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Michael A. Arbib
Shun-ichi Amari
Editors

Dynamic Interactions in Neural Networks: Models and Data



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Dynamic Interactions in Neural Networks: Models and Data

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PREFACE

This is an exciting time. The study of neural networks is enjoying a great renaissance, both in *computational neuroscience* — the development of information processing models of living brains — and in *neural computing* — the use of neurally inspired concepts in the construction of "intelligent" machines. Thus the title of this volume, *Dynamic Interactions in Neural Networks: Models and Data* can be given two interpretations. We present models and data on the dynamic interactions occurring in the brain, and we also exhibit the dynamic interactions between research in computational neuroscience and in neural computing, as scientists seek to find common principles that may guide us in the understanding of our own brains and in the design of artificial neural networks. In fact, the book title has yet a third interpretation. It is based on the U.S.-Japan Seminar on "Competition and Cooperation in Neural Nets" which we organized at the University of Southern California, Los Angeles, May 18-22, 1987, and is thus the record of interaction of scientists on both sides of the Pacific in advancing the frontiers of this dynamic, re-born field.

The book focuses on three major aspects of neural network function: learning, perception, and action. More specifically, the chapters are grouped under three headings: "Development and Learning in Adaptive Networks," "Visual Function", and "Motor Control and the Cerebellum." In Chapter 1, we have provided a brief outline of the contents of each chapter in this book, placing it in the perspective of current developments in the field of neural networks. Here we simply offer a quick glimpse of how the contributions in each of the three parts of this volume hang together.

Part I, Development and Learning in Adaptive Networks, begins with a mathematical perspective on "Dynamical Stability of Formation of Cortical Maps" by Amari. We then turn to some amazing empirical data which encourages the search for general principles of neural development as Sur reports on the functional properties of visual inputs that he has induced into auditory thalamus and cortex. Schmajuk reports on his modeling of "The Hippocampus and the Control of Information Storage in the Brain" to give us fresh insight into the role of this region in the formation of long term memories. We then turn to three contributions to neural computing.

In "A Memory with Cognitive Ability," Shinomoto studies learning rules which satisfy the physiological constraint that excitatory synapses must remain excitatory and inhibitory synapses inhibitory. In "Feature Handling in Learning Algorithms," Hampson and Volper add an important new chapter in the study of computational complexity of neural networks. Finally,

Miyake and Fukushima build on earlier work on the Neocognitron to present "Self-Organizing Neural Networks with the Mechanism of Feedback Information Processing."

Part II, Visual Function, starts with Arbib's "Interacting Subsystems for Depth Perception and Detour Behavior," another chapter in the evolution of *Rana computatrix*, the computational frog. The rest of Part II presents important neurophysiological data ripe for modeling. Hikosaka analyzes the "Role of Basal Ganglia in Initiation of Voluntary Movement," while the final two papers analyze the visual mechanisms in monkey cortex that lie beyond the primary visual areas. Desimone, Moran and Spitzer probe "Neural Mechanisms of Attention in Extrastriate Cortex of Monkeys," while Miyashita discusses "Neuronal Representation of Pictorial Working Memory in the Primate Temporal Cortex."

The last Part of the volume deals with Motor Control and the Cerebellum. Kawato, Isobe, and Suzuki apply models of "Hierarchical Learning of Voluntary Movement by Cerebellum and Sensory Association Cortex" to learning trajectory control of an industrial robotic manipulator. The role of the cerebellum in adapting the control of eye movements is taken up by Fujita in his paper on "A Model for Oblique Saccade Generation and Adaptation," and by Miyashita and Mori in their study of "Cerebellar Mechanisms in the Adaptation of the Vestibulo-Ocular Reflex." Paulin offers a more abstract mathematical perspective by arguing for "A Kalman Filter Theory of the Cerebellum." To close the volume, Moore and Blazis again integrate a theory of adaptation in neural networks with data on animal conditioning experiments to provide new insights into "Conditioning and the Cerebellum."

We close this preface with a number of acknowledgements. The U.S.-Japan Seminar held at USC in May of 1987 was the sequel to an earlier one held in Kyoto in February of 1982. The Proceedings of the 1982 meeting were published as *Competition and Cooperation in Neural Nets* (S. Amari and M. A. Arbib, Eds.) in the Springer Lecture Notes in Biomathematics. We wish to record our thanks to the National Science Foundation (USA) and the Japan Science Foundation for their support of both meetings, and to Dean Wagner and the USC program in Neural, Informational and Behavioral Sciences (NIBS) for supplementary funding of the USC Meeting. Finally, special thanks to Lori Grove and Debbie O'Rear for all they did to make our meeting such a success.

