TOPOLOGICAL AND DYNAMICAL ASPECTS OF A NEURAL NETWORK MODEL FOR GENERATION OF PURSUIT MOTOR PROGRAMS

R. ECKMILLER
University of Düsseldorf, FRG

ABSTRACT

A computational model of a motor program generator (MPG) for horizontal pursuit eye movements (PEM) is proposed. The MPG model consists of two neural networks (velocity maps). Neurons are arranged in a single circular layer with lattice structure and connected only to their immediate neighbors. During PEM one of the two maps always features an activity peak (AP) which travels with constant velocity from one neuron to the next. A memory trace of the most recent portion of the trajectory is created by means of a temporary increase of the interneuronal connectivity strength between previously activated neurons. This novel MPG model may be useful for designing parallel processors for motor control of robots.

INTRODUCTION

The new areas of Cognitive Science, Artificial Intelligence, and Robotics share a common interest with Neuroscience in the various topological (structural) and functional principles of the primate central nervous system, which uses the general concept of parallel processing and a hierarchical organization of numerous neural maps. One important function of the primate brain that has concerned neuroscientists for many years is Motor Control. Assuming the predominantly accepted view is correct that movements in primates are based on internally generated motor programs rather than on reflectory responses to sensory stimuli, the fundamental and still open question is: How are motor program generators (MPG) (which certainly consist of neurons and synapses) designed in detail to control the motor activity time courses of various sets of muscles for speech movements, eye movements, or limb movements?

Neither neurophysiological nor neuroanatomical research has so far been able to offer answers or even plausible hypotheses regarding the architecture and dynamics of motor program generators, although an enormous amount of data has been compiled (Miles & Evarts, 1979; Tatton & Bruce, 1981). One possible exception is the generation of locomotion programs at the level of the spinal cord (Grillner & Wallén, 1985; Herman et al., 1976; Miller & Scott, 1977). By means of cognitive modelling several groups have recently begun to identify the problem of motor program generation and to search for neural networks with appropriate parallel processing features (Anderson, 1983; Arbib, 1981; Feldman & Ballard, 1982).

The present study leads to a proposal of a MPG for pursuit eye movements (PEM). This MPG model was developed on the basis of extensive single unit studies and accompanying lesioning and neuroanatomical studies on the pursuit control system in trained monkeys (Macaca fascicularis). Accordingly, the necessary assumptions concerning the network topology and dynamics of the MPG model are neurophysiologically plausible or even supported by direct neurophysiological evidence.

