Biol. Cybern. 69, 517–524 (1993)

Biological Cybernetics

A dynamical neural network model for motor cortical activity during movement: population coding of movement trajectories

A. V. Lukashin *, A. P. Georgopoulos

Brain Sciences Center, Department of Veterans Affairs Medical Center, One Veterans Drive, Minneapolis, MN 55417, USA; and Departments of Physiology and Neurology, University of Minnesota Medical School, Minneapolis, MN 55455, USA

Received: 28 November 1992/Accepted in revised form: 15 March 1993

Abstract. As a dynamical model for motor cortical activity during hand movement we consider an artificial neural network that consists of extensively interconnected neuron-like units and performs the neuronal population vector operations. Local geometrical parameters of a desired curve are introduced into the network as an external input. The output of the model is a time-dependent direction and length of the neuronal population vector which is calculated as a sum of the activity of directionally tuned neurons in the ensemble. The main feature of the model is that dynamical behavior of the neuronal population vector is the result of connections between directionally tuned neurons rather than being imposed externally. The dynamics is governed by a system of coupled nonlinear differential equations. Connections between neurons are assigned in the simplest and most common way so as to fulfill basic requirements stemming from experimental findings concerning the directional tuning of individual neurons and the stabilization of the neuronal population vector, as well as from previous theoretical studies. The dynamical behavior of the model reveals a close similarity with the experimentally observed dynamics of the neuronal population vector. Specifically, in the framework of the model it is possible to describe a geometrical curve in terms of the time series of the population vector. A correlation between the dynamical behavior of the direction and the length of the population vector entails a dependence of the "neural velocity" on the curvature of the tracing trajectory that corresponds well to the experimentally measured covariation between tangential velocity and curvature in drawing tasks.

1 Introduction

Although individual neurons in the motor cortex are broadly tuned with respect to the direction of movement (Georgopoulos et al. 1982) and a particular direction involves the activation of a large ensemble of cells, the high accuracy of a movement performance can be explained by means of the "population coding" hypothesis (Georgopoulos et al. 1983, 1986, 1988). In this hypothesis the contribution of each ith directionally tuned neuron is represented as a vector pointing in its preferred direction $\mathbf{C}_i$ with the length given by the change in cell frequency of discharge associated with a particular movement direction. For a given movement $\mathbf{M}$, these contributions add vectorially to yield the "neuronal population vector" $\mathbf{P}$, which is a measure of the combined directional tendency of the whole neuronal ensemble:

$$\mathbf{P}(\mathbf{M}; t) = \sum_i V_i(\mathbf{M}; t)\,\mathbf{C}_i \tag{1}$$

where $V_i(\mathbf{M}; t)$ is the activity of the ith neuron at time bin t (usually 10- or 20-ms bin). Now it is well established that the neuronal population vector accurately predicts the direction of movement under a variety of conditions (Georgopoulos 1990).

Remarkably, the population vector can be used as a probe to monitor the directional tendency of the neuronal ensemble, as it changes in time. For example, in a task that required a movement to be made at a given angle from a stimulus direction, the population vector rotated from the stimulus direction to the direction of the movement (Georgopoulos et al. 1989; Lurito et al. 1991). Moreover the "neural trajectories" reconstructed from the time series of neuronal population vectors attached to each other tip-to-tail correspond well to the actual movement trajectories produced in reaching (Georgopoulos et al. 1988) as well as in drawing tasks (Schwartz and Anderson 1989; Schwartz 1993). All of these findings indicate that the ongoing direction and length of the neuronal population vector could predict the tangential

---

Correspondence to: A. P. Georgopoulos

* On leave of absence from the Institute of Molecular Genetics, Russian Academy of Sciences, Moscow, Russia

velocity vector of the movement that is made approximately 120 ms later (Schwartz 1993). In its turn, a stable covariation between the tangential velocity of the hand movement and the curvature of a drawn trajectory has been well documented (Viviani and Terzuolo 1982; Lacquaniti et al. 1983; Soechting and Terzuolo 1986; Massey et al. 1992). Qualitatively, this correlation reflects the fact that the movement tends to slow down when the trajectory is more curved. It was hypothesized (Massey et al. 1992) that the underlying mechanisms of the covariation between geometrical and kinematic parameters of the movement could be neural constraints. Namely, if indeed the neuronal population vector predicts the tangential velocity vector of the real movement, then the reason of the tendency to slow down at the curved sections of a trajectory could be explained by the additional time, compared with straight-line movement, needed for the rotation of the neuronal population vector. However, the neural basis which would explain qualitative and quantitative aspects of the problem remains to be explored.

The distributed coding of the direction of movement as well as stationary properties of the ensemble of motor cortical units has been well reproduced in the framework of simple three-layered model trained through a supervised learning algorithm (Lukashin 1990), by means of the model of arrays of adjustable pattern generators (Berthier et al. 1991) and within a more biological model that computes visuomotor transformations for arm-reaching movements (Burnod et al. 1992). The purpose of this paper is to propose a simple *dynamical* neural network model which consists of extensively interconnected neuron-like units and performs the neuronal population vector operations as a response to some input information. Specifically, we consider a model of neural network which receives the input in terms of geometrical features of a trajectory and produces the dynamical behavior of the neuronal population vector as the output. The dynamical properties of the neuronal population vector as well as a relation between the curvature of a trajectory and tangential velocity obtained in the framework of the model reveal close correspondence with the experimental findings mentioned above.