Los Angeles and Tokyo,
June 1988

Michael A. Arbib
Shun-ichi Amari

Table of Contents

Preface	v
Dynamic Interactions in Neural Networks: An Introductory Perspective	
Michael A. Arbib	1
I. Development and Learning in Adaptive Networks	13
Dynamical Stability of Formation of Cortical Maps	
Shun-ichi Amari	15
Visual Plasticity in the Auditory Pathway: Visual Inputs Induced into Auditory Thalamus and Cortex Illustrate Principles of Adaptive Organization in Sensory Systems	
Mriganka Sur	35
The Hippocampus and the Control of Information Storage in the Brain	
Nestor A. Schmajuk	53
A Memory with Cognitive Ability	
Shigeru Shinomoto	73
Feature Handling in Learning Algorithms	
S.E. Hampson and D.J. Volper	87
Self-Organizing Neural Networks with the Mechanism of Feedback	
Information Processing	
Sei Miyake and Kunihiko Fukushima	107
II. Visual Function	121
Interacting Subsystems for Depth Perception and Detour Behavior	
Michael A. Arbib	123
Role of Basal Ganglia in Initiation of Voluntary Movements	
Okihide Hikosaka	153
Neural Mechanisms of Attention in Extrastriate Cortex of Monkeys	
Robert Desimone, Jeffrey Moran and Hedva Spitzer	169
Neuronal Representation of Pictorial Working Memory in the Primate Temporal Cortex	
Yasushi Miyashita	183
III. Motor Control and the Cerebellum	193
Hierarchical Learning of Voluntary Movement by Cerebellum and Sensory Association Cortex	
Mitsuo Kawato, Michiaki Isobe and Ryoji Suzuki	195

A Model for Oblique Saccade Generation and Adaptation	
Masahiko Fujita	215
Cerebellar Mechanisms in the Adaptation of Vestibuloocular Reflex	
Yasushi Miyashita and Koichi Mori	227
A Kalman Filter Theory of the Cerebellum	
Michael Paulin	239
Conditioning and the Cerebellum	
John W. Moore and Diana E.J. Blazis	261

Dynamic Interaction in Neural Networks: An Introductory Perspective

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It is the purpose of this introduction to briefly review the papers in each of the three parts of the volume, and then conclude with a brief unifying perspective.

1. Development and Learning in Adaptive Networks

In "Dynamical Stability of Formation of Cortical Maps," Shun-ichi Amari emphasises mathematical models. These are important because they point to intrinsic mechanisms — simple models provide a basis for understanding details. In particular, Amari stresses a field theory of self-organizing neural nets. An important case is a layered network, with field equations set up for each layer. The aim is to solve these equations and/or provide a stability analysis. Studies in the dynamics of learning and self-organization include the learning of input-output relations.

Turning to neural representation of signals, Amari notes that local self-organization of a field may yield the representation of a localized pattern in the external world by a localized "grandmother cell" representation (e.g. orientation- selective cells; retinotopy), or by a distributed representation (i.e., a pattern distributed across all or part of the network). He thinks that the brain uses both types of representation, and offers a mathematical demonstration that neural networks can form both types. Key questions here are: How can topological arrangements be reflected in a localized representation — especially when the topology is of higher dimension than the two dimensions of the neural layer? And how does the resolution of such a representation reflect the varying interest of different signals?

Amari studies three properties of a cortical map formed by self-organization: the topology of a signal space is preserved in some sense in the map; frequently applied signals occupy wide areas in the map with fine resolution; and, even when both the signal space and the neural field are continuous, a mosaic or block structure emerges in both spaces, and similar signals are categorized and represented by one mosaic. The last part of the paper treats associative memory. Earlier work emphasized the statistical neurodynamics of similarity. His results treated the stable states, but now he stresses that the real interest is in the transients, and these are addressed in recent computer simulations.

