

A Neural Network for Coding of Trajectories by Time Series of Neuronal Population Vectors

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The neuronal population vector is a measure of the combined directional tendency of the ensemble of directionally tuned cells in the motor cortex. It has been found experimentally that a trajectory of limb movement can be predicted by adding together population vectors, tip-to-tail, calculated for successive instants of time to construct a neural trajectory. In the present paper we consider a model of the dynamic evolution of the population vector. The simulated annealing algorithm was used to adjust the connection strengths of a feedback neural network so that it would generate a given trajectory by a sequence of population vectors. This was repeated for different trajectories. Resulting sets of connection strengths reveal a common feature regardless of the type of trajectories generated by the network: namely, the mean connection strength was negatively correlated with the angle between the preferred directions of neuronal pair involved in the connection. The results are discussed in the light of recent experimental findings concerning neuronal connectivity within the motor cortex.

1 Introduction

The activity of a directionally tuned neuron in the motor cortex is highest for a movement in a particular direction (the neuron's preferred direction) and decreases progressively with movements farther away from this direction. Quantitatively, the change of neuron activity can be approximated by the cosine of the angle between the movement direction and the neuron's preferred direction (Georgopoulos *et al.* 1982). The direction of an upcoming movement in space can be represented in the motor cortex as the neuronal population vector which is a measure of the combined directional tendency of the whole neuronal ensemble (Georgopoulos *et al.* 1983, 1986). If C_i is the unit preferred direction vector for the i th neuron,

then the neuronal population vector \mathbf{P} is defined as the weighted sum of these vectors:

$$P(t) = \sum_i V_i(t)C_i \quad (1.1)$$

where the weight $V_i(t)$ is the activity (frequency of discharge) of the i th neuron at time bin t . The neuronal population vector has proved to be a good predictor of the direction of movement (for a review see Georgopoulos 1990; Georgopoulos *et al.* 1993). Moreover, the population vector can be used as a probe by which to monitor in time the changing directional tendency of the neuronal ensemble. One can obtain the time evolution of the population vector by calculating it at short successive intervals of time or continuously, during the periods of interest. Adding these population vectors together, tip-to-tail, one may obtain a neural trajectory. It was shown that real trajectories of limb movement can be accurately predicted by neural trajectories (Georgopoulos *et al.* 1988; Schwartz and Anderson 1989; Schwartz 1993).

It was hypothesized (Georgopoulos *et al.* 1993) that the observed dynamic evolution of the neuronal population vector is governed by the interactions between directionally tuned neurons in motor cortex while extrinsic inputs can initiate the changes in activity and contribute temporarily or constantly to the ongoing activity. Two types of neural network models could be suggested in the framework of the hypothesis. Within a model of the first type, the movement is decomposed in piecewise parts, and local geometric parameters of a desired trajectory are introduced into the network by the mechanism of continuous updating of the current position (Bullock and Grossberg 1988; Lukashin and Georgopoulos 1993). The main disadvantage of this model is that it needs a mechanism for relatively fast local changes of synaptic weights during the movements. The second type of models may be treated as an opposite limiting case. It could be supposed that subsets of synaptic weights in the motor cortex permanently store information about possible trajectories or at least about its essential parts, and synaptic weights do not change during the movement. Then for realization of a particular trajectory, only one external command is needed: namely, a global activation of an appropriate neuronal subset.

The purpose of the present paper is to simulate dynamic evolution of the neuronal population vector in the framework of the second model above. We consider a one-layer feedback network that consists of fully interconnected neuron-like units. In full analogy with experimental approaches, the neuronal population vector is calculated at successive instants of time in accordance with equation 1.1 as a vector sum of activities of units. A neural trajectory is computed by attaching these vectors tip-to-tail. The network is trained to generate the neural trajectory that coincides with a given curve, and its synaptic weights are adjusted until it does. This is repeated for different trajectories. It is obvious that practically any kind of reasonable dynamic evolution could be reached by

appropriate learning procedure; for example, rather complex dynamics of trained neuronal ensembles have been demonstrated by Jordan (1986), Pineda (1987), Dehaene *et al.* (1987), Massone and Bizzi (1989), Pearlmutter (1989), Williams and Zipser (1989), Fang and Sejnowski (1990), and Amirkian and Lukashin (1992). For the same network design, learning different trajectories entails different sets of synaptic weights. Moreover, one and the same trajectory can be generated by the network with different sets of connection strengths. The main question we address in the present paper is whether these sets of connection strengths reveal common features. The results of this analysis are compared with experimental data (Georgopoulos *et al.* 1993) concerning functional connections between directionally tuned neurons in the motor cortex.

