

A Dynamical Neural Network Model of Sensorimotor Transformations in the Leech

Shawn R. Lockery, Yan Fang, and Terrence J. Sejnowski

Computational Neurobiology Laboratory
Salk Institute for Biological Studies
Box 85800, San Diego, CA 92138

ABSTRACT

Interneurons in leech ganglia receive multiple sensory inputs and make synaptic contacts with many motor neurons. These "hidden" units coordinate several different behaviors. We used physiological and anatomical constraints to construct a model of the local bending reflex. Dynamical networks were trained on experimentally derived input-output patterns using recurrent back-propagation. Units in the model were modified to include electrical synapses and multiple synaptic time constants. The properties of the hidden units that emerged in the simulations matched those in the leech. The model and data support distributed rather than localist representations in the local bending reflex. These results also explain counterintuitive aspects of the local bending circuitry.

INTRODUCTION

Neural network modeling techniques have recently been used to predict and analyze the connectivity of biological neural circuits (Zipser and Andersen, 1988; Lehky and Sejnowski, 1988; Anastasio and Robinson, 1989; Lockery et al., 1989). Neurons are represented as simplified processing units and arranged into model networks that are then trained to reproduce the input-output function of the reflex or brain region of interest. After training, the receptive and projective field of hidden units in the network often bear striking similarities to actual neurons and can suggest functional roles of neurons with inputs and outputs that are hard to grasp intuitively. We applied this approach to the local bending reflex of the leech, a three-layered, feed-forward network comprising a small number of identifiable neurons whose connectivity and input-output function have been determined physiologically. We found that model local bending networks trained using recurrent back-propagation (Pineda, 1987; Pearlmutter, 1989) to reproduce a physiologically determined input-output function contained hidden units whose connectivity and temporal response properties closely resembled those of identified neurons in the biological network. The similarity between model and actual neurons suggested that local bending is produced by distributed representations of sensory and motor information.

THE LOCAL BENDING REFLEX

In response to a mechanical stimulus, the leech withdraws from the site of contact (Fig. 1a). This is accomplished by contraction of longitudinal muscles beneath the stimulus and relaxation of longitudinal muscles on the opposite side of the body, resulting in a U-shaped local bend (Kristan, 1982). The form of the response is independent of the site of stimulation: dorsal, ventral, and lateral stimuli produce an appropriately oriented withdrawal. Major input to the local bending reflex is provided by four pressure sensitive mechanoreceptors called P cells, each with a receptive field confined to a single quadrant of the body wall (Fig. 1b). Output to the muscles is provided by eight types of longitudinal muscle motor neurons, one to four excitatory and inhibitory motor neurons for each body wall quadrant (Stuart, 1970; Ort et al., 1974). Motor neurons are connected by chemical and electrical synapses that introduce the possibility of feedback among the motor neurons.

Dorsal, ventral, and lateral stimuli each produce a pattern of P cell activation that results in a unique pattern of activation and inhibition of the motor neurons (Lockery and Kristan, 1990a). Connections between sensory and motor neurons are mediated by interneurons (Kristan, 1982). The latency from sensory neurons to motor neurons suggests that interneurons are arranged in one or at most two layers. Nine types of local bending interneurons have been identified (Lockery and Kristan, 1990b). These comprise the subset of the local bending interneurons which contribute to dorsal local bending because they are excited by the dorsal P cell and in turn excite the dorsal excitatory motor neuron. Pairwise electrophysiological recordings from a substantial subset of the many possible interneuron pairs revealed no functional connections between interneurons since pairwise recordings. Other interneurons in the network remain to be identified, such as those which *inhibit* the dorsal excitatory motor neurons.