In evaluating these results, it should be noted that they are based on very general field equations. However, circuits in different parts of the brain have different characteristics. As we develop different models for hippocampus (Chapter 4), cerebellum (Part III of this volume), cerebral cortex, brainstem, etc., it will be interesting to see to what extent Amari's statistical neurodynamics can be adapted to these more specific circuitries.

Turning from general mathematical theory to experimental data on the development of neural wiring systems, Mriganka Sur argues that "Visual Inputs induced into Auditory Thalamus and Cortex Illustrate Principles of Adaptive Organization in Sensory Systems." By adapting surgical procedures developed in hamster by Schneider, he has been able to induce retinal projections in newborn ferrets to enter the medial geniculate nucleus (MGN), the principal auditory thalamic nucleus. Electrophysiological recordings reveal that the "visual cells" in the MGN have large, diffuse receptive fields and receive input from retinal ganglion cells with slow conduction velocities. Visual cells with long conduction latencies and large receptive fields can also be recorded in the primary *auditory* cortex! Importantly, these receptive fields are confined to the contralateral visual field, indicating that the cortical visual responses arise from input through the MGN and not from the intact hemisphere via the corpus callosum. Finally, some visual cells in auditory cortex have oriented receptive fields that resemble those of complex cells in the primary visual cortex. These findings prompted John Moore to ask at the USC meeting "What do the lights sound like?"

These results suggest that some of the operations considered "wired into" the visual thalamus and cortex may in fact be the result of general developmental mechanisms responding to structured visual inputs. In other words, what is intrinsically visual about central visual circuitry may not be so much intrinsic to the circuitry itself but rather the result of receiving visual input. Such results are encouraging for general models which explain the brain's wiring in terms of general mechanisms (e.g., those that involve excitation from below and recurrent inhibition as suggested by von der Malsburg and Amari) without making any assumption about the *visual* nature of the input.

Sur speculates that at least some aspects of intrinsic connectivity may be quite similar across thalamic and cortical areas, and one function of sensory cortex, for example, may be to perform stereotypical transformations of input akin to the simple and complex transformations done by visual cortex. What might the function of complex cells be in the auditory system? There are cells in the auditory system which respond either to sweeps from low to high or high to low, and this may be the auditory analog of orientation-tuning; while Merzenich has found auditory cells with broad tuning curves, but which respond to any input within the range.

Nestor Schmajuk provides an important bridge between the study of neural networks and the experimental data on animal conditioning as he analyzes "The Hippocampus and the Control

of Information Storage in the Brain." The general idea is that different information is stored in different areas of the brain and that the hippocampus acts as coordinator. In the 60's, Sokolov proposed that we model the world, generating an orienting response when input differs from model. The q-rhythm in hippocampus seems proportional to the size of the orienting response. Schmajuk models hippocampus in terms of attentional-associative networks for higher-order conditioning and sensory preconditioning — he call these S-P-H networks, the Schmajuk version of Pearce and Hall networks. A given CS_i can yield both a direct first-order prediction of some US, and a second-order prediction via some intervening CS_r . This involves prediction of which CS_k s occur and which do *not* occur. The model makes assumptions as to how attentional terms change with hippocampal lesions. Also, it assumes that CS-CS associations vanish with hippocampal lesions. Schmajuk develops a top-down approach: he tunes the model to yield the effects of hippocampal lesions, LTP, etc. He then tries bottom-up to relate the model to plausible hippocampus circuitry. The model seems to fit well about 80% of the phenomena of conditioning.

With the next three papers, we turn to studies in the theory of learning networks in general; not of specific brain regions or of realistic neural circuitry. The role of learning is to build "memory structures" that fill the gap between information supplied by the environment and that required to get the job done. In his study of "A Memory with a Cognitive Ability," Shigeru Shinomoto joins that growing group of physicists who provide mathematical analyses of auto-correlation matrix memories. Where many such memories are constructed with the possibility of arbitrary coupling between the neurons, Shinomoto introduces the physiological constraint that the sign of the synaptic coupling is uniquely determined by presynaptic neuron — i.e., neurons must be either excitatory or inhibitory. For a novel pattern, the Hopfield model gets trapped in spurious attractors. However, Shinomoto's networks have the property that they can signal non-retrieval — if an input signal has little correlation with any of the stored memories, it gives a clear response by going into a special mode which may be stationary or periodic, depending on a population of excitatory or inhibitory neurons. Thus the system acquires a new computational ability to determine whether an input pattern is identifiable or not, and thus tends to get rid of spurious memories. In concluding his talk at the USC meeting, Shinomoto quoted Confucius: "To recognize a thing, you should first identify whether or not it is one with which you are acquainted."

