

# Neural Networks Controlling Wrist Movements

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## Abstract

In monkeys performing a step-tracking task, the discharge patterns of forearm motor units and connected premotoneuronal cells in cortex and red nucleus (identified by post-spike facilitation of EMG) fall into characteristic classes: tonic, phasic-tonic, decrementing, etc. We used dynamic neural network models incorporating these discharge patterns to investigate networks that could transform a step input of target position to the observed discharge patterns of flexor and extensor motoneurons. These networks have interconnected hidden units with either excitatory or inhibitory connections to each other and to the motoneurons. The activity of many hidden units resembles discharge patterns that are observed in monkey recordings. The network solutions typically involve preferential connectivity within synergistic groups and often include reciprocal inhibition of antagonists. A network trained on a specific input step level does not necessarily produce a proportional output for other step sizes; however, the networks can be trained to generate motor responses proportional to a target step size. The role of the hidden units can also be investigated by selective lesions or stimulation.

## Introduction

The primate's ability to perform a sophisticated variety of tasks involving wrist and finger movements depends on the neural circuitry controlling forelimb muscles. The response properties of cells during movements have been investigated in monkeys performing specific types of movements. These have revealed a remarkable variety of response patterns in relation to even simple movements. To obtain a quantitative picture of the contributions of cells to control of wrist muscles, it is helpful to identify those cells whose output affects muscle activity. These premotoneuronal cells can be identified by spike-triggered averaging of EMG, which can reveal post-spike facilitation or suppression of target muscles. The response patterns of corticomotoneuronal (CM) cells and rubromotoneuronal (RM) cells have been documented during a simple alternating flexion/extension task designed to relate activity to changes in force and to sustained static force (Cheney & Fetz, 1980). The types of discharge patterns observed in CM and RM cells, as well as in single motor units (MU) of agonist muscles, fall into specific classes (Cheney et al 1988; Fetz et al 1990). During a ramp-and-hold movement, all three groups include cells that show phasic-tonic discharge. The phasic component is related to the changing force and the tonic component is proportional to the amount of static force exerted. All groups also include tonic cells which show steady discharge throughout the hold period in proportion to the active force. Each region also has cells with unique firing properties. A large proportion of motor units show decrementing discharge, which decreases gradually through the hold period. The RM population is unique in having cells that fire during both flexion and extension. In particular, an unmodulated group of RM cells shows steady discharge during active movement that is not modulated with the task (Cheney, et al, 1988). CM cells include a subset whose activity is steadily incrementing during the static hold period. Other response patterns have been observed in additional cells that do not facilitate motoneurons. In cerebral cortex many non-CM cells fire phasically at onset of movement and many of these fire bidirectionally with flexion and extension.

## Network Models

To investigate the functional role of these cells and to infer the types of discharge patterns that might be required to transform a step signal to the observed output of motoneurons, we developed a model that can incorporate these firing patterns. The network utilizes a generalization of the back-propagation algorithm developed by Watrous (1986) in the temporal flow model, and is similar to the networks recently described by Williams and Zipser (1989). These networks allow arbitrary interconnectivity of all elements; in addition to feed-forward connections, they can also have cross-connections within layers as well as feedback. Secondly, the networks incorporate time-varying

activity of cells representing the firing rates of neurons. In our simulations we have used averaged firing rates of motoneurons recorded in monkeys performing a step-tracking task.

The input-output function of each unit is the standard sigmoidal function, with an offset to assure that units generate negligible output in the absence of input activity. The input to a unit consists of the activation of all other cells connected to the unit times their synaptic weight; steady input may also be derived from a bias element with variable weight. The network is initialized with random synaptic weights and the back propagation algorithm is used to modify the connectivity to reduce the error for the specified target output activations.

### Reciprocal movements

The simulation in Figure 1 was designed to derive a neural network that transformed a step change in target position at the input to the observed response patterns of motor units at the output. This simulates the step-tracking task between alternating flexion and extension target zones, and has each of the four types of motor units: tonic, phasic-tonic, decrementing and phasic for both flexor and extensor movements. The network consists of twelve excitatory and twelve inhibitory neurons. We found that using sign constraints on the outputs of units, i.e., that outputs from a given unit be either all excitatory or all inhibitory, provided more interpretable activation patterns. The squares in the matrix symbolize the strength of the synaptic connection from the unit in the row to the unit in the column. Excitatory weights are in black and inhibitory weights are open squares, and the size of the square is proportional to the strength of the connection. The absence of self-recurrent connections corresponds to the absence of diagonal elements. All the excitatory hidden units affect the output cells, and half also connect to the inhibitory group. Half of the inhibitory hidden units connect to the excitatory units and the other half connect only to the output cells.

