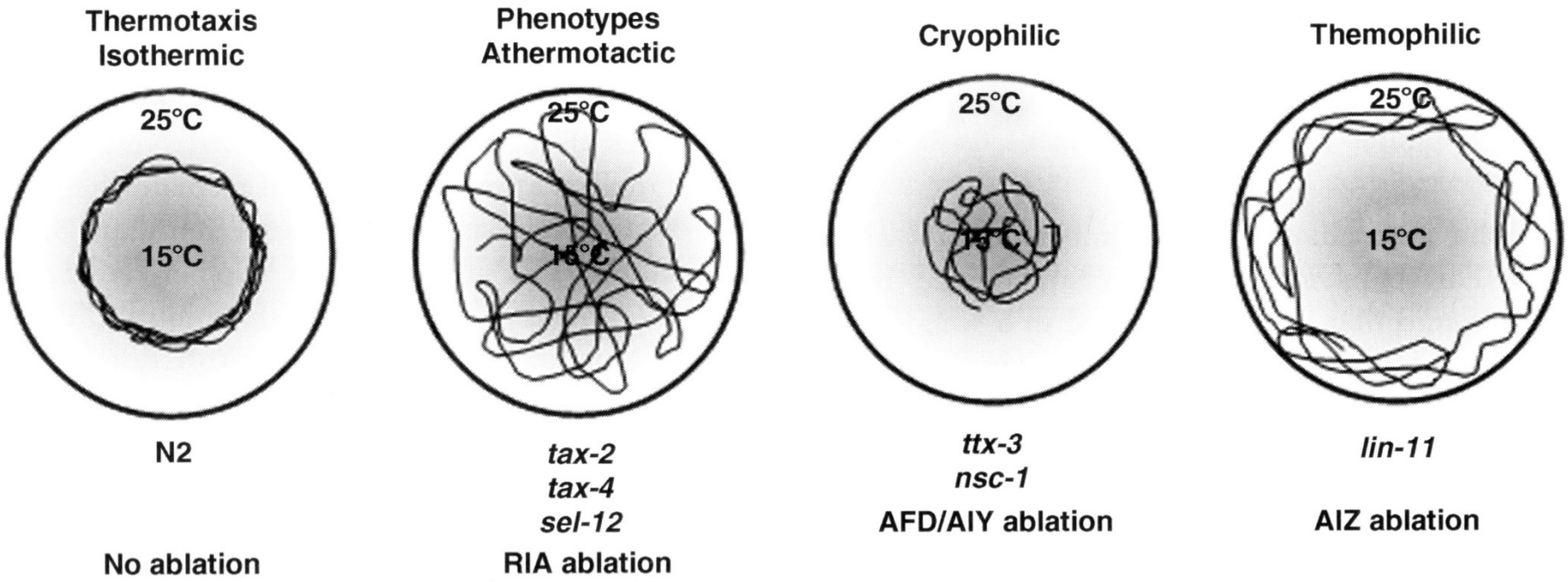
Thermosensory neurons

- Thermotaxis results from activities of mainly **two** amphid **interneurons**:
  - **AIY:** drives movement towards **warmer temperature** (T)
  - **AIZ:** drives movement towards **colder temperatures** (C)



Thermosensory neurons

Genes and neurons involved in thermotaxis



- Worms maintained at 20˚C and transferred to a **radial thermal gradient**
- Ablation = precise elimination of neurons by a laser pulse

Behaviour	Assay
Locomotion	Qualitative inspection
	Radial dispersal rate
	Wave frequency
	Wave amplitude
Egg-laying	Egg stage
	Egg retention (serotonin-test)
	Egg-laying rate (liquid)
Defecation	Constipation
	Ethogram (direct inspection)
Chemoattraction	Point source gradient
	Step gradient grid
Chemorepulsion	Ring crossing
	Gradient
	Step gradient grid
Thermotaxis	Radial gradient
	Linear gradient
Body-touch response	Plate tapping
	Eyelash
	Pick prod
Nose-touch response	Eyelash bumping
Pharyngeal pumping	Pump count
	Detailed inspection
	EPG
Male mating	Reproductive efficiency
	Direct inspection
Dauer formation	Uncrowded growth
	Crowding/starvation
	Pheromone response
	Epistasis with *daf* genes

Using *C. elegans* behavior for mutant analysis

- When a new mutant is identified, much knowledge can be gained from testing for a variety of behavioral defects
- This process is not unlike a routine for neuronal examination in mouse or human

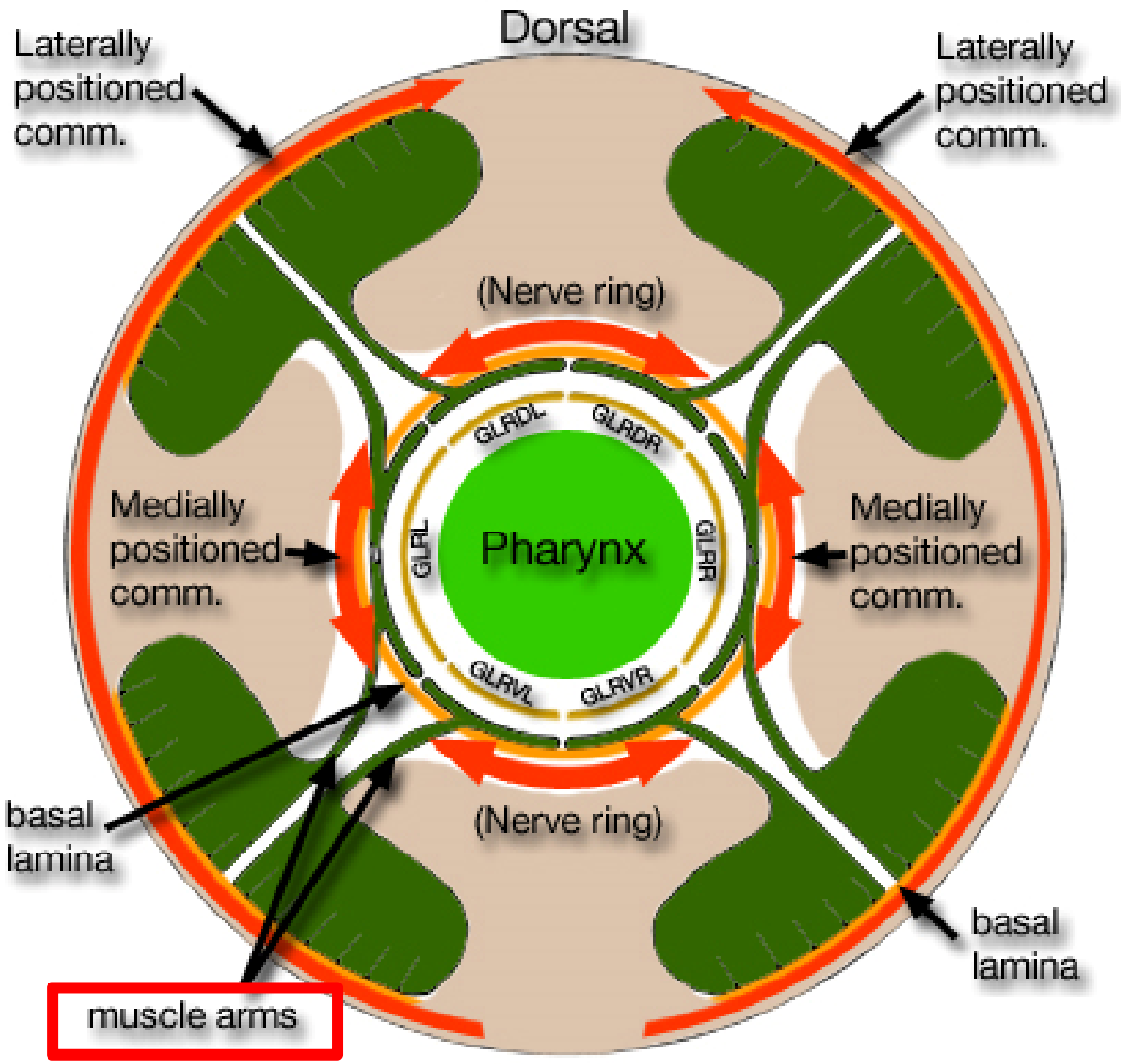
(Aldicarb resistance: defects in ACh neurotransmission)

Special feature of the *C. elegans* nervous system:

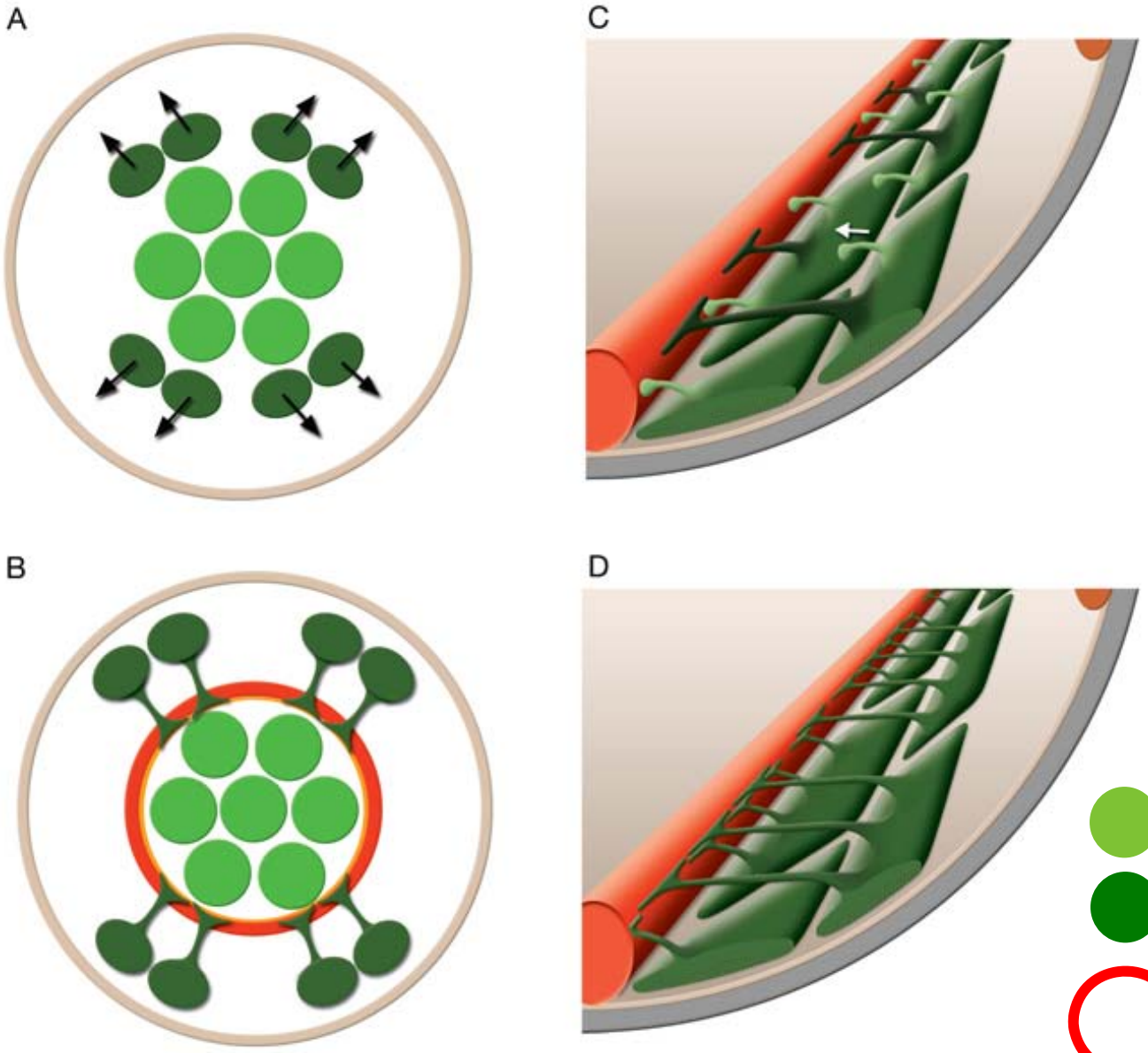
Muscle arms and muscle arm chemotropism

Muscle arms

In higher animals neurons send processes to the muscle, in *C. elegans* muscles send processes to neurons receiving their input