Hampson and Volper, in their paper on "Feature Handling in Learning Algorithms," extend the theoretical analysis of learning networks by offering a complexity analysis of connectionistic representation and learning schemes. They note that the Perceptron convergence theorem gives a bound on the number of trials required to achieve convergence, but that the bound $M \|w\|^2/a^2$ has the unfortunate property that it depends on the choice of a solution w , and it is such a w we seek. However, one can use the upper bound to evaluate various learning schemes. Empirical results generally reflect the time complexity based on the upper bound. They note that one aspect

that slows Perceptron convergence is that learning does not occur for features absent on a given trial. An alternative model codes absence by -1 instead of 0. Thus a feature gets adjusted whether present or absent. Another model is the two-vector model using two vectors of length d . It is representationally equivalent, but has a different learning character.

They have also analysed neuron learning schemes based on conditional probabilities, relating them to laws in the animal learning literature. Adding nodes to express conditional probabilities speeds learning *dramatically*: they call the result an OT (operator training) algorithm. Neurons which respond most strongly to a new input also learn the most from that new input. For the multiplexer, Barto's 4 node network takes 130,000 presentations; whereas an OT net with 5 nodes needs only 524 presentations. It thus seems possible to speed up learning by use of salience.

In their analysis of "Self-Organizing Neural Networks with the Mechanism of Feedback Information Processing," Sei Miyake and Kunihiro Fukushima study several neural network models in which a feedback signals are used to emphasize novel features. (1) A multilayered network which has both feedforward connections and feedback connections from the deepest-layer cells to the front-layer cells, with both types of connection being self-organized. (2) In another algorithm, the growth of connections is controlled by feedback information from postsynaptic cells. Even if a new pattern is presented, resembling one of the learning patterns with which the network has been organized, the network is capable of being self-organized again, and a cell in the deepest layer comes to acquire a selective responsiveness to the new pattern. (3) A third model has modifiable inhibitory feedback connections between the cells of adjoining layers. If a feature-extracting cell is excited by a familiar pattern, the cell immediately feeds back inhibitory signals to its presynaptic cells. On the other hand, since the feature-extracting cell does not respond to an unfamiliar pattern, and so circuits detecting novel features develop. (4) Finally, a self-organizing neural network which has an ability of symbol information processing has been proposed to, in some sense, take "context" into account. Even if an imperfect word is given to the network after completion of the self-organization, the network should be able to estimate its omitted letter by contextual information.

2. Visual Function

Providing a novel perspective on the notion of "sensory fusion," Michael Arbib starts his study of "Interacting Subsystems for Depth Perception and Detour Behavior" with an analysis of neural networks for depth perception. The problem for many models of binocular perception is to suppress ghost targets. The Cue Interaction Model uses two systems, each based on a cooperative computation stereopsis model, to build a depth map. One is driven by disparity cues, the other by accommodation cues, but corresponding points in the two maps have excitatory

cross-coupling. The model is so tuned that binocular depth cues predominate where available, but monocular accommodative cues remain sufficient to determine depth in the absence of binocular cues. The Prey Localization Model incorporates a triangulation hypothesis. Each side of the brain selects a prey target based on output of the contralateral retina, and computes a depth estimate by triangulation to adjust lens focus. If the selected retinal points correspond to the same prey-object, then the depth estimate will be accurate and the object will be brought into clearer focus, "locking on" to the target. If the points do not correspond, the resulting lens adjustment will tend to bring one of the external objects into clearer focus, and the two halves of the brain will tend to choose that object over the other.

Arbib then introduces the notion of a *schema* as a unit of analysis intermediate between overall behavior and the details of neural networks. Various models of detour behavior are presented in which the above depth models may be seen as subschemas which help a toad locate worms and barriers as it determines the path to its prey. Such schema/neural considerations are relevant to the design of "perceptual robots."