Figure 1 illustrates the weight matrix and the activation patterns of all units after 2000 training iterations. The discharge patterns of the units are shown at left; from top to bottom, these are the input steps (fs, es), the excitatory and inhibitory hidden units (a's and b's), and the output units (ft to ep). The activation patterns are repeated along the top, above the column representing the input weights to each unit. To better visualize the relationships between units, the hidden units were sorted in order of the strength of their effect on the tonic output units. The sorting algorithm used the product of activation and weight to the flexion tonic output unit minus activation times weight to the extension unit. Thus, the first hidden unit (a3) makes the maximal contribution to the tonic flexion motoneuron. The grouping of the connections indicates that the units which contributed most to tonic flexion activity also made the strongest contribution to the response patterns of all other flexor output units. In the matrix representing interconnection between hidden units, it is clear that units more strongly related to flexion were also more strongly interconnected to each other and least strongly connected to the extension units and vice versa.

The activation patterns of the hidden units show several interesting features. Most hidden units are active during either flexion or extension, although some, (e.g., a9, b10, b8) show appreciable activity through both phases of movement. Secondly, although the profiles of the target motor units are identical for the flexion and the extension groups, the network solution involves an asymmetric assignment of hidden units devoted to each. There are appreciably more hidden unit activations related to flexion than to extension, yet they produce essentially identical output effects. Third, the discharge patterns in the hidden units involve some recognizable variants of the output patterns. Thus, during the extension phase the excitatory hidden units exhibit phasic, phasic-tonic, and tonic patterns (a2, a4 & a1). In the flexion phase none of the hidden units show phasic components. Instead the phasic component of the motoneuron activity is derived from the difference between early onset of excitatory tonic units and later onsets of inhibitory tonic units. Even within the excitatory flexion cells, there is a considerable variety of onset times and rates, which corresponds to physiological observations on CM cells (Cheney & Fetz, 1980).

### Magnitude scaling

We also investigated a network's ability to generate output activation patterns proportional to the input step. In the step tracking task, monkeys learned to generate force levels proportional to the size of the target step, and did so by a proportional scaling of discharge levels of the task-related cells. Such linearity was tested in a simpler network that transforms a step input to a phasic-tonic output (Fig. 2). Testing a given network trained on one force level with inputs representing other force levels yielded outputs that deviate rapidly from a proportional phasic-tonic pattern (Fig. 2, left). Going from