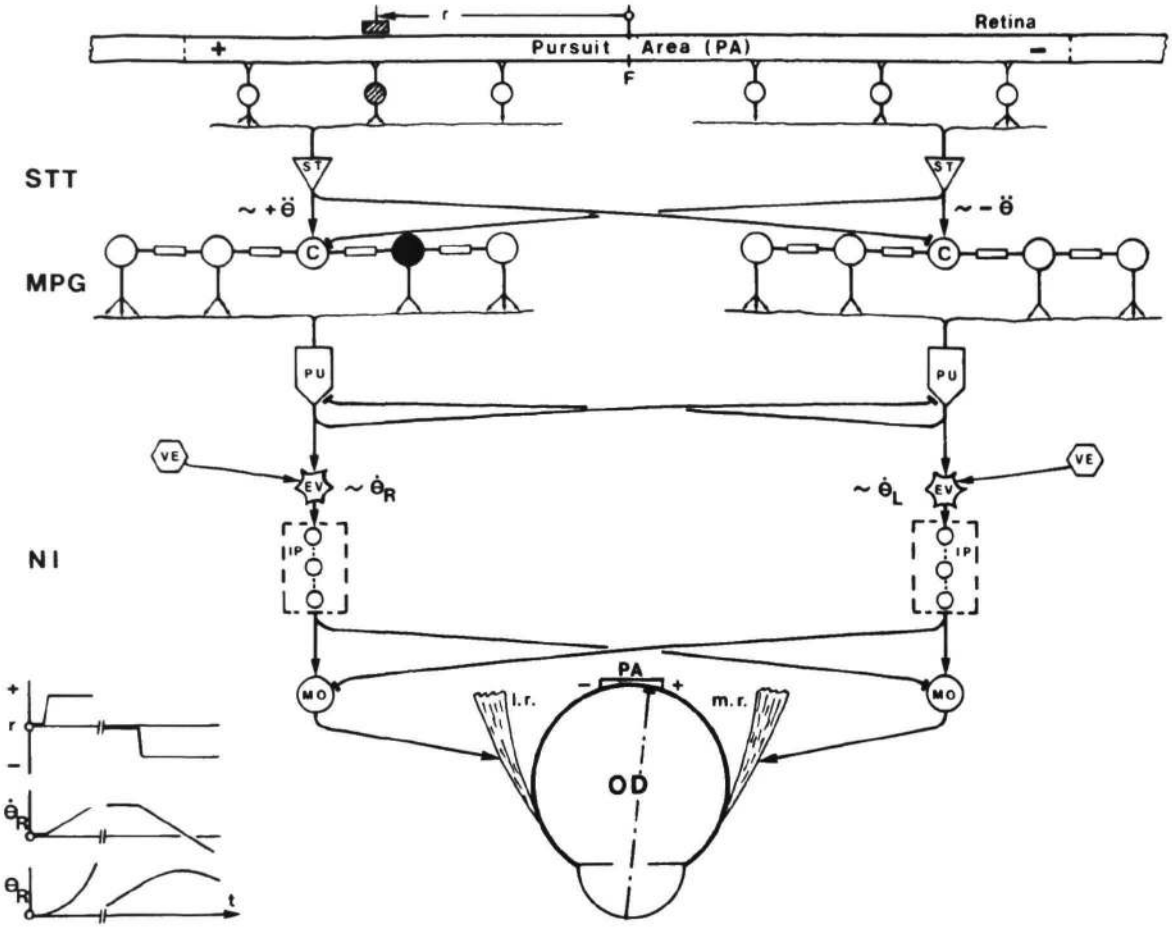

FIG. 1: Model of the oculomotor pursuit system in primates for horizontal pursuit of the right eye (OD). STT: spatio-temporal translation; MPG: motor program generation; NI: neural integration. Details, see text. Inset bottom left: relationship between position error r, eye velocity to the right θ_R, and eye position θ_R.

A) Neurophysiological, Neuroanatomical, and Behavioral PEM Data

PEM in the horizontal head plane (oblique or vertical PEM are assumed to be generated by additional signals from a vertical PEM system) in pursuit of maneuverable or predictable (e.g. sinusoidal) moving targets against a homogeneous background continuously minimize the position error r between the center of the fovea centralis on the retina and the retinal target projection. PEM approximately yields a continuous fixation of the moving target for the purposes of pattern recognition (Eckmiller, 1981; Eckmiller, 1986a). PEM can follow a continuous time course without large correctional saccadic eye movements as long as target velocity $\dot{\theta}_t$ is less than $\pm$ 50 deg/sec at target accelerations $\ddot{\theta}_t$ below $\pm$ 250 deg/sec^2. These maximal values imply that sinusoidal PEM at an amplitude of 10 deg will be possible for frequencies up to at least 0.8 Hz (Eckmiller, 1983; Eckmiller & Mackeben, 1978).

Recent neurophysiological studies in trained monkeys revealed that PEM must be controlled by two MPG for eye velocity to the left $\dot{\theta}_L$ and to the right $\dot{\theta}_R$. These two separate velocity signals are probably represented by two clusters of pursuit neurons (PU) close to the abducens nuclei in the brain stem (Eckmiller, 1983; Eckmiller & Bauswein, 1985). In fact, all oculomotor control signals at the pre-motor level exist only as eye velocity signals and have to be transformed into eye position time courses by means of a neural integrator (Eckmiller, 1986b; Robinson, 1981).