2 Model

2.1 *Basic requirements*

Generally, the present model belongs to a well-known class of neural networks which are able to generate sequential patterns of neural activity (Jordan 1986; Kleinfeld 1986; Sompolinsky and Kanter 1986; Dehaene et al. 1987; Guyon et al. 1988; Kleinfeld and Sompolinsky 1988; Schoner and Kelso 1988; Massone and Bizzi 1989; Pearlmutter 1989; Williams and Zipser 1989; Amirikian and Lukashin 1992). Therefore, we will concentrate only on those features of the model that are essential for the problem in question.

Let K_x and K_y be the x and y components of a unit length tangential vector **K** taken at a point K on a trajectory (Fig. 1). Let M_x and M_y be the same values for a subsequent point M. Receiving components of the vectors **K** and **M** as external input, the desired network has to produce components of the neuronal population vector **P** as a sum of the responses of the ensemble directionally tuned neurons [see (1)]. The basic qualitative requirements for the dynamical behavior of the neuronal population vector follow from experimental findings concerning the dynamical behavior of the neuronal population vector during a transformation task (Georgopoulos et al. 1989; Lurito et al. 1991). The observed dynamical behavior of the neuronal population vector in the case with externally assigned initial (stimulus) and final (movement) directions consists of the rotation of the population vector from an initial to a final direction, followed by the stabilization of the direction and the length of the population vector. Hence, we suppose that at the motor cortical level the tracing of the section of a trajectory between point K with tangential vector **K** and point M with tangential vector **M** corresponds to the rotation of the neuronal population vector **P** from the direction **K** to the direction **M** with subsequent stabilization in the direction **M**. The stabilization of the direction of the population vector triggers the change of the external signals: now the direction **M** is considered by the network as the initial direction, and a new final desired direction (for example, tangential vector **N** of the next point N on the trajectory) is given as a new external input. This assumption is conceptually in accord with the mechanisms of continuous updating of the current position commands to arm muscles, introduced by Bullock and Grossberg (1988) in a model of the circuit that automatically generates arm-movement trajectories.

2.2 *Architecture*

A schematic representation of a neural network obeying the above requirements is shown in Fig. 2. In order to avoid overloading of the figure, only those neurons and connections of the network are shown that realize its

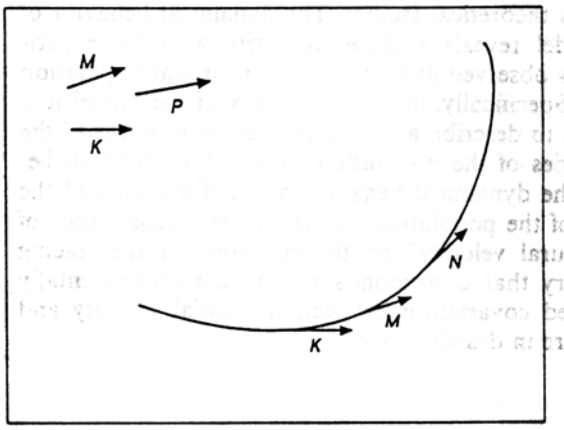

Fig. 1. A desired movement trajectory. **K**, **M**, and **N** are tangential vectors. While tracing the section between points K and M, the neuronal population vector **P** rotates from the direction **K** to the direction **M** with subsequent stabilization in the direction **M**

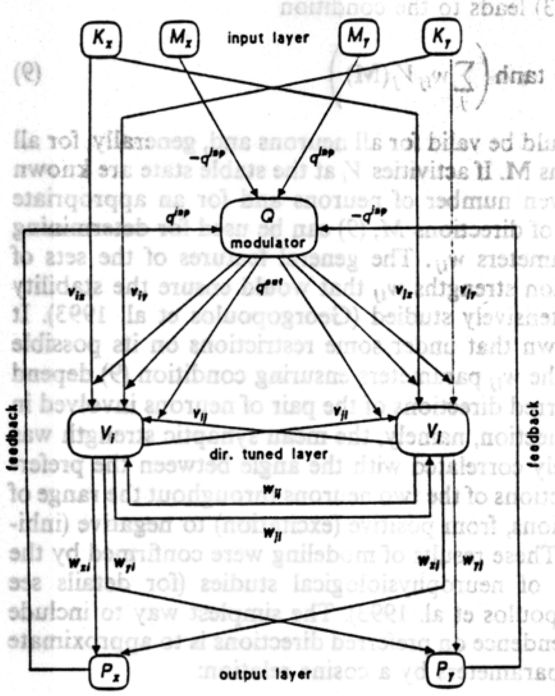

Fig. 2. Architecture of the neural network that models dynamical behavior of the neuronal population vector during movement. Directions of connections are shown by arrows. All modulated connections are designated by v; all nonmodulated connections are designated by w. The neuronal population vector is an integral representation of activities of units V_i located in directionally tuned layer (only two units are shown). Efficacy of modulated connections depends on activities of units Q located in modulator layer (only one unit is shown)

main functions, namely, the neuronal population vector operations when the initial and final directions of movement are given. The straightforward part of the network which realizes the change of external signals is not shown. The input (upper) layer of the network consists of four neurons, the activities of which code components of vectors **K** and **M**. Only the activities of these neurons are assigned externally. The output (lowest) layer consists of two neurons with linear activation functions. The activities of these neurons are supposed to code components of the neuronal population vector **P**. There are two hidden layers in the network: a layer of modulators whose activities are designated by Q (only one of them is shown) and a layer of directionally tuned neurons whose activities are designated by V_i, where index i enumerates neurons in the layer (only two of them are shown in Fig. 2). The activities of all neurons in both hidden layers are determined by a nonlinear activation function which is chosen as a hyperbolic tangent function.