Okihide Hikosaka's paper on "Role of Basal Ganglia in Initiation of Voluntary Movements" returns us to the experimental analysis of neural mechanisms, this time in the study of eye movements. Wurtz trained a monkey to fixate a light while holding a lever and then release the lever when the light dims to get water reward. The substantia nigra is a very busy region, with incessant activity at 100 Hz even when the animal is sleeping. But one sees cessation of activity there after the target dims, there is then a saccade, after which substantia nigra background resumes. The cessation of substantia nigra activity occurs at the same time as a burst of activity of superior colliculus neurons. Since substantia nigra projects to superior colliculus this strongly suggests an inhibitory connection. But how do the nigral neurons stop discharging? The nigra receives input from other regions of the basal ganglia, including the caudate nucleus. So Hikosaka worked on the caudate with a similar paradigm. Caudate is a quiet area; but he found cells which discharge just before saccadic movements. This suggests that the caudate acts by disinhibiting the phasic inhibition of superior colliculus by substantia nigra. It is the phasic inhibition from the nigra that stops superior colliculus from yielding constant eye movements in response to its bombardment of excitation.

Many units in the basal ganglia are related to movement, but are not purely motor. Hikosaka found a cell which did not fire for a *visually* - directed saccade, but did fire for a "memory-guided saccade," i.e., a saccade to a *recalled* target position. Another unit started discharging on receiving an instruction to saccade to a yet-to-be-presented, and continued firing until the target appeared at the anticipated location. There is reciprocal interaction between basal ganglia and cortex; as well as mutually excitatory connections between thalamus and cortex. Caudate activity can release the cortical-thalamic system from substantia nigra inhibition. These substantia nigra cells seem to act as a short-term memory. They fire when a target is flashed

before it can be used, but not if a saccade can follow immediately. A sequence of substantia nigra disinhibitions may be involved in complex movements. The loop from cortex-thalamus to caudate to substantia nigra could act as a flip-flop circuit to hold short-term information in the brain.

The experimental analysis of vision continues with the study of "Neural Mechanisms for Preattentive and Attentive Vision in Extrastriate Cortex of the Primate" by Robert Desimone, Jeffrey Moran, and Hedva Spitzer. Since we are aware of only a small portion of the information on our retinas at any one moment, most of this information must be filtered out centrally. Yet, this filtering cannot easily be explained by the known physiological properties of visual cortical neurons. At each successive stage along the pathway from the primary visual cortex into the temporal lobe, the pathway known to be crucial for pattern perception, there is an increase in receptive field size. Moran and Desimone recorded from this pathway, studying *covert* attention: without eye movements, it is possible to attend to one or other of two stimuli. The locus of attention has dramatic effect on activity of V4 cells. They found V4 cells which, for a fixed stimulus, respond when the focus of attention is in one subfield, but not the other. The animal effectively shrinks its receptive field, so that the cell gives a response only inside the RF to a "good" stimulus. However, when the animal attends outside the overall RF of a cell, the cell seem to fire its normal response to any and all stimuli within that RF.

In plotting a histogram for the response of a V4 cell to attended and ignored stimuli, Desimone et al. see a difference with latency of 90 msec., which may thus be thought of as the time required for selective attention to turn off the cell's response. They posit that the V4 cell receives input both from the unattended stimulus and the attended stimulus, but with the unattended stimulus gated out by the attentional filter. In the chronic filter model, the attentional filter is chronically active; while in the triggered filter model, it requires a signal from the unattended stimulus to activate the filter. The data favor the triggered filter model. In discussion at the USC meeting, Desimone asserted that he does not think selective attention works at the geniculate level. The "ignored" data can yield interference effects even at quite late stages. Thinks attention may only operate after segmentation of the input into objects. Suppressive surrounds for cortical cells seem to come from other cells in the same area for figure-ground, color constancy, etc. — one does not want to turn off visual input before it enters into inter-areal processing. He thinks suppression acts at the module level: gating cells within the module containing the locus of attention, but not affecting other modules.

Our tour of "modeling-rich" experimental data on the visual system concludes with Yasushi Miyashita's account of "Neuronal Representation of Pictorial Working Memory in the Primate Temporal Cortex." It has been proposed that visual memory traces are located in the temporal lobes of cerebral cortex, but in the past neuronal responses to specific complex objects such as hands and faces have been found to cease soon after the offset of stimulus presentation.

Miyashita has recently found a group of shape-selective neurons in an anterior ventral part of monkey temporal cortex which exhibit maintained activity during the delay period of a visual working memory task. He thus argues that working visual memory is encoded in temporary activation of an ensemble of neurons in visual association cortex, rather than in a brain area specialized for working memory *per se*.