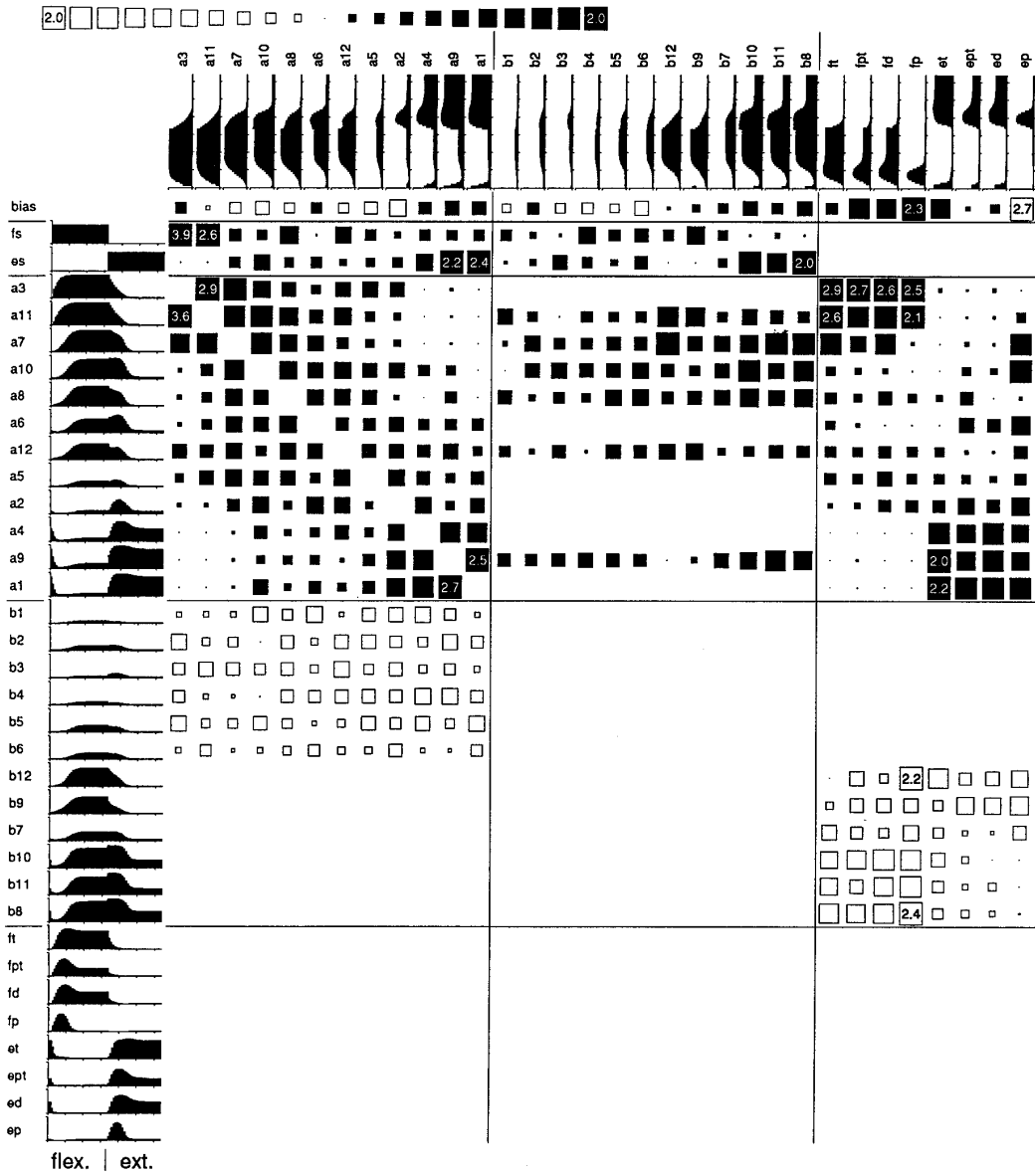


Fig 1. Connectivity matrix and activation patterns (left column and along top) for a network transforming alternating step inputs (fs, es) to eight motor unit discharge patterns (ft to ep; bottom left and top right). The synaptic weight from row unit to column unit is symbolized by the size of the square in the range calibrated at the top, and by a number for weights outside this range. Excitatory and inhibitory connections are represented by solid and open squares respectively. This is the state of the network after 2000 training iterations. Units were sorted within the excitatory and inhibitory groups by their net contribution to unit ft minus their net contribution to unit et.