B) Concept of the MPG model

The MPG model consists of two neural networks (velocity maps), which represent a continuum of velocity values $\dot{\theta}_R$ and $\dot{\theta}_L$ respectively, as locations on the map with zero in the center and increasing velocity (up to 50 deg/sec) at increasing radius R. The only input to each MPG network comes from ST neurons (Eckmiller, 1983) that carry the position error r to the center neuron C. Fig. 1 shows that positive values of r activate the left ST neuron. Its output is proportional to $\ddot{\theta}$ in the sense that it causes a change of $\dot{\theta}_R$ that is generated by the MPG network. If r becomes negative, then the ST neuron on the opposite side is activated and inhibits the center neuron in the left MPG network while exciting the center neuron in the right network.

C) Network Topology

Neurons are arranged in a single circular layer with lattice structure and connected only to their immediate neighbors as indicated in Fig. 2.

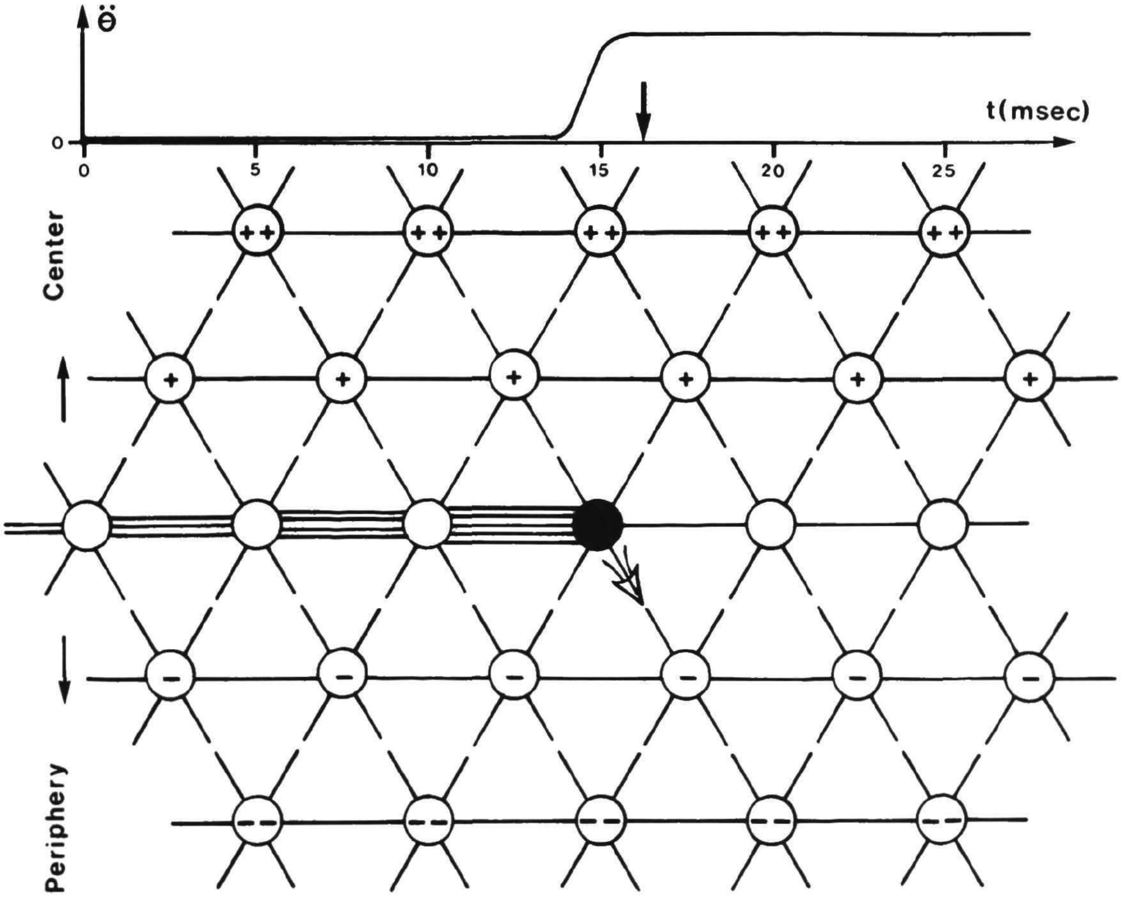

FIG. 2: Spatial distribution of neurons in the MPG network. Horizontal connections follow circles about the center. Activity peak, which is presently (see large arrow on the time scale) located at the central neuron (filled circle) of this network portion, had travelled from the left and is about to move downwards because of the sudden acceleration increase (time course at the top). The potential gradient is indicated by (++), (+), and (-), (--).

