Altering Rhythmicity: Slow Dance, Fast Dance, Hither and Yon

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Overarching Theme for Talk = A Key Concept in the Grand Challenges in Organismal Biology:

Stability versus Change

as bent by my thinking on

Neural Control of Locomotory Activity

Organisms of Choice for the talk:

- the Pteropod Mollusc, *Clione limacina*
- Cnidarian Medusae

How I will interpret Stability versus Change:

Stability – evaluation of neural circuitry that produces appropriate biomechanical movements to propel an organism in an appropriate direction and in an appropriate time frame. In simple terms – the basic neural and muscular machinery for rhythmic locomotory movements

Change – sensory and integrative circuitry that alters the basic locomotory rhythm to produce advantageous changes in behaviors, such as for feeding, escape, protection, migration, etc.

Class Gastopoda

Subclass Opisthobranchia

Order Gymnosomata

Clione limacina

"Naked" Pteropod

Holoplanktonic

Vertical Migrator

Extreme Feeding Specialist -

Only Eats Shelled Pteropods

(Order Thecosomata)

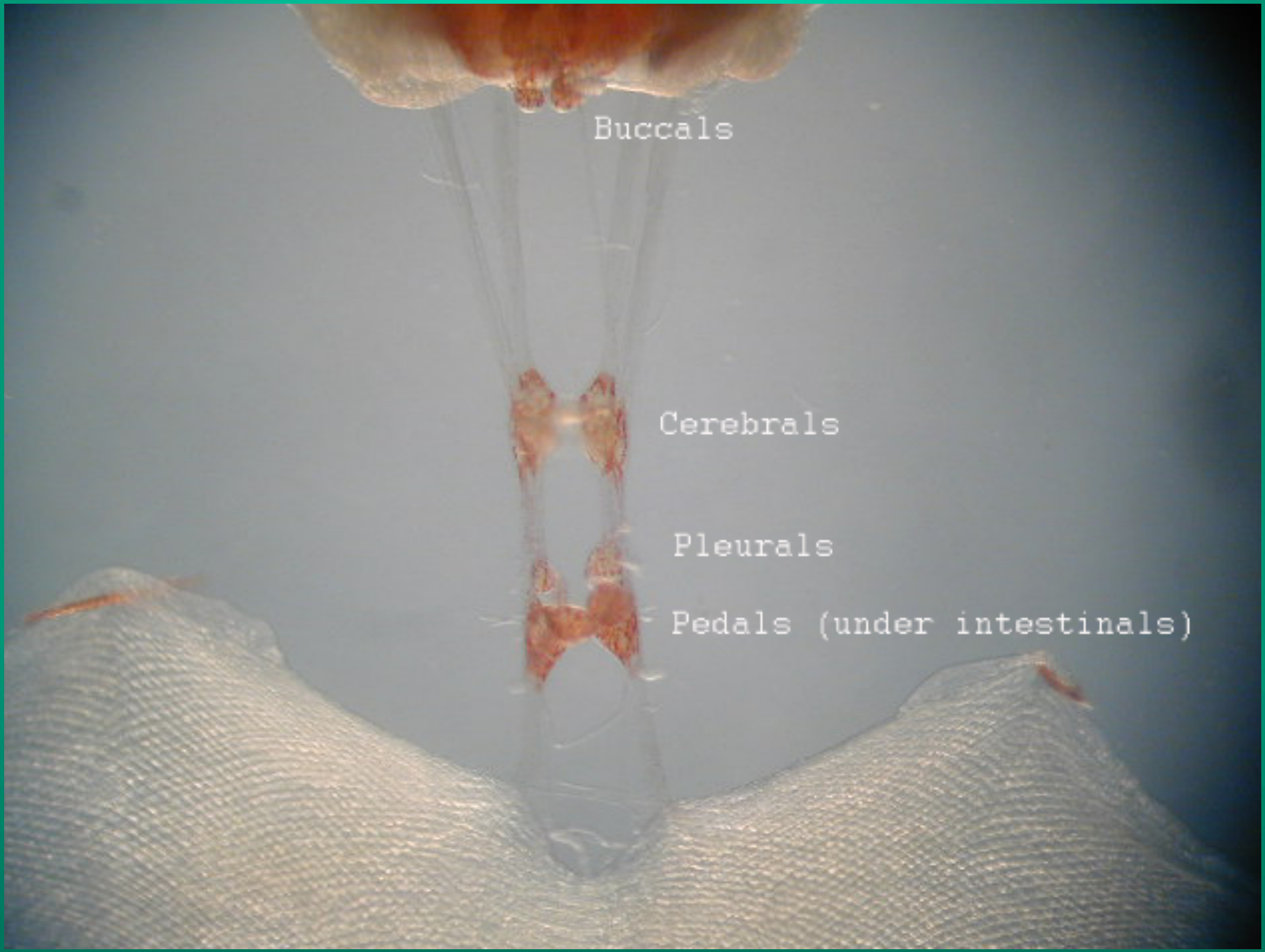
"Wings" – Modified Foot Tissue

"Ptero" – Wing; "Pod" - Foot

Relaxed, Pinned *Clione*

Pins from the fruit of the prickly pear cactus Opuntia sp.

Central Ganglia – Live (anesthetized) Dissection

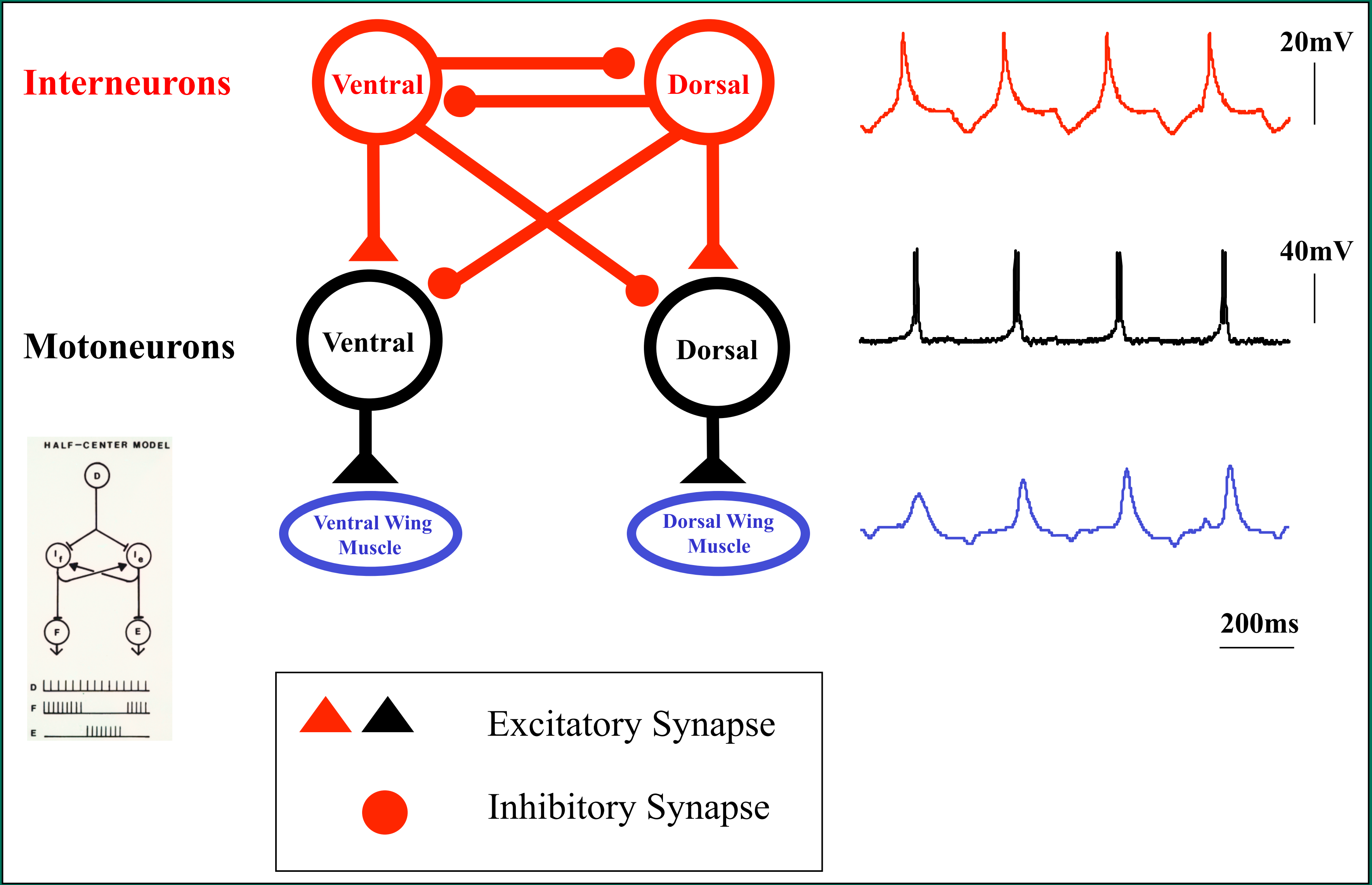


Baseline Activity – Representing Stabilty

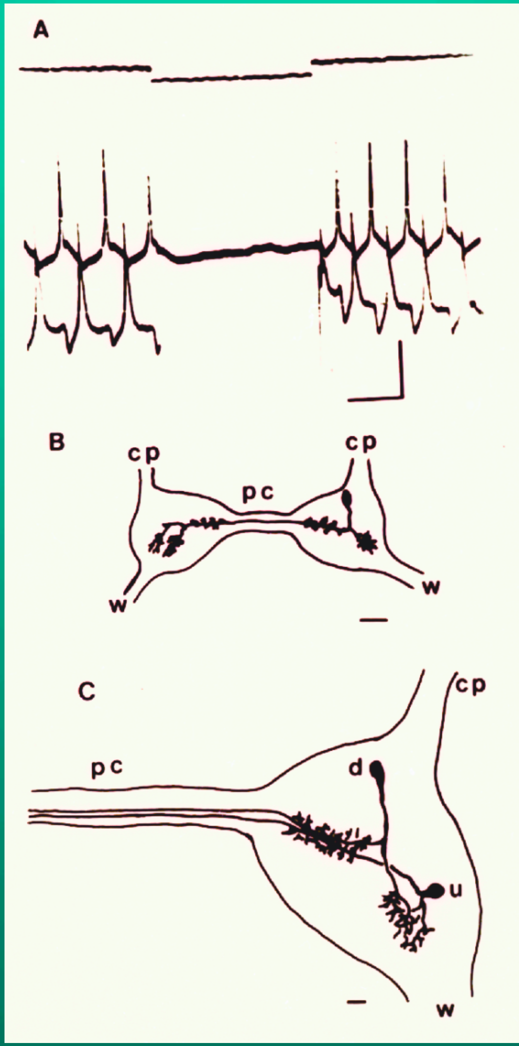
Slow Swimming

- Wing-beat frequency ~ 1 Hz
- Animal movement – hovering or slowly moving upward or downward