2 Model and Learning Procedure

We consider a network of N neurons whose dynamics is governed by the following system of coupled differential equations:

$$\tau \frac{du_i}{dt} = -u_i(t) + \sum_j w_{ij} V_j(t) + E_i \quad (2.1)$$

$$V_i(t) = \tanh[u_i(t)] \quad (2.2)$$

$$E_i = \cos(\theta - \alpha_i) \quad (2.3)$$

Argument t is shown for values which depend on time. The variable $u_i(t)$ represents internal state (for example, the soma membrane potential) and the variable $V_i(t)$ represents correspondingly the output activity (for example, firing frequency) of the i th neuron, τ is a constant giving the time scale of the dynamics, and w_{ij} is the strength of interaction between neurons ($j \rightarrow i$).

External input E_i (2.3) serves to assign preferred direction for the i th neuron. Indeed, in the simplest case, $w_{ij} = 0$, one has $u_i(t \gg \tau) = E_i$ and $V_i \approx \cos(\theta - \alpha_i)$. Thus, if the angle θ is treated as a direction of "movement" that is given externally, then the angle α_i can be regarded as the preferred direction for the i th neuron. It is noteworthy that preferred directions of motor cortical neurons range throughout the directional continuum (Georgopoulos *et al.* 1988). The same type of distribution was obtained for a network that learns arbitrary transformations between input and output vectors (Lukashin 1990). Therefore, below we use random uniform distribution of angles α_i .

Once preferred directions are assigned, components of the neuronal population vector \mathbf{P} can be calculated as the decomposition (equation 1.1) over preferred directions:

$$P_x(t) = \sum_i V_i(t) \cos \alpha_i \quad P_y(t) = \sum_i V_i(t) \sin \alpha_i \quad (2.4)$$

where the time dependence of the V_i values is determined by equations 2.1–2.3. Equations 2.4 may be interpreted as an addition of two output units with assigned synaptic weights.

Let a desired two-dimensional trajectory be given as a sequence of points with coordinates $X_d(t_k), Y_d(t_k), k = 1, \dots, K$. In accordance with the above consideration corresponding points $X_a(t_k), Y_a(t_k)$ of the actual trajectory generated by the network should be calculated by attaching successive population vectors:

$$X_a(t_k) = \sum_{n=1}^k P_x(t_n) \quad Y_a(t_k) = \sum_{n=1}^k P_y(t_n) \quad (2.5)$$

The goal of a training procedure is to find a set of connection strengths w_{ij} that ensures that the difference between desired and actual trajectories is as small as possible. We minimized this difference by means of the simulated annealing algorithm (Kirkpatrick *et al.* 1983) treating the chosen cost function

$$F(w) = \frac{1}{K} \left\{ \sum_{k=1}^K [(X_d(t_k) - X_a(t_k))^2 + (Y_d(t_k) - Y_a(t_k))^2] \right\}^{1/2} \quad (2.6)$$

as the “energy” of the system. The optimization scheme is based on the standard Monte Carlo procedure (Aart and van Laarhoven 1987) that accepts not only changes in synaptic weights w_{ij} that lower the energy, but also changes that raise it. The probability of the latter event is chosen such that the system eventually obeys the Boltzmann distribution at a given temperature. The simulated annealing procedure is initialized at a sufficiently high temperature, at which a relatively large number of state changes are accepted. The temperature is then decreased according to a cooling schedule. If the cooling is slow enough for equilibrium to be established at each temperature, the global minimum is reached in the limit of zero temperature.

Although the achievement of the global minimum cannot be guaranteed in practice when the optimal cooling rate is unknown, the simulated annealing algorithm seems to be the most adequate procedure for our specific purposes. We wish to extract the common features of the sets of synaptic weights ensuring different trajectories. In general, each given trajectory can be realized by different sets of synaptic weights. A complete analysis of the problem needs exhaustive enumeration of all possible network configurations that can be done only for sufficiently simple systems (Carnevali and Patarnello 1987; Denker *et al.* 1987; Baum and Haussler 1989; Schwartz *et al.* 1990). The advantage of the simulated annealing method is that during the procedure a treated system at each temperature (including zero-temperature limit) tends to occupy likeliest (in a thermodynamical sense) regions of the phase space (Kirkpatrick *et al.* 1983; Aart and van Laarhoven 1987). Thus the algorithm provides a useful tool for obtaining likeliest or “typical” solution of the problem.