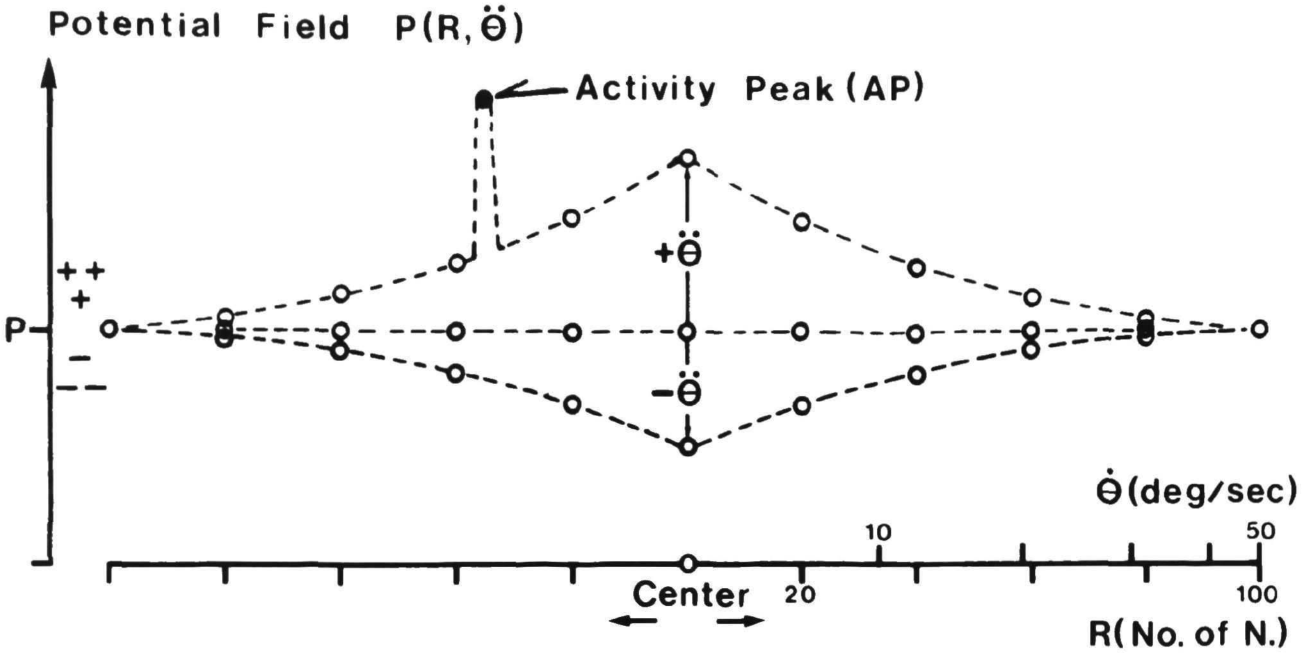

FIG. 3: Potential field P(R,$\ddot{\theta}$) along a cross section of the MPG map through the center at three different values of the input signal (+$\ddot{\theta}$, 0, −$\ddot{\theta}$). Abscissa gives the radius R as the number of neurons from the center as well as the eye velocity $\dot{\theta}$(deg/sec) with a possible non-linear scale. The activity peak AP is about to travel towards the periphery due to the potential gradient.