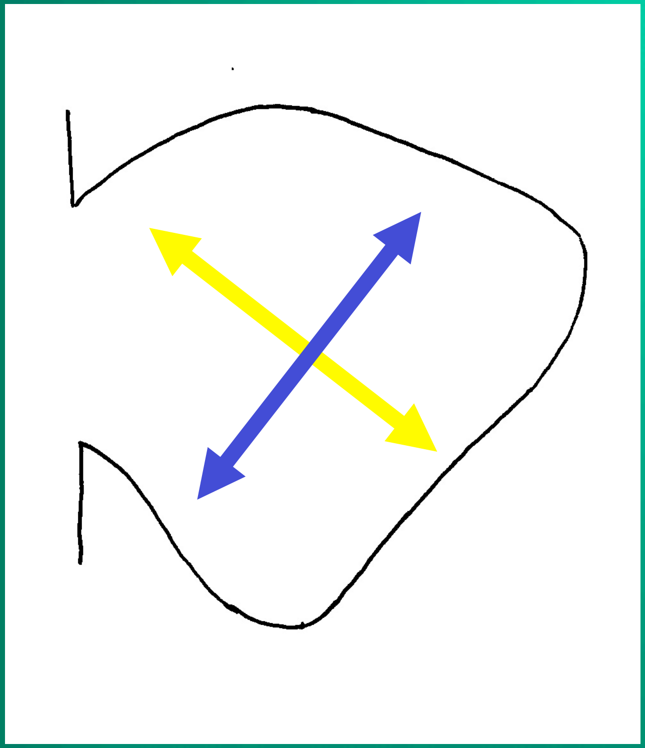
Clione Swim Central Pattern Generator

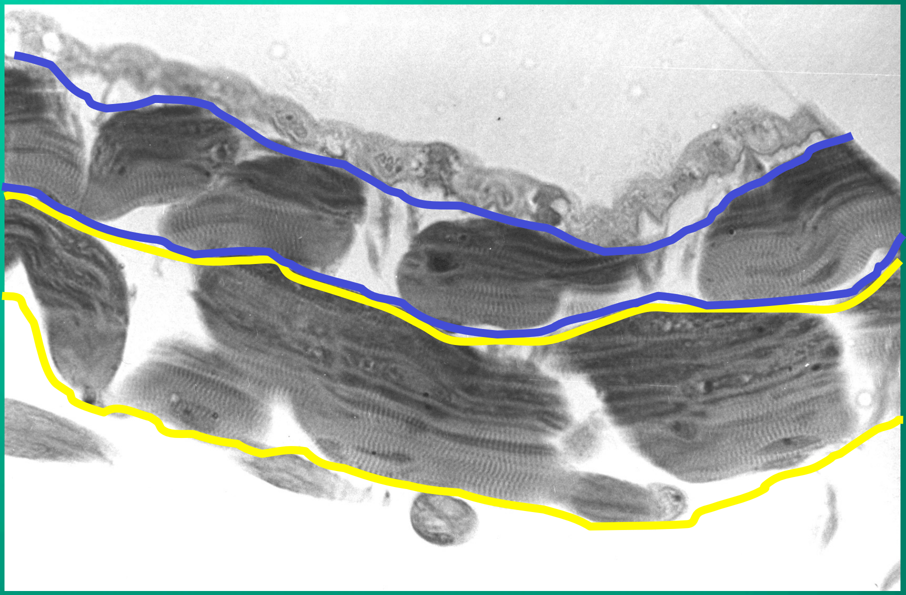


Central Pattern Generator Interneurons

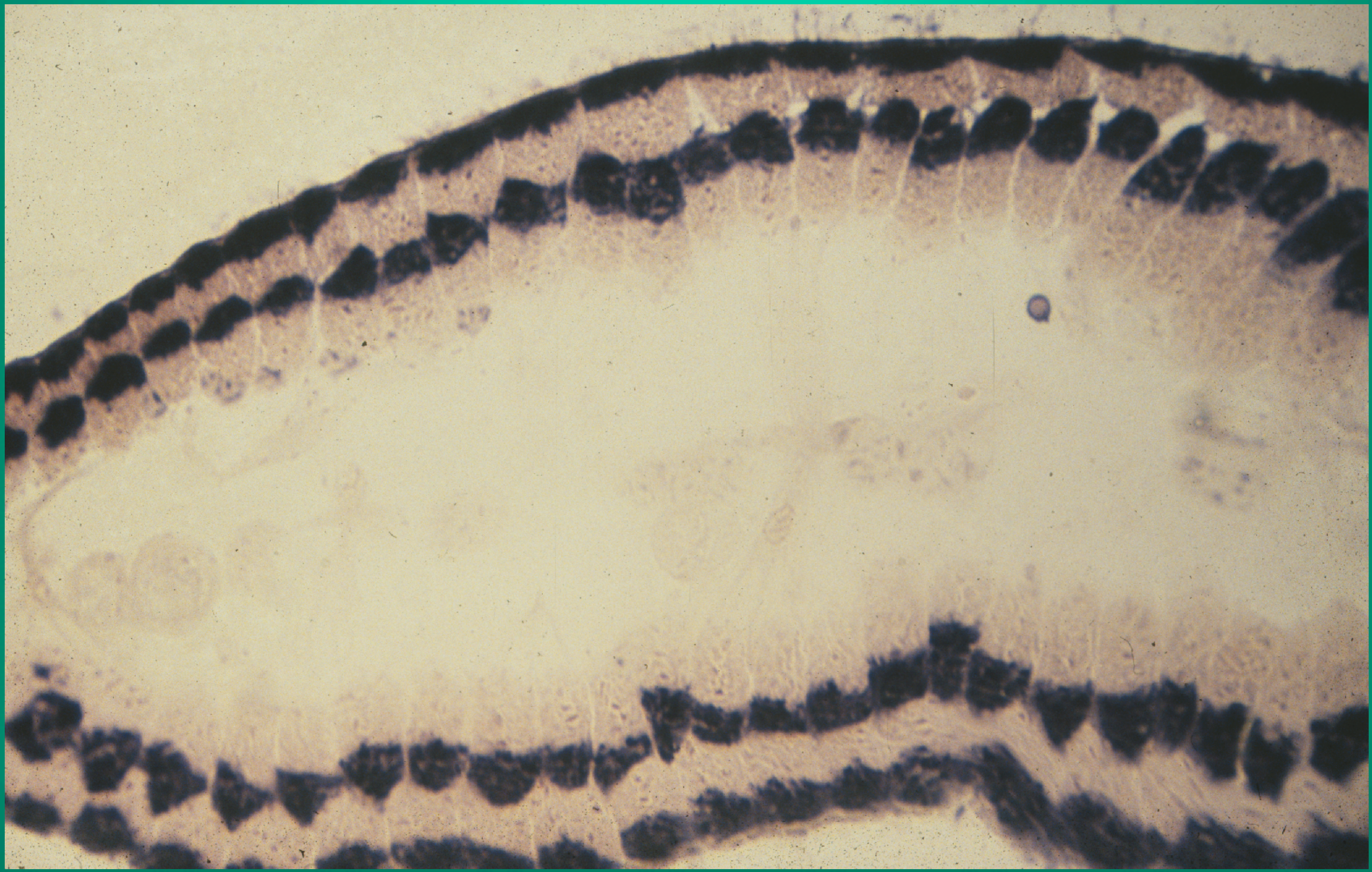


Orientation of Swim Musculature

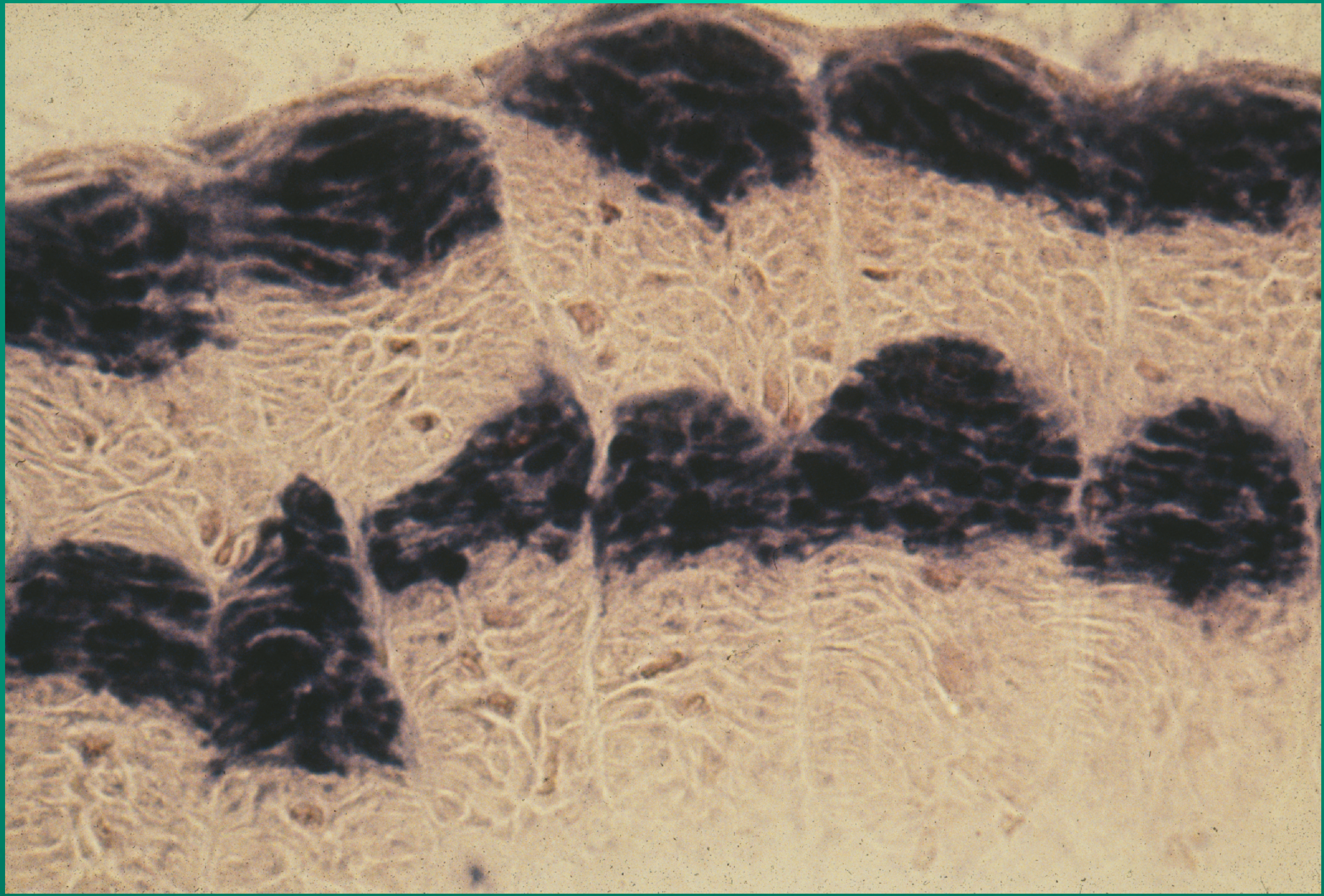




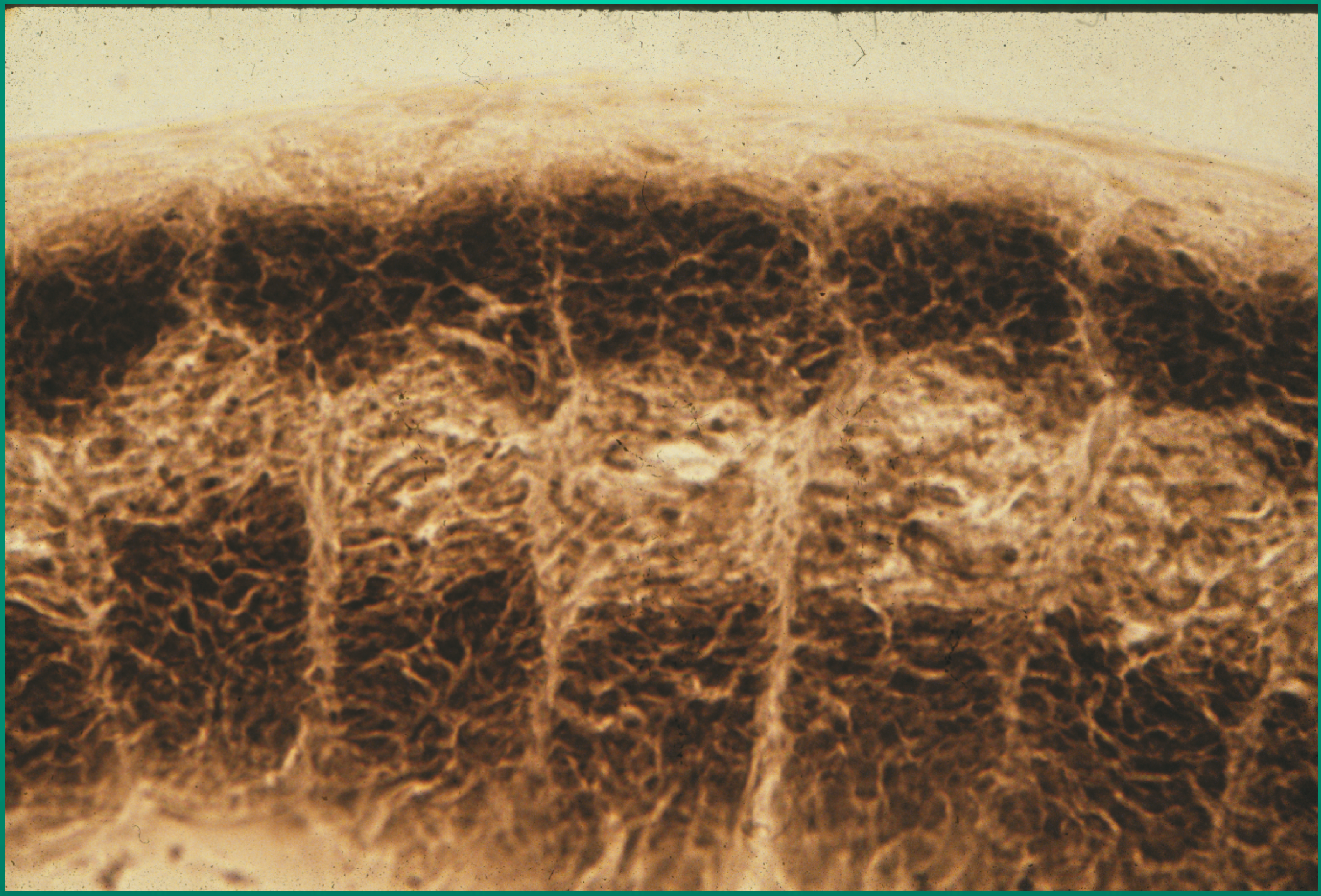
Clione Wing – Oxidative Enzyme Stain (NADH diaphorase)



Oxidative Stain - Detail



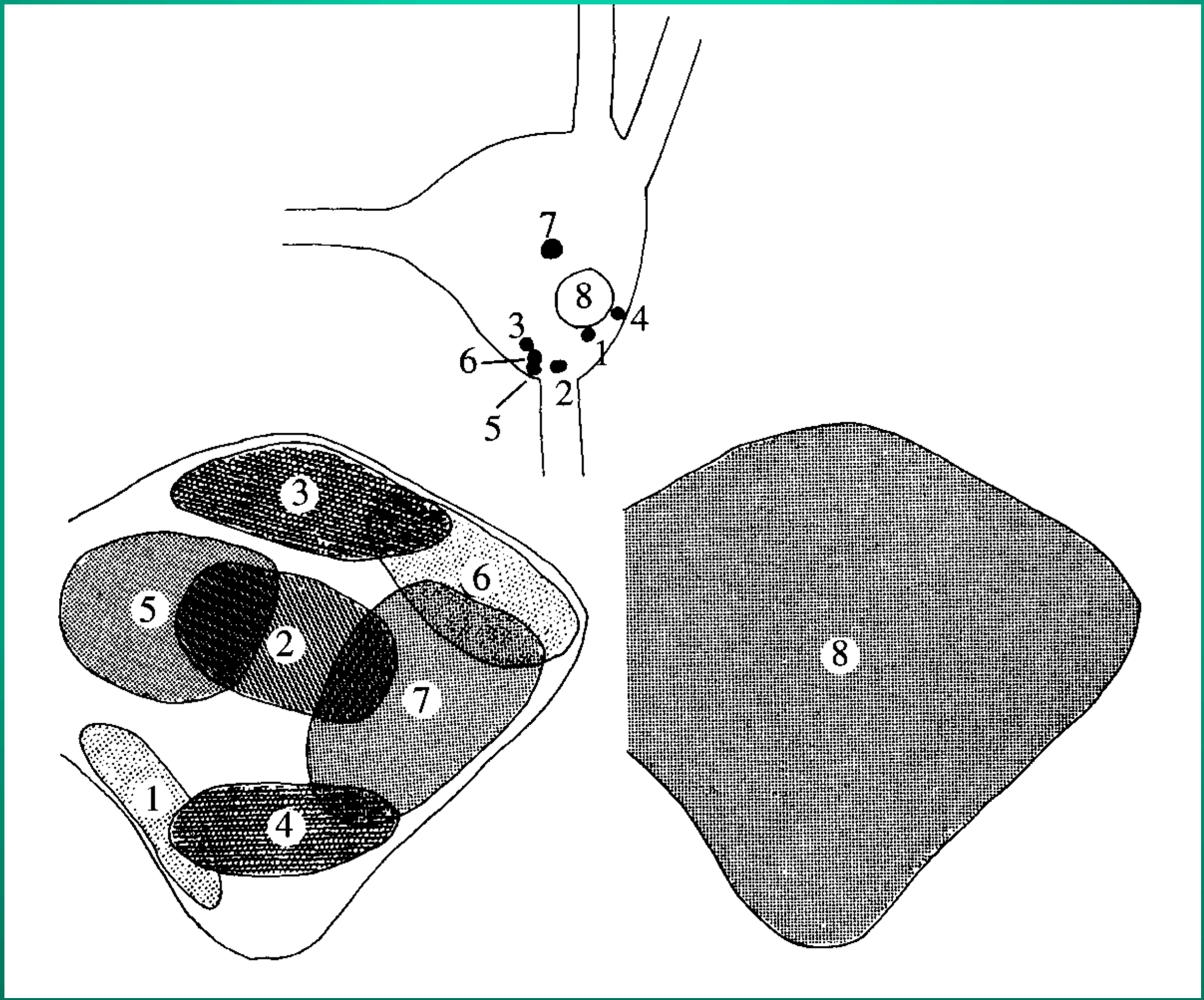
Clione Wing – Myosin ATPase Stain



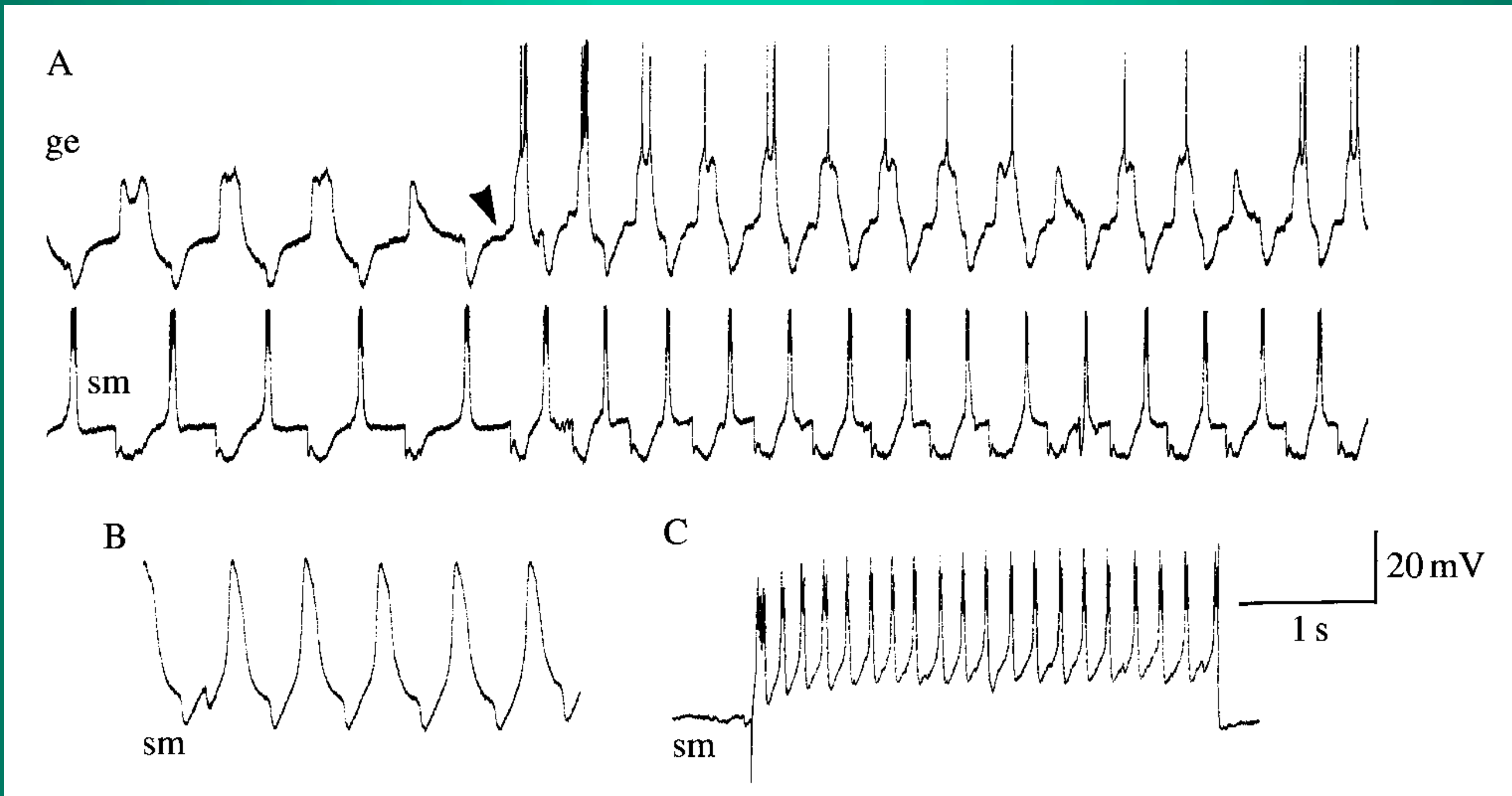
Physiological Properties of Two Types of Muscle Cells

	Slow-Twitch	Fast-Twitch
Time to Peak Tension	73.8 ± 24 ms	20.0 ± 6 ms
One-half Relaxation Time	70.5 ± 14 ms	31.0 ± 8 ms
Size of 10th twitch (5 Hz) [Relative to Initial Twitch]	62%	30%
Size of 20th twitch (5 Hz) [Relative to Initial Twitch]	31%	19%