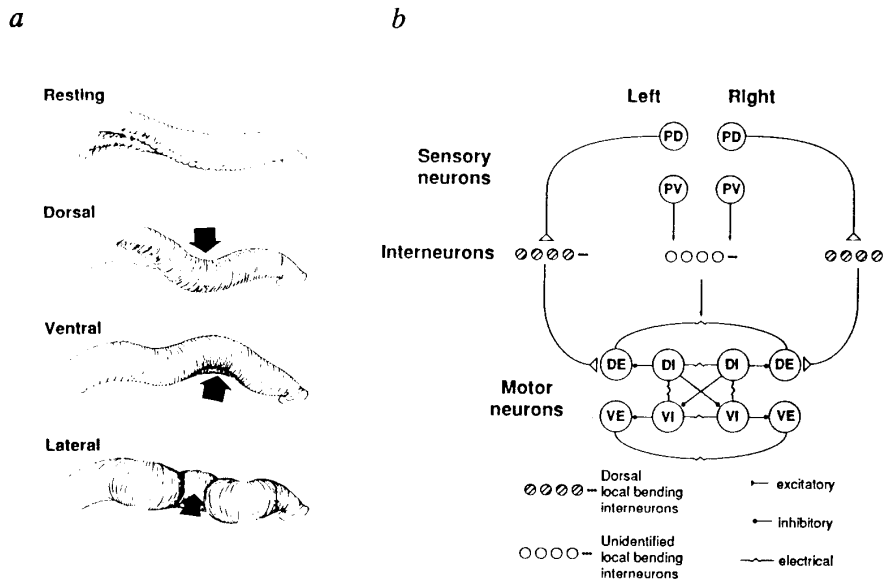


Figure 1: *a.* Local bending behavior. Partial view of a leech in the resting position and in response to dorsal, ventral, and lateral stimuli. *b.* Local bending circuit. The main input to the reflex is provided by the dorsal and ventral P cells (PD and PV). Control of local bending is largely provided by motor neurons whose field of innervation is restricted to single left-right, dorsal-ventral quadrants of the body; dorsal and ventral quadrants are innervated by both excitatory (DE and VE) and inhibitory (DI and VI) motor neurons. Motor neurons are connected by electrical and chemical synapses. Sensory input to motor neurons is mediated by a layer of interneurons. Interneurons that were excited by PD and which in turn excite DE have been identified (hatched); other types of interneurons remain to be identified (open).

The local bending network thus appears to be organized like a three-layered, feed-forward perceptron (Minsky and Papert, 1969). Interneuron input connections were determined by recording the amplitude of the postsynaptic potential in an interneuron while each of the P cells was stimulated with a standard train of impulses (Lockery and Kristan, 1990b). Output connections were determined by recording the amplitude of the postsynaptic potential in each motor neuron when an interneuron was stimulated with a standard current pulse. Interneuron input and output connections are shown in Figure 2, where white squares are excitatory connections, black squares are inhibitory connections, and the size of each square indicates connection strength. Most interneurons received substantial input from three or four P cells, indicating that the local bending network forms a distributed representation of sensory input.

NEURAL NETWORK MODEL

Because sensory input is represented in a distributed fashion, most interneurons are active in all forms of local bending. Thus, in addition to contributing to *dorsal* local bending, most interneurons are also active during *ventral* and *lateral* bending when some or all of their output effects are inappropriate to the observed behavioral response. This suggests that the inappropriate effects of the dorsal bending interneurons must be offset by other as yet unidentified interneurons and raises the possibility that local bending is the result of simultaneous activation of a population of interneurons with multiple sensory inputs and both appropriate and inappropriate effects on many motor neurons. It was not obvious, however, that such a population was sufficient, given the well-known nonlinearities of neural elements and constraints imposed by the input-output function and connections known to exist in the network. Additionally, the fact that most interneurons received substantial input from most sensory neurons suggested that the differences in activity pattern across all the interneurons in response to different sensory inputs would be small. The possibility remained that interneurons specific for each form of the behavior were

required to produce each output pattern. To address this issue, we used recurrent back-propagation (Pearlmutter, 1989) to train a dynamical network of model neurons (Fig 3a). The network had four input units representing the four P cells, and eight output units representing the eight motor neuron types. Between input and output units was a single layer of 10 hidden units representing the interneurons. Neurons were represented as single electrical compartments with an input resistance and time constant. The membrane potential (V_i) of each neuron was given by