The connectivity strength c of tangential (horizontal in Fig. 2) connections c_t and radial connections c_r are initially constant, whereby c_t is slightly larger (indicated by a continuous line) than c_r (indicated by an interrupted line). This arrangement gives a slight preference to activity movements along a tangential trajectory. The time course at the top of Fig. 2 indicates an abrupt change in $\ddot{\theta}$ just before the movement (large arrow) at which the distribution of connectivity strength between the neurons and the activity state of each neuron is indicated. The activity state of each neuron is given by its potential P, which is initially constant throughout the network.

Fig. 3 indicates the potential field P(R,$\ddot{\theta}$) of the MPG network in a cross section through the center. The abscissa gives two possible and plausible scales: the radius R is measured by the number of neurons from the center; the eye velocity signal $\dot{\theta}$ can have a non-linear scale along the radius R as exemplified in Fig. 3. The topology can be changed by the input signal to the center neuron as indicated in Fig. 3 for several neurons at a positive (+$\ddot{\theta}$) and negative (−$\ddot{\theta}$) acceleration value. The potential field P(R,$\ddot{\theta}$) of all neurons is analogous to a flat circular membrane whose center can be pushed up or down by an amount proportional to the retinal position error r. The activity peak (AP) will be discussed later.

D) Network Dynamics

During PEM one of the two MPG networks, which are connected in a push-pull fashion (Fig. 1), always features an activity peak (AP) which travels with constant velocity v_T from one neuron to the next. The shape of the potential field defines whether AP travels in a circle ($\dot{\theta}$ = constant) in case of $\ddot{\theta}$ = 0, towards the periphery ($\dot{\theta}$ increase) or towards the center ($\dot{\theta}$ decrease). The topology of the network assures that only one AP can exist at a time and that AP always travels with v_T = constant.

These two postulates are neurophysiologically plausible and can be simulated with little effort. The constant travel velocity of AP represents a linear passage of real time, which is an essential feature of any generator of time functions. AP is indicated in Fig. 2 as the filled circle neuron. This figure also shows that the connectivity strength of the most recently active connections is temporarily increased, as indicated by the number of connection lines. AP came along a circle (horizontal line in Fig. 2) from the left at a suggested travel velocity of v_T = 5 msec per jump between neighboring neurons

