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The control structure of the nematode *Caenorhabditis elegans*: neuro-sensory integration and proprioceptive feedback

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1 The control structure of the nematode *Caenorhabditis elegans*: 2 neuro-sensory integration and proprioceptive feedback

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7 Abstract

We develop a biophysically realistic model of the nematode *C. elegans* that includes: (i) its muscle structure and activation, (ii) key connectomic activation circuitry, and (iii) a weighted and time-dynamic proprioception. In combination, we show that these model components can reproduce the complex waveforms exhibited in *C. elegans* locomotive behaviors, chiefly omega turns. This is achieved via weighted, time-dependent suppression of the proprioceptive signal. Though speculative, such dynamics are biologically plausible due to the presence of neuromodulators which have recently been experimentally implicated in the escape response, which includes an omega turn. This is the first integrated neuromechanical model to reveal a mechanism capable of generating the complex waveforms observed in the behavior of *C. elegans*, thus contributing to a mathematical framework for understanding how control decisions can be executed at the connectome level in order to produce the full repertoire of observed behaviors.

8 1. Introduction

9 Of general interest to the biology community is understanding how biomechanical
10 systems process sensory input to produce behavioral outcomes and robust control strate-
11 gies. Seemingly simple behavioral paradigms such as flying, crawling, and walking all
12 involve complex interactions between neuronal networks of sensory neurons, propriocep-
13 tive feedback, and muscle activation. Understanding how these various networks interact

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