Muscle arm development



Muscle arms are formed during the migration of myoblasts at mid embryo-genesis:
As the myoblast moves towards the hypodermis **cell-trunks** (attachments) **are left behind** near the area where the nerve ring will form

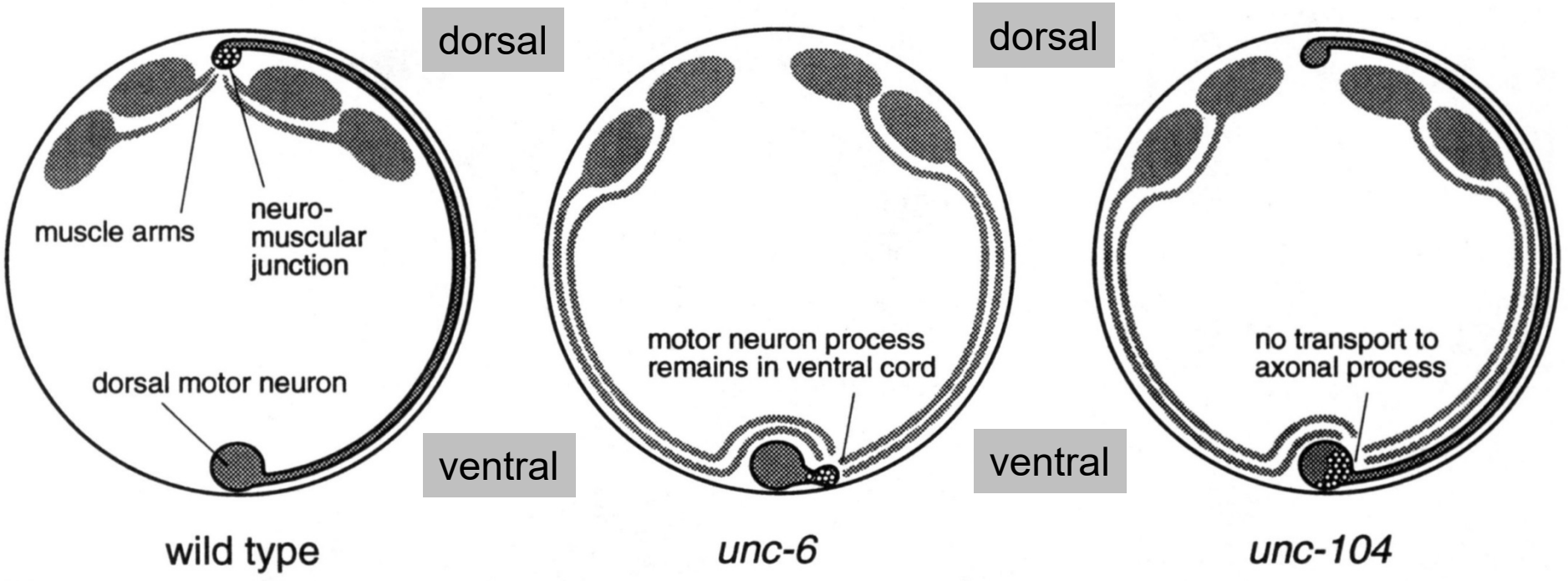
primordial pharynx cells

myoblasts

nerve ring

Muscle arm chemotropism

Muscle arms follow to vesicle-rich areas by an unknown chemoattractant process



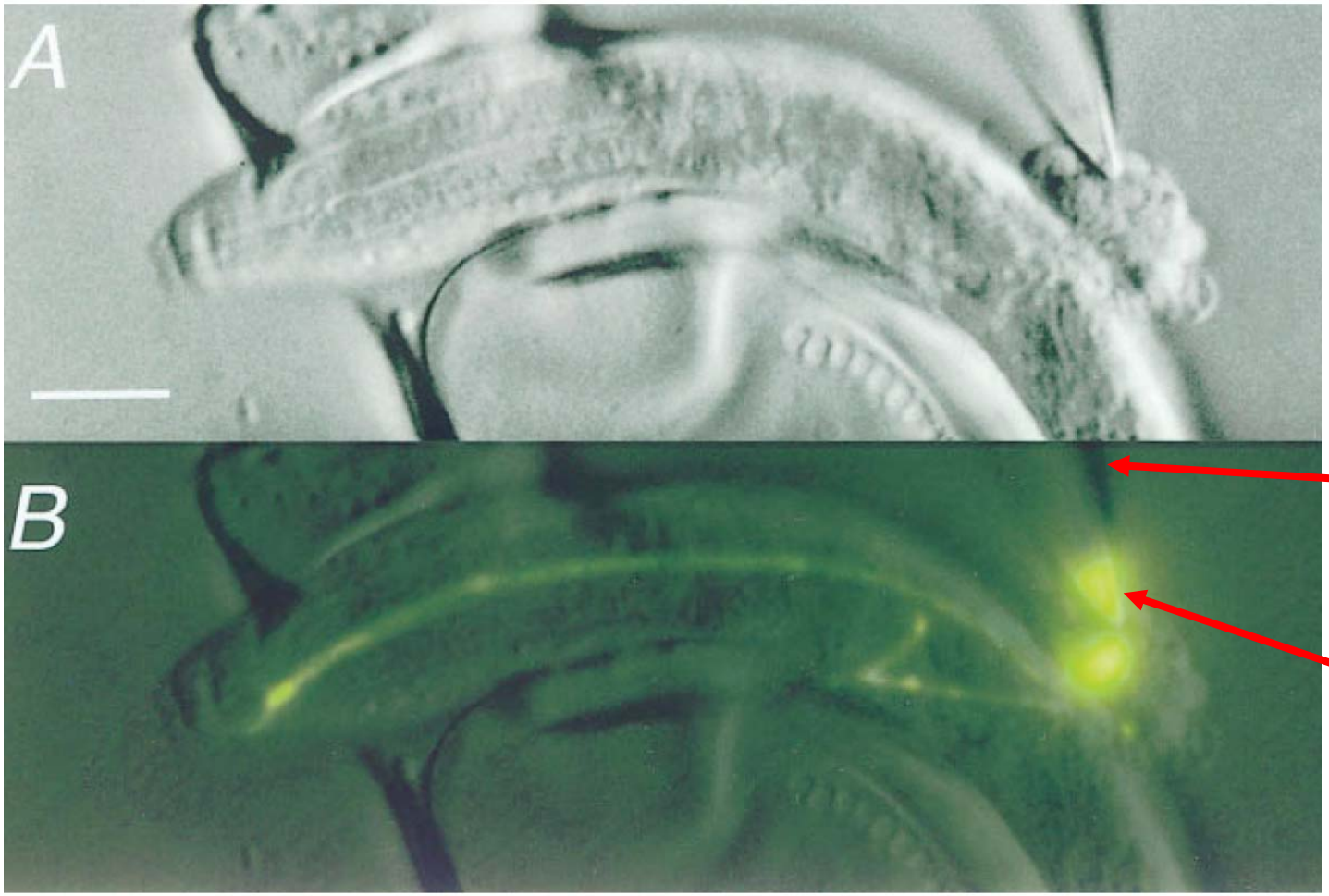
• Muscle arms connect to dorsal synapses formed by a motor neuron with its cell body located ventrally

• In *unc-6* mutants axonal outgrowth is impeded
• Muscle arms follow to the small axonal trunk located ventrally
• *unc-6* encodes the guidance molecule **netrin**

• In *unc-104* mutants axonal outgrowth is normal but vesicle transport is impeded
• Muscle arms follow to the vesicle rich area at the axon hillock

Studying the *C. elegans* nervous system

1) **Laser ablation**: using a laser microbeam, single neurons can be destroyed without damage of the nervous system => assessment of behavioral function of any neuron
2) Recording neuronal activity using electrophysiological **patch clamp** methods:
   - Worms are immobilized with cyanoacrylate **glue** and immersed in physiological saline (so called **M9 buffer**) and the cuticle cut near the GFP-marked neuron



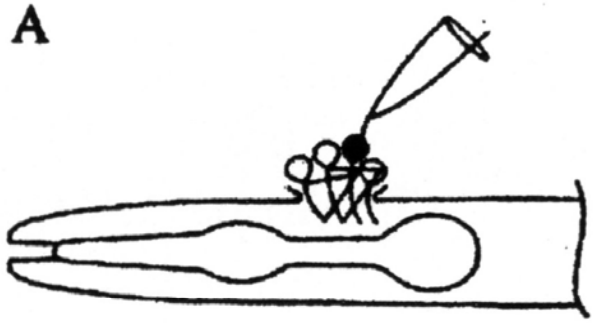
- After cutting the cuticle a bouquet of several neurons appear
- Only the GFP-marked neuron is patched