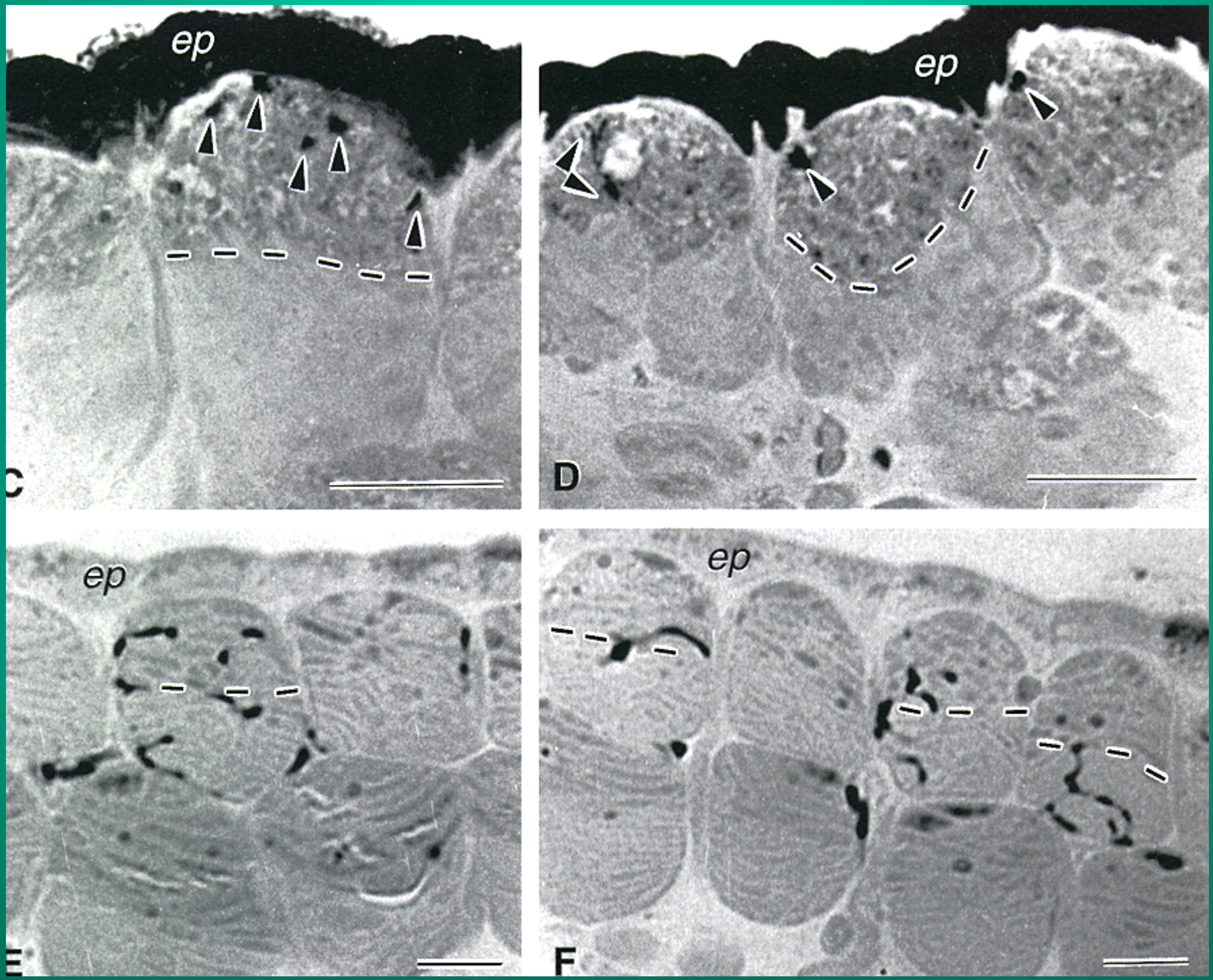
Innervation Fields of Swim Motoneurons

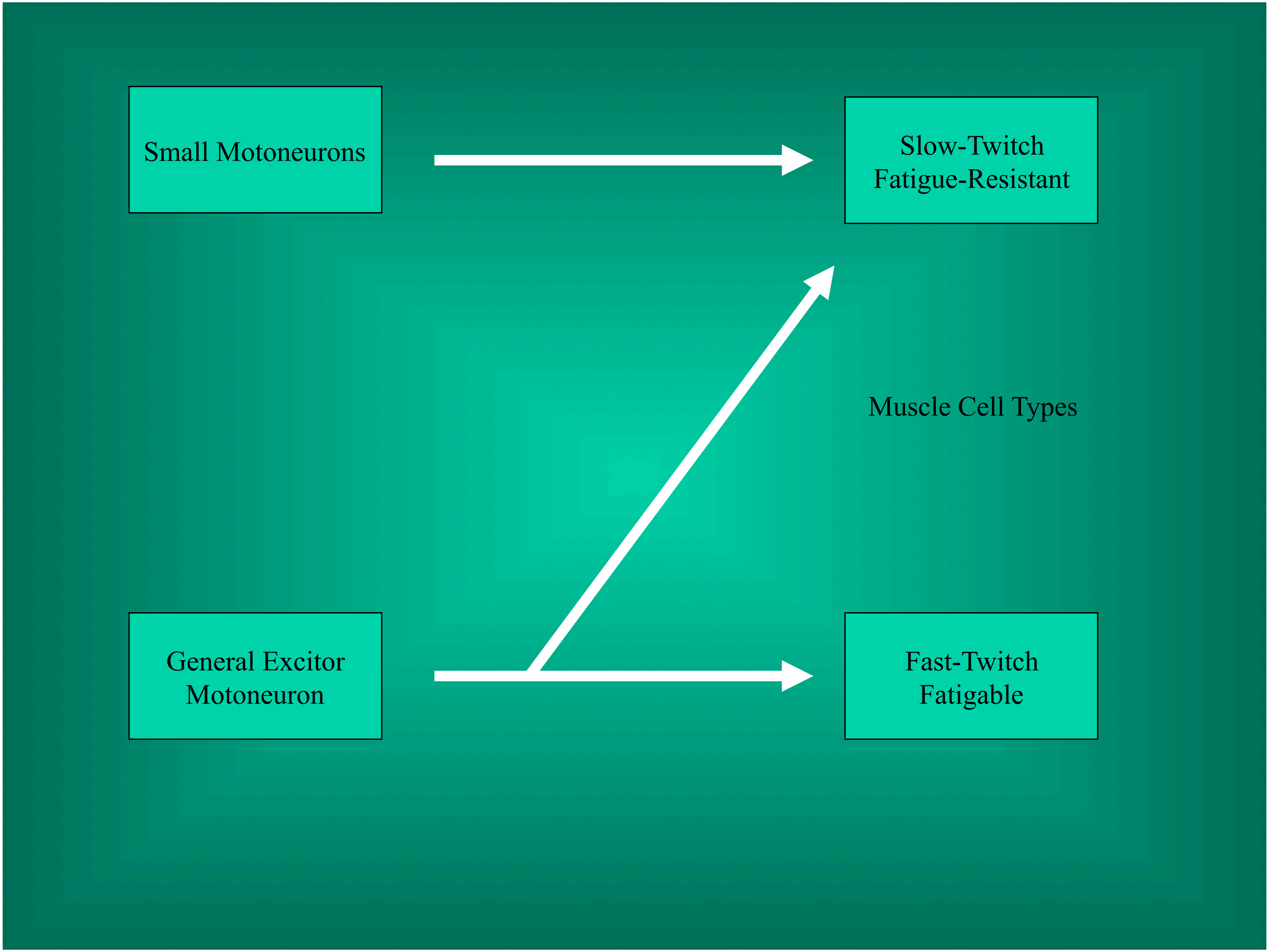


Motoneuron Recruitment During Swim Acceleration



Neurobiotin Injections of Motoneurons



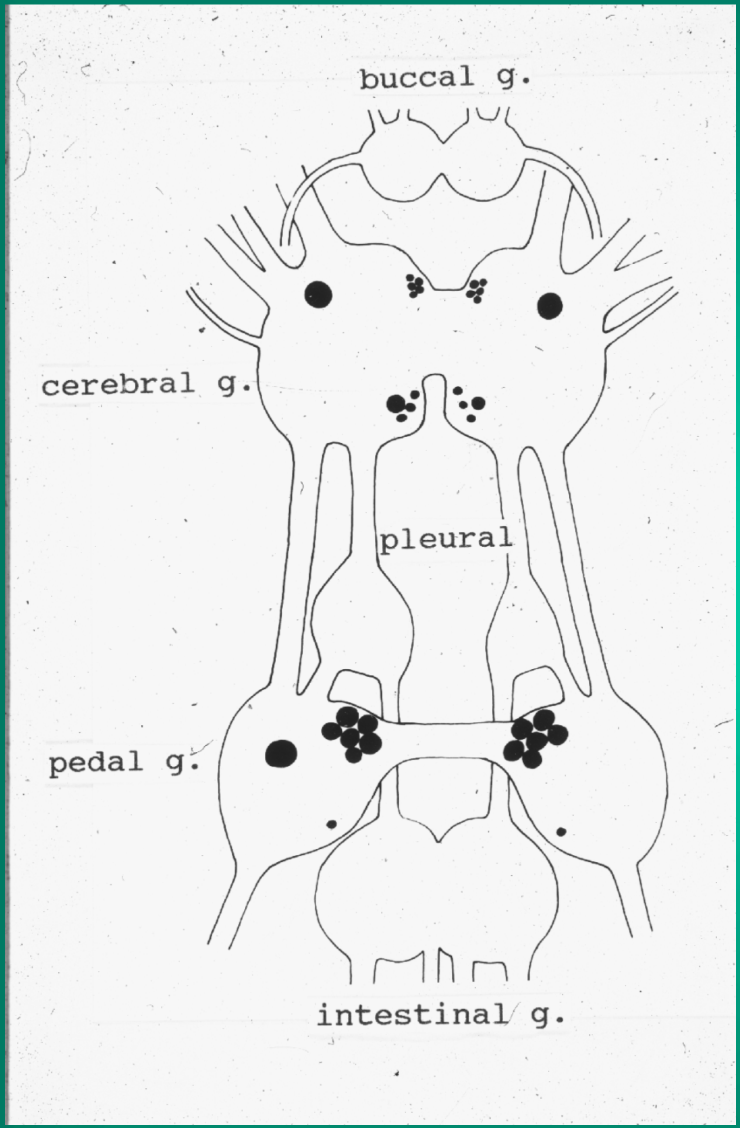

Small Motoneurons
Slow-Twitch Fatigue-Resistant
Muscle Cell Types
General Excitor Motoneuron
Fast-Twitch Fatigable

Change #1

Reflex-type activity – acceleration within the slow swimming speed.

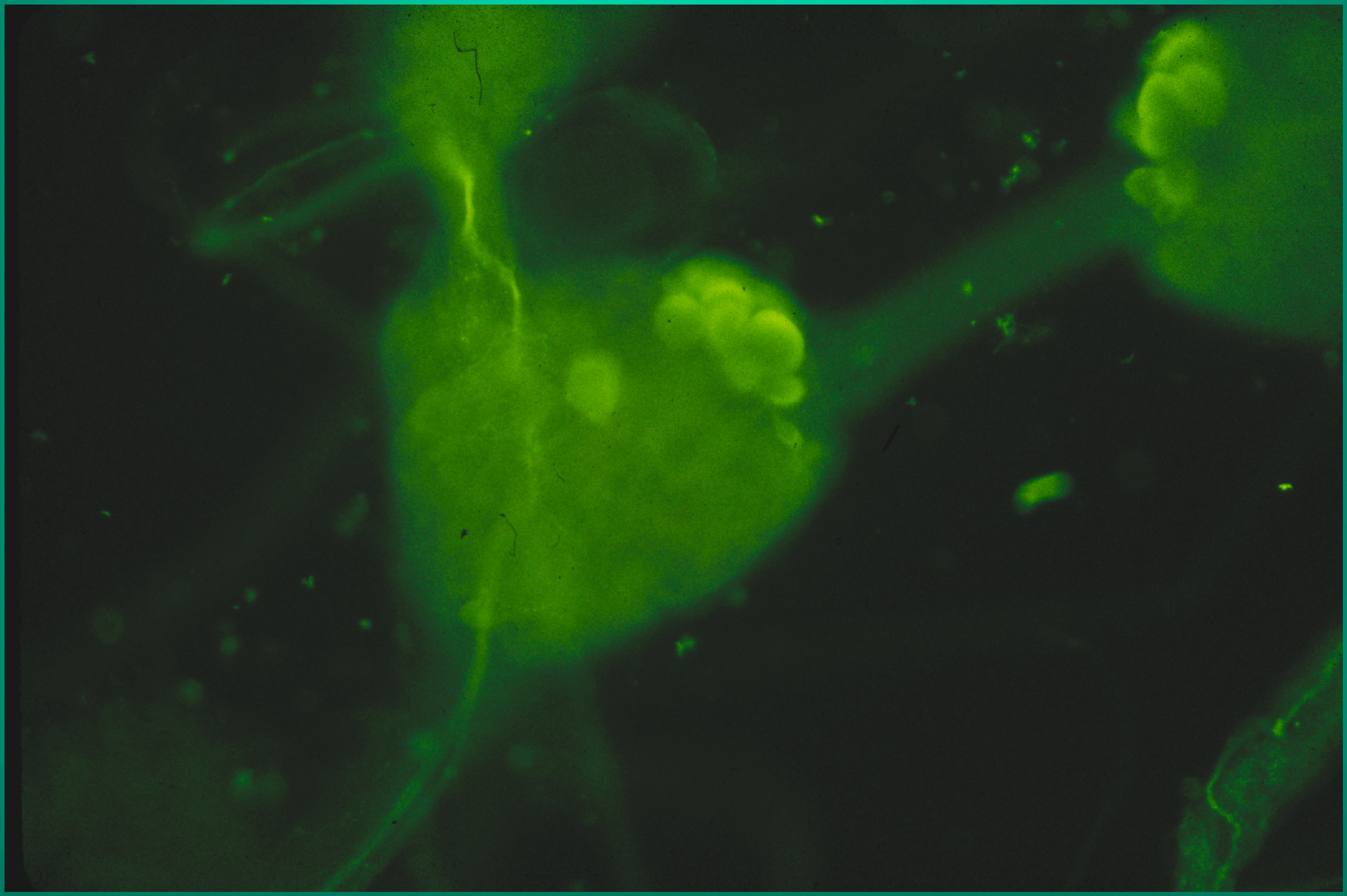
Triggered by mechanical stimulation of wing (below the threshold for wing withdrawal)

Involves a threshold-related behavioral switch

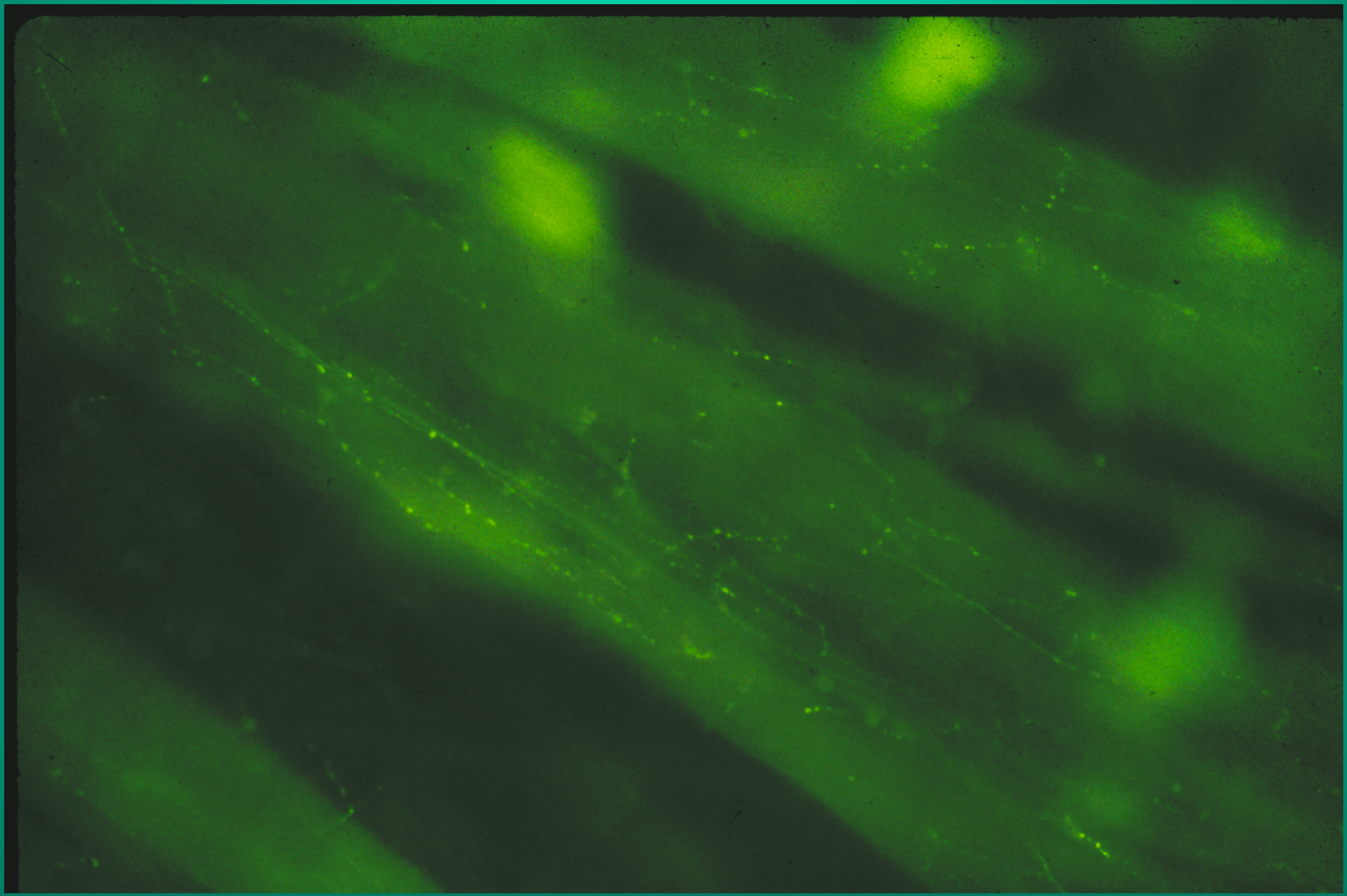


Location of Serotonergic Neurons in the CNS of *Clione*

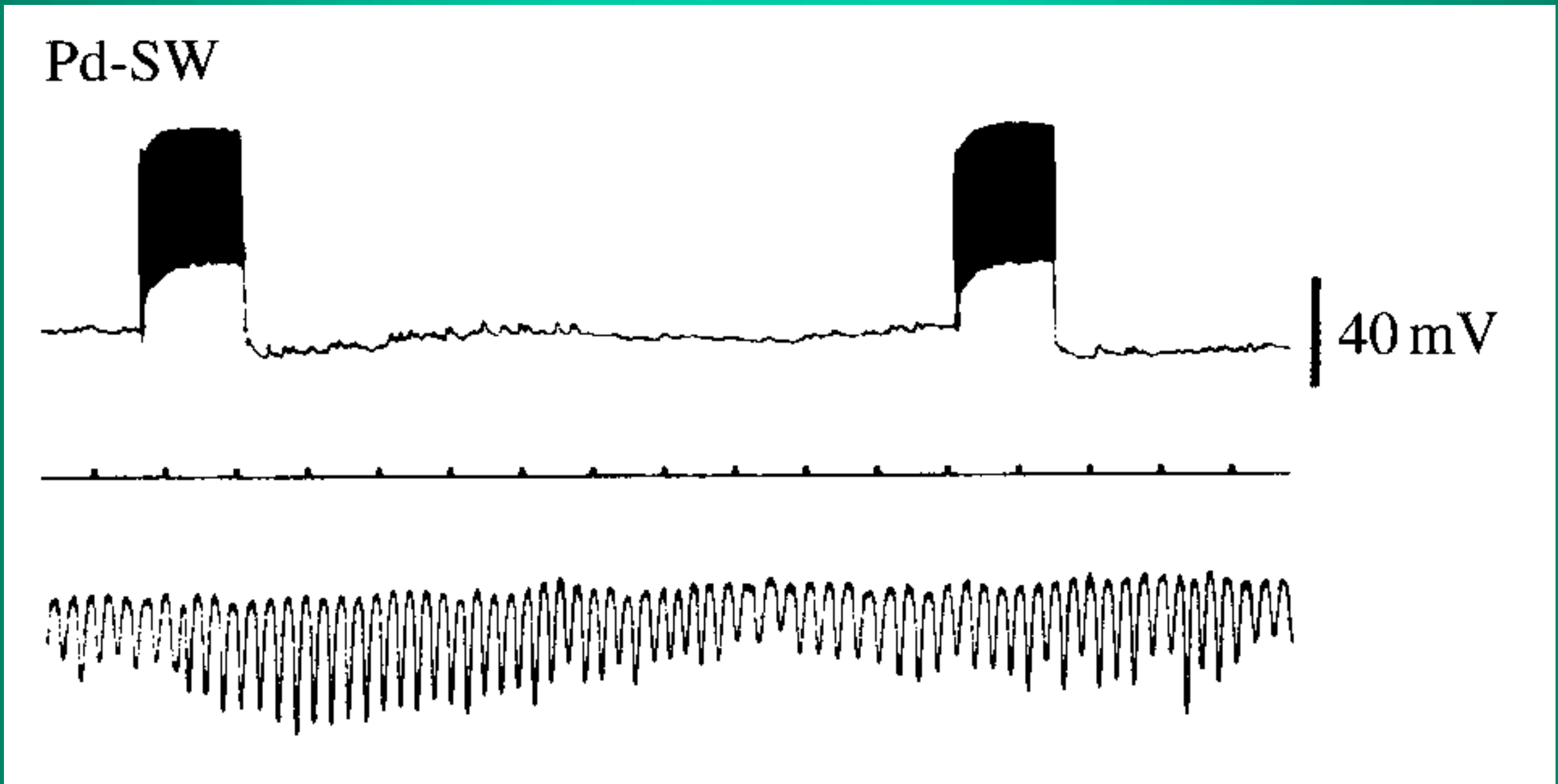
Serotonin Immunohistochemistry – Pedal Ganglia