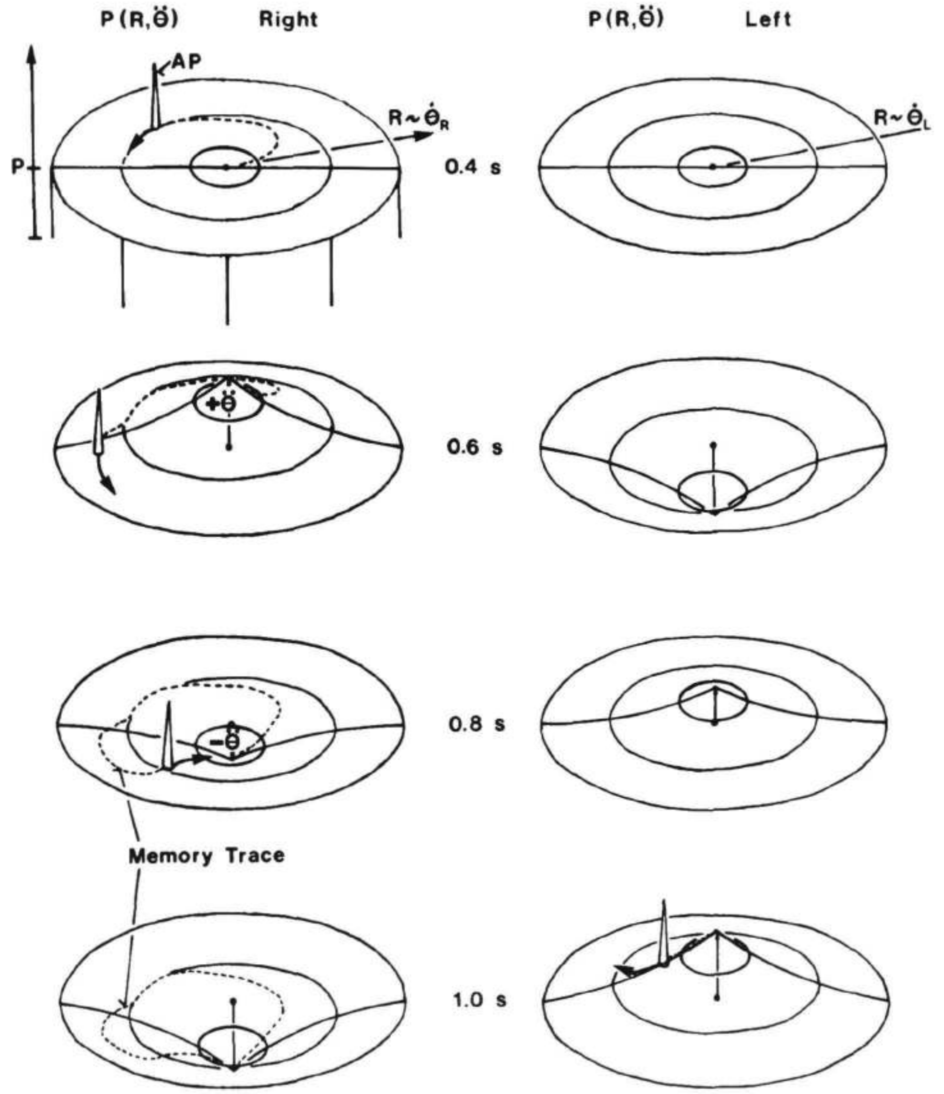

FIG. 4: Potential fields $P(R,\ddot{\theta})$ of the two MPG networks for generation of eye velocity time courses to the right ($\dot{\theta}_R$) and to the left ($\dot{\theta}_L$) at four different times. At 0.4 sec the activity peak AP is travelling in a circle since the potential field is flat. At 0.6 sec AP travels towards the periphery and at 0.8 sec towards the center. At 1.0 sec AP has already left the map for $\dot{\theta}_R$ and is travelling on the other map. Note that the potential fields of both maps are always identical except for the sign. The most recent trajectory is temporarily existent as a memory trace.

at $P(R,\ddot{\theta})$ = constant, when $\ddot{\theta}$ changed suddenly from zero to a positive value. This change led to the occurrence of a potential gradient as indicated in Fig. 2. AP will now travel towards the periphery. Depending on the size of the potential gradient, AP can travel always, or only occasionally towards more peripheral (or central) neurons, thereby generating trajectories with varying curvature on the velocity map. Alternating phases of $\dot{\theta}_R$ and $\dot{\theta}_L$ are made possible by repeated transfers of AP from the center neuron of one map to that of the other.

A memory trace of the most recent portion of the trajectory is created by means of a temporary increase of the connectivity strength as already mentioned. A small portion of such a memory trace is indicated in Fig. 2. Fig. 4 gives the events on both maps including the location of AP at four different times and the gradually increasing length of the memory trace.

Several features are noteworthy with regard to Fig. 4:

a) Trajectories on a map always start and end in the center,
b) the topology of both networks changes in opposite directions when $\ddot{\theta}$ changes from zero to a positive or negative value.
c) It is assumed that AP travels away from the center in the same angular direction under similar potential field conditions.
d) The memory trace gradually fades with a time constant of about 1 sec. Given a small potential gradient towards the center, AP can be pulled out of a weak memory trace and travel towards the center in a spiral after target disappearance.

This memory trace is used as explanation for the neural predictor mechanism (Eckmiller & Mackeben, 1978; Westheimer, 1954). Once a memory trace exists it can be used to reduce the amount of necessary updating (position error signals) during periodical pursuit movements, which are generated by repeated generation of the same two velocity trajectories on both maps. In such a case sudden and temporary target disappearance episodes can be bridged since AP simply follows the memory trace in the absence of a retinal input.