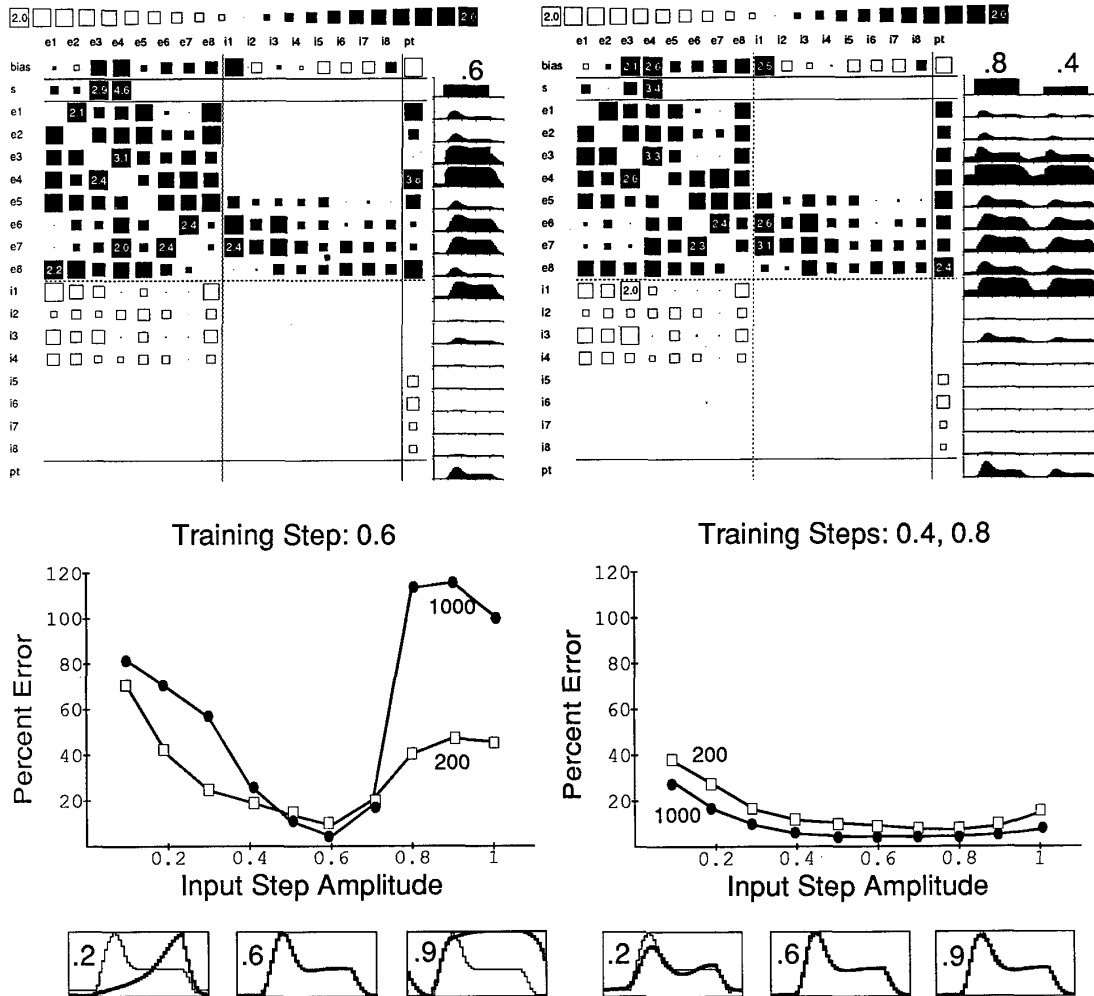


Fig 2. Neural networks transforming step input to phasic-tonic patterns. Left: network trained on one step size (0.6). Right: network trained from same starting point on two step sizes (0.4 and 0.8). Bottom graphs give percent error between the actual output and a phasic-tonic pattern proportional to the step input, after 200 training iterations (white boxes) and 1000 iterations (black circles). Samples below show normalized outputs (dark lines) with their target phasic-tonic patterns (light lines) for input step sizes 0.2, 0.6, and 0.9 using the 1000-iteration networks.

200 to 1000 training iterations produced a slight improvement in accuracy at the training level (0.6) but resulted in greater deviations at other levels. We obtained a network that generates output in proportion to the input by simultaneous training at two step levels (Fig. 2, right). Training at both a high and a low force level (0.8 and 0.4) yielded a network solution similar to the network trained at a single level, although the excitatory hidden units contributed more equitably to the output (compare left and right networks). When tested with intermediate force levels, the second network generated proportional outputs. However, when tested with steps outside the range straddled by the training levels, the output still deviates slightly from a proportional response.

#### Concluding comments

In these dynamic networks the function of hidden units can be tested by making selective lesions -- i.e., by eliminating the activation of particular units and analyzing the behavior of the remaining network. For large networks with distributed weights, the lesion of a particular unit may have relatively little effect. However, for networks in which a few units with similar activations (e.g., phasic) are strongly interconnected, the lesion of one can drastically reduce activity of the others and can eliminate corresponding components of activity in the output units.

The output effects of a given unit can also be tested by delivering a simulated stimulus and analyzing the propagated network response. The activation pulse can be delivered during various phases of the ongoing task to determine how the impulse response is modulated by changing cell activations.

These network simulations provide a useful tool for analyzing neural mechanisms that could generate patterns of activity in motoneurons. By incorporating profiles of physiological activity and observing anatomical connectivity, they can be constrained to produce plausible models of sensorimotor integration.

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