There are connections v_{ix}, v_{iy} between neurons K_x, K_y of the input layer, which code the initial direction **K**, and all neurons V_i of directionally tuned hidden layer. Correspondingly, there are connections w_{xi}, w_{yi} between all V_i neurons and the two neurons P_x, P_y in the output layer. The essential feature of the model is the existence of intralayer connections between neurons V_i in the directionally tuned layer. These connections are of two types: modulated, v_{ij}, and nonmodulated, w_{ij} (see below). The modulator neuron Q receives inputs from neurons M_x, M_y, which code the required final direction **M**, and, by means of feedback connections, from the two neurons P_x, P_y of the output layer, which code the current direction of the neuronal population vector. For the sake of simplicity the absolute values of all these connections are supposed to have the same strength q^{inp}. Possible signs of the connections are shown in Fig. 2. The modulated neuron Q sends signals to directionally tuned neurons V_i in a way such that the efficacy of modulated connections v_{ij} between neurons V_i and the efficacy of connections v_{ix}, v_{iy} between neurons V_i and neurons K_x, K_y depend on the activity of modulator Q and on the connection strengths between neuron Q and neurons V_i. Again, the latter connections are supposed to have the same strength q^{out}.

2.3 *Dynamical equations*

In the framework of standard theory of neural networks (see, for instance, Amari 1972; Sejnowski 1976; Grossberg and Cohen 1983; Hopfield 1984; Hopfield and Tank 1986; Atiya and Baldi 1989) the dynamical behavior of the model described above is governed by the following system of coupled nonlinear differential equations:

$$\tau \frac{du_i}{dt} = -u_i(t) + \sum_j w_{ij} V_j(t) + \left(\sum_j v_{ij} V_j(t) + v_{ix} K_x + v_{iy} K_y\right) q^{out} Q(t) \quad (2)$$

$$V_i(t) = \tanh[u_i(t)] \quad (3)$$

$$Q(t) = \tanh[q^{inp}(|M_x - \tilde{P}_x(t)| + |M_y - \tilde{P}_y(t)|)] \quad (4)$$

$$P_x(t) = \sum_i w_{xi} V_i(t); \quad P_y(t) = \sum_i w_{yi} V_i(t) \quad (5)$$

Argument t is shown for variables which depend on time. Equation (2) is a resistance-capacitance equation for the ith neuron of the directionally tuned layer (variable u_i, for example, might represent the soma membrane potential of the neuron averaged over a reasonable time interval). The time constant τ is a characteristic time for the individual neuron. To simplify the equations, characteristic times for neurons in other layers are supposed to be much shorter than the τ value. We checked that this approximation does not change the main results presented below. Equation (3) shows the relation between the internal state of the ith neuron and its output activity V_i (this value might correspond to the change of discharge rate of a real cell averaged over a reasonable time interval). In accordance with the model (Fig. 2), the activity of the modulator Q at time t (4) is the function of the components of the constant vector **M** and the components of vector **P** at time t. [The tilde above means that vector **P** is normalized to unity in (4)]. The components of vector **P** are linear functions of activities $V_i(t)$, as can be seen from (5).

Once (2)–(5) are written, the dynamical behavior of the model completely depends on the set of connection strengths. In the next section we explain the motivation for our choice of these parameters.

3 Connection strengths

3.1 *Directional tuning of neurons*

Suppose that there are no intralayer connections between neurons V_i (or $w_{ij} = 0$, $v_{ij} = 0$) and no feedback connections to modulator $[Q(t) \approx 1]$. Then (2) is reduced to ordinary differential equations having a straightforward solution, which for $t \gg \tau$ and $q^{out} \ll 1$ leads to the relations:

$$V_i(t \gg \tau) \approx q^{out}(v_{ix}K_x + v_{iy}K_y) = q^{out}k_i \cos(\theta_K - \alpha_i) \quad (6)$$

where θ_K is the angle characterizing the direction of the input vector **K** (Figs. 1, 2), and parameters k_i and α_i are expressed through connection strengths v_{ix}, v_{iy}. Since (6) gives the same response activity to the external direction **K** as has been observed in numerous experiments (Georgopoulos et al. 1982; Schwartz et al. 1988; Schwartz 1992), the angle α_i can be regarded as the *preferred direction* of the *i*th neuron. The important property of the real ensemble of directionally tuned neurons is the uniform distribution of preferred directions in space (Schwartz et al. 1988; Burnod et al. 1992). The same type of distribution was obtained in the framework of the simplified model (without intralayer connections) by means of adjusting the set of the v_{ix}, v_{iy} parameters through a supervised learning algorithm (Lukashin 1990). In accordance with these results, we use for the complete model [(2)–(5)] the following expressions for connection strengths [compare with (6)]:

$$v_{ix} = \cos\alpha_i; \qquad v_{iy} = \sin\alpha_i \quad (7)$$

where angles α_i are randomly and uniformly distributed over the interval $[-\pi, \pi]$. Since the preferred directions are given, connection strengths w_{xi}, w_{yi} [see (5)] should lead to the standard definition of the neuronal population vector (1), namely,

$$w_{xi} = \frac{2}{N}\cos\alpha_i; \qquad w_{yi} = \frac{2}{N}\sin\alpha_i \quad (8)$$

where $2/N$ is a normalizing coefficient and N is the number of neurons in the directionally tuned layer. Equations (8) and (5) are completely equivalent to (1).