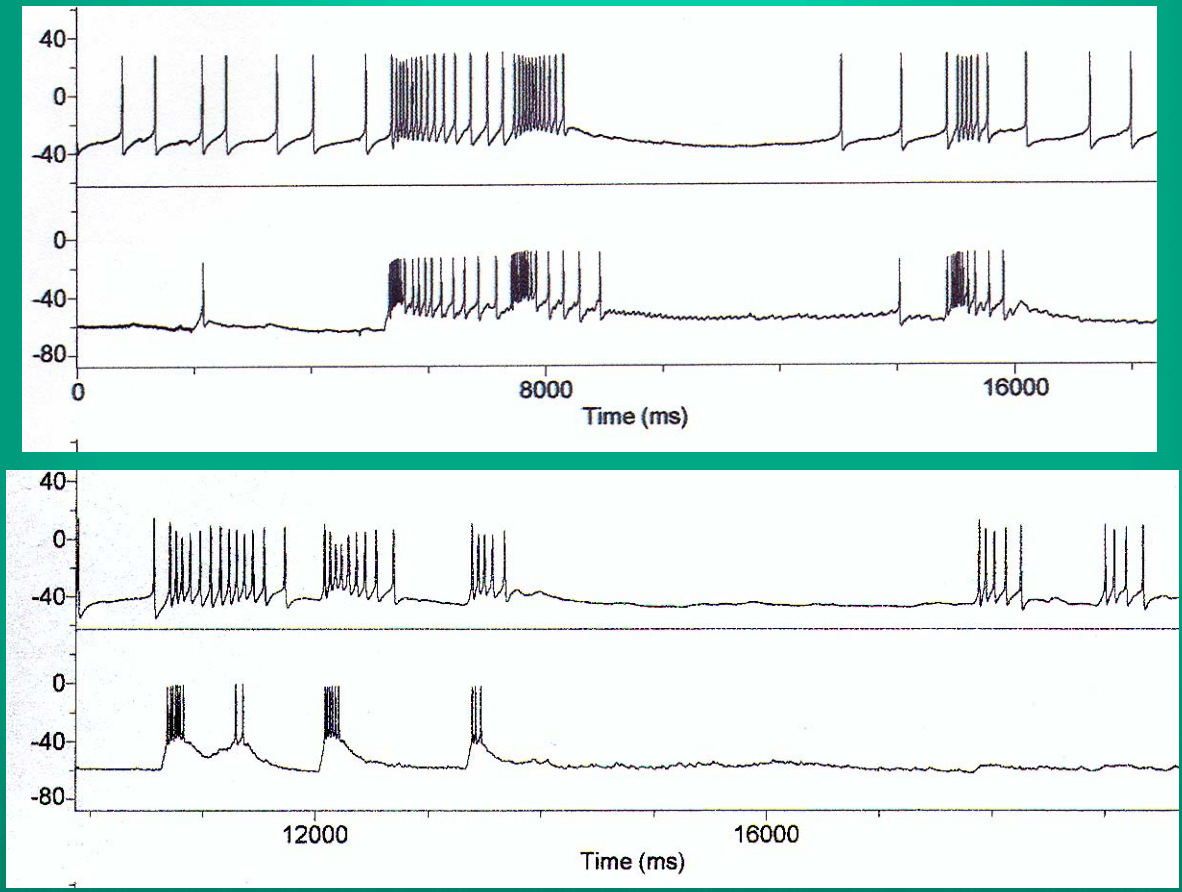
Serotonin Immunohistochemistry – Wing Muscle Bundles



Modulation of Wing Contractility by Pedal Serotonergic Neuron (Pd-SW)



Mechanical Stimulation of the Wing Activates Peripheral 5-HT Cells



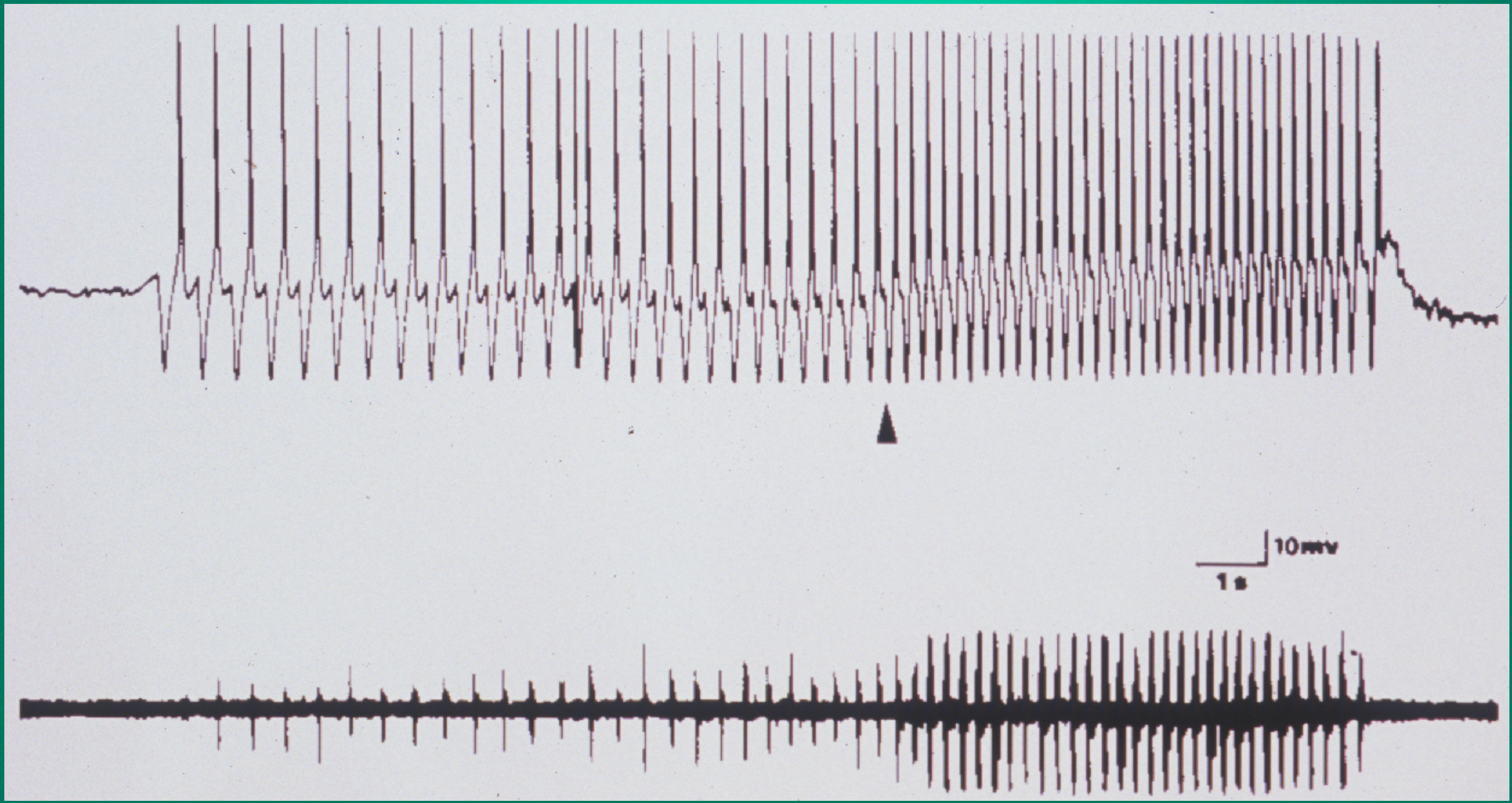
Change #2

Mechanical Stimulation of Tail – swim acceleration (equivalent to a gait change)

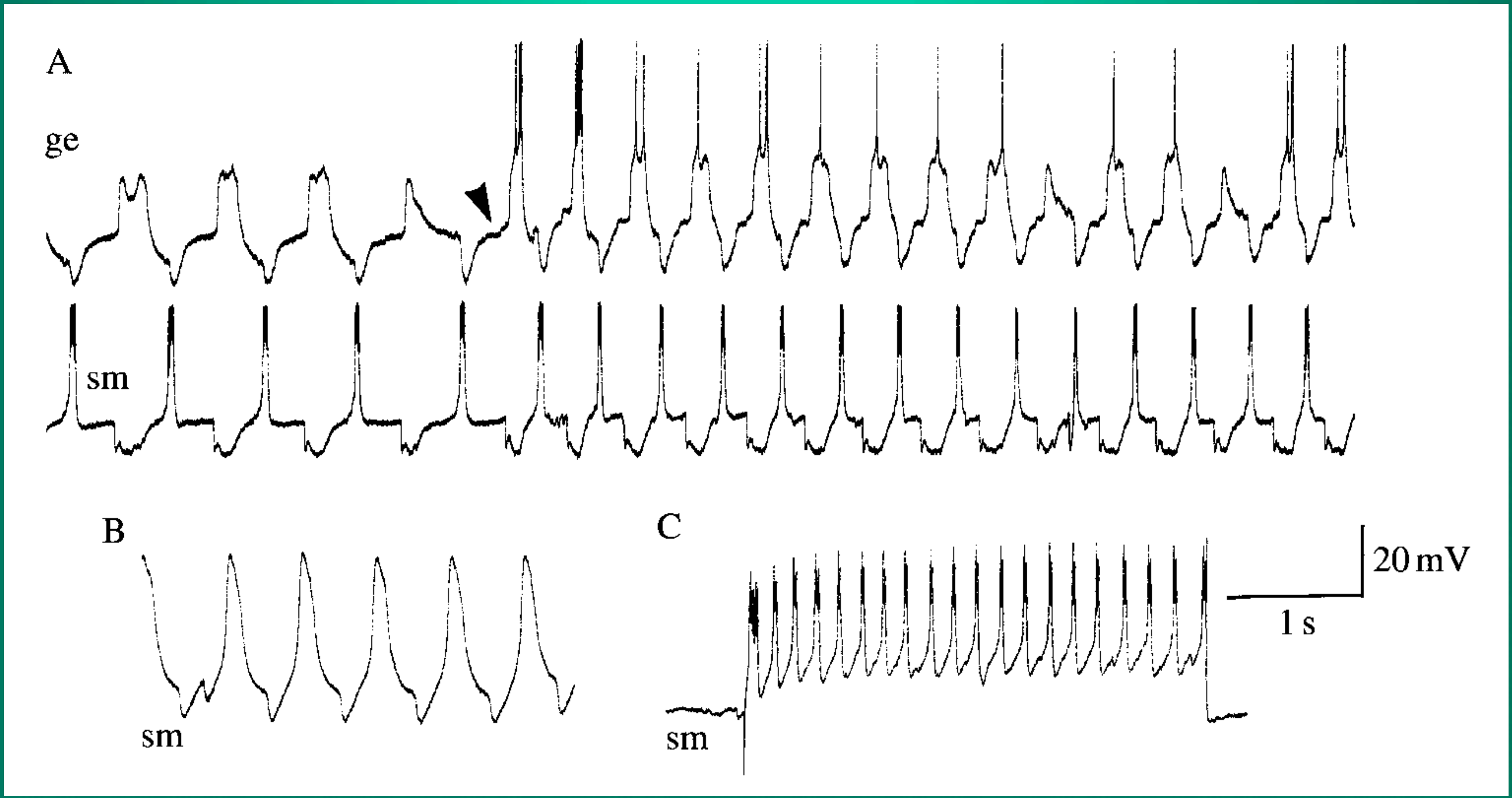
- Increase in wing-beat frequency
- Increase in wing contractility
- Moves animal forward at up to 3-4 body lengths per second

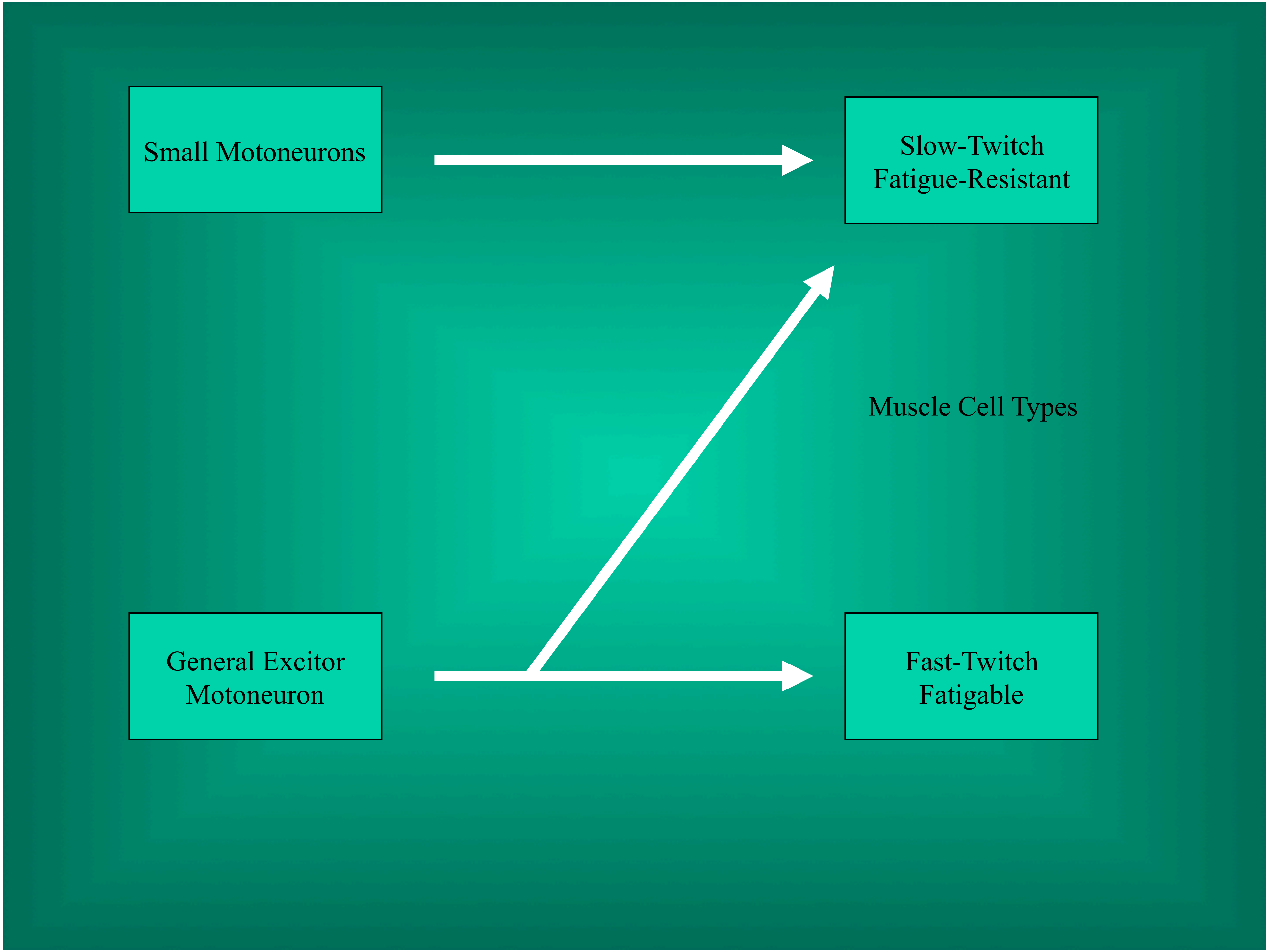
Involves central activation of a general arousal system with variable output (strength and duration)

Electrical Correlate of Swim Acceleration (Arrow)
Top – CPG Interneuron
Bottom – Wing Nerve Recording