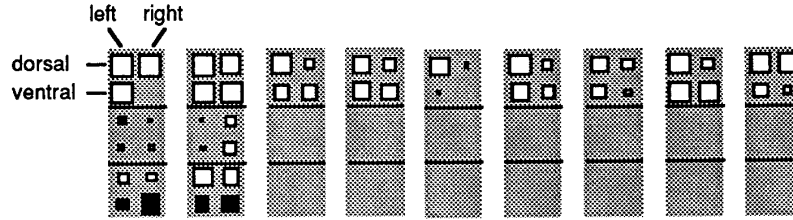


Figure 2: Input and output connections of the nine types of dorsal local bending interneurons. Within each gray box, the upper panel shows input connections from sensory neurons, the middle panel shows output connections to inhibitory motor neurons, and the lower panel shows output connections to excitatory motor neurons. Side-length of each box is proportional to the amplitude of the connection determined from intracellular recordings of interneurons or motor neurons. White boxes indicate excitatory connections and black boxes indicated inhibitory connections. Blank spaces denote connections whose strength has not been determined because the relevant pair of interneurons are not simultaneously accessible to electrophysiological recording.

$$T_i \frac{dV_i}{dt} = -V_i + R_i(I_e + I_c)$$

where T_i and R_i are the time constant and input resistance of the neuron and I_e and I_c are the sum of the electrical and chemical synaptic currents from presynaptic neurons. Current due to electrical synapses was given by

$$I_e = S_j g_{ij} (V_j - V_i)$$

where g_{ij} is the coupling conductance between neuron i and j . To implement the delay associated with chemical synapses, synapse units (s-units) were inserted between pairs of neurons connected by chemical synapses. The activation of each s-unit was given by

$$T_{ij} \frac{dS_{ij}}{dt} = -S_{ij} + f(V_j)$$

where T_{ij} is the synaptic time constant and $f(V_j)$ was a physiologically determined sigmoidal function ($0 \leq f \leq 1$) relating pre- and postsynaptic membrane potential at an identified monosynaptic connection in the leech (Granzow et al., 1985). Current due to chemical synapses was given by

$$I_c = S_j w_{ij} S_{ij}$$

where w_{ij} is the strength of the chemical synapse between units i and j . Thus, synaptic current is a graded function of presynaptic voltage, a common feature of neurons in the leech (Friesen, 1985; Granzow et al., 1985; Thompson and Stent, 1976) and other invertebrates (Katz and Miledi, 1967; Burrows and Siegler, 1978; Nagayama and Hisada, 1987).

Chemical and electrical synaptic strengths between motor neurons were determined by recording from pairs of motor neurons and were not adjusted by the training algorithm. Interneuron input and output connections were given small initial values that were randomly assigned and subsequently adjusted during training. During training, input connections were constrained to be positive to reflect the fact that only excitatory interneuron input connections were seen (Fig. 2), but no constraints were placed on the number of input or output connections. Synaptic time constants were assigned fixed values. These were adjusted by hand to fit the time course of motor neuron synaptic potentials (Lockery and Kristan, 1990a), or determined from pairwise motor neuron recordings (Granzow et al., 1985).