3.2 *Stabilization of the neuronal population vector*

Suppose that the direction of the neuronal population vector **P** is close enough to the desired final direction **M**, or $Q(t) \approx 0$ [see (4)]. Then only the first and second terms in the right-hand side of (2) are retained. In accordance with experimental findings in this case (Georgopoulos et al. 1989; Lurito et al. 1991), the direction of the neuronal population vector should be stable. During this steady-state period activities of directional neurons cease to change, so that $du_i/dt = 0$ for all i, which together with (2) and (3) leads to the condition

$$V_i(\mathbf{M}) = \tanh\left(\sum_j w_{ij}V_j(\mathbf{M})\right) \quad (9)$$

that should be valid for all neurons and, generally, for all directions **M**. If activities V_i at the stable state are known for a given number of neurons and for an appropriate number of directions M, (9) can be used for determining the parameters w_{ij}. The general features of the sets of connection strengths w_{ij} that would ensure the stability were extensively studied (Georgopoulos et al. 1993). It was shown that under some restrictions on its possible values, the w_{ij} parameters ensuring condition (9) depend on preferred directions of the pair of neurons involved in the connection, namely, the mean synaptic strength was negatively correlated with the angle between the preferred directions of the two neurons throughout the range of connections, from positive (excitation) to negative (inhibition). These results of modeling were confirmed by the findings of neurophysiological studies (for details see Georgopoulos et al. 1993). The simplest way to include the dependence on preferred directions is to approximate the w_{ij} parameters by a cosine relation:

$$w_{ij} = \frac{2}{N}\cos(\alpha_i - \alpha_j) \quad (10)$$

However, we checked that sets of the parameters w_{ij} obtained in Georgopoulos et al. (1993) led to the same results as the set (10).

3.3 *Rotation of the neuronal population vector*

The dynamical behavior of the system producing the rotation of the neuronal population vector can be ensured by connections that induce the phase shift violating steady-state conditions. Again, the simplest way to include this phase shift is to assign modulated intralayer connection strengths v_{ij} by the relations:

$$v_{ij} = \frac{2}{N}\sin(\alpha_i - \alpha_j), \quad (i \neq j) \quad (11)$$

To allow for the possibility of changing the length of the population vector we introduce a self-inhibition for activities of neurons in the directionally tuned layer (nonzero negative values of the diagonal elements v_{ii}). The self-inhibition is under control by the feedback loop in the same way as it is realized for the modulator Q (this loop is not shown in Fig. 2).

4 Results of simulations and discussion

In this section we give the results of calculations of the dynamical behavior of the model described by (2)–(5) with connection strengths given by (7), (8), (10), and (11). Preferred directions α_i are randomly and uniformly distributed over the interval $[-\pi, \pi]$. The number of neurons in the directionally tuned layer in routine calculations is $N = 100$.

4.1 *Adjustable parameters*

Only three adjustable parameters remain to be established: the characteristic time τ (2), the input, q^{inp}, and the output, q^{out}, connections of the modulator [see (2) and (4)]. The parameter τ determines the time scale of the dynamics. A reasonable value is $\tau \approx 5$ ms. We checked that the results do not depend on a particular value of the q^{inp} parameter if it is large enough. All the results presented below have been obtained for $q^{inp} = 50$. In contrast, the model reveals a strong sensitivity to the value of the q^{out} parameter. Figure 3 shows the time dependence of the direction of the neuronal population vector in a particular case without feedback connections [$Q(t) \approx 1$], for different values of q^{out}. The chosen set of connection strengths provides dynamics such as a movement toward an attractor. It can be seen that the population vector rotates from the direction of vector **K** toward the direction of vector **M** and then stabilizes. The shape of the curves as well as the saturation level essentially depends on the value of the q^{out} parameter. It makes sense to adjust this parameter so as to obtain the angular velocity of rotation at initial moments of time close to the experimentally measured value which is of the order of 500 deg/s (Georgopoulos et al. 1989; Lurito et al. 1991). From this point of view the curve corresponding to $q^{out} = 0.05$ gives the best fit. Indeed, in this case the angular velocity is around 2.5 deg per τ unit or 500 deg/s, if $\tau \approx 5$ ms. All the results shown below were obtained for $q^{out} = 0.05$.

4.2 *Feedback connections*

Figure 4 illustrates the underlying dynamical behaviors for the complete model with feedback connections. The curves correspond to three different directions of the final vector **M** and the same initial direction of the vector **K**. In the beginning of the dynamics, when the current direction of population vector is far enough from the desired final direction, the population vector rotates with constant angular velocity. Without the feedback connections, the dynamics would be the same as curve *c* in Fig. 3. When the direction of population vector becomes close to the assigned final direction **M**, the activity of the modulator Q tends to zero [see Fig. 2 and Eq. (4)]. The third term in the right-hand side of the basic equation (2) ceases to affect the dynamics, and the process enters into the steady-state phase. The stabilized directions of the population vector coincide with the directions of vector **M**. In the light of experimental data concerning the dynamical behavior of the population vector during a transformation task (Georgopoulos et al. 1989) we consider the steady-state phase as the necessary part of the whole dynamics.