3 Results of Simulations

The minimal size of the network that still allows the realization of the desired dynamics is about 10 units. In routine calculations we used networks with number of neurons N from 16 to 48. Since in this range the size of the network was not an essential parameter, below we show the results only for $N = 24$. During the learning procedure, the randomly chosen set of preferred directions α_i was not varied. For each selected set of connection strengths w_{ij} , the system of equations 2.1–2.3 was solved as the initial value problem, $u_i(0) = 0$, using a fifth-order Runge–Kutta–Fehlberg formula with automatic control of the step size during the integration. Components of the neuronal population vector (equation 2.4), current positions on the actual trajectory (equation 2.5), and the addition to the cost function (equation 2.6) were calculated at time instances separated from each other by the interval $\tau/100$. The total running time ranged from τ ($K = 100$) to 5τ ($K = 500$). Below we show results for $K = 300$. The time constant, τ , is usually thought of as the membrane time constant, about 5 msec. At this point one should take into account that the running time in the model is completely determined by the time that it takes for a desired trajectory to complete, and may be given arbitrarily. Since the crucial parameter for us was the shape of trajectories, we considered short (or fast) trajectories in order to make the training procedure less time-consuming. Slower trajectories can easily be obtained. Nevertheless, we note that a direct comparison of the velocity of the real movement and the velocity obtained in the model is impossible. The model operates with neural trajectories, and the question of how the “neural” length is related to the real length of a trajectory cannot be answered within the model.

For each learning trial, the connection strengths w_{ij} were initialized to uniform random values between -0.5 and 0.5 . The temperature at the initial stages of the simulated annealing was chosen so that practically all states of the system were accepted. During the simulated annealing procedure, values w_{ij} were selected randomly from the same interval $[-0.5, 0.5]$ without assuming symmetry. The angle θ (equation 2.3) was also treated as a variable parameter on the interval $[0, \pi]$. We used the standard exponential cooling schedule (Kirkpatrick *et al.* 1983): $T_{n+1} = \beta T_n$, where T_n is the temperature at the n th step and the value $1 - \beta$ is varied within the interval from 5×10^{-4} to 10^{-5} . Each step of the simulated annealing procedure included a change of one parameter and the entire recalculation of the current trajectory. We checked the robustness of the results with respect to different series of random numbers used for the generation of particular sets of preferred directions α_i and during the realization of the simulated annealing procedure (about 10 trials for each desired trajectory; data not shown).

Figure 1 shows three examples of desired curves and trajectories produced by the trained network described above. It is seen that actual

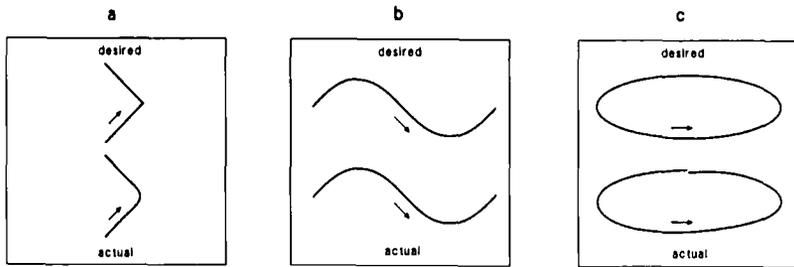


Figure 1: The (X, Y) -plots of desired (upper) and actual (lower) trajectories. Arrows show directions of tracing. The actual curves shown were obtained after the following number of steps of the simulated annealing procedure: 2×10^4 for the orthogonal bend (a), 9×10^4 for the sinusoid (b), and 4×10^5 for the ellipse with the relation between axes 3 : 1 (c).

trajectories generated by the network reproduce the desired ones very well. The trajectories generated by the network (Fig. 1) do not correspond to the global minimum of the cost function (equation 2.6). In all cases these are local minima. This is the reason why the corner in Figure 1a is rounded and the curve in Figure 1c is not closed. If allowed to continue, Figure 1c would trace a finite unclosed trajectory. However, we have found that a limit cycle close to the desired elliptic trajectory can be obtained if the network is trained to trace twice the elliptic trajectory.

To extract the common features of the sets of synaptic weights giving the dynamics shown in Figure 1 we calculated the mean value of the synaptic weight as a function of the angle between the preferred directions of the two neurons in a pair. Corresponding results are shown in Figure 2a, b, c for each trajectory presented in Figure 1a, b, c. Regardless of the type of trajectories generated by the network, the mean connection strength is negatively correlated with the angle between preferred directions: $r = -0.86$ for the orthogonal bend (Fig. 2a), -0.90 for the sinusoid (Fig. 2b), and -0.95 for the ellipse (Fig. 2c).