recording pipette sealed to a ASE neuron

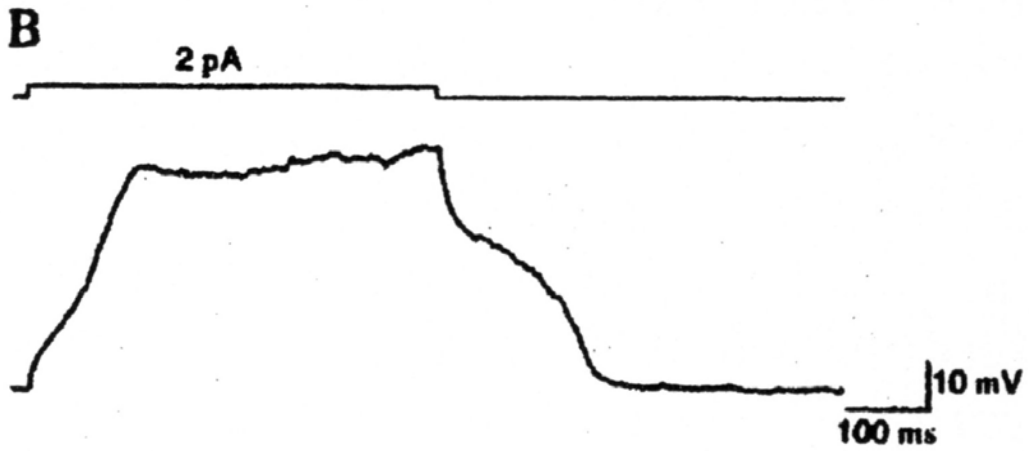
membrane patch inside the pipette

Doing electrophysiology with *C. elegans* neurons

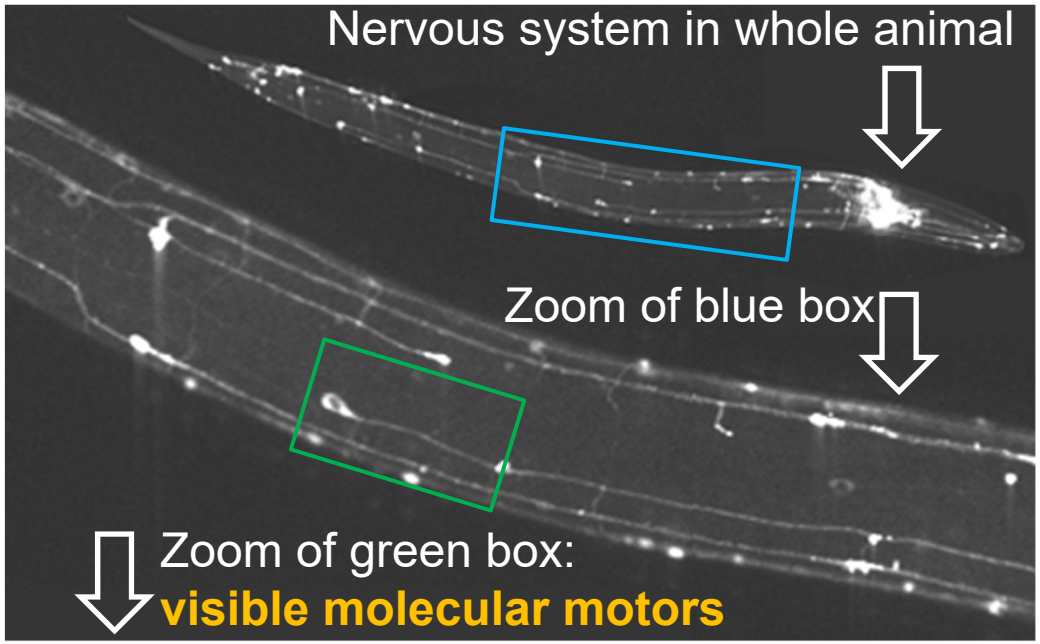
Patch-clamp recording scheme from GFP-labeled neurons after cutting the head epidermis



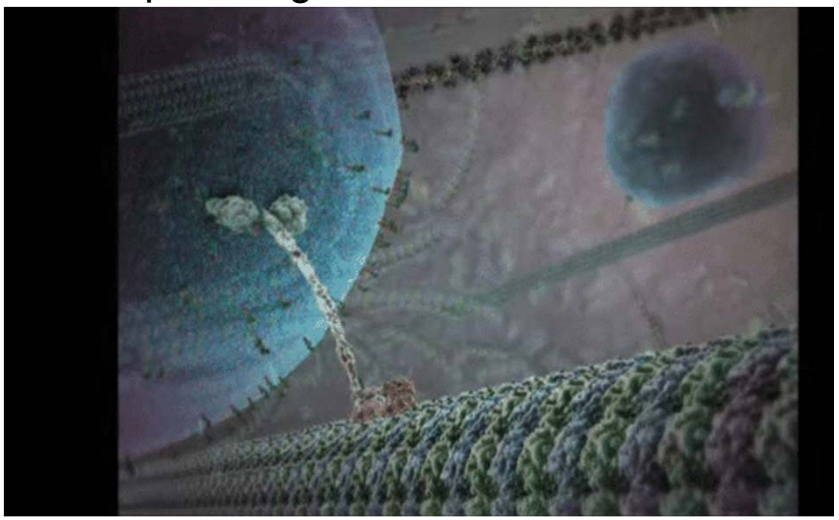
Voltage response of the chemosensory neuron ASE to current application (2 pA)

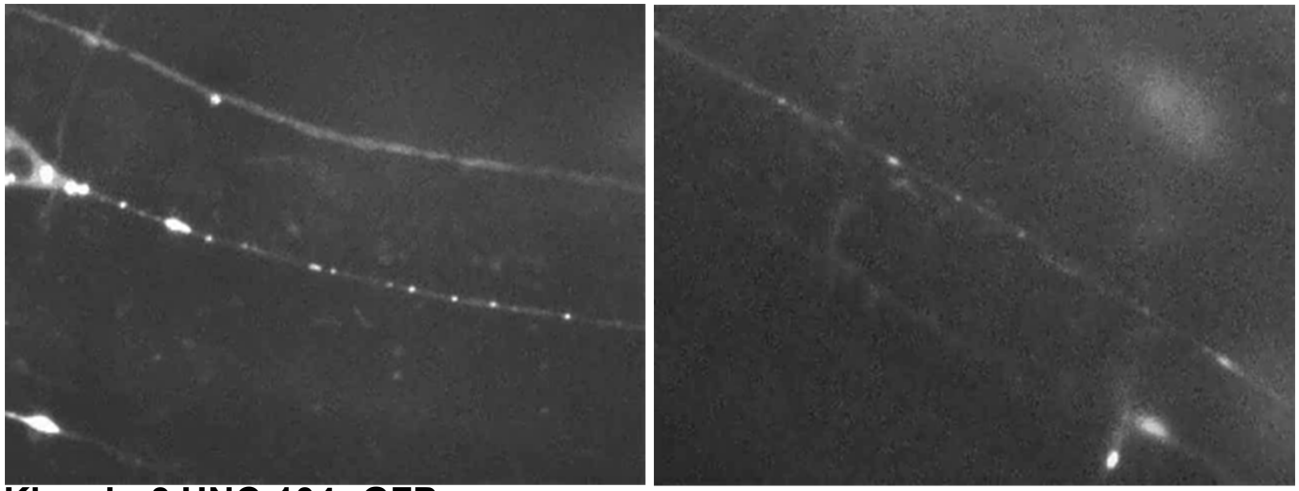


Wagner-Lab: How are molecular motors regulated in *C. elegans* neurons?



Kinesins are molecular motors that transport cargo and walk on microtubule

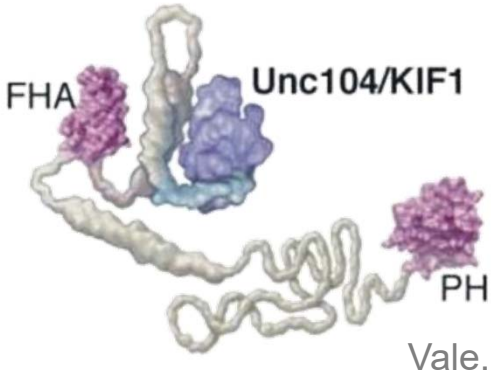




Kinesin-3 UNC-104::GFP

http://life.nthu.edu.tw/~laboiw/

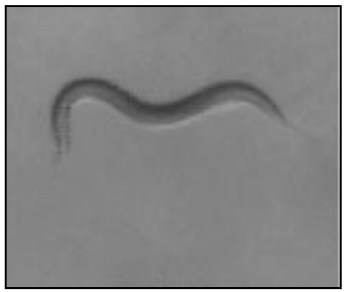
Importance of kinesin-3 UNC-104 (KIF1A)



Vale. **2003**. *Cell*

- Anterograde transport of synaptic vesicles
- *unc-104*/kif1A loss-of-function mutants have **severe synaptic vesicle transport defects** (death or paralysis)

KIF1A knockout mice (Yonekawa et al. **1998**. *JCB*)

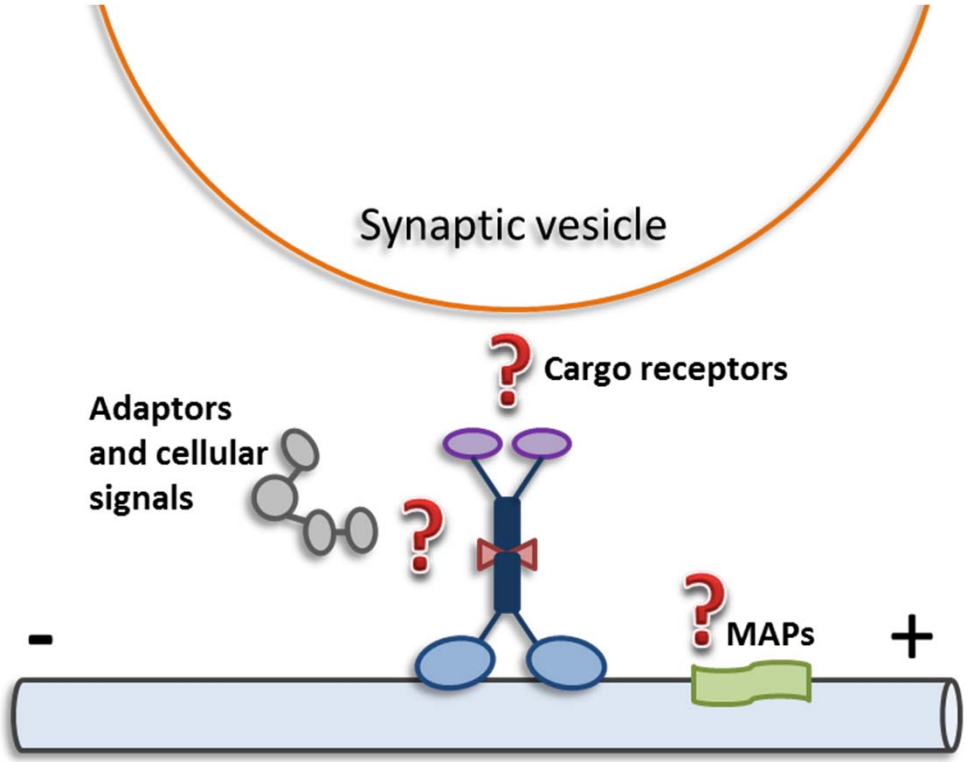


C. elegans wild type

C. elegans unc-104

Synaptic vesicle retention in neuronal cell bodies

Questions Wagner-Lab



How do motors recognize their cargo?

•Membrane receptors, scaffolding proteins, lipids…

How is cargo/vesicle transport regulated?