4.3 *Population coding of movement trajectories*

The aim of this section is to check the ability of the model to describe trajectories in terms of time series of the neuronal population vectors attached to each other tip-to-tail if the geometrical features of a trajectory are introduced into the network as external input. Here, as an example, we consider closed elliptic trajectories. We checked that all the results remain valid for other curves.

Let a desired trajectory be given (Fig. 5 curve a). Let *K*, *M*, *N*, ... be points along the trajectory separated from each other by equal arc lengths (in routine calculations we used 100 points per trajectory). The beginning of the dynamics is considered to be the instant at which the components of the first two tangential vectors **K** (initial) and **M** (final) are introduced into the network as

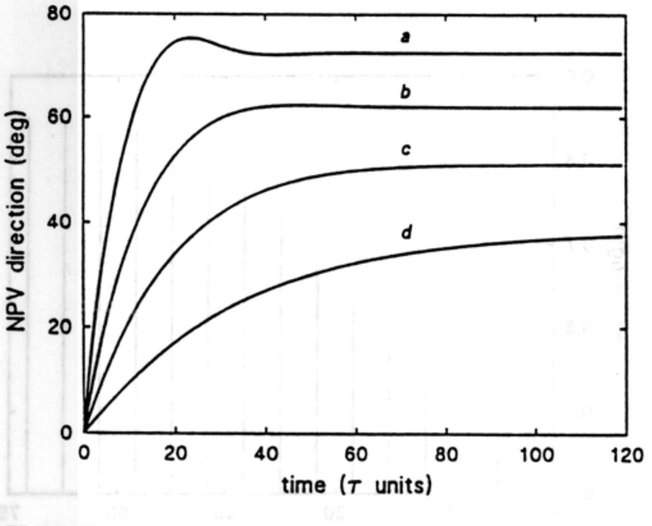

Fig. 3. Time dependence of the direction of the neuronal population vector calculated from (2)–(5), (7), (8), (10) and (11), without feedback connections. Angle $\theta_P = \arctan(P_y/P_x)$ is plotted against t measured in τ units. Activities of the input neurons K_x, K_y and M_x, M_y are chosen so that $\theta_K = 0$ deg, $\theta_M = 90$ deg. Different curves correspond to different values of q^{out}: 0.2 (*a*), 0.1 (*b*), 0.05 (*c*), and 0.02 (*d*)

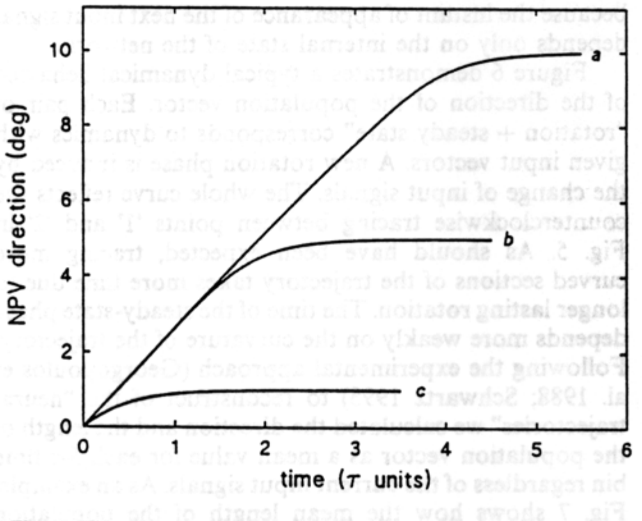

Fig. 4. Time dependence of the direction of the neuronal population vector calculated from (2)–(5), (7), (8), (10), and (11), with feedback connections $q^{inp} = 50$, $q^{out} = 0.05$. Angle $\theta_P = \arctan(P_y/P_x)$ is plotted against t measured in τ units. Activities of the input neurons K_x, K_y are chosen so that $\theta_K = 0$ deg. Different curves correspond to different sets of the values M_x, M_y: angle $\theta_M = 10$ deg (*a*), 5 deg (*b*), and 1 deg (*c*)

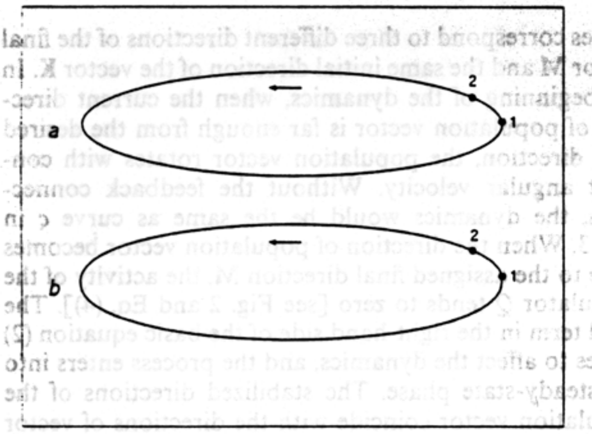

Fig. 5. a Real given trajectory of movement: ellipse with the relation between axis 4:1. Components of tangential vectors taken sequentially at 100 points counterclockwise along the trajectory are introduced into the network as external inputs. **b** Corresponding neural trajectory reconstructed from the 5-τ bin time series of neuronal population vectors attached to each other tip to tail (266 vectors). The length of neural trajectory is normalized to the units of length of real trajectory. Counterclockwise tracing between points 1 and 2 corresponds to the dynamics shown in Figs. 6 and 7

activities of corresponding neurons. Then the dynamics described by (2)–(5), (7), (8), (10), and (11) begins. When the current direction of population vector **P** becomes close to the direction **M**, the activity of the modulator Q rapidly tends to zero. On the one hand, this entails the stabilization of the population vector **P**. On the other hand, the low value of the activity of the modulator Q triggers the change of the input signals (this straightforward part of the network is not shown in Fig. 2). Now vector **M** serves as the initial direction, and the next tangential vector **N** is introduced as a desired final direction, and so on. It is important to note that in the framework of this procedure the relative velocity of tracing of the trajectory is determined by the network itself because the instant of appearance of the next input signal depends only on the internal state of the network.