DISCUSSION

The key feature of the proposed MPG model is the existence of an activity peak AP which travels with constant velocity on a neural map along a modifiable trajectory (Eckmiller, 1986c). This MPG model may also prove applicable to limb movements in addition to eye movements. A comparison of the model with the technical solutions that are presently available for generating various movement trajectories (including trajectory learning, memory, and prediction) indicates that it may be used for designing parallel processors for motor control of robots.

It is evident that the neural network as proposed for the MPG cannot be detected by means of single unit recordings. Simultaneous recordings from larger ensembles of neurons, however, may be able to monitor an AP as it travels over the map.

Desired velocity trajectories can be permanently stored by means of neurons that gradually develop connections only to those neurons in the map that are repeatedly activated by an AP during a learning phase (Eckmiller, 1986c). These pattern retrieval (PR) neurons can later be used to reactivate a strong memory trace with a single activation burst.

ACKNOWLEDGEMENT

This research was supported by the Deutsche Forschungsgemeinschaft, SFB 200/A1.

REFERENCES

1. Anderson, J.A. (1983) Cognitive and psychological computation with neural models. IEEE Trans. SMC-13, 799-815.
2. Arbib, M.A. (1981) Perceptual structures and disturbed motor control. In: Hdb. Physiology, Section 1: The nervous system, Vol. II, Motor control, Part 2, J.M. Brookhart , V.B. Mountcastle, and V.B. Brooks (eds.) Baltimore: Williams & Wilkins, ch.33, pp. 1449-1480.
3. Eckmiller, R. (1981) A model of the neural network controlling foveal pursuit eye movements. In: Prog. Oculomotor Res., (Fuchs & Becker, eds.), Elsevier: New York, pp. 541-550.
4. Eckmiller, R. (1983) Neural control of foveal pursuit versus saccadic eye movements in primates - single unit data and models. IEEE Trans. SMC-13, 980-989.
5. Eckmiller, R. (1986a) Neural control of pursuit eye movements. Physiological Reviews (submitted).
6. Eckmiller, R.(1986b) The transition between pre-motor eye velocity signals and oculomotor eye position signals in primate brain stem neurons during pursuit. In: Adaptive processes in visual and oculomotor systems. (Keller & Zee, eds.), Pergamon Press: New York, in press.
7. Eckmiller, R. (1986c) Computational properties of a neural net with a triangular lattice structure and a travelling activity peak. Proc. 1986 IEEE Int. Conf. Systems, Man, and Cybernetics.
8. Eckmiller, R., & Bauswein, E. (1985) Smooth pursuit eye movements. In: Oculomotor and skeletomotor system - Differences and similarities (Freund et al., eds.), Prog. Brain Res. 64, 313-323.
9. Eckmiller, R., & Mackeben, M. (1978) Pursuit eye movements and their neural control. Pflügers Arch. Eur. J. Physiol. 377, 15-23.
10. Feldman, J.A., & Ballard, D.H. (1982) Connectionist models and their properties. Cognitive Sci. 6, 205-254.
11. Grillner, S., & Wallén, P. (1985) Central pattern generators for locomotion, with special reference to vertebrates. Ann. Rev. Neurosci. 8, 233-261.
12. Herman, R.M., Grillner, S., Stein, P.S.G., & Stuart, D.G. (eds.) (1976) Neural control of locomotion. Plenum: New York.
13. Miles, F.A., & Evarts, E.V. (1979) Concepts of motor organization. Ann. Rev. Psychol. 30, 327-362.
14. Miller, S., & Scott, P.D. (1979) The spinal locomotor generator. Exp. Brain Res. 30, 387-403.
15. Robinson, D.A. (1981) Control of eye movements. In: Hdb. Physiology see ref. 2, ch. 28, pp. 1275-1320.
16. Tatton W.G., & Bruce I.C. (1981) Comment: A scheme for the interactions between motor programs and sensory input. Can. J. Physiol. Pharmacol. 59, 691-699.
17. Westheimer, G. (1954) Eye movement responses to a horizontally moving visual stimulus. Arch Ophthalmol. 52, 932-941.