There was also agreement between the time course of the response of model and actual interneurons to P cell stimulation (Fig. 4b). In the actual network, interneuron synaptic potentials in response to trains of P cell impulses had a fast and slow component. Some interneurons showed only the fast component, some only the slow, and some showed both components (mixed). Although no constraints were placed on the temporal response properties of interneurons, the same three types of interneuron were found in the model network. The three different types of interneuron temporal response were due to different relative connection strengths of fast and slow s-units impinging on a given interneuron (Fig. 3a). The difference in temporal response properties suggests that the real network could

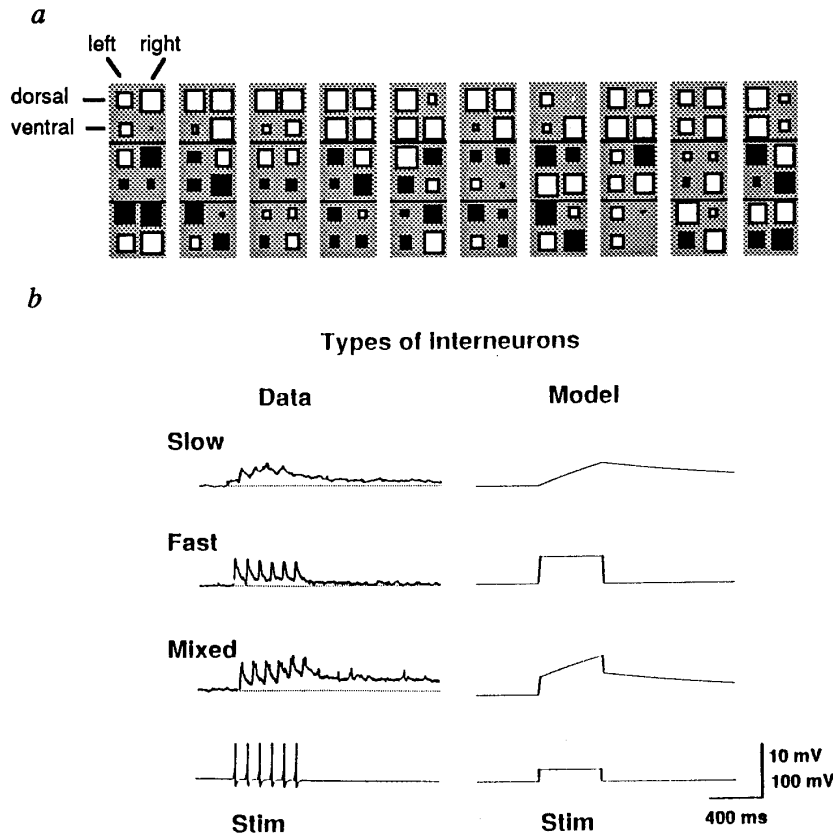


Figure 4: *a.* Input and output connections of model local bending interneurons. Model interneurons, like the actual interneurons, received substantial inputs from three or four sensory neurons and had significant effects on most of the motor neurons. Symbols as in figure 2. *b.* Actual (data) and simulated (model) synaptic potentials recorded from three types of interneuron. Actual synaptic potentials were recorded in response to a train of P cell impulses. Simulated synaptic potentials were recorded in response to a pulse of current in the P cell which simulates a step change in P cell firing frequency.

respond differently to stimuli of different durations. This can be tested theoretically by training the network to produce qualitatively different response to stimuli of different durations.

CONCLUSION

Our results show that the network modeling approach can be adapted to models with more realistic neurons and synaptic connections, including electrical connections, which occur in both invertebrates and vertebrates. The main differences between our model and previous neural network models is that synaptic current is passed between nodes in the network, rather than simple activation, and the state variable of each unit is voltage rather than activation. Leech

neurons are well suited to this formalism because neurotransmitter is released in the absence of action potentials but the approach could in principle be extended to neurons that require action potentials to release neurotransmitter. The qualitative similarity between model and actual interneurons demonstrates that a population of interneurons resembling the identified dorsal local bending interneurons could mediate local bending in a distributed processing system without additional interneurons specific for different forms of local bending. Interneurons in the model also displayed the diversity in temporal responses seen in interneurons in the leech. Clearly, the training algorithm did not produce exact matches between model and actual interneurons, but this was not surprising since the identified local bending interneurons represent only a subset of the interneurons in the reflex. More exact matches could be obtained by using two pools of model interneurons, one to represent identified neurons, the other to represent unidentified neurons. Model neurons in the latter pool would constitute testable physiological predictions of the connectivity of unidentified local bending interneurons.