Figure 6 demonstrates a typical dynamical behavior of the direction of the population vector. Each pair of "rotation + steady state" corresponds to dynamics with given input vectors. A new rotation phase is induced by the change of input signals. The whole curve reflects the counterclockwise tracing between points '1' and '2' in Fig. 5. As should have been expected, tracing more curved sections of the trajectory takes more time due to longer lasting rotation. The time of the steady-state phase depends more weakly on the curvature of the trajectory. Following the experimental approach (Georgopoulos et al. 1988; Schwartz 1993) to reconstruct of the "neural trajectories" we calculated the direction and the length of the population vector as a mean value for each 5-τ time bin regardless of the current input signals. As an example, Fig. 7 shows how the mean length of the population vector changes in time during the tracing between points 1 and 2 in Fig. 5. The dependence of the mean length on the current curvature is clearly seen. Finally, curve b in Fig. 5 represents 266 mean neuronal population vectors calculated as described above and attached to each other tip-to-tail. To compare with the real curve the "neural trajectory" is normalized to the same length units. The difference between the two curves is minimal.

4.4 Relation between "neural velocity" and curvature

Since the length of the population vector was calculated as the average over equal time bins, the neural velocity can be presented as the population vector length divided by the value of time bin (5 τ) and normalized to the length units of the real trajectory. The similarity between real and "neural" trajectories and Figs. 6 and 7 demonstrates

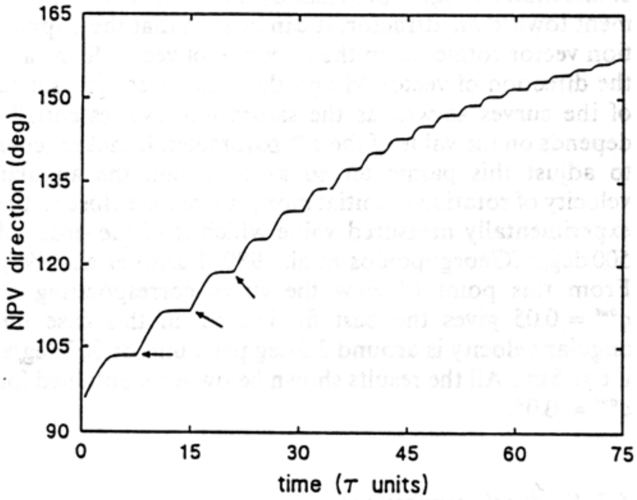

Fig. 6. Time dependence of the direction of the neuronal population vector calculated from (2)–(5), (7), (8), (10), and (11), $q^{inp} = 50$, $q^{out} = 0.05$. Angle $\theta_P = \arctan(P_y/P_x)$ is plotted against t measured in τ units. The curve corresponds to the tracing between points 1 and 2 in Fig. 5. Eighteen changes of the input signals are seen. Three of them are shown by *arrows*

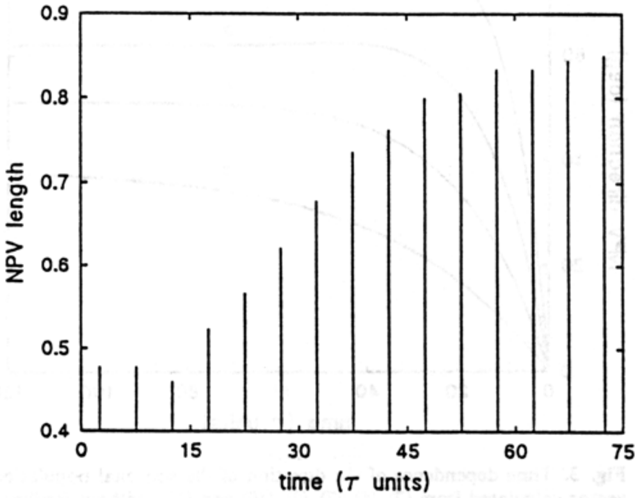

Fig. 7. Time dependence of the mean value of the neuronal population vector length during tracing between points 1 and 2 in Fig. 5. Each *bar* corresponds to the averaging of the length over 5-τ time bin

the correspondence between the changes of the direction and the length of the population vector, namely, the larger the angle, the shorter the length. In other words, a correlation exists between the neural velocity of tracing and the curvature of the resulting trajectory. The reciprocal of the neural velocity is plotted in Fig. 8 against the curvature. This dependence corresponds well to experimental data concerning the relation between the velocity of hand movement and the curvature of the drawn trajectory. Indeed, it was shown that the tangential velocity of the hand movement is approximately proportional to the radius of curvature (Viviani and Terzuolo 1982; Lacquaniti et al. 1983; Soechting and Terzuolo 1986; Massey et al. 1992).