•Direct motor phosphorylation

•Cargo binding triggers motor activity and directionality

•Scaffolding proteins and adaptor binding

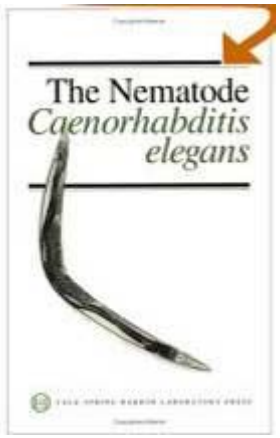
•Calcium binding and phosphorylation of motor adaptors

•Signaling events

•Tug-of-war between opposing motors

Literature

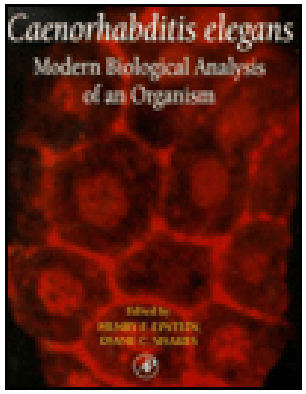
The Nematode *Caenorhabditis elegans*
(The Cold Spring Harbor Monograph Series)
by **William B. Wood**



667 pages

June **1988**

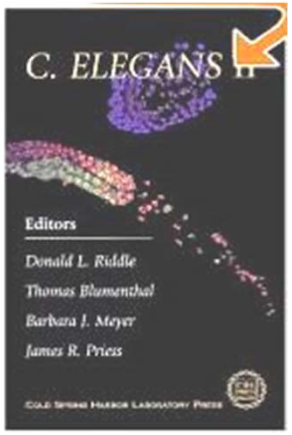
Caenorhabditis elegans:
Modern Biological Analysis of an Organism
(Methods in Cell Biology)
by **Henry F. Epstein**



659 pages

October **1995**

C. ELEGANS II
(Cold Spring Harbor Monograph)
by **Donald L. Riddle**

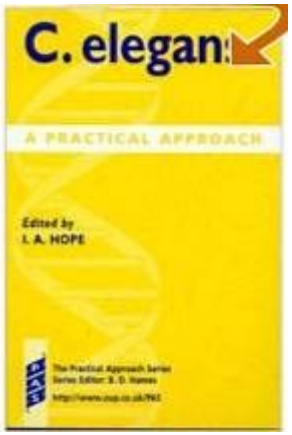


1222 pages

January **1998**

Literature

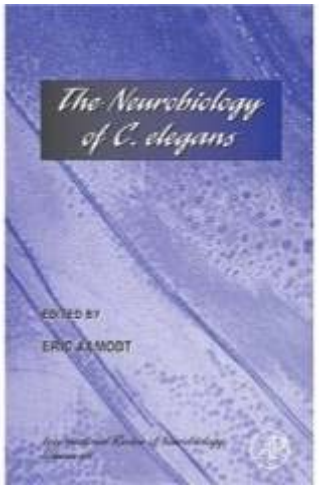
C. elegans: A Practical Approach
(Oxford University Press)
by **Ian A. Hope**



304 pages

December **1999**

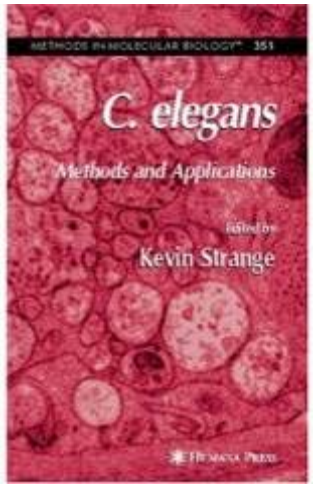
The Neurobiology of *C. elegans*
(Academic Press)
by **Eric James Aamodt**



248 pages

January **2006**

C. elegans: Methods and Applications
(Methods in Molecular Biology)
by **Kevin Strange**



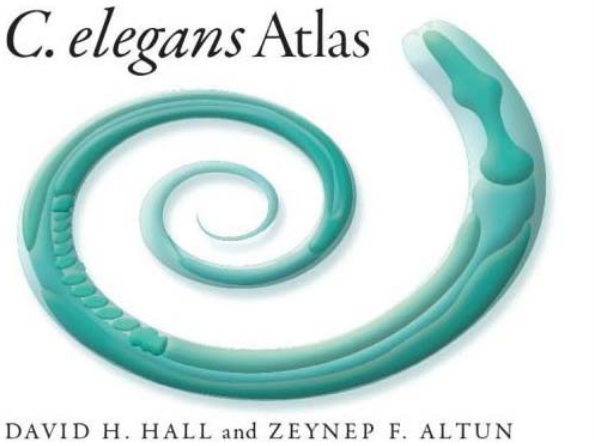
308 pages

August **2006**

Literature

C. elegans Atlas
(CSH press)
by **David H. Hall** and **Zeynep F. Altun**

http://www.wormatlas.org/



300 pages

Nov. **2007**

WormBook
THE ONLINE REVIEW OF *C. elegans* BIOLOGY

WormBook

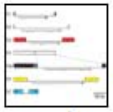
THE ONLINE REVIEW OF *C. elegans* BIOLOGY

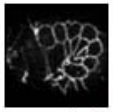
WormBook is a comprehensive, open-access collection of original, peer-reviewed chapters covering topics related to the biology of *Caenorhabditis elegans* and other nematodes. **Wormbook** also contains: **WormMethods**, a collection of protocols for nematode researchers; **WormHistory**, personal perspectives on *C. elegans* research; and the **Worm Breeder's Gazette**, an informal, non-refereed, biannual newsletter for the interchange of ideas and information related to *C. elegans* and other nematodes.

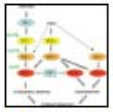
http://www.wormbook.org/

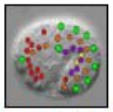
WormBook Sections

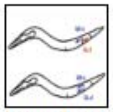
C. elegans


Genetics and genomics

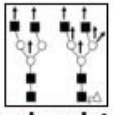

Developmental control


Signal transduction


Molecular biology


Post-embryonic development


Neurobiology and behavior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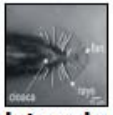
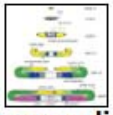

Sex determination


Evolution and ecology


Cell biology


The germ line


Disease models and drug discovery

Other nematodes

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WormBook: The Online Review of C. elegans Biology [Internet].
Pasadena (CA): WormBook; 2005-.
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2. 
C. elegans II. 2nd edition.
Riddle DL, Blumenthal T, Meyer BJ, et al., editors.
Cold Spring Harbor (NY): Cold Spring Harbor Laboratory Press; 1997.
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3. 