Acknowledgements

Supported by the Bank of America-Giannini Foundation, the Drown Foundation, and the Mathers Foundation.

References

- Anastasio, T. and Robinson, D. A. (1989) Distributed parallel processing in the vestibulo-oculomotor system. *Neural Comp.* 1:230-241.
- Burrows, M., and M.V.S. Siegler (1978) Graded synaptic transmission between local interneurons and motor neurones in the metathoracic ganglion of the locust. *J. Physiol.* 285:231-255.
- Friesen, W.O. (1985) Neuronal control of leech swimming movements: interactions between cell 60 and previously described oscillator neurons. *J. Comp. Physiol.* 156:231-242.
- Jacob, R.A. (1988) Increased rates of convergence through learning rate adaptation. *Neural Networks* 1:295-307.
- Fang, Y. and T.J. Sejnowski (1990) Faster learning for dynamical recurrent back-propagation. *Neural Comp.* (in press).
- Granzow, B., W.O. Friesen, and W.B. Kristan Jr. (1985) Physiological and morphological analysis of synaptic transmission between leech motor neurons. *J. Neurosci.* 5:2035-2050.
- Katz, B., and Miledi, R. (1967) Synaptic transmission in the absence of nerve impulses. *J. Physiol.* 192:407-436.
- Kristan Jr., W.B. (1982) Sensory and motor neurons responsible for the local bending response in leeches. *J. Exp. Biol.* 96:161-180.
- Kristan, W.B. Jr., S.J. McGirr, and G.V. Simpson (1982) Behavioral and mechanosensory neurone responses to skin stimulation in leeches. *J. Exp. Biol.* 96:143-160.
- Lehky, S.R., and T.J. Sejnowski (1988) Network model of shape-from-shading: neural function arises from both receptive and projective fields. *Nature* 333:452-454.
- Lockery, S.R., Wittenberg, G., Kristan, W.B., Jr., and Cottrell, G.W. Function of identified interneurons in the leech elucidated using neural networks trained by back-propagation. *Nature* 340:467-471.
- Lockery, S.R., and W.B. Kristan Jr. (1990) Distributed processing of sensory information in the leech. I. Input-output relations of the local bending reflex. *J. Neurosci.* (in press).
- Lockery, S.R., and W.B. Kristan Jr. (1990) Distributed processing of sensory information in the leech. II. Identification of interneurons contributing to the local bending reflex. *J. Neurosci.* (in press).
- Minsky, M and S. Papert (1969). *Perceptrons*. Cambridge, MA: MIT Press.
- Nagayama, T., and M. Hisada (1987) Opposing parallel connections through crayfish local nonspiking interneurons. *J. Comp. Neurol.* 257:347-358.
- Nicholls, J.G., and D. Purves (1970) Monosynaptic chemical and electrical connexions between sensory and motor cells in the central nervous system of the leech. *J. Physiol.* 209:647-667.
- Nicholls, J.G., and B.G. Wallace (1978) Quantal analysis of transmitter release in an inhibitory synapse in the CNS. *J. Physiol.* 281:157-170.
- Ort, C.A., W.B. Kristan Jr., and G.S. Stent (1974) Neuronal control of swimming in the medicinal leech. II. Identification and connections of motor neurones. *J. Comp. Physiol.* 94:121-154.
- Stuart, A.E. (1970) Physiological and morphological properties of motoneurons in the central nervous system of the leech. *J. Physiol.* 209:627-646.
- Thompson, W.J., and G.S. Stent (1976) Neuronal control of heartbeat in the medicinal leech. *J. Comp. Physiol.* 111:309-333.
- Zipser, D., and R.A. Andersen (1988) A back-propagation programmed network that simulates response properties of a subset of posterior parietal neurons *Nature* 331:679-684.