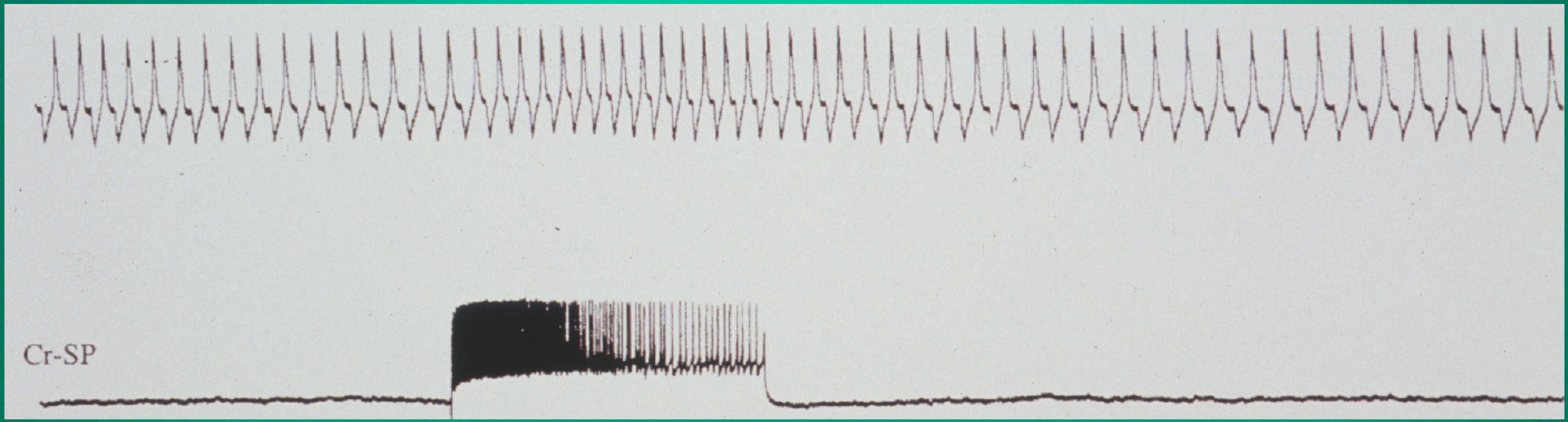
Motoneuron Recruitment During Swim Acceleration



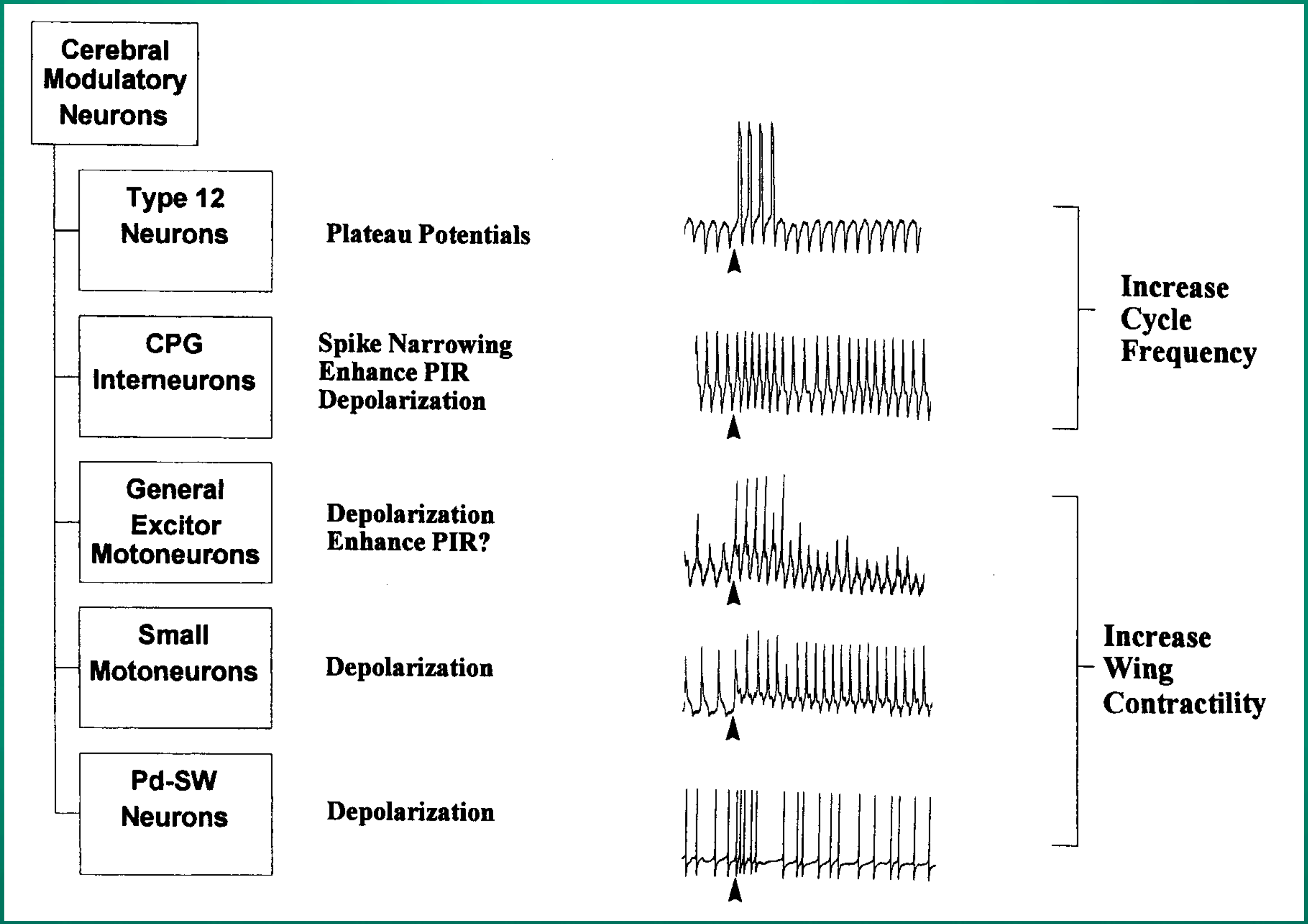

Small Motoneurons
Slow-Twitch
Fatigue-Resistant
Muscle Cell Types
General Excitor
Motoneuron
Fast-Twitch
Fatigable

Serotonin-Immunoreactive Neurons (Stereo Pairs)

Swim Acceleration Induced by Stimulation of Cerebral Serotonergic Neuron (Cr-SP)



Postsynaptic Targets of Cerebral Serotonergic Neurons (Cr-SA and Cr-SP)

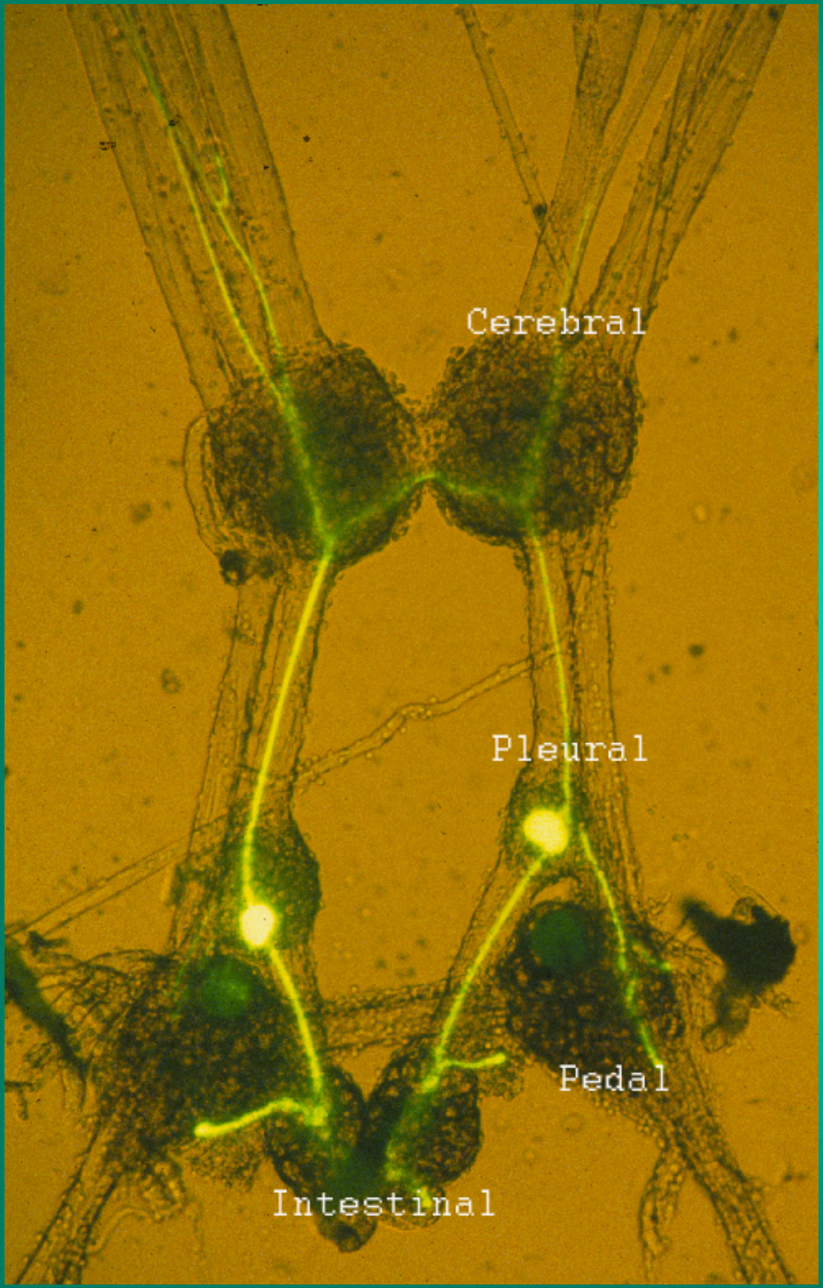


Change #3

Whole Body Withdrawal

- Activated by either nociceptive or repeated mechanical stimulation of the head
- Swimming is inhibited
- Wings are withdrawn into body
- Body is contracted longitudinally
- Passive sinking due to negative buoyancy

Key feature – reciprocal inhibition between circuitry for mutually exclusive behaviors



Whole-Body Withdrawal Neurons

Located in the Pleural Ganglia

Inhibit swimming

Change #4

Food acquisition behavior

- Higher order behavior that involves an internal motivational state
- Includes swim acceleration using the serotonergic arousal state
- Involves tail bending to produce fast, looping swimming movements (statocyst override)

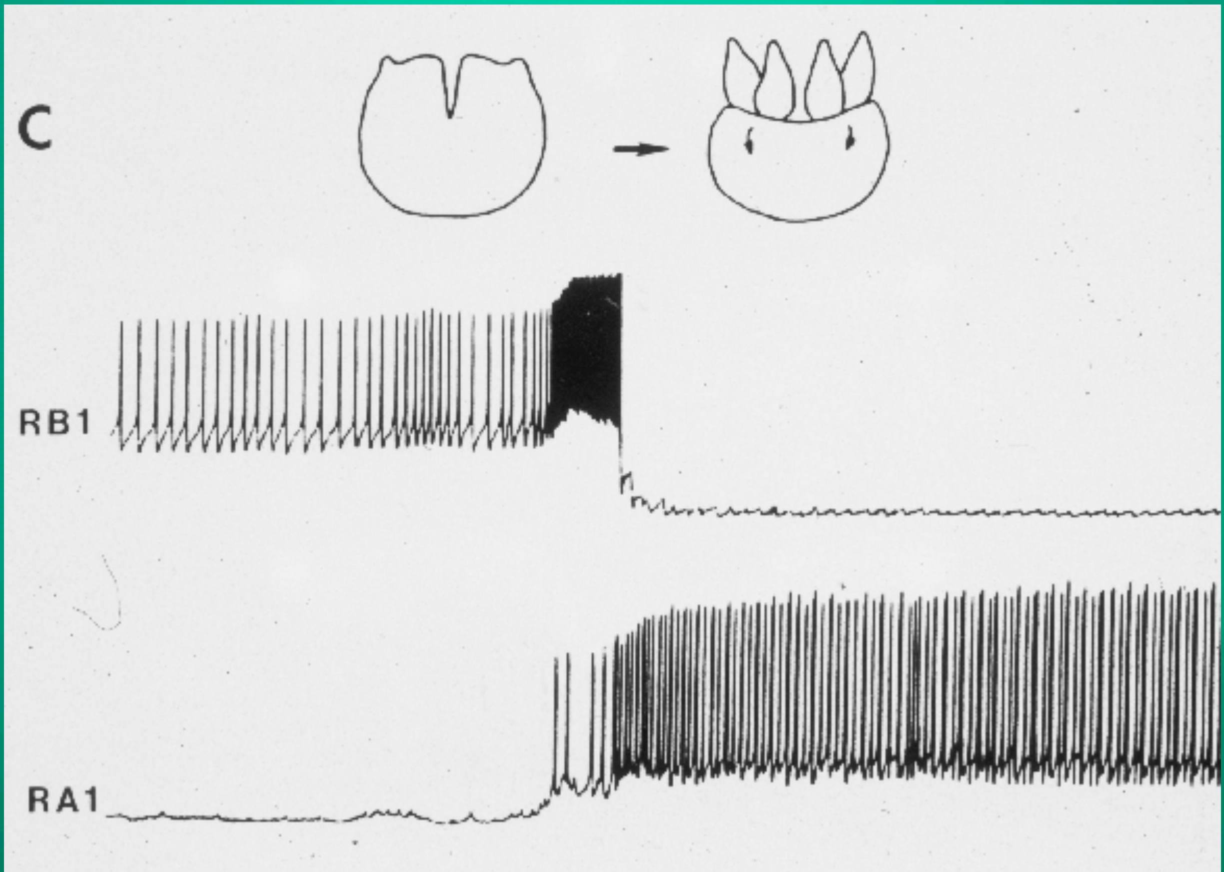
Non-Feeding Animal

Lips Closed, Buccal Cones Withdrawn

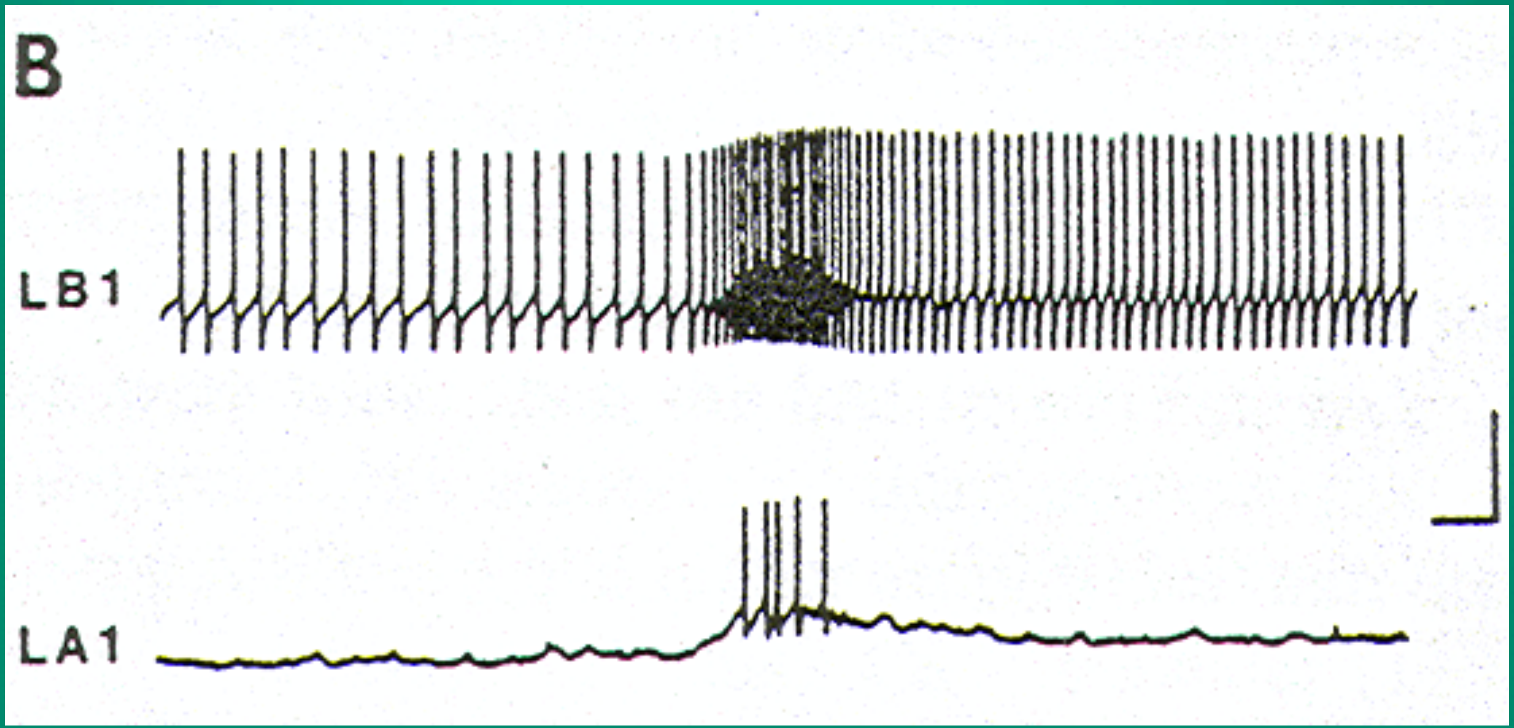
Feeding on a Shelled Pteropod (*Limacina*)

Buccal Cone Expansion – 50ms!