Madame Curie Bioscience Database [Internet].
Austin (TX): Landes Bioscience; 2000-.
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4. 
Molecular Biology of the Cell. 4th edition.
Alberts B, Johnson A, Lewis J, et al.
New York: Garland Science; 2002.
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5. 
Molecular Cell Biology. 4th edition.
Lodish H, Berk A, Zipursky SL, et al.
New York: W. H. Freeman; 2000.
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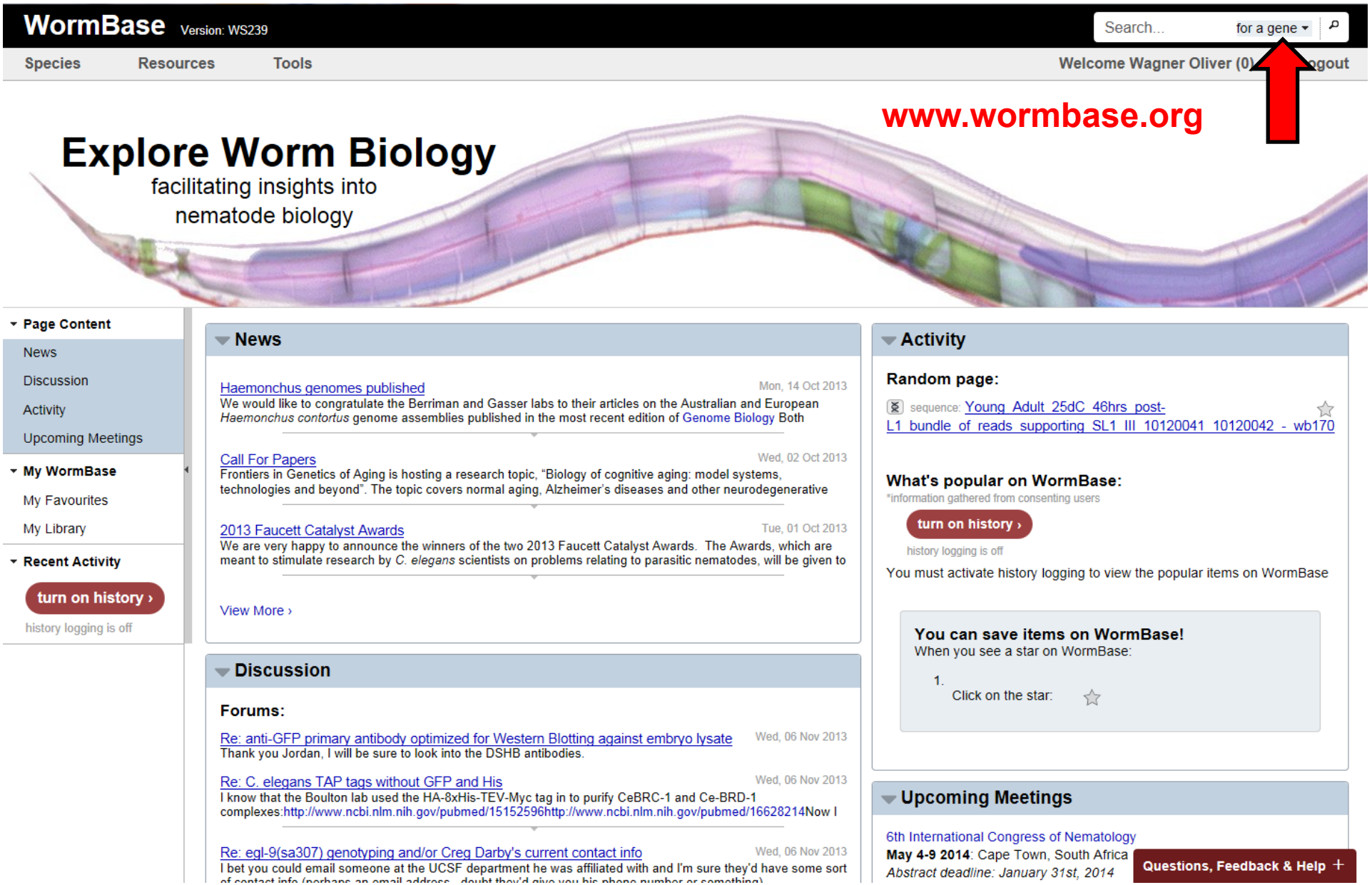
6. 
TRP Ion Channel Function in Sensory Transduction and Cellular Signaling Cascades.
Liedtke WB, Heller S, editors.
Boca Raton (FL): CRC Press; 2007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Wed, 06 Nov 2013
Thank you Jordan, I will be sure to look into the DSHB antibodies.
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Re: egl-9(sa307) genotyping and/or Creg Darby's current contact info
Wed, 06 Nov 2013
I bet you could email someone at the UCSF department he was affiliated with and I'm sure they'd have some sort
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Random page:
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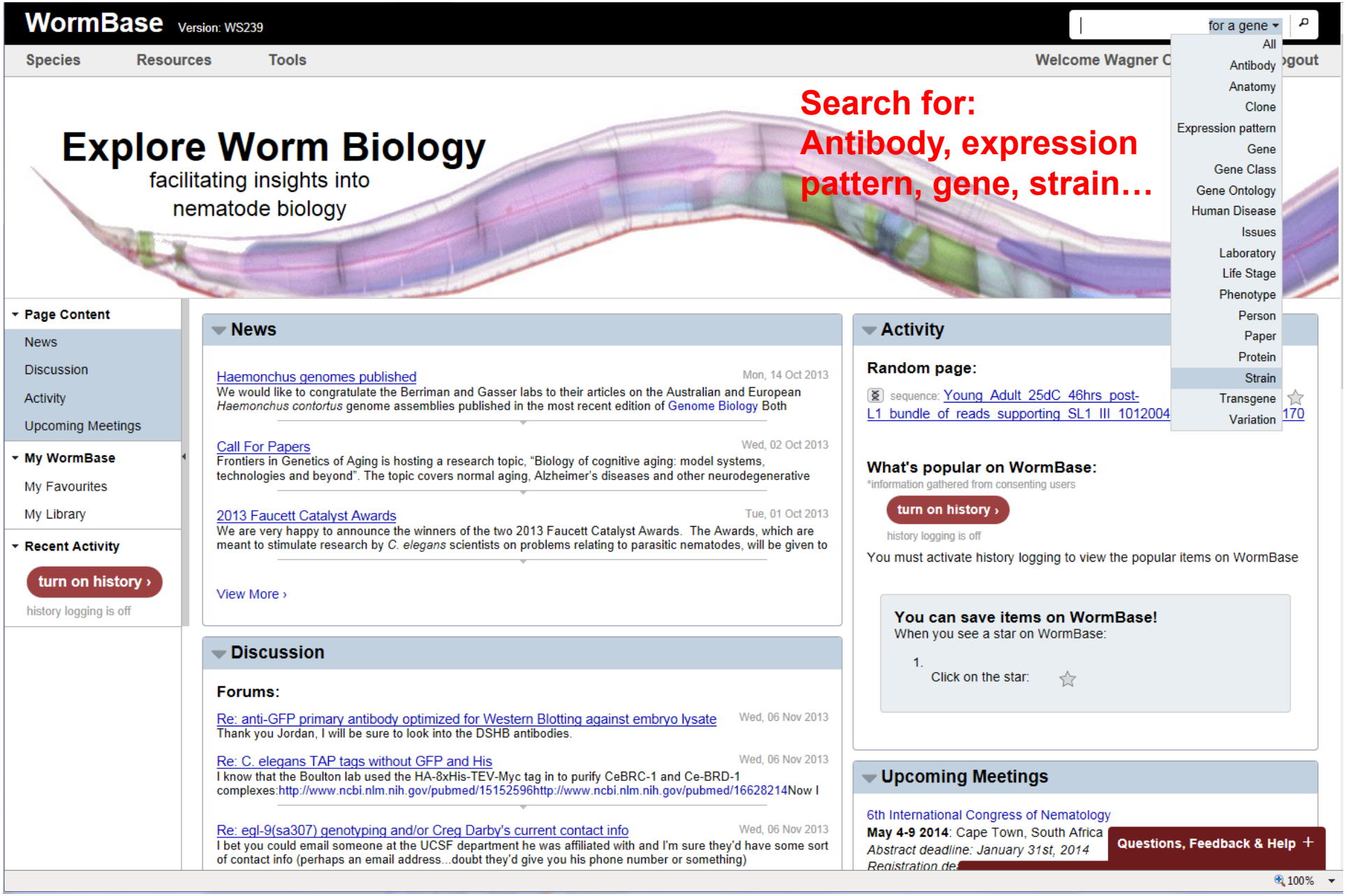
May 4-9 2014: Cape Town, South Africa
Abstract deadline: January 31st, 2014
Questions, Feedback & Help +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Wed, 06 Nov 2013
I bet you could email someone at the UCSF department he was affiliated with and I'm sure they'd have some sort of contact info (perhaps an email address...doubt they'd give you his phone number or something)
Activity
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170
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*information gathered from consenting users
turn on history ›
history logging is off
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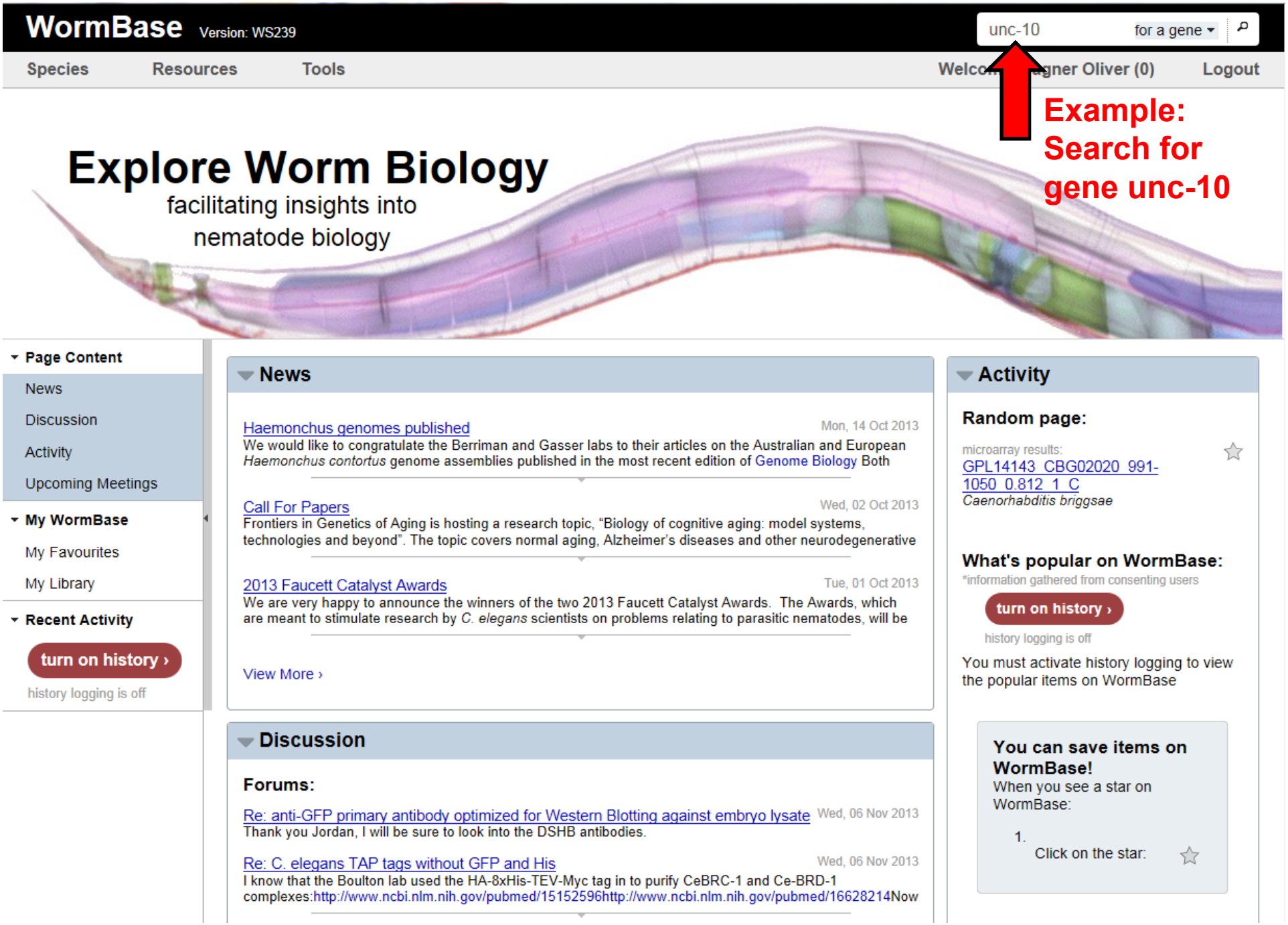
1. Click on the star:
Upcoming Meetings
6th International Congress of Nematology
May 4-9 2014: Cape Town, South Africa
Abstract deadline: January 31st, 2014
Questions, Feedback & Help +
100%


WormBase Version: WS239
unc-10
for a gene
Species
Resources
Tools
Logout
Example: Search for gene unc-10
Explore Worm Biology
facilitating insights into nematode biology
Page Content
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My Library
Recent Activity
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News
Haemonchus genomes published
Mon, 14 Oct 2013
We would like to congratulate the Berriman and Gasser labs to their articles on the Australian and European Haemonchus contortus genome assemblies published in the most recent edition of Genome Biology Both
Call For Papers
Wed, 02 Oct 2013
Frontiers in Genetics of Aging is hosting a research topic, "Biology of cognitive aging: model systems, technologies and beyond". The topic covers normal aging, Alzheimer's diseases and other neurodegenerative
2013 Faucett Catalyst Awards
Tue, 01 Oct 2013
We are very happy to announce the winners of the two 2013 Faucett Catalyst Awards. The Awards, which are meant to stimulate research by C. elegans scientists on problems relating to parasitic nematodes, will be
View More ›
Discussion
Forums:
Re: anti-GFP primary antibody optimized for Western Blotting against embryo lysate
Wed, 06 Nov 2013
Thank you Jordan, I will be sure to look into the DSHB antibodies.
Re: C. elegans TAP tags without GFP and His
Wed, 06 Nov 2013
I know that the Boulton lab used the HA-8xHis-TEV-Myc tag in to purify CeBRC-1 and Ce-BRD-1 complexes:http://www.ncbi.nlm.nih.gov/pubmed/15152596http://www.ncbi.nlm.nih.gov/pubmed/16628214Now
Activity
Random page:
microarray results:
GPL14143_CBG02020_991-1050_0.812_1_C
Caenorhabditis briggsae
What's popular on WormBase:
*information gathered from consenting users
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When you see a star on WormBase:
1. Click on the star:

Gene » *unc-10*

Page Content
- Overview
- Expression
- External Links
- Gene Ontology
- Genetics
- History
- Homology
- Human Diseases
- Interactions
- Location
- Phenotypes
- Reagent
- References
- Sequences

Tools
- Tree Display
- Genetic Map
- Nucl. Aligner

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Recent Activity
turn on history ›
history logging is off

Overview

unc-10 (UNCoordinated)

Short description

unc-10 encodes a protein with zinc-finger, Q/N-rich, PDZ, and C2 domains that is homologous to vertebrate Rim1, a presynaptic protein which binds, and effects the activity of, synaptic vesicle-associated GTP-Rab3; UNC-10 is required for normal locomotion and synaptic transmission, and localizes to a subdomain of presynaptic termini, where it probably acts to regulate the priming step of presynaptic vesicle fusion by promoting conformational changes in syntaxin.

