THE NEURAL BASIS OF THE
LOCOMOTION OF NEMATODES

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Abstract: A model of electrotonic neurons is presented which allows computer simulation of
a physiologically realistic neural network, such as that found in nematodes. The undulatory
locomotion of Caenorhabditis elegans is investigated by solving the equations of motion of a
segmented model of the discretized body taking into account all internal and external forces.
The spatio-temporal muscle excitation patterns which produce locomotion are determined, and
it is concluded that these are most probably generated by stretch receptor cells and signals
which globally turn on or off the neural circuitry governing forward or backward motion. The
results are illustrated in the form of a computer generated videotape and compared with the
observed motion of a nematode.

I. Introduction

The purpose of this work is to contribute towards an understanding of neural net-
works occurring in nature. Our first consideration was to determine an appropriate
starting point. Fig. 1 shows three nerve cells: (a) of the nematode Caenorhabditis ele-
gans (C.e.), (b) of the shark, (c) of man. Note, that for obvious reasons, the synapses,
where the cell transmits information to another cell, are only shown for C.e. Besides the
increase of dendritization clearly visible in Fig. 1, at some stage of evolution towards
species with more and more complex nervous systems, probably two important tran-
sitions have taken place: the transition from electrotonic neurons to a combination of
electrotonic and spiking neurons with electrochemical compensation of signal attenua-
tion; and the transition from a completely deterministic, genetically pre-wired nervous
system to a net with an, at least, partially random connectivity. As a result of the in-
creased complexity of the nervous systems of advanced organisms as noted above, we
have chosen, as a starting point, to consider the nematode C.e. which has a very simple
nervous system.
Fig. 1. Three nerve cells. (a) schematic diagram of a nerve cell of the nematode *Caenorhabditis elegans*. Arrows indicate in- or outgoing chemical synapses, H-symbols denote electrical synapses. The alphanumeric code identifies other neurons, to which the synapses connect. (b) nerve cell of shark. (c) nerve cell of man.

The nematode *C.e.* is an animal for which the wiring diagram of the whole nervous system is known [1]. *C.e.* is a worm of ~1mm length and ~0.08mm diameter. Each individual has 302 neurons. Each neuron has, on the average, 20 synapses. Through laser ablation experiments (i.e. selective killing of neurons), the function of many of the neurons is known. We have reasons to believe that the neurons are electrotonic, i.e. transmit graded electric signals which are attenuated along the axons, and not spikes.

Related to its simple nervous system is the simple lifestyle of *C.e.* Its only observable activities are locomotion, feeding, digesting (bacteria), and reproduction. This makes the study of its nervous system more tractable than that of higher species, for instance vertebrates, which may engage in activities other than those listed above.

Our second consideration, therefore, was to select the neural basis for one specific activity of *C.e.* to investigate. Several reasons led us to choose locomotion. Among these, the primary reason was the fact that the innervation by 69 motor neurons and