Two parameters determine the dependence between the neural velocity of tracing and the curvature of the resulting trajectory, shown in Fig. 8. The slope of the linear part reflects the average angular velocity for a curved trajectory performance (~ 500 deg/s). Extrapolation to zero curvature gives the velocity of straight-line movement (~ 1 unit length/s). In the framework of the hypothesis that the neuronal population vector predicts the tangential velocity of the real movement, both values could be compared with similar parameters obtained in hand-movement experiments. The average angular velocity of hand movement is of the same order, ~ 500 deg/s (Massey et al. 1992). The absolute value of the straight-line movement depends on the scale length, which can be chosen arbitrarily within the present model. Nevertheless, a reasonable choice of the characteristic length of the hand-drawn trajectory, say 10 cm, leads to a value of the straight-line movement of 10 cm/s which is comparable to 10–30 cm/s obtained experimentally (Corradini et al. 1992; Schwartz 1992).

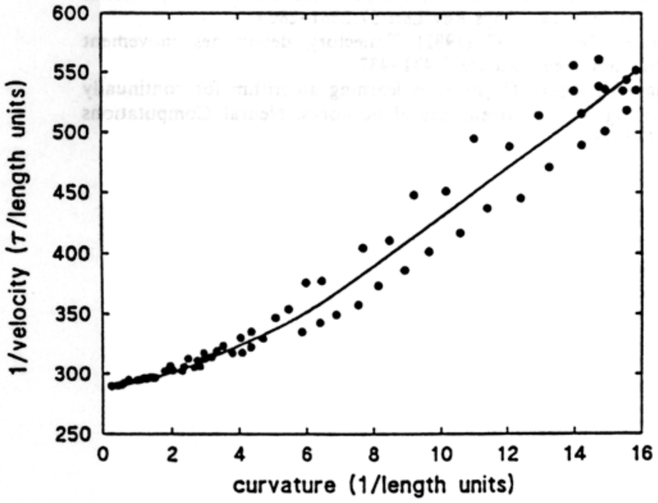

Fig. 8. The reciprocal of the neural velocity as a function of the curvature of the elliptic trajectory. Velocity is normalized so that it is measured in real length units divided to τ units of time. Curvature is measured in reciprocal units of length. The large axis of the ellipse is taken as a unit of length. *Points*, results of calculations; *solid line*, best fit

5 Conclusion

The main feature of the proposed model is that the neuronal population vector operations produced by the network are the result of the interactions between directionally tuned neurons rather than being imposed by external inputs. Connections between neurons were assigned in the simplest and most common way so that actually only one numerical parameter, namely q^{out}, has been adjusted. The network receives inputs as a sequence of tangential vectors of a curve which is to be traced out, but the neural velocity of the tracing is a function of internal parameters of the model. The output of the network is the current direction and length of the population vector. The correspondence between the changes of these parameters during tracing a trajectory makes it possible to describe a drawn geometrical curve in terms of the time series of the population vector in full agreement with experimental findings (Georgopoulos et al. 1988; Schwartz and Anderson 1989; Schwartz 1993). Moreover, the dependence of the neural velocity on the curvature obtained in the framework of the model reveals close correspondence with the similar covariation observed experimentally for hand movement in drawing tasks (Viviani and Terzuolo 1982; Lacquaniti et al. 1983; Soechting and Terzuolo 1986; Massey et al. 1992).

The network considered in this paper possesses three major characteristics that are biologically relevant for cortical operations in general and two properties that are important for the motor cortex in particular. The general characteristics include the massive interconnectivity among the network elements, the weak strength of synaptic connections and the correlated interactions: indeed, these seem to be general features of cortical processing (Martin 1988). The specific properties of the network that correspond to motor cortical operations include the directional tuning of individual elements and the computation of the neuronal population vector. Altogether then, this network combines biologically meaningful aspects which are embedded within a dynamical behavior that evolves in time. This temporal evolution combines an experimentally observed operation (i.e., the rotation of the neuronal population vector) and applies it to the neural representation of curvature in a planned movement trajectory. However, for this application an internal feedback mechanism is proposed that signals the completion of a unit rotation; this hypothesized feedback mechanism needs to be identified experimentally. It is this interplay between theory and experiment that lies in the heart of the present attempt to bridge artificial and real neural networks within the domain of the motor cortex.

Acknowledgements. This work was supported by United States Public Health Service grants NS17413 and PSMH48185, Office of Naval Research contract N00014-88-K-0751, and a grant from the Human Frontier Science Program.

References

Amari S (1972) Characteristics of random nets of analog neuron-like elements. IEEE Trans Syst Man Cybern 2:643–657

Amirikian BR, Lukashin AV (1992) A neural network learns trajectory of motion from the least action principle. Biol Cybern 66:261–264

Atiya A, Baldi P (1989) Oscillations and synchronization in neural networks: an exploration of the labelling hypothesis. Int J Neural Syst 1:103–124

Berthier NB, Singh SP, Barto AG, Houk JC (1991) Distributed representation of limb motor programs in arrays adjustable pattern generators. Technical Reports from the Center for Neuroscience Research on Neuronal Populations and Behavior, Northwestern University Medical School, Chicago, IL 60611, USA

Bullock D, Grossberg S (1988) Neural dynamics of planned arm movements: emergent invariants and speed-accuracy properties during trajectory formation. Psycol Rev 95:49–90