Date last updated: 17 Jun 2004
Curator: Kimberly Van Auken
Paper evidence: Schafer, Sanchez, & Kenyon, 1996; Koushika et al., 2001; Karlin, Brocchieri, Bergman, Mrazek, & Gentles, 2002; Serio & Lindquist, 1999; Michelitsch & Weissman, 2000; Serio & Lindquist, 2001; Scheibel & Lindquist, 2001; Osherovich & Weissman, 2002

Paper evidence

- Details
- From *C. elegans I* and *II*
- Curatorial remarks

Species: *Caenorhabditis elegans*
Sequence: T10A3.1
Other names: *rim-1*, CELE_T10A3.1
Type: protein coding
Gene class: unc
Clone: T10A3
Parent seq: T10A3
Named by: Jonathan Hodgkin
WormBase ID: WBGene00006750

Genetics

Reference allele: *e102*

Alleles:

Search: Save table

Show 10 entries

Allele	Molecular change	Locations	Protein effects	Protein change	Amino acid position	Isoform	# of Phenotypes	Method
ad591	Not curated						1	Allele
cn257	Not curated						0	Allele
e102	Substitution	Intron	Splice_site				11	Substitution allele
e126	Not curated						0	Allele
gk284830	Substitution	UTR 3						

Questions, Feedback & Help +

WBVar00047961	SNP, Predicted SNP	Substitution	Coding exon	Silent	0
WBVar00047966	SNP, Predicted SNP	Substitution	Coding exon	Silent	0
WBVar00047971	SNP, Predicted SNP	Substitution	Intron		0
WBVar00047976	SNP, Predicted SNP	Substitution	Intron		0
WBVar00047981	SNP, Predicted SNP	Substitution	Intron		0
WBVar00080358	SNP, Predicted SNP	Substitution	Intron		0
WBVar00080361	SNP, Predicted SNP	Substitution	Coding exon	Silent	0
WBVar00098970	SNP, Predicted SNP	Substitution	Intron		0
WBVar00098971	SNP, Predicted SNP	Substitution	Intron		0

Strains:

Carrying *unc-10* alone		
	Available from the CGC	**Other strains**
CB102, DA591, NM1657	DA711, DA726, MT5222	BC13829

Save table

Strain	Genotype	Available from CGC?
BC13829		no
CB102	unc-10(e102)X.	yes
DA591	unc-10(ad591)X.	yes
DA711	unc-10(e102) dpy-6(e14) X.	yes
DA726	unc-10(e102) eat-13(ad522) X.	yes
MT5222	sem-5(n2030)/unc-10(e102) xol-1(y9) dpy-6(e14) X.	yes
NM1657	unc-10(md1117) X.	yes

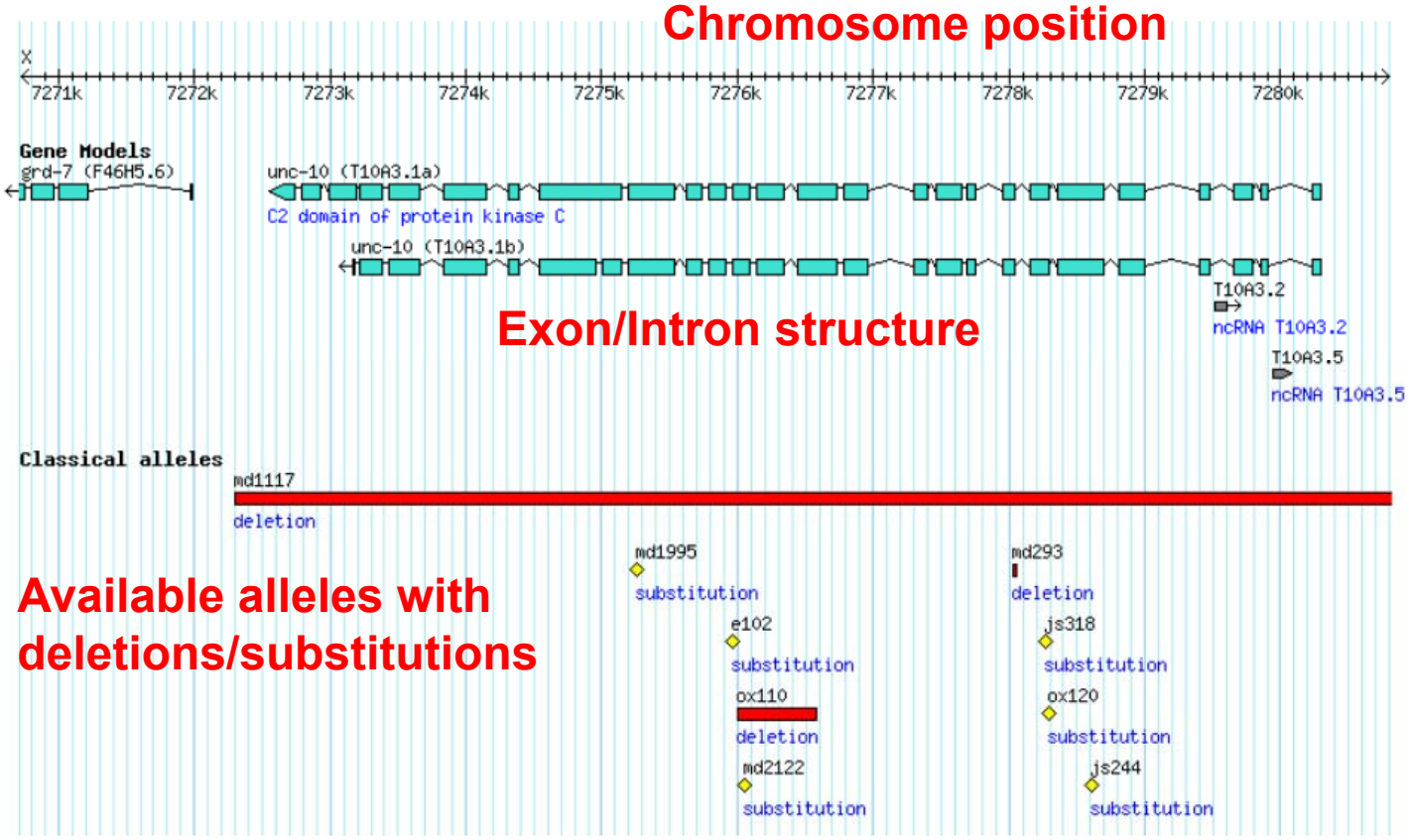
Location

Genetic position: X:-1.78 +/- 0.001 cM
Genomic position: X:7272324..7280320

DA726	unc-10(e102) eat-13(ad522) X.	yes
MT5222	sem-5(n2030)/unc-10(e102) xol-1(y9) dpy-6(e14) X.	yes
NM1657	unc-10(md1117) X.	yes

Location

Genetic position: X:-1.78 +/- 0.001 cM
Genomic position: X:7272324..7280320



Tree Display

expand all nodes | collapse all nodes | view schema

Name WBGene00006750 **Class** Gene Change

Homology

Best BLASTP matches:

BLAST e-value	Species	Hit	Description	% Length
0	*C. remanei*	RP:RP40439	CRE-UNC-10	100.0%
0	*C. japonica*	JA:JA63550	CJP-UNC-10	100.0%
0	*C. brenneri*	CN:CN17997	CBN-UNC-10	92.6%
0	*C. briggsae*	BP:CBP29870	CBR-UNC-10	100.0%
2.7e-152	*B. malayi*	BM:BM22651	Bm5702, isoform d	43.5%
4.8e-130	*D. melanogaster*	FLYBASE:CG33547	Flybase gene name is Rim-PK	78.4%
4e-123	*H. sapiens*	ENSEMBL:ENSP00000384892	regulating synaptic membrane exocytosis protein 2 isoform a **(RIM)**	71.2%
1.4e-115	*R. norvegicus*	SW:Q9JIR4	Regulating synaptic membrane exocytosis protein 1	56.9%
3.3e-109	*P. pacificus*	PP:PP33892	PPA00369	40.9%
4.9e-23	*C. elegans*	WP:CE43920	PQN-15	28.9%
4e-15	*S. cerevisiae*	SGD:YKL054C	RNAPII degradation factor, forms a complex with Rad26p in chromatin, enables ubiquitination and proteolysis of RNAPII present in an elongation complex; mutant is deficient in Zip1p loading onto chromosomes during meiosis	28.0%

▸ View full BLASTP List

Human Orthologs:

Ortholog	Method
ENSEMBL:ENSP00000361769	EnsEMBL-Compara Panther
ENSEMBL:ENSP00000439287	EnsEMBL-Compara
RIMS1	EnsEMBL-Compara TreeFam
RIMS2	EnsEMBL-Compara TreeFam
ENSEMBL:ENSP00000264839	Inparanoid_7 Panther
ENSEMBL:ENSP00000383959	Inparanoid_7
RIMS4	Panther
RIMS3	Panther
ENSEMBL:ENSP00000371553	Panther

Curated Nematode Orthologs:

Species	Ortholog	Method
C. remanei	*Cre-unc-10*	Inparanoid_7 OMA TreeFam WormBase-Compara Hillier-set

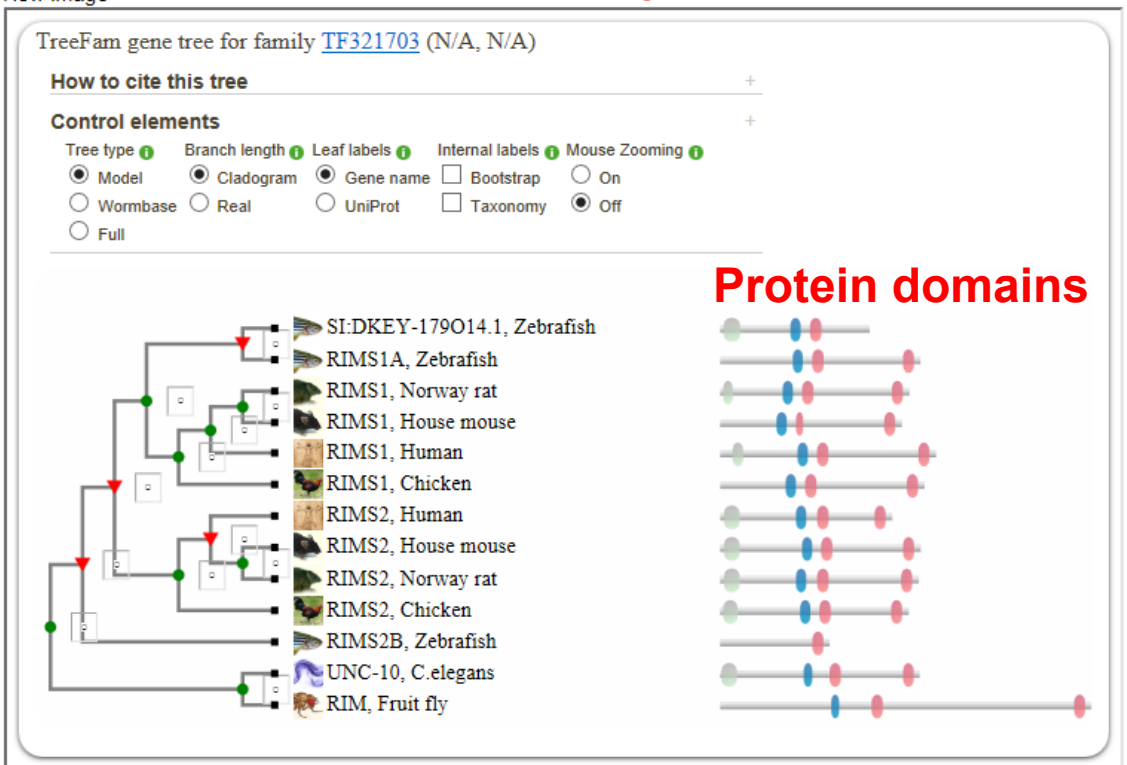
C. sp.5	Csp5_scaffold_00022.g1323.t2	WormBase-Compara
C. angaria	Cang_2012_03_13_09484.g22094.t1	WormBase-Compara

Protein domains: C2 calcium-dependent membrane targeting
C2 calcium/lipid-binding domain, CaLB
PDZ domain
Zinc finger, FYVE/PHD-type
Zinc finger, RING/FYVE/PHD-type

TreeFam: **Treefam (ID:TF321703)**

Gene family tree

View image



Phylogenetic trees provided by theTreefam project.

