

[NOTE: The following is an unpublished summary about nervous system design and function in the blackworm, *Lumbriculus variegatus* (Class Oligochaeta). This worm is being used at high school and college levels for student laboratory exercises and research projects. It has proven quite useful and reliable for studies of segment regeneration, circulatory physiology, locomotion, eco-toxicology, and neurobiology (Drewes, 1996a; Lesiuk and Drewes, 1998; Drewes and Cain, 1998). The following article provides students and instructors with general information about this worm's nervous system which is not currently available in any biology texts. Correspondence or questions about this information are welcome. Please address to: Charles Drewes, Zoology & Genetics, Room 339 Science II Building, Iowa State University, Ames, IA, 50011; or phone: (515) 294-8061; or email: cdrewes@iastate.edu].

Functional organization of the nervous system in *Lumbriculus variegatus*

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The gross anatomy of the nervous system in *Lumbriculus variegatus* was originally described more than 70 years ago by Isossimow (1926), with an English summary of that work given in Stephenson's book, *The Oligochaeta* (1930). Virtually no published studies of this worm's neurophysiology or behavior were done until the late 1980's. The central nervous system in *Lumbriculus* consists of a cerebral ganglion (or "brain"), located in segment #1, and a ventral nerve cord that extends through every body segment (Figure 1). In each segment, except the first two, the ventral nerve cord gives rise to four pairs of segmental nerves. [Comparative note: In the earthworm, *Lumbricus terrestris*, there are three pairs of segmental nerve in each segment.] The segmental nerves extend laterally into the body wall where they form a series of parallel rings that extend within and around the body wall (for review, see Stephenson, 1930.). Some fibers in these nerves are sensory in function and detect stimulation of the body surface. Other fibers are motor in function and innervate circular muscle, longitudinal muscle, or chaetal muscles in the body wall.

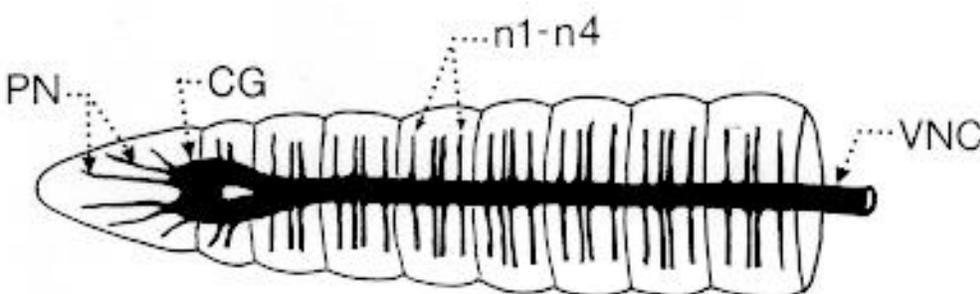


Fig. 1. Dorsal view of the central nervous system in the anterior end of *Lumbriculus variegatus*. Abbreviations: PN, prostomial nerves; CG, cerebral ganglion; n1-n4, segmental nerves 1-4; VNC, ventral nerve cord.

Clusters of neurons are found in the ventral nerve cord of each segment. Some of these are sensory neurons, others are motor neurons, and many are interneurons. Some of the fibers arising from motor and sensory neurons extend into segmental nerves, while other fibers from these neurons extend into a central region of the ventral nerve cord, termed the neuropile. The neuropile is a region where many synaptic connections are made between all types of neurons. Some of these connections involve neurons within the same segment, and others involve connections between neurons in neighboring segments. These pathways and connections are formed in an orderly fashion, thus providing an anatomical basis for the neuronal circuits and reflex pathways that control the worm's coordinated movements and behavior.

A cross-section through the ventral nerve cord reveals three exceptionally large diameter nerve fibers in the dorsal part of the cord (Figure 2). These are the worm's so-called giant nerve fibers that are seen in the ventral nerve cord of nearly all oligochaetes; these fibers have a key role in the worm's rapid escape responses (Drewes, 1984; Zoran and Drewes, 1987; Drewes and Fourtner, 1990; Drewes and