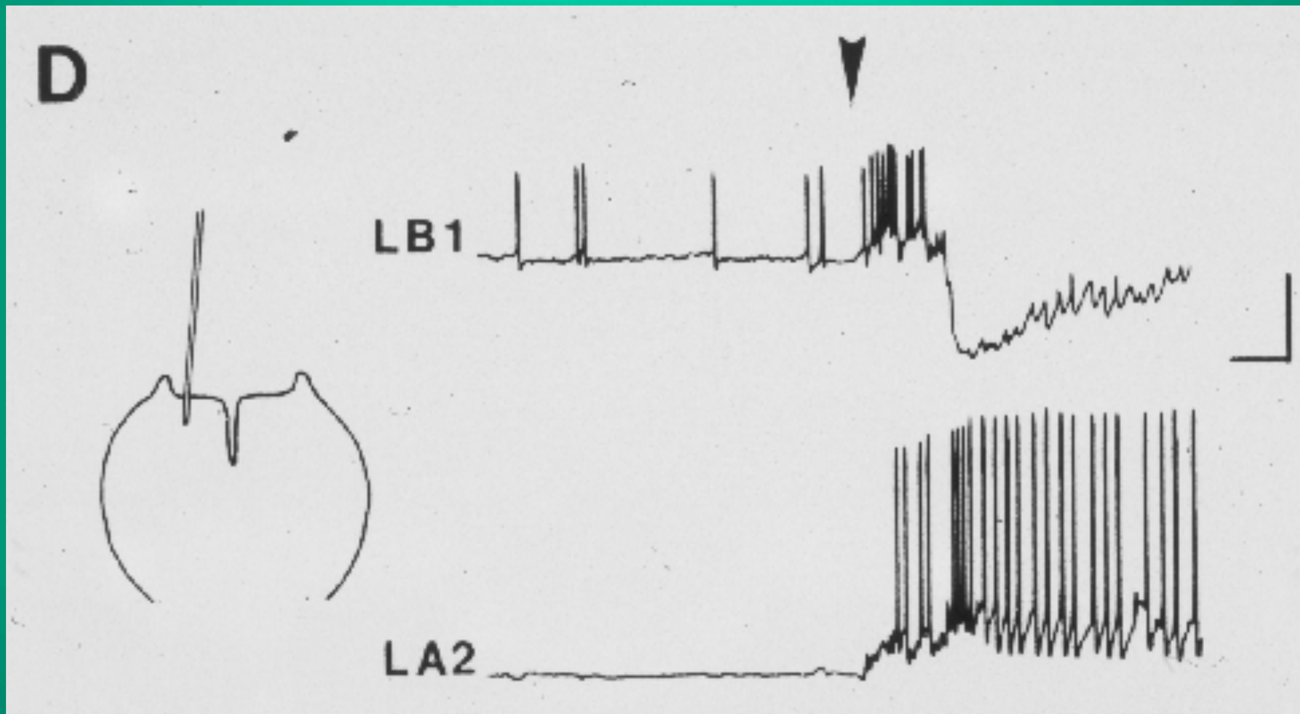
Spontaneous Protraction of Buccal Cones



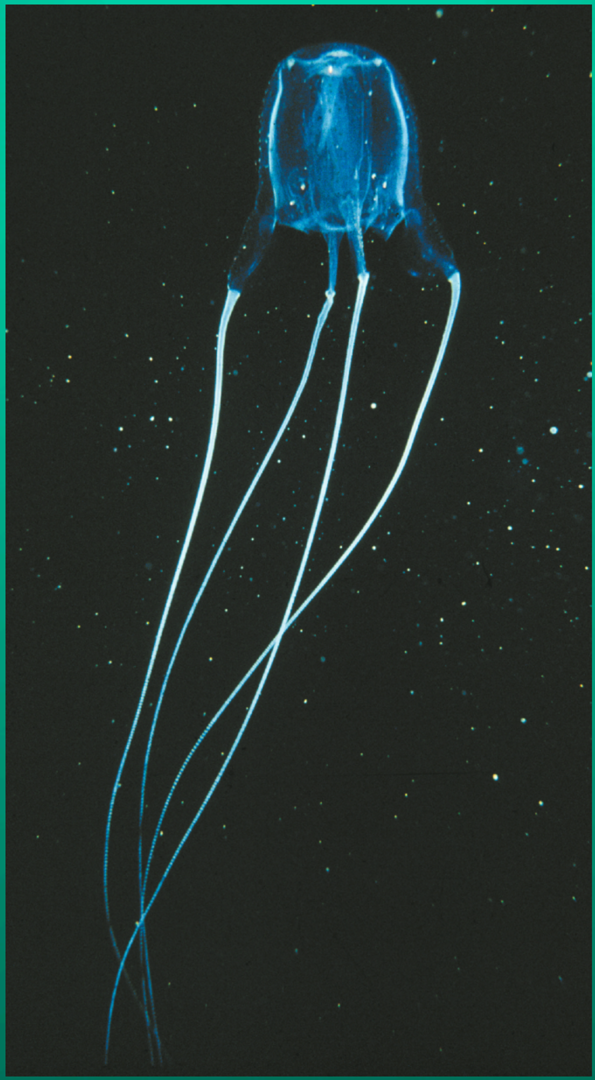
Mechanical Stimulation of Head
No Serotonin



Mechanical Stimulation of Head With Serotonin or Prey "Juice"

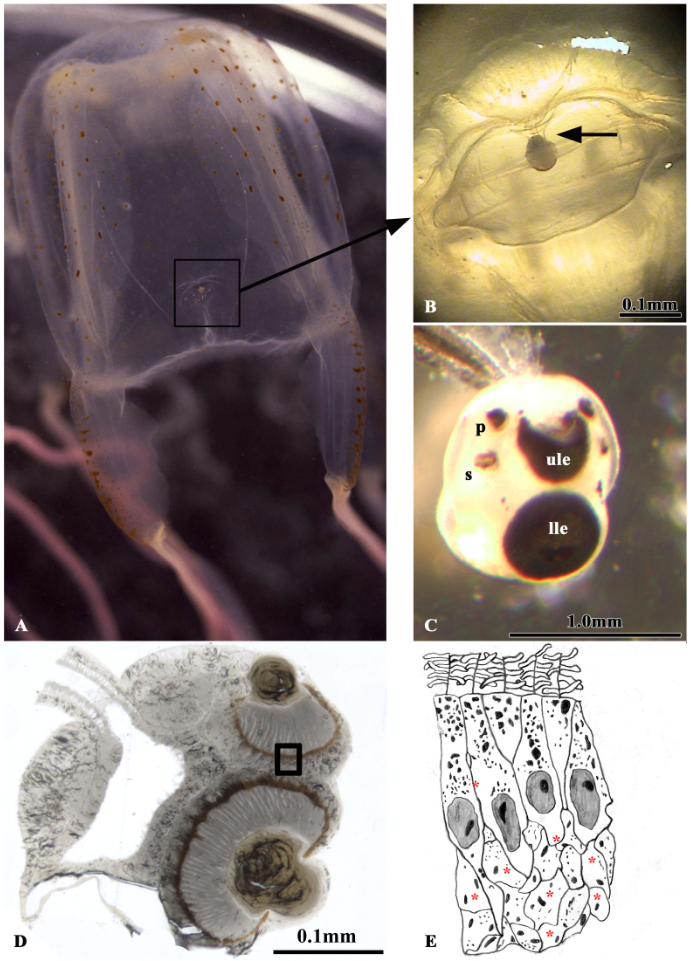


Carybdea marsupialis (Cubozoa)



Stability – rhythmic contractions in cubozoan and scyphozoan jellyfish

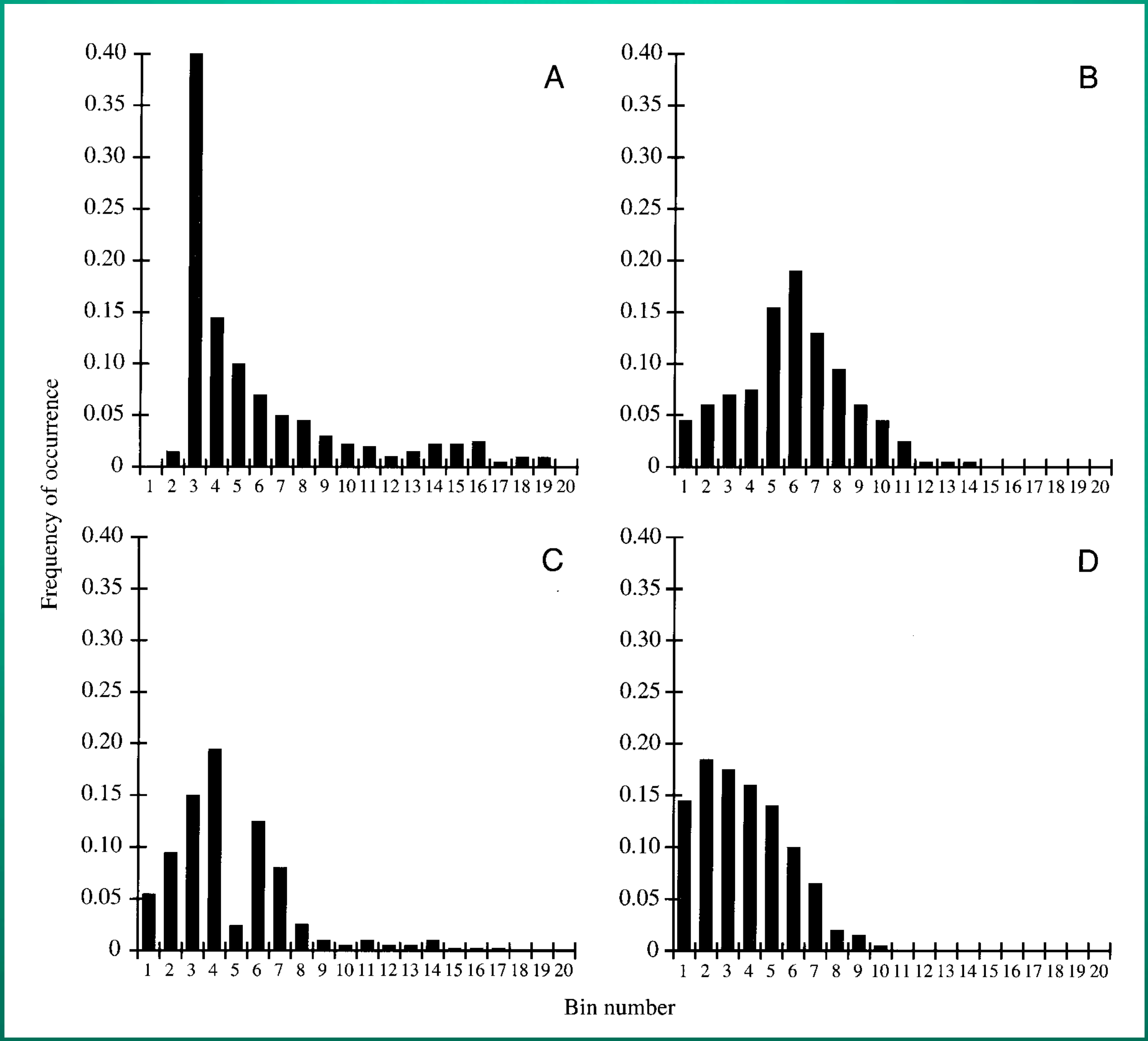
- Impulses originate in marginal rhopalia (4 in cubomedusae, 8 or more in scyphomedusae)
- Swim musculature lines subumbrellar cavity and is activated by diffuse, non-polarized nerve nets



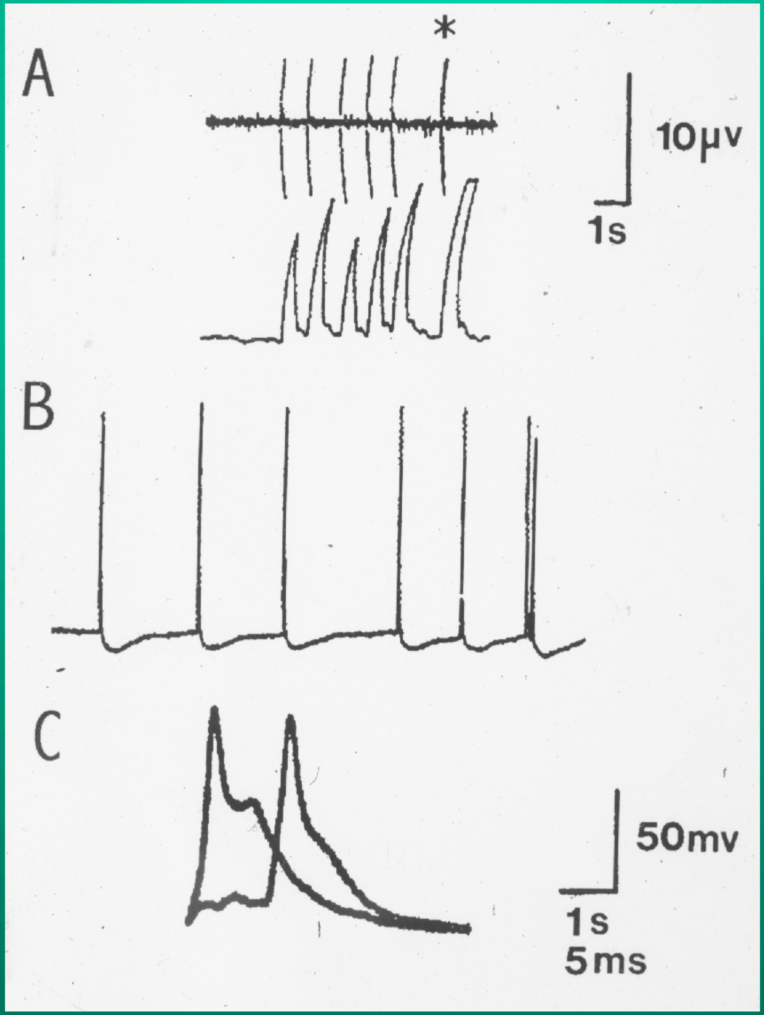
Tamoya haplonema

Rhopalial structure

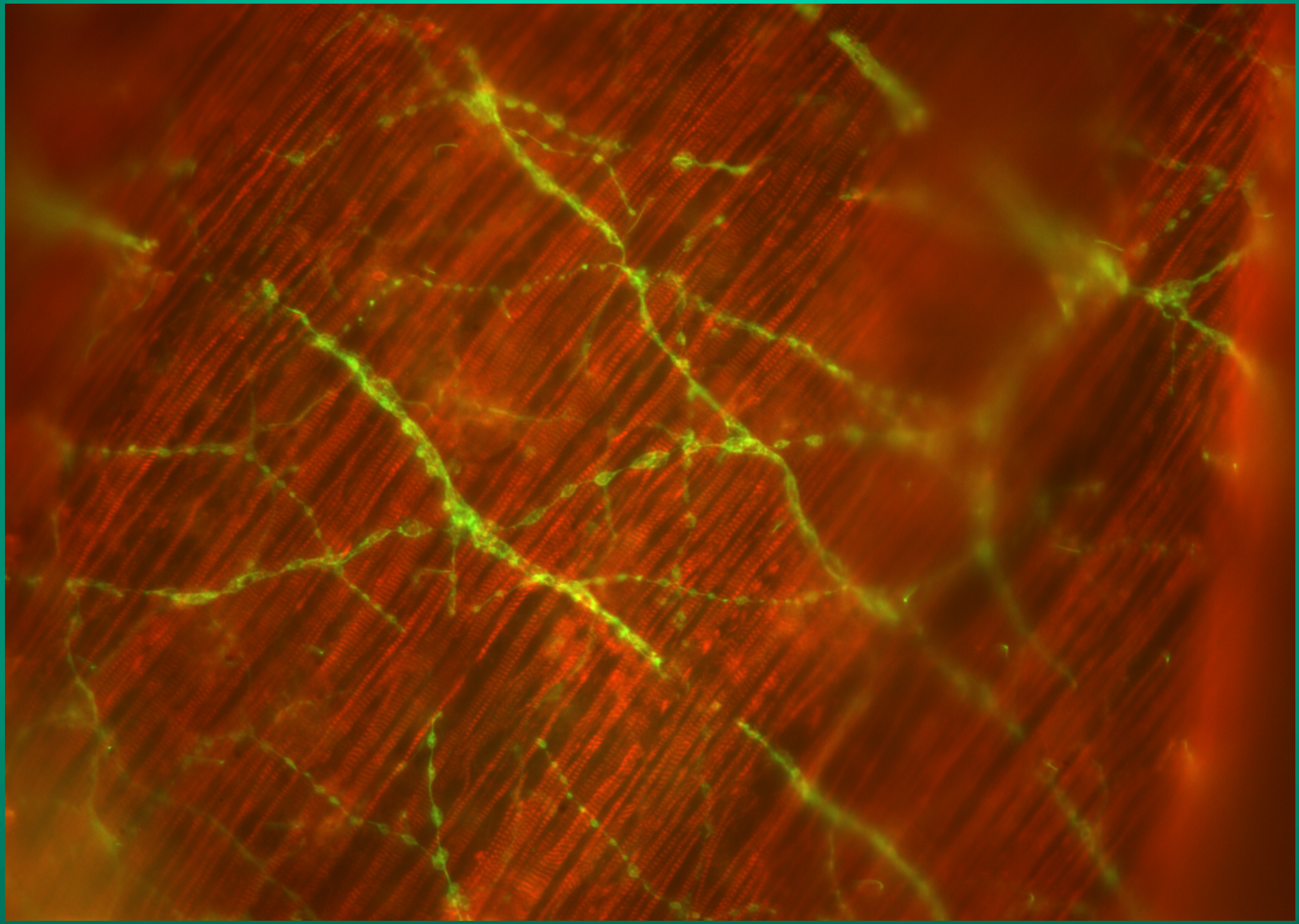
Sequential Rhopalial Removal Alters Interpulse Interval Distribution of Swim Contractions