Burnod Y, Grandguillaume P, Otto I, Ferraina S, Johnson PB, Caminiti R (1992) Visuomotor transformations underlying arm movement toward visual targets: a neural network model of cerebral cortical operations. J Neurosci 12:1435–1453

Corradini ML, Gentilucci M, Leo T, Rizzolatti G (1992) Motor control of voluntary arm movements. Kinematic and modelling study. Biol Cybern 67:347–360

Dehaene S, Changeux JP, Nadal JP (1987) Neural networks that learn temporal sequences by selection. Proc. Natl Acad Sci USA 84:2727–2731

Georgopoulos AP (1990) Neural coding of the direction of reaching and a comparison with saccadic eye movements. Cold Spring Harbor Symp Quant Biol 55:849–859

Georgopoulos AP, Kalaska JF, Caminiti R, Massey JT (1982) On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. J Neurosci 2:1527–1537

Georgopoulos AP, Caminiti R, Kalaska JF, Massey JT (1983) Spatial coding of movement: a hypothesis concerning the coding of movement direction by motor cortical populations. Exp Brain Res [Suppl] 7:327–336

Georgopoulos AP, Schwartz AB, Kettner RE (1986) Neuronal population coding of movement direction. Science 233:1416–1419

Georgopoulos AP, Kettner RE, Schwartz AB (1988) Primate motor cortex and free arm movement to visual targets in three-dimensional space. II. Coding of the direction of movement by a neuronal population. J Neurosci 8:2928–2937

Georgopoulos AP, Lurito JT, Petrides M, Schwartz AB, Massey JT (1989) Mental rotation of the neuronal population vector. Science 243:234–236

Georgopoulos AP, Taira M, Lukashin AV (1993) Cognitive neurophysiology of the motor cortex. Science 260:47–52

Grossberg S, Cohen M (1983) Absolute stability of global pattern formation and parallel memory storage by competitive neural networks. IEEE Trans Syst Man Cybern 13:815–826

Guyon I, Personnaz L, Nadal JP, Dreyfus G (1988) Storage and retrieval of complex sequences in neural networks. Phys Rev A 38:6365–6372

Hopfield JJ (1984) Neurons with graded response have collective computational properties like those of two state neurons. Proc Natl Acad Sci USA 81:3088–3092

Hopfield JJ, Tank DW (1986) Computing with neural circuits: a model. Science 233:625–633

Jordan MI (1986) Attractor dynamics and parallelism in a connectionist sequential machine. In: Proceedings of the 8th Annual Conference of the Cognitive Science Society. Erlbaum, Hillsdale, NJ, pp 531–546

Kleinfeld D (1986) Sequential state generation by model neural networks. Proc Natl Acad Sci USA 83:9469–9473

Kleinfeld D, Sompolinsky H (1988) Associative neural network model for the generation of temporal patterns. Biophys J 54:1039–1051

Lacquaniti F, Terzuolo C, Viviani P (1983) The law relating kinematic and figural aspects of drawing movements. Acta Psychol 54:115–130

Lukashin AV (1990) A learned neural network that simulates properties of the neuronal population vector. Biol Cybern 63:377–382

Lurito JT, Georgakopoulos T, Georgopoulos AP (1991) Cognitive spatial-motor process. 7. The making of movement at an angle from a stimulus direction: studies of motor cortical activity at the single cell and population levels. Exp Brain Res 87:562–580

Martin KAC (1988) From single cells to simple circuits in the cerebral cortex. Q J Exp Physiol 73:637–702

Massey JT, Lurito JT, Pellizzer G, Georgopoulos AP (1992) Three-dimensional drawing in isomeric conditions: relation between geometry and kinematics. Exp Brain Res 88:685–690

Massone L, Bizzi E (1989) A neural network model for limb trajectory formation. Biol Cybern 61:417–425

Pearlmutter BA (1989) Learning state space trajectories in recurrent neural networks. Neural Computations 1:263–269

Schoner G, Kelso JAS (1988) Dynamic pattern generation in behavioral and neural systems. Science 239:1513–1520

Schwartz AB (1992) Motor cortical activity during drawing movements: single-unit activity during sinusoid tracing. J Neurophysiol 68:528–541

Schwartz AB (1993) Motor cortical activity during drawing movements: population representation during sinusoid tracing. J Neurophysiol (in press)

Schwartz AB, Anderson BJ (1989) Motor cortical images of sinusoidal trajectories. Soc Neurosci Abstr 15:788

Schwartz AB, Kettner RE, Georgopoulos AP (1988) Primate motor cortex and free arm movements to visual targets in three-dimensional space. I. Relations between single cell discharge and direction of movement. J Neurosci 8:2913–2927

Sejnowski TJ (1976) On the stochastic dynamics of neuronal interaction. Biol Cybern 22:203–211

Soechting JF, Terzuolo CA (1986) An algorithm for the generation of curvilinear wrist motion in arbitrary plane in three-dimensional space. Neuroscience 19:1393–1405

Sompolinsky H, Kanter I (1986) Temporal association in asymmetric neural networks. Phys Rev Lett 57:2861–2864

Viviani P, Terzuolo C (1982) Trajectory determines movement dynamics. Neuroscience 7:431–437

Williams RJ, Zipser D (1989) A learning algorithm for continually running fully recurrent neural networks. Neural Computations 1:270–280