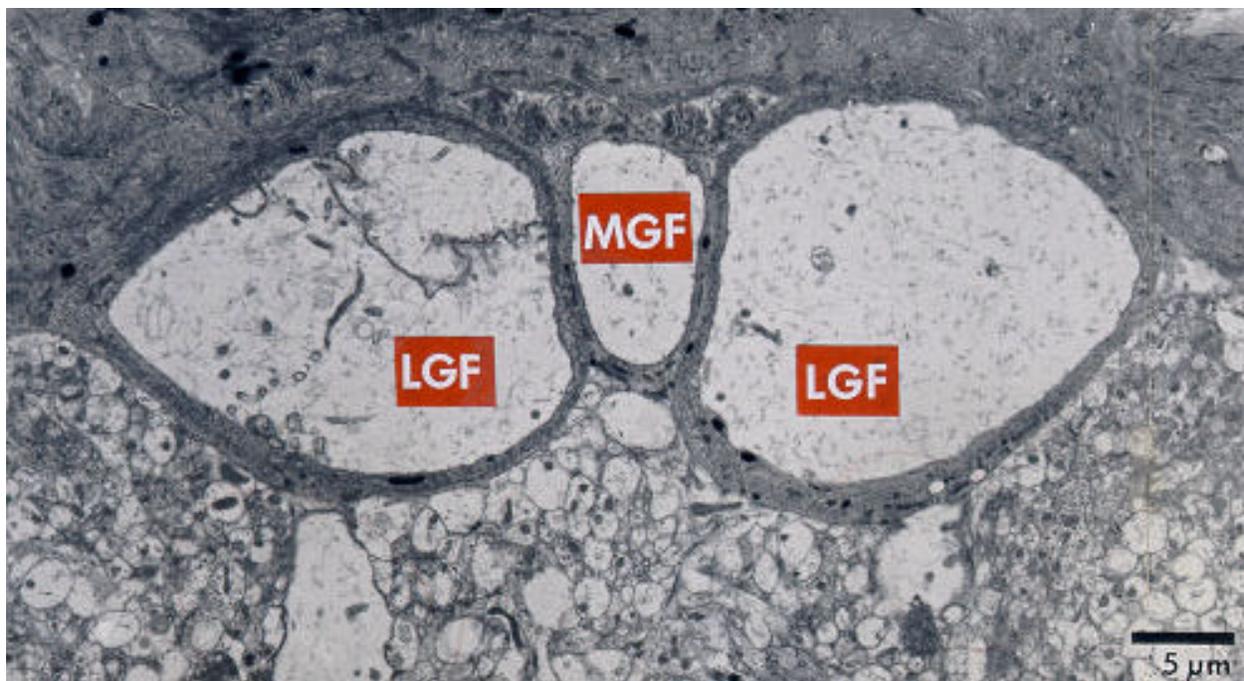


Fig. 2. Cross-sectional view of *Lumbriculus* ventral nerve (dorsal portion of posterior ventral nerve cord). MGF, medial giant fiber; LGF lateral giant fiber. Note the small-diameter fibers in the neuropil region below the giant nerve fibers. Also note the heavy myelin-like sheath surrounding the giants fibers.

Brinkhurst, 1990). Each of the three giant fibers is derived from an aligned, tandem sequence of enlarged axons that arise from segmentally arranged interneurons (Fig. 3).

Electrical synapses interconnect these axons, thus allowing uninterrupted impulse conduction along the entire fiber. The giant nerve fibers in *Lumbriculus* are tightly wrapped by glial cell membranes, except at points where small branches emerge ventrally from the fibers (see anterior left LGF in Fig. 2). This glial wrapping gives the same appearance and probably serves the same function (increased conduction velocity) as the myelin sheath in vertebrate nerve fibers. In *Lumbriculus*, as in other oligochaetes, the giant fiber branches that emerge ventrally and interrupt the glial wrapping appear to have a dual function: they may act as functional “nodes” in initiating action potentials and they may receive synaptic connections from other neurons (Zoran et al., 1988; Drewes, 1997).

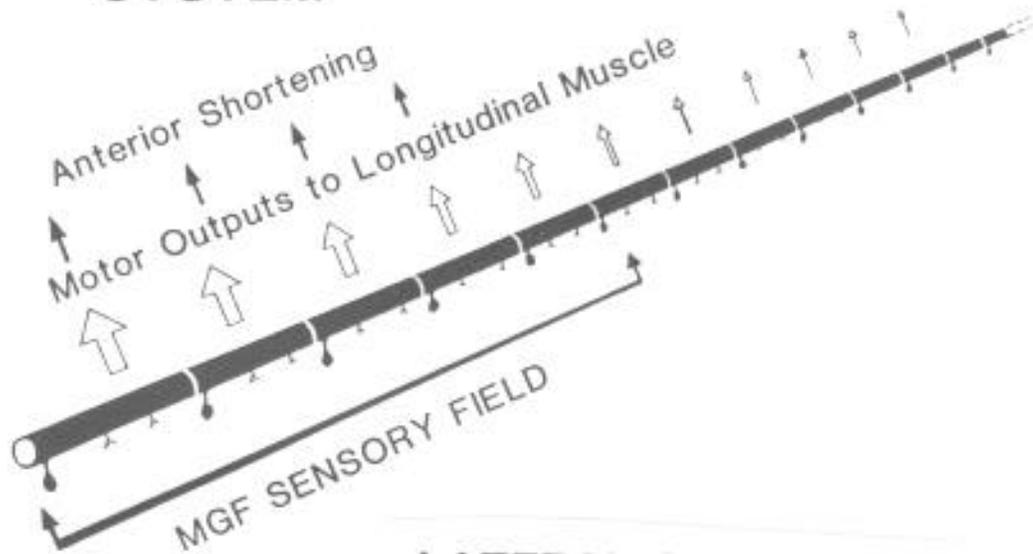
The giant nerve fibers form two functionally different pathways, as shown in Figure 3. The medial giant fiber (or MGF) is excited by touch sensory stimuli to anterior segments. Once excited, the MGF conducts impulses along the ventral nerve cord and excites segmental motor neurons which, in turn, excite longitudinal muscle, resulting in rapid shortening and withdrawal of anterior segments. In contrast, the two lateral giant fibers (or LGFs) are excited by touch stimuli to posterior segments. The LGFs are excited together and conduct impulses as a single unit along the ventral nerve cord. LGF impulses also excite motor neurons and longitudinal muscle, thus leading to rapid shortening of posterior segments. In addition to touch sensory stimulation, the LGFs are also be excited by a shadow stimulus when the worm’s tail is projected to the water surface. Photoreceptors in the worm’s tail detect the shadow. This triggers LGF impulses and rapid shortening of the tail (Drewes and Fournier, 1989).