4 Discussion

Increasing efforts have been recently invested in neural network models for motor control (see, for example, Bullock and Grossberg 1988; Massone and Bizzi 1989; Kawato *et al.* 1990; Burnod *et al.* 1992; Corradini *et al.* 1992). An important question is whether the neural networks that control different types of movements share many or few neuronal subsets. At one end of the spectrum, quite different behavior could be produced by

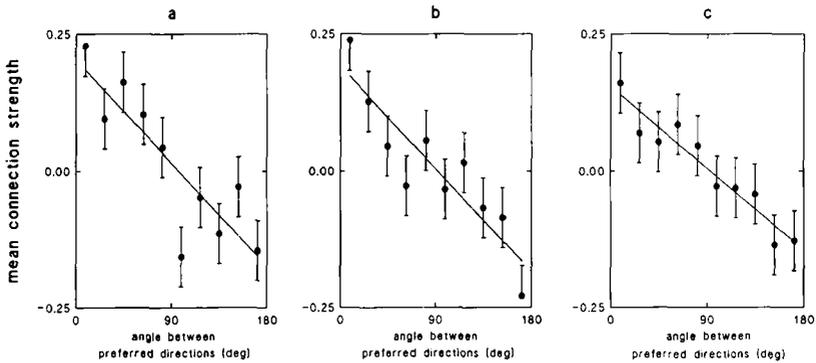


Figure 2: The dependence of the mean value (\pm SEM) of connection strength on the angle between preferred directions of neurons involved in the connection. The mean value of connection strength was calculated by averaging over connections between neurons the preferred directions of which did not differ from each other by more than 18° . Straight lines are linear regressions. Connection strengths w_{ij} used in the calculation of mean values were the same w_{ij} parameters that gave actual trajectories presented in Figure 1: (a) orthogonal bend, (b) sinusoid, and (c) ellipse.

continuous modulation of a single network. At the other end, different subsets could generate each type of movement or “movement primitive.” Taking together in sequential chains or in parallel combinations these movement primitives may provide a variety of natural behavior. Both types of organization have been found experimentally (for a discussion see, for example, Alexander *et al.* 1986; Harris-Warrick and Marder 1991; Bizzi *et al.* 1991). Clearly, intermediate cases involving multiple networks with overlapping elements are likely.

The model we have used implies that synaptic weights do not change during the movement. This means that at the level of the motor cortex different trajectories are realized by different neuronal subsets or by different sets of synaptic weights which store the information about trajectories. Our main result is that although different trajectories correspond to different sets of synaptic weights, all of these sets have clearly a common feature: namely, neurons with similar preferred directions tend to be mutually excitatory, those with opposite preferred directions tend to be mutually inhibitory, whereas those with orthogonal preferred directions tend to be connected weakly or not at all (see Fig. 2). Remarkably, the same structure of the synaptic weights matrix was obtained in modeling

studies of connection strengths that would ensure the stability of the neuronal population vector (Georgopoulos *et al.* 1993).

The results of this study are relevant to those obtained experimentally in the motor cortex (Georgopoulos *et al.* 1993). In those studies, the connectivity between cells was examined by recording the impulse activity of several neurons simultaneously. The correlation between the firing times of pairs of neurons was examined. The correlation reveals the net effect of the whole synaptic substrate through which two neurons interact, including both direct and indirect connections; it represents the "functional connection" between the two neurons. The weight of a connection was estimated by calculating the "difference distribution" between the observed and randomly shuffled distributions of waiting times (for details see Note 34 in Georgopoulos *et al.* 1993). It was found that the mean connection strength was negatively correlated with the difference between preferred directions of the neurons in a pair ($r = -0.815$). This result is in good agreement with the results of our calculations (Fig. 2). Although the weight of the functional connection estimated experimentally is not completely equivalent to the efficacy of single synapse that is implied in the model, our simulations show how this type of the organization of connections in the motor cortex can provide a dynamic evolution of the neuronal population vector during the limb movement. The correlations between the strength of interaction and a similarity among units observed in the experiments and in our simulations might reflect a general principle of the organization of connections in the central nervous system (for a discussion see Tso *et al.* 1986; Martin 1988; Sejnowski *et al.* 1988; Douglas *et al.* 1989; Georgopoulos *et al.* 1993).

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