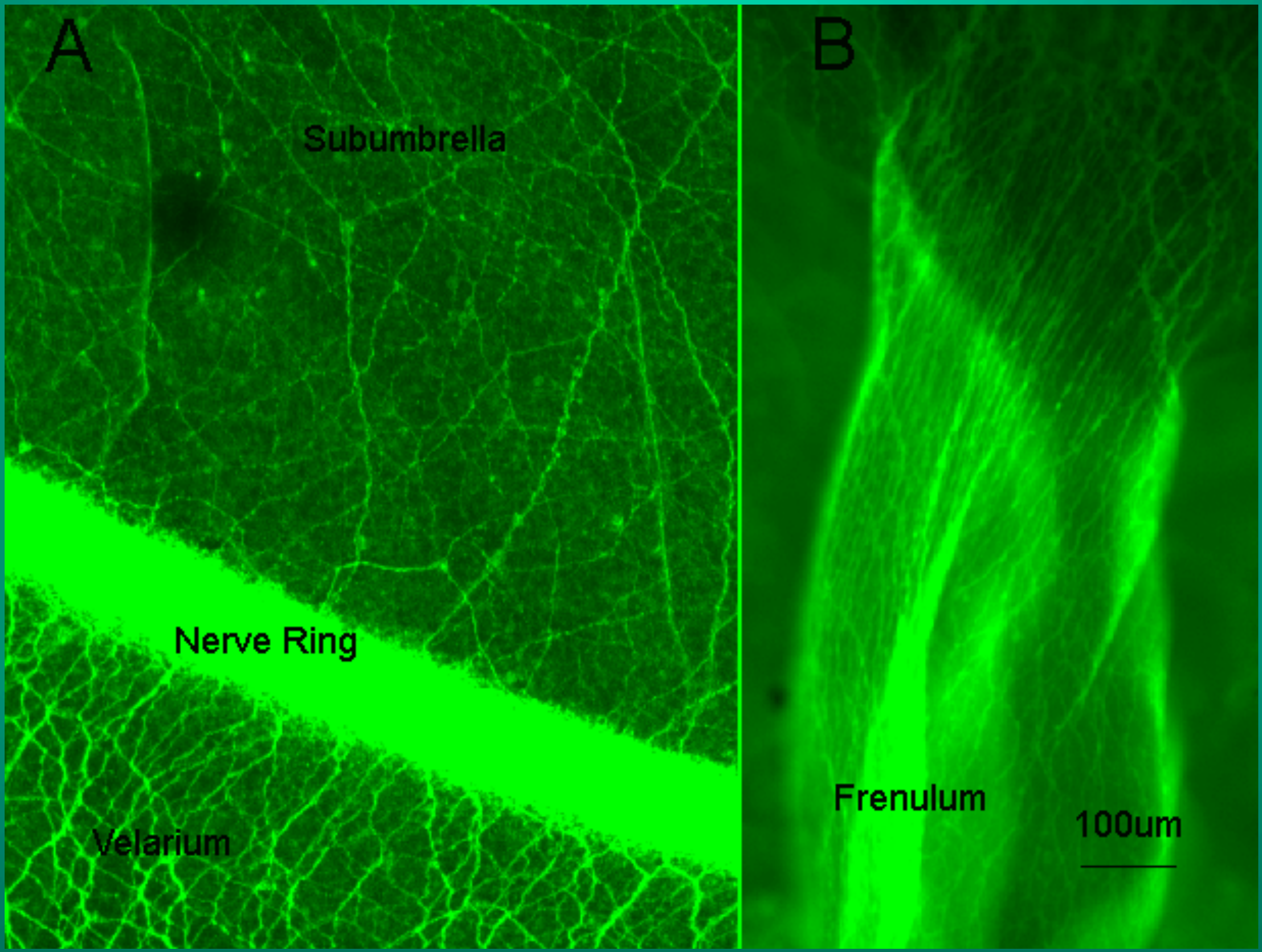
Carybdea – Motor Neuron Recordings



Tripedalia cystophora
Actin-Tubulin Double Stain



Relative Density of Nerve Nets in Subumbrella, Velarium and Frenulum

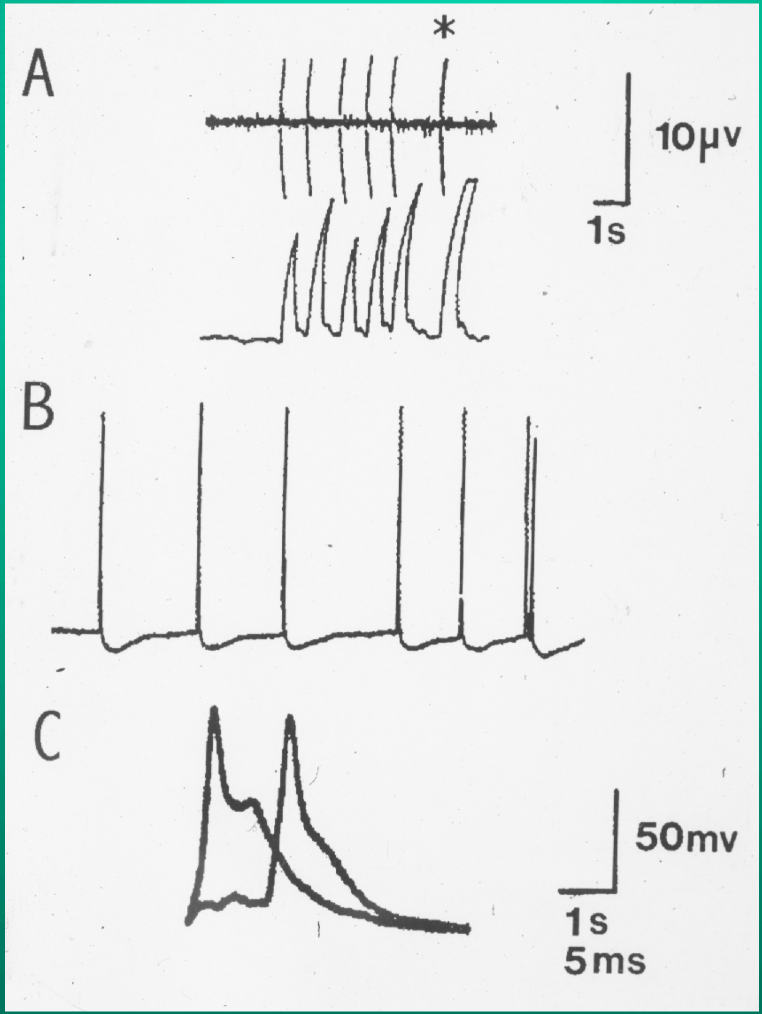


Change #1

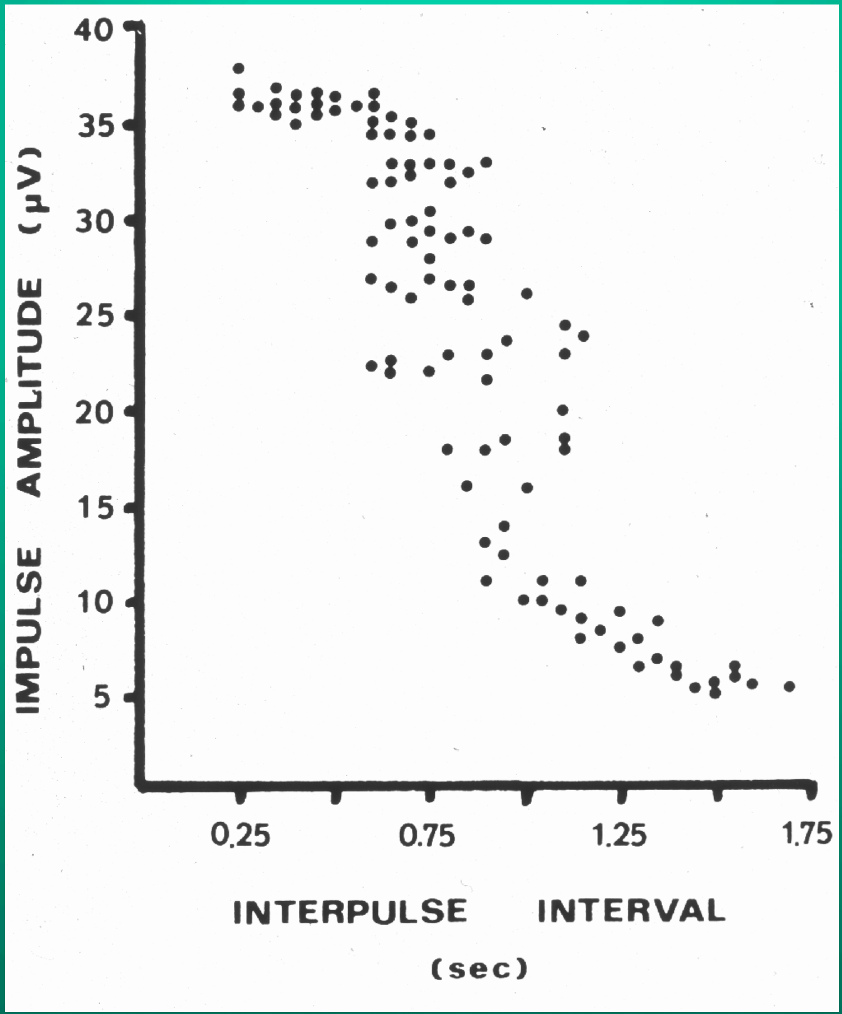
Alteration of force of contractions

- Peripheral neuromuscular facilitation

Carybdea – Motor Neuron Recordings



Carybdea – Neuromuscular Facilitation Properties



Change #2

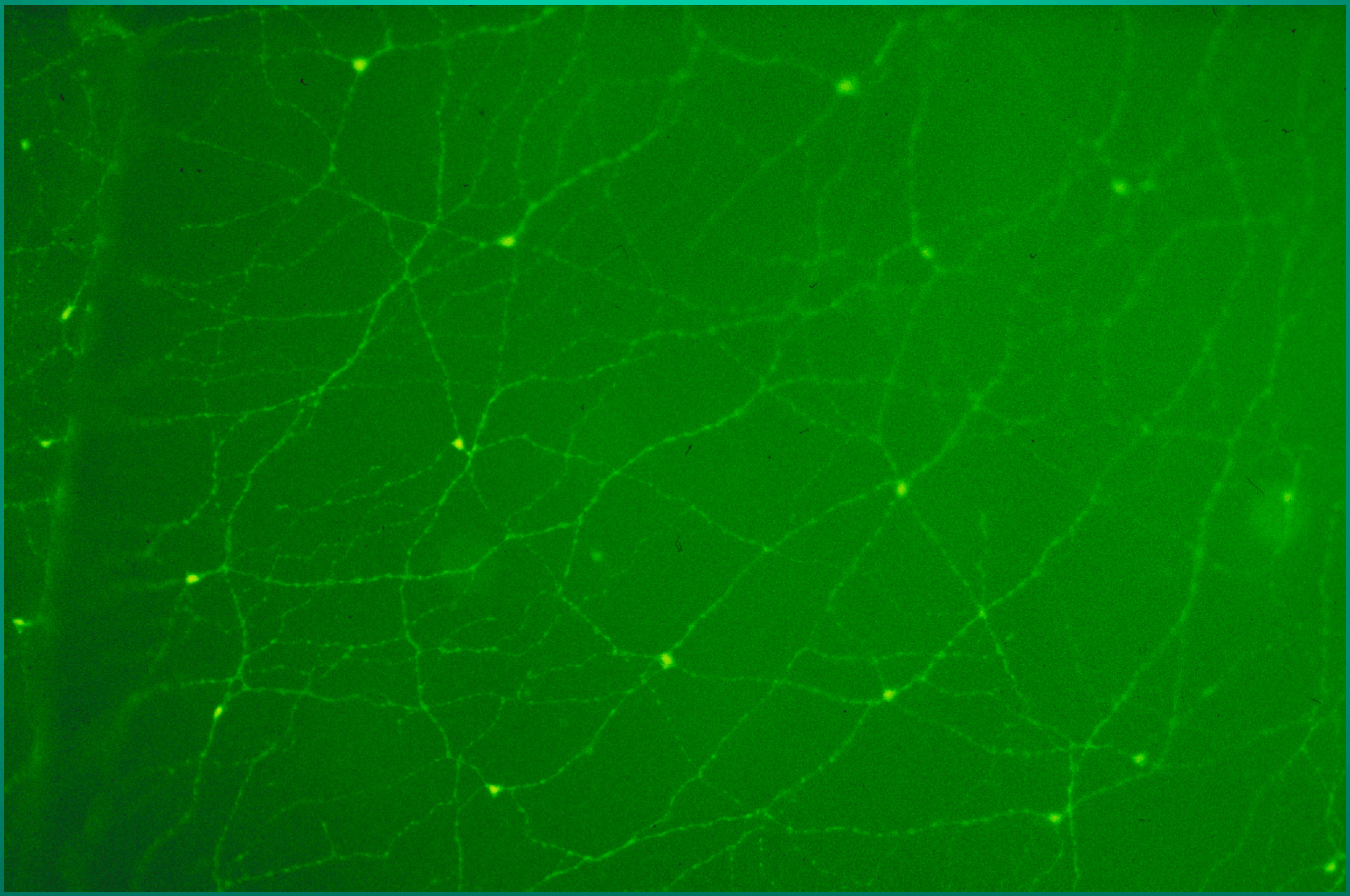
Turning behavior

•Asymmetrical contraction of subumbrella in scyphomedusae

•Asymmetrical contraction of velarium creating a directional nozzle in cubomedusae

• Involvement of a second peripheral nerve net, the "Diffuse Nerve Net" - modulatory function.

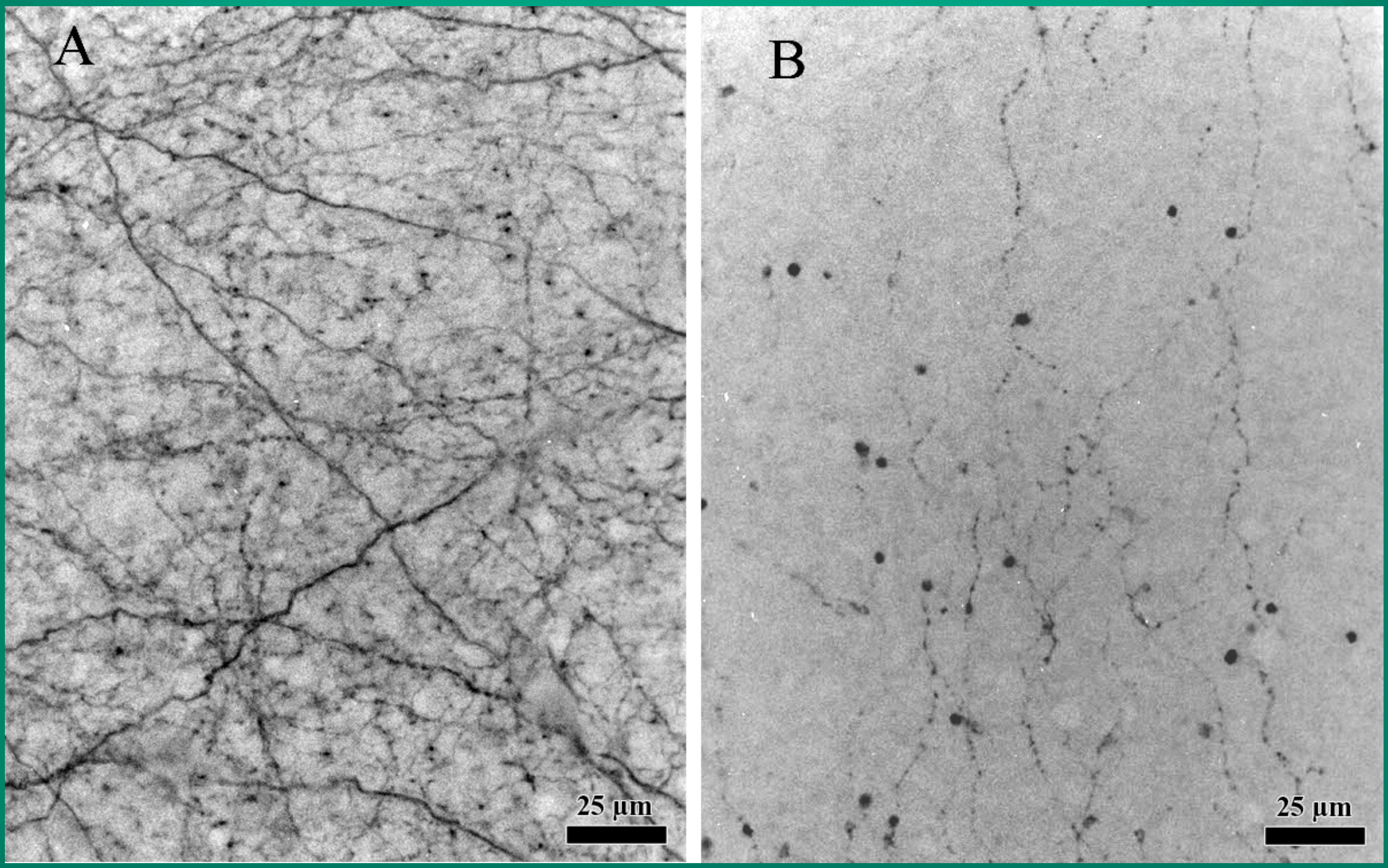
Cyanea capillata
FMRFamide Immunoreactivity



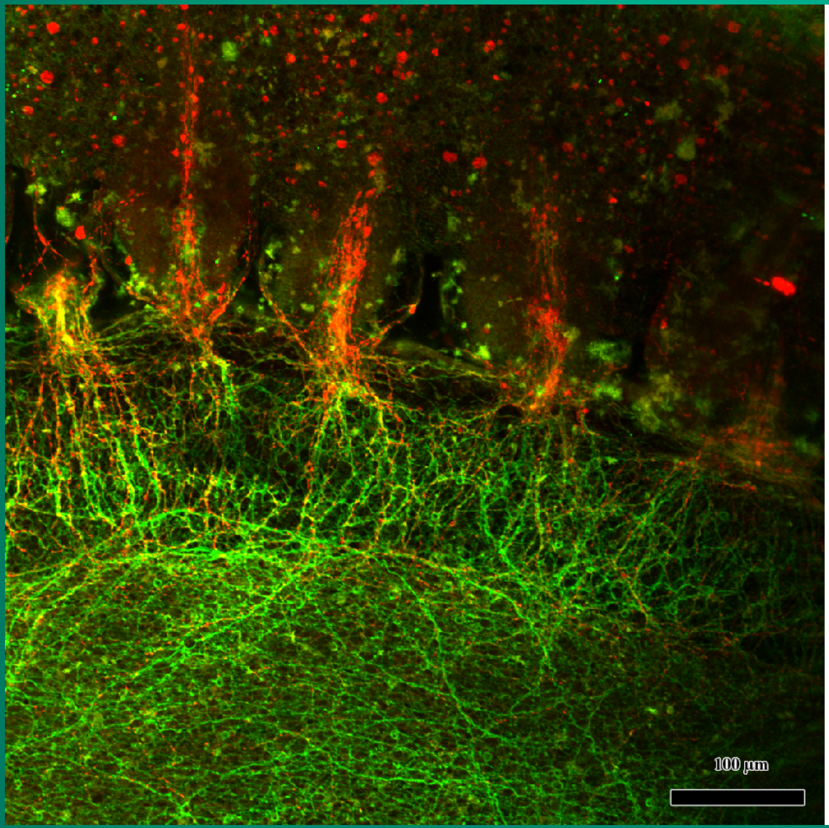
Double label with Tubulin (A) and FMRFamide (B) antibodies