The giant fibers in *Lumbriculus* offer a rare technical opportunity for neurophysiological study. All-or-none action potentials from the MGF or LGF can be detected non-invasively in freely moving worms, thus eliminating the need for anesthesia, dissection, and restraint. MGF and LGF conduction velocities increase in relation to increased fiber diameter. Diameter, in turn, varies in relation to location along the worm’s body, age, and stage of segment regeneration (Zoran and Drewes, 1987; Drewes and Brinkhurst, 1990; Drewes and Fournier, 1990). Conduction velocity may also be momentarily increased to “super-normal” values as a result of previous impulse conduction (Turnbull and Drewes, 1996). Giant fiber excitability and conduction velocity may be decreased by exposure to a wide variety of environmental toxicants (Rogge and Drewes, 1993; Drewes, 1997).

Although there have been numerous studies of giant fiber-mediated rapid escape behavior in *Lumbriculus*, there have been no physiological studies of the neural control of other movements or locomotor behaviors that are also important to this animal. For example, the neuronal circuits that control this worm’s swimming and crawling behaviors have not been studied. Since swimming and crawling are rhythmic and patterned movements (Drewes and Cain, 1998), we would expect and assume that each of these behaviors is controlled by some type of central pattern generator in the worm’s ventral nerve cord. The term “central pattern generator” (abbreviated CPG) refers to any network of neurons that generates patterned, and usually rhythmic outputs of neuronal activity which, in turn, control a particular behavior. Examples in invertebrates include the CPG’s for rhythmic feeding in snails, swimming in leeches, as

well as walking, running and flying in many arthropods. In *Lumbriculus*, CPG's probably control forward and rearward peristaltic crawling movements which are produced by coordinated waves of circular and longitudinal muscle contraction. The helical swimming movements in *Lumbriculus* (Drewes, 1996b) are probably also under the control of a different CPG. The biomechanics and timing of helical swimming movements are indirect reflections of the outputs of the CPG for swimming. The timing and mechanics of swimming movements in various ages of *Lumbriculus* have been recently described (Drewes, 1998).

MEDIAL GIANT FIBER SYSTEM



LATERAL GIANT FIBER SYSTEM

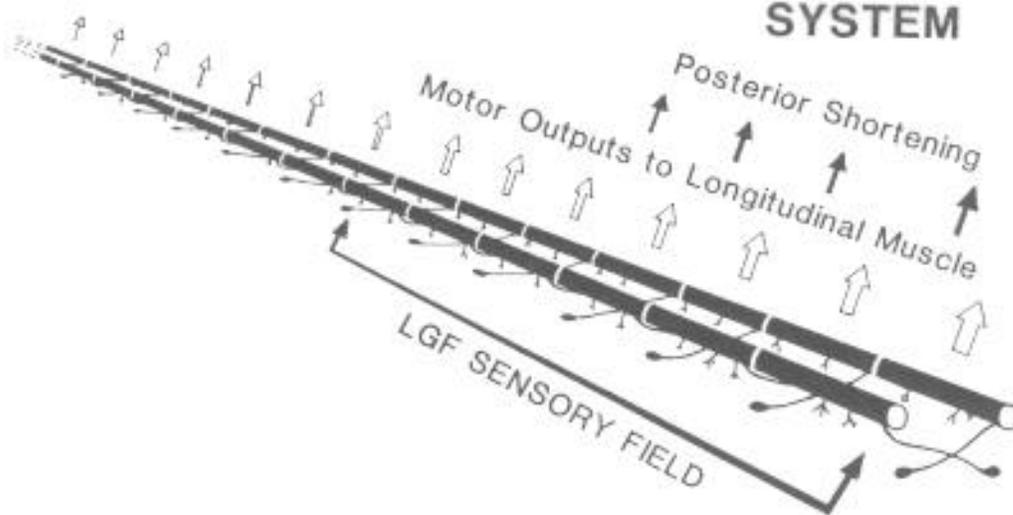


Fig. 3. Generalized diagrams of escape reflex organization in *Lumbriculus*. Note the segmentally arranged cell bodies (CB) of the medial (M) and lateral (L) giant nerve fibers.

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