Expression

Anatomic Expression Patterns:

Clickable

Pattern	Type	Description	Expressed in	Life stage	GO term	Transgene
Chronogram1591 view images	Reporter gene	Original chronogram file: chronogram.473.xml details				sEx13829
Expr2418 view images	Antibody	Rim staining was restricted to discrete puncta in synapse-rich regions of the nervous system including the nerve ring, the ventral nerve cord and the dorsal nerve cord. Localized Rim protein was observed in all larval stages. details	ventral nerve cord nerve ring dorsal nerve cord	L1 larva L4 larva L2 larva L3 larva	synaptic vesicle details	
Expr1017493 view images		Developmental gene expression time-course. Raw data can be downloaded from ftp://caltech.wormbase.org/pub/wormbase/datasets-published/levin2012 details				

Anatomy terms: nerve ring
ventral nerve cord
dorsal nerve cord

Expression Cluster: ▸ 37 expression clusters

Microarray, Tiling Array and RNAseq: Perform Clustering Analysis in SPELL (documentation)

Microarray "topology map" data: T10A3.1
K03A1.3

Phenotypes

Phenotypes: Alleles for which the sequence change is known are listed in **boldface**.

The following phenotypes have been observed in unc-10:

Phenotype	Supporting Evidence

Phylogenetic trees provided by theTreefam project.

Expression

Anatomic Expression Patterns:

Clickable

UNC-10 is solely expressed in the nervous system

Expr1017493
view images

data can be downloaded from ftp://caltech.wormbase.org/pub/wormbase/datasets-published/levin2012

details

Anatomy terms: nerve ring
ventral nerve cord
dorsal nerve cord

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The following phenotypes have been observed in unc-10:

Phenotype	Supporting Evidence

Phenotypes

Phenotypes: Alleles for which the sequence change is known are listed in **boldface**.

The following phenotypes have been observed in unc-10:

Phenotype	Supporting Evidence
acetylcholinesterase inhibitor resistant	Allele: ***e102*** — details
locomotion variant	Allele: ***e102*** — details RNAi: 89808 — details
pharyngeal pumping irregular	Allele: ***e102*** — details
antihelmintic response variant	Allele: ***e102*** — details
backing increased	Allele: ***e102*** — details
small	Allele: ***e102*** — details
activity level variant	Allele: ***e102*** — details
presynaptic vesicle cluster localization variant	Allele: ***md1117*** — details
thin	Allele: ***e102*** — details
aldicarb resistant	RNAi: 60642 — details 60639 — details 60644 — details 60643 — details 60640 — details 60641 — details 60638 — details

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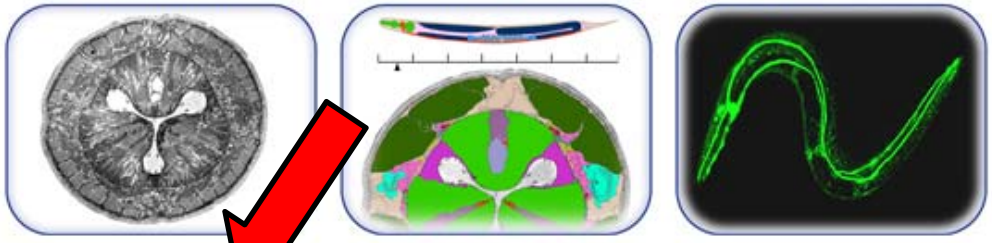
Worm Image | Slidable Worm | Gene Expression



Individual Neurons | Cell Identification | Glossary

Neuronal Wiring | Movie Gallery | Cell Lineages

Individual Neurons

Neuron	Lineage	Description
ADAL	AB.plapaaaapp	Ring interneuron
ADAR	AB.prapaaaapp	Ring interneuron
ADEL	AB.plapaaaapa	Anterior deirid, sensory neuron
ADER	AB.prapaaaapa	Anterior deirid, sensory neuron
ADFL	AB.alpppppaa	Amphid neuron
ADFR	AB.praaappaa	Amphid neuron
ADLL	AB.alpppaad	Amphid neuron
ADLR	AB.praaapaad	Amphid neuron
AFDL	AB.alpppapav	Amphid finger cell
AFDR	AB.praaaapav	Amphid finger cell
AIAL	AB.plppaappa	Amphid interneuron
AIAR	AB.prppaappa	Amphid interneuron
AIBL	AB.plaapappa	Amphid interneuron
AIBR	AB.praapappa	Amphid interneuron
AIML	AB.plpaapppa	Ring interneuron
AIMR	AB.prpaapppa	Ring interneuron
AINL	AB.alaaaalal	Ring interneuron
AINR	AB.alaapaaar	Ring interneuron
AIYL	AB.plpapaaap	Amphid interneuron
AIYR	AB.prpapaaap	Amphid interneuron
AIZL	AB.plapaaapav	Amphid interneuron
AIZR	AB.prapaaapav	Amphid interneuron
ALA	AB.alapppaaa	Neuron, sends processes laterally and along dorsal cord
ALML	AB.arppaappa	Anterior lateral microtubule cell
ALMR	AB.arpppappa	Anterior lateral microtubule cell
ALNL	AB.plapappppap	Neuron associated with ALM
ALNR	AB.prapappppap	Neuron associated with ALM

Individual Neurons List

Select Cell A-C

Select Cell D-P

Select Cell R-V

All Neurons Image - pdf

Longitudinal Tracts - pdf

Pharyngeal Neurons - pdf

Neuronal Wiring and Connectivity

Postembryonic Neurons

Serotonergic Neurons - Loer Lab

Dopaminergic Neurons - Loer Lab

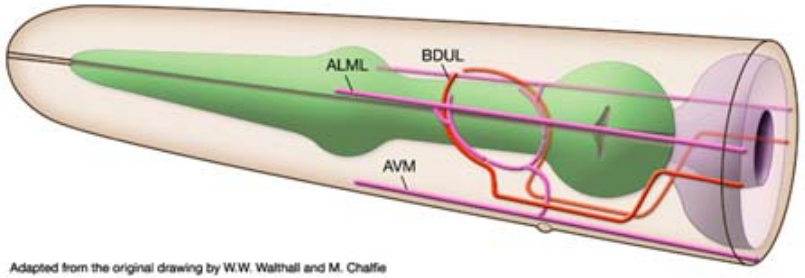
Neurotransmitters Table

Neuropeptide-like Protein Expression Table

Actions of Neurotransmitters Table

ALML, ALMR

Type: Sensory neuron (Mechanosensory)
In MoW: ALM
Male Wiring Project: ALML, ALMR
In Wormbase: ALM, ALML, ALMR
Lineage: AB arppaappa, AB arpppappa
Location: Lateral in mid-body
Description: Anterior lateral microtubule cells, touch receptor neurons
Neurotransmitter: Glutamate. Expresses VGluT, EAT-4 (Lee et al., 1999).
Function: Along with AVM and PLM, sense touch to the body and provide input to the command (inter) neurons (PVC, AVB, AVD, AVA) via both synaptic connections and gap junctions (Chalfie et al., 1985). The touch cells form gap junctions with agonist interneurons and chemical synapses with the antagonist interneurons. Hence, the anterior touch cells ALML/R and AVM form gap junctions with the backward movement interneuron AVD, but they provide synaptic input to the forward interneurons (AVB and PVC) (Kaplan and Driscoll, 1997; Goodman, 2006). See body touch circuit here.
Receptor Expression: Express MEC-2 (stomatin-like), MEC-4 (degenerin), MEC-10 (degenerin) which comprise part of a



Adapted from the original drawing by W.W. Walthall and M. Chalfie

Longitudinal Tracts - pdf

Pharyngeal Neurons - pdf

Neuronal Wiring and Connectivity

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Neurotransmitters Table

Neuropeptide-like Protein Expression Table

Actions of Neurotransmitters Table

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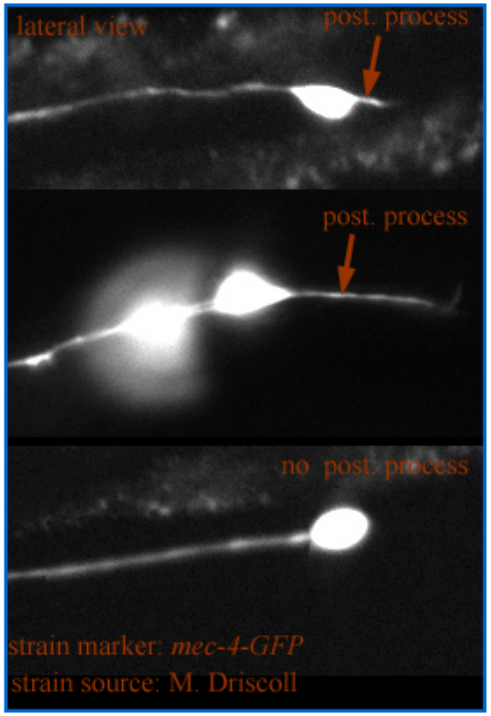
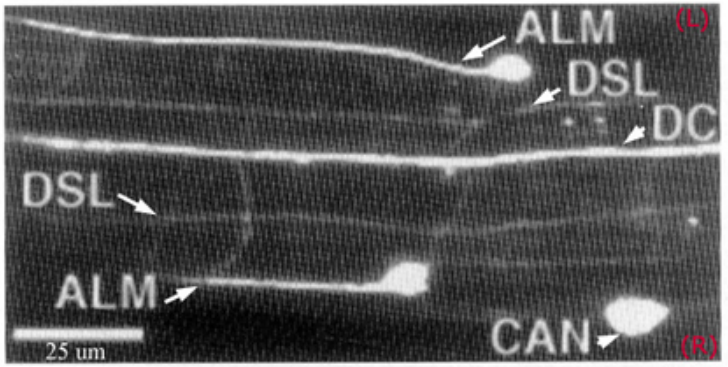
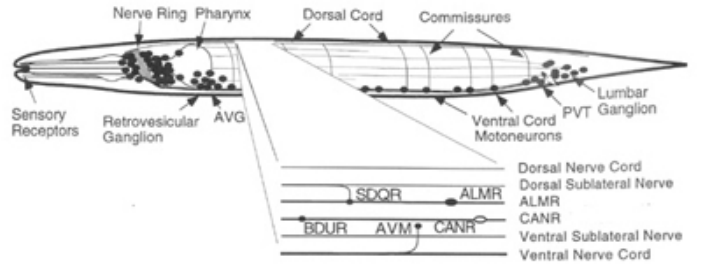
The posterior process coming out of ALM cell body (red arrows, below) is infrequently seen and can be at random legths:



Dorsal view



strain: urIs13 (*unc-119::GFP; pRF4*) source: W. G. Wadsworth



(Right side neurons as visualized from the left side of the animal)
image source: W. G. Wadsworth

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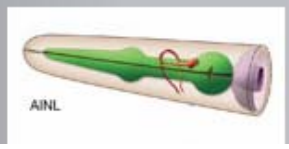

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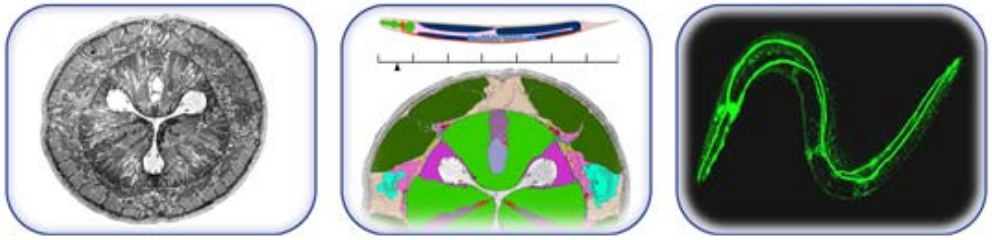

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SW Guide

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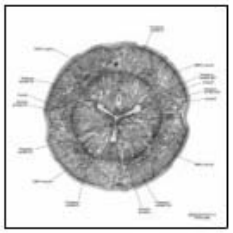
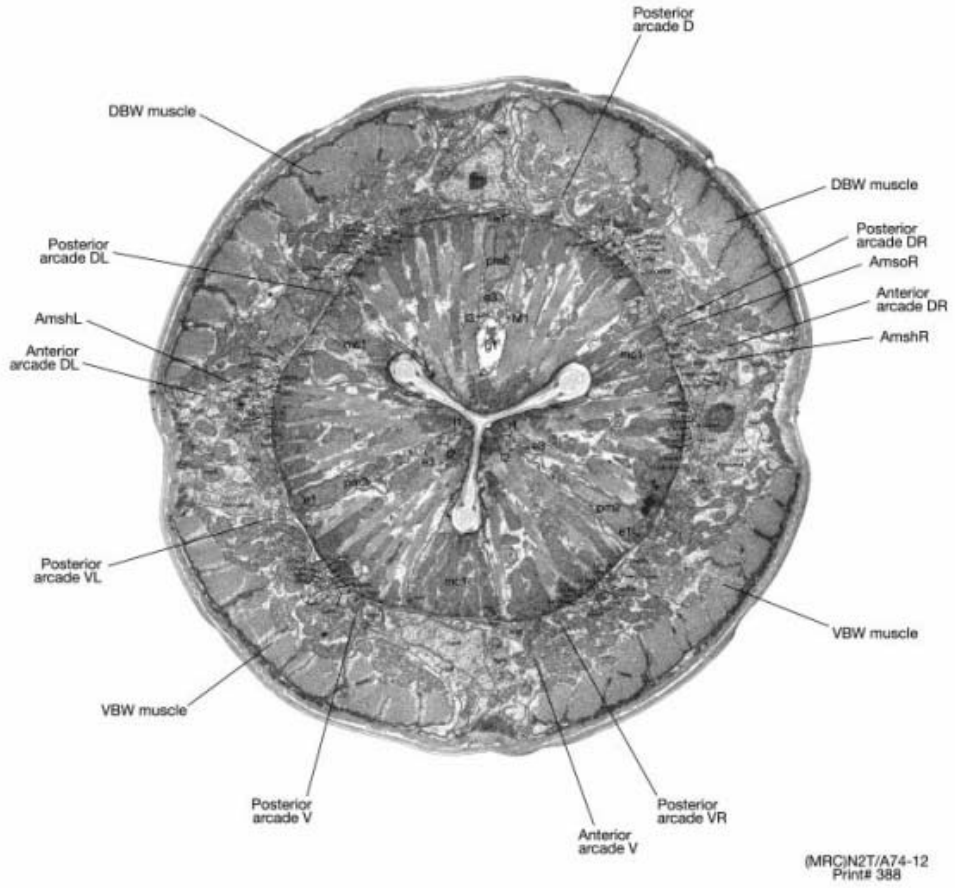
SlidableWorm

Slice #: 30 Go to: Off Labels Transparent Opaque

No. 793





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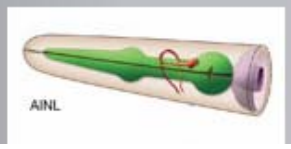
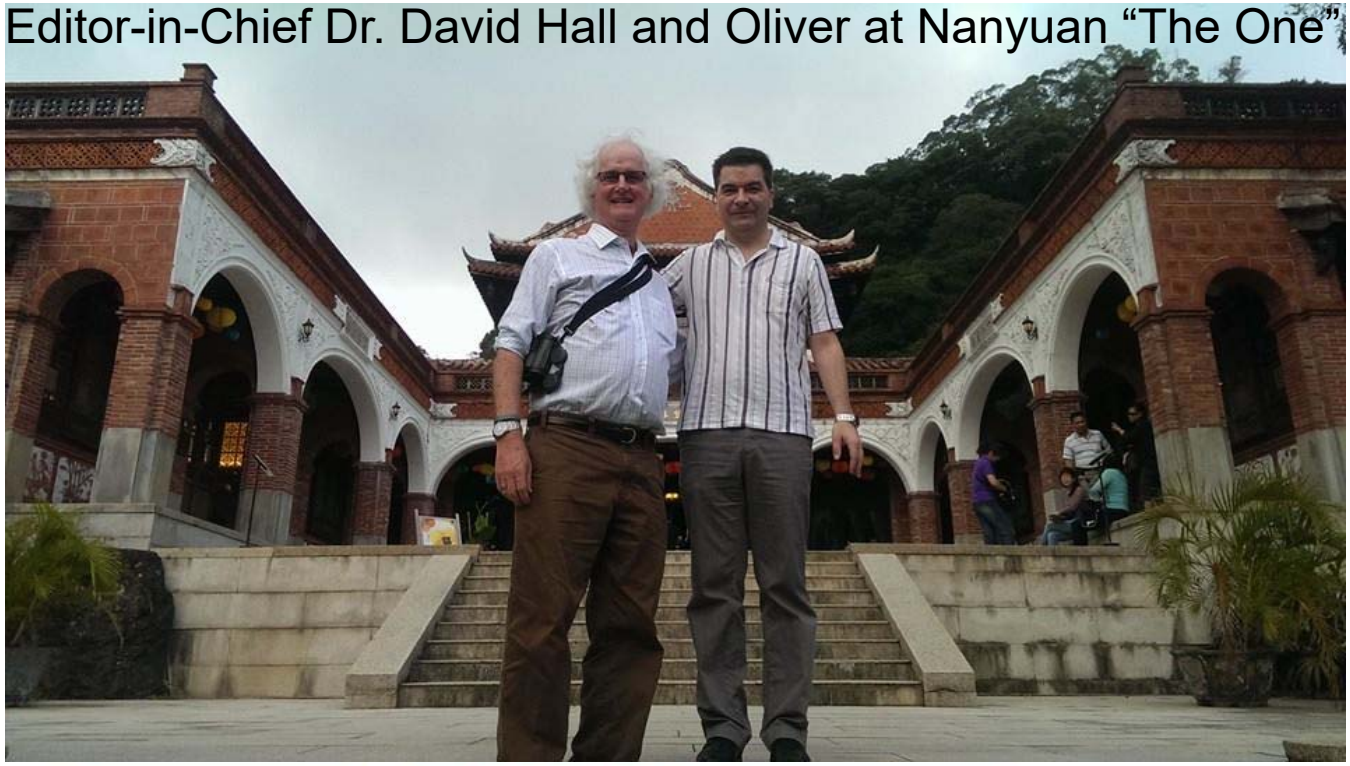


Editor-in-Chief Dr. David Hall and Oliver at Nanyuan "The One"



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- endosome markers for mouse T cells (by Jinshu)
- How to immunoisolate Golgi (by Jinshu)
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- Suspension cells (by scifi)
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Mug
Mug $12.00

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Large Mug $12.00
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C. elegans DNA Large Mug
Large Mug $12.99

C. elegans Yin Yang Mug
Mug $12.00

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Stackable Mug Set (4 mugs) ~~$32.99~~
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c. elegans core facility taiwan

A SERVICE FROM NTU, NTHU, CGU and NCKU

October 29, 2013

http://cecore.life.nthu.edu.tw/

- welcome
- goals and missions
- overview of services
- announcements
- E-learning
- database (login)
- contact us

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C. elegans publications from TAIWAN

Welcome to the CECF Taiwan

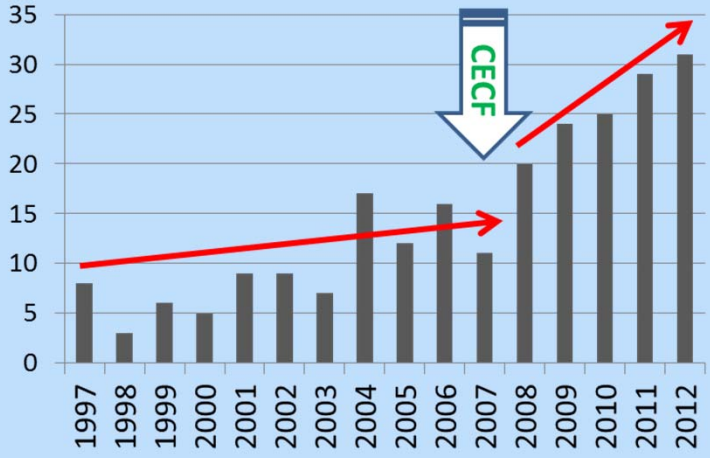
The nematode worm *Caenorhabditis elegans* has become an important tool in the scientific world resulting in over 23,000 publications until now. Fully sequenced genome, 3-day life cycle and a considerable high amount of protein-coding genes (21,000) with high homology to humans making it an attractive model organism.

Our goal is to increase scientific awareness about this important model organism and our mission is to assist creating up new *C. elegans* labs in Taiwan and to offer **non-profit** services for existing worm-labs.

Using worm as a research tool is highly beneficial based on its low cost and its easiness to be adapted after several training courses. We wish to support investigators during their transition from single cell research to *C. elegans* based model organism research providing methodically assistance, sharing mutant strains and plasmids, training students and offering lectures about *C. elegans* based research.

Our mission is to provide knowledge to help researchers to design and conduct experiments without *C. elegans* experience. We assist in developing experiments to test various hypothesis in the nematode that have been otherwise investigated only in cell culture or other models.

C. elegans publications in Taiwan (past 15 years)



OUR SERVICES

Microinjection Facility at NTHU.
Read more >

Gene Gun (Biolistic Particle Delivery System) at NCKU.
Read more >

Center for Strain and Vector Collection at NTU.
Read more >

https://www.facebook.com/CECoreTW

You?

*191 as of 2017 ☺

Thanks for your attention

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Department of Life Science