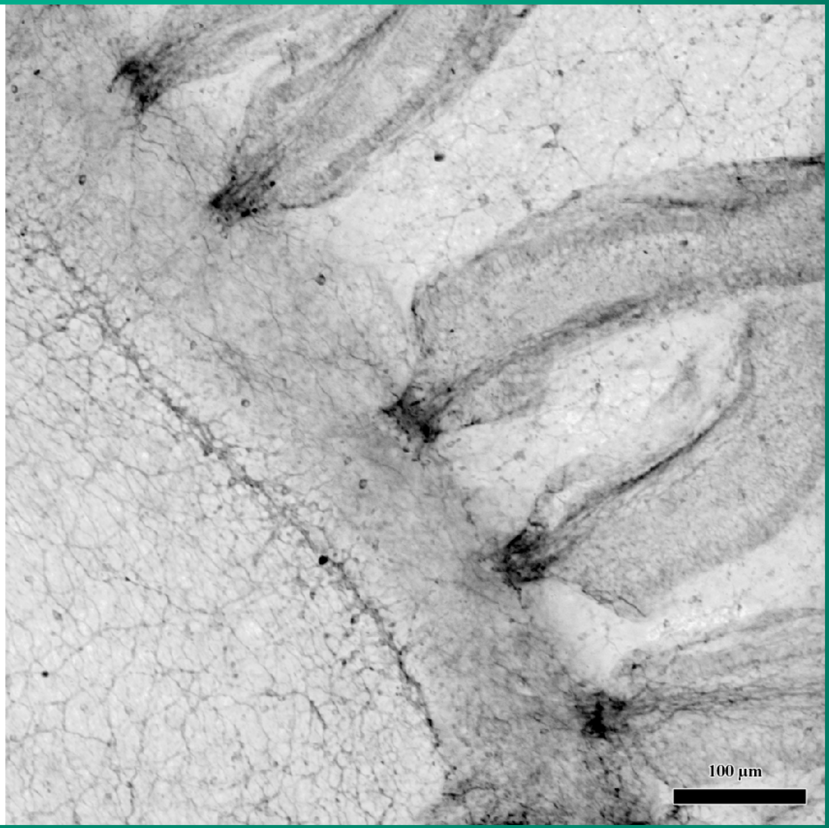
A – motor nerve net in subumbrella

B – diffuse nerve net in exact same position



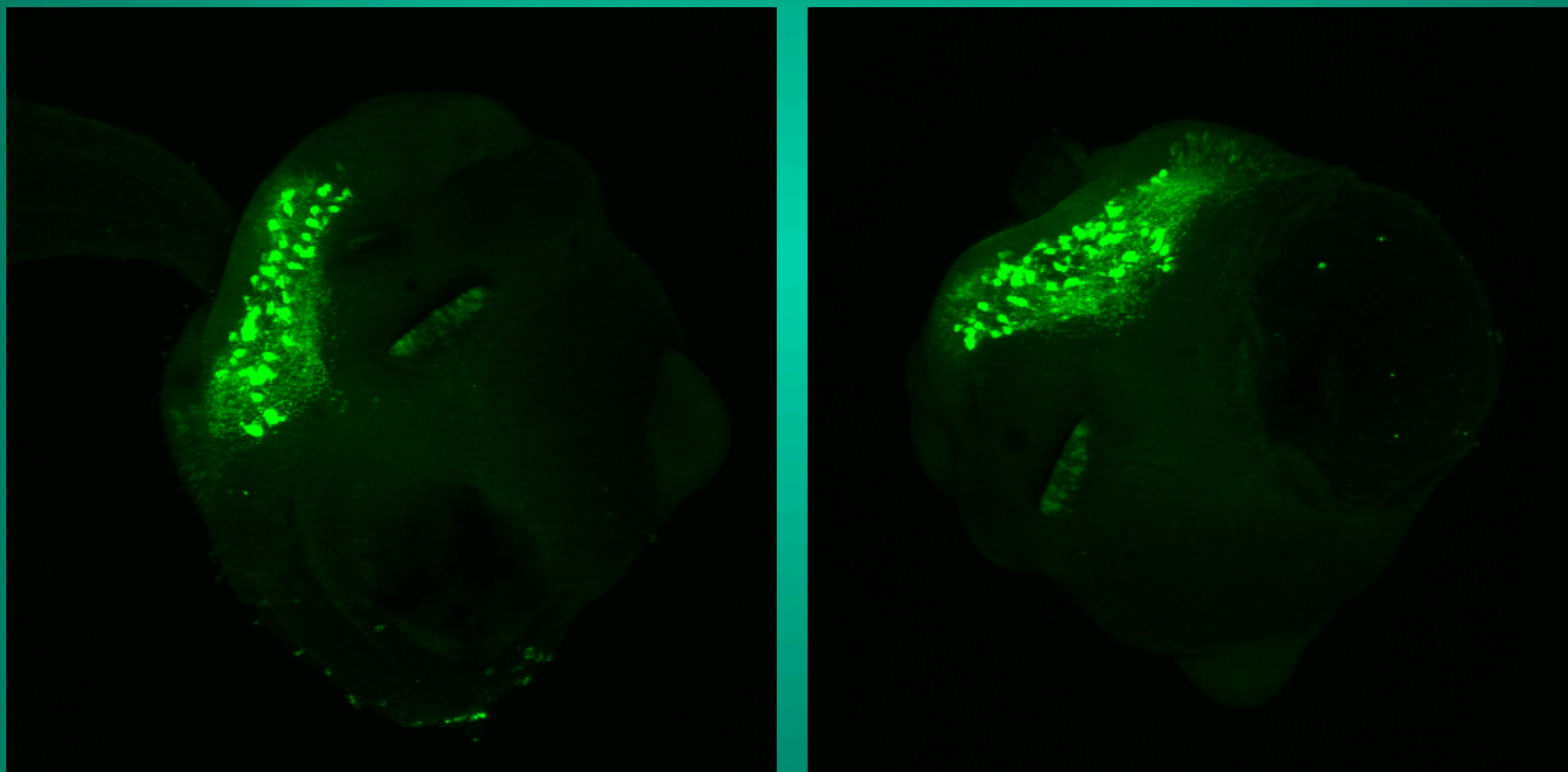
Double label with Tubulin (motor nerve net – green) and FMRFamide (diffuse nerve net – red) antibodies. Marginal region with tentacles bases, and marginal zone lacking swim musculature.





Tripedalia Rhopalia

FMRFamide Immunohistochemistry



Cephalization and the "no-headed" cnidarians.

If we borrow the concept of cephalization (whether it is considered a driving force or a consequence), we can see that integrative centers tend to align with sensory specializations more than with effector elaborations. Even nerve net compressions seem to follow this general organizational rule.

Where does this leave the nerve net in terms of nervous system organization in Cnidarians?

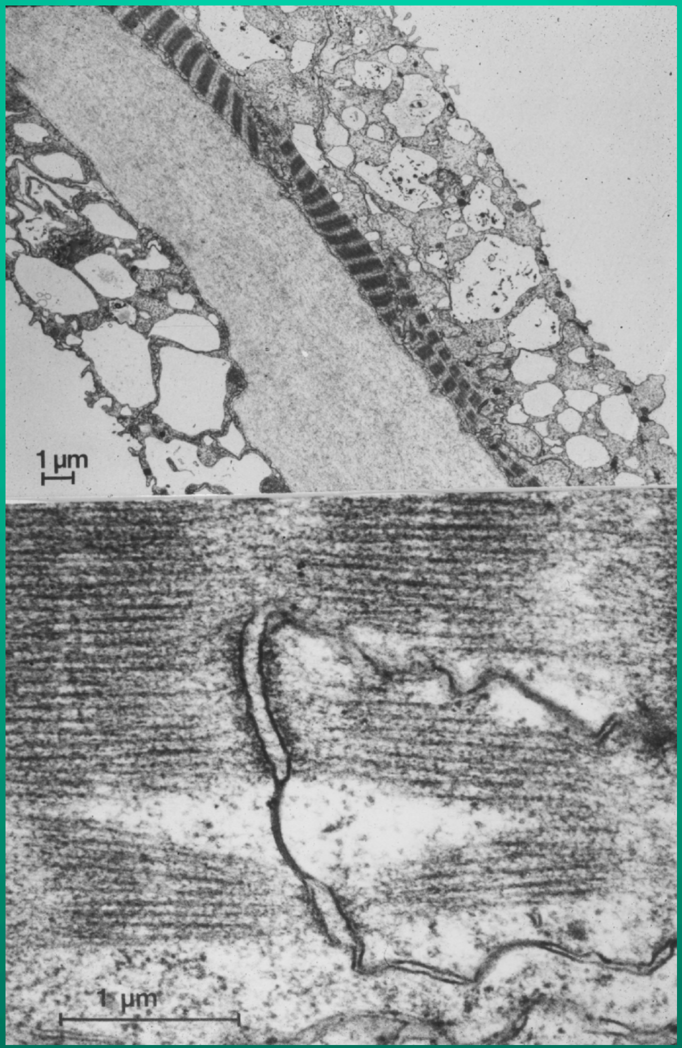
Primitive form of nervous system organization?

Alternate idea – simply the most efficient way to activate a broad, two-dimensional sheet of effectors (diffuse conduction) when excitation can originate from a variety of sources around the margin of the medusa (non-polarized conduction).

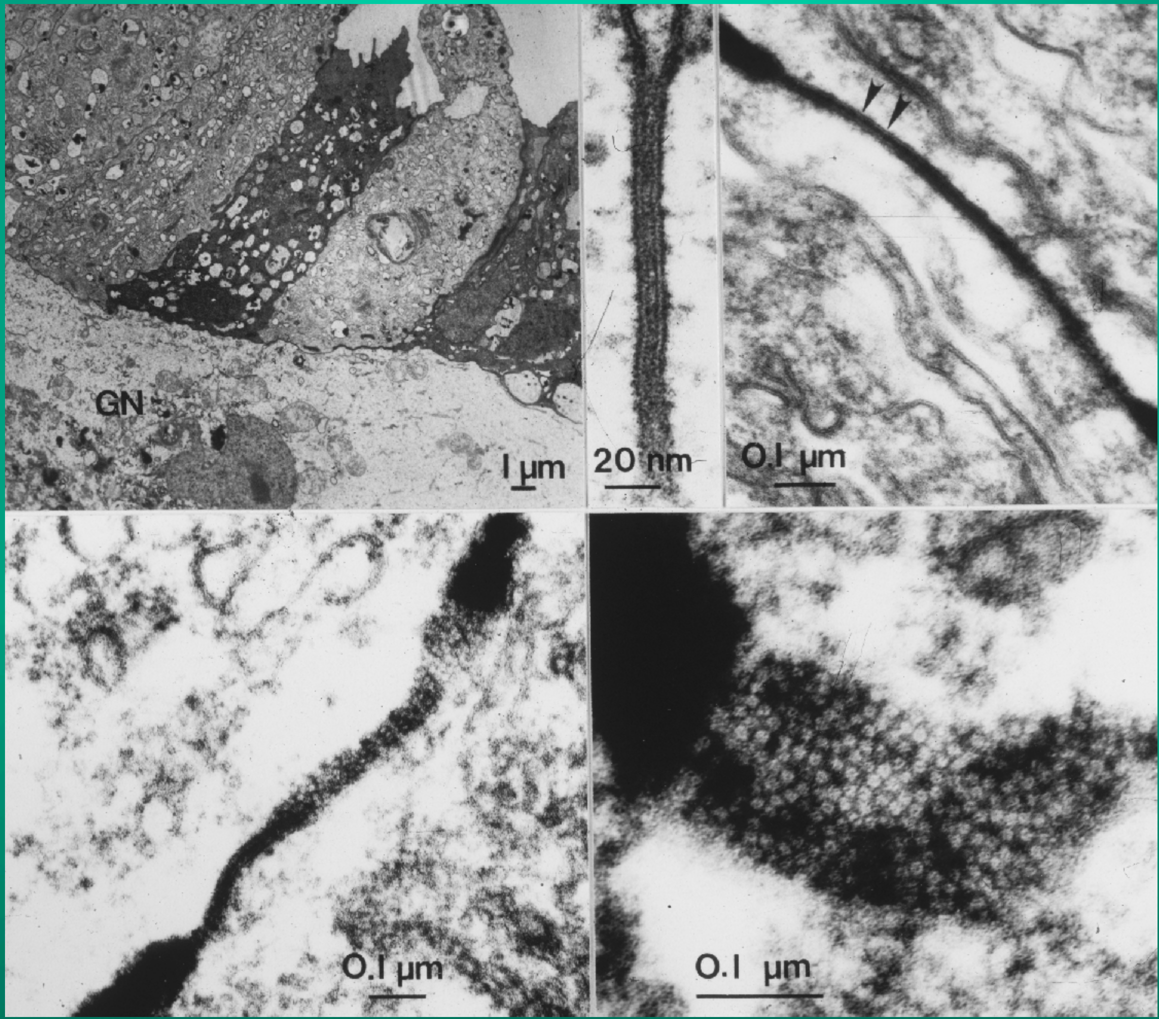
In molluscs and other invertebrates, sheets of effectors are frequently innervated by central motorneurons and a peripheral neuronal plexus.

Is there an alternate way to innervate broad sheets in effectors in cnidarians?

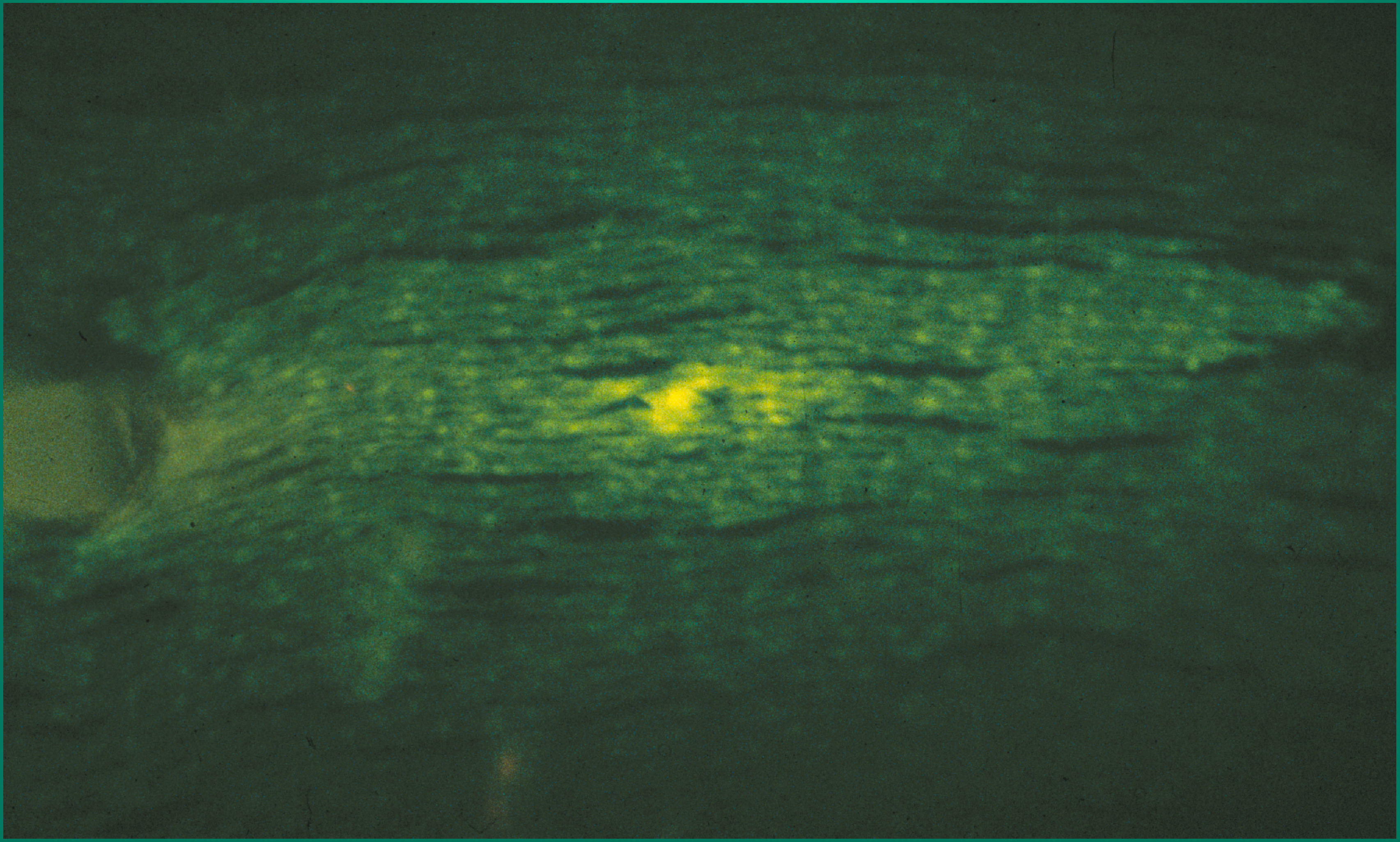
Polyorchis – Subumbrellar Ultrastructure



Polyorchis Gap Junctions



Aequorea – Subumbrellar Dye-Coupling



Stability and Change in Locomotory Systems

Rhythmic activities rely on some form of pattern generation to produce reliable and efficient motor patterns.

This background activity is subject to modification through simple reflexes, through central arousal systems, through hierarchical interactions between complementary and mutually-exclusive circuits, and through internal motivational states.

Changes are typically organized so the resultant modification in the baseline activity confers some behavioral advantage to the organism, either on the short term, or through learned responses, with longer duration.

When considering the overall functions of nervous systems, we can underline a couple of items on our lists, that are inclusive of the earliest animal forms that had distinct, multicellular nervous systems.

•The ability to modify activity of a neural circuit based on specific sensory perturbations in ways that favor a beneficial change in behavioral output of either short or longer term.

•The accumulation of neural tissue (and integrative circuitry) in association with the elaboration of sensory structures allows more centralized control of the interaction between the external senses and internal drives to provide fast and meaningful changes in behavioral output. **This holds regardless of the body symmetry of the animal (radial or bilateral).**

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Contemplating a Career in Aquatic Biology?

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