3. Motor Control and the Cerebellum

The analysis of motor control and the cerebellum commences with the presentation of "A Hierarchical Neural-Network Model for Control and Learning of Voluntary Movement and its Application to Robotics" by Mitsuo Kawato, Michiaki Isobe and Ryoji Suzuki. The approach is to study trajectory formation and control of human and robotic arms as an optimization problem with constraints in nonlinear dynamics. Abend, Bizzi, and Morasso studied human planar horizontal arm movements between a pair of targets, and observed a straight line trajectory with bell-shaped velocity curve. Flash and Hogan proposed that the trajectory minimizes "jerk;" but Uno, Kawato and Suzuki offered an alternative, the minimum-torque change model, and developed an iterative learning algorithm to determine the optimal trajectory, constrained by the dynamics of the arm. Their model is better than the minimum jerk model in predicting the bowed trajectory humans use to bring the arm from side to front.

The two steps of coordinate transformation and generation of motor command can be solved simultaneously by trial and error learning. Kawato et al. postulate that learning control by iteration in *body* space might be achieved in Area 2; while learning control by iteration in *visual* space might occur in Areas 5 and 7.

At the Kyoto meeting in 1982, Tsukuhara and Kawato gave a model of rubro-cerebellar learning, a neural identification algorithm structured as a hierarchical neural network model. Association cortex sends the desired trajectory in body coordinates to motor cortex, which in turn sends muscle commands. The cerebro-cerebellum and parvocellular red nucleus generate an internal model of the inverse dynamics. The spino-cerebellum and magnocellular red nucleus build an internal model of dynamics. The learning equation involves heterosynaptic plasticity. More recently, Kawato and his colleagues have applied such a controller to a robot manipulator. Control performance improved, and the feedback mode changed to feedforward as learning proceeded. Moreover, the learning generalized from a few taught trajectories to yield smooth control of new trajectories. With a 6 degree of freedom manipulator, they used 925 synaptic weights. They predict that, with parallel implementation, the method is 100-fold-faster than the computed torque method.

Before outlining the other papers in this section, we first recall a presentation that James Bloedel made at the USC meeting, summarizing a variety of viewpoints on the question "The Operation of the Climbing Fibers: Establishment of an Engram for Motor Learning or an Interaction Critical for Real Time Processing?" The basic organizational point is that cerebellar cortex receives two types of input fiber: MFs (mossy fibers) originate in brainstem, spinal cord, cerebellar nuclei, etc. They synapse on granule cells, which have axons forming parallel fibres which contact Purkinje cells along their course. By contrast, CFs (climbing fibers) originate from only one site, the inferior olive. Each Purkinje cell has its dendrites entwined with the branches of one climbing fiber — a unique synaptic relationship. Current debate over the involvement of cerebellar cortex in motor learning focuses on three general issues:

1. Is the cerebellum involved in motor learning?
2. Is the cerebellum the site of learning?
3. What is the role of the climbing fiber system?

Bloedel summarized the viewpoints on these issues as follows:

- (1): *Involvement* : All investigators accept that cerebellum is involved in some way in some aspects of motor learning.
- (2) *Site* : There are three camps: camp A strongly advocates cerebellum as the site of motor learning; camp B sees such a role for cerebellum as strongly supportive of their data; while camp C argues that cerebellum is not the site of learning.
- (3) *Role of CF system* : Here the debate is between storage theories which hold that the action of the CF on the dendrites of the PC (Purkinje cell) produces long-lasting changes in the parallel fibre synapses, especially with concurrent activation with them; and the notion that the CF system is involved in real-time processing operations.

Masahiko Fujita proposes "A Model for Oblique Saccade Generation and Adaptation." It explains a possible neural mechanism which successfully decomposes a vectorial eye movement velocity into horizontal and vertical eye velocities. Functional roles and neural mechanisms of the cerebellar vermis in saccadic eye movements in adaptation will also be discussed on the basis of such model. He stresses the importance of the idea of population coding in motor systems, in contrast with the idea of feature extracting in sensory systems. A saccade of 1 -40° takes 20-100 msc. What is the spatial-to-temporal transformation? Fujita studies the logical structure for the generation of oblique saccades.

Building on a model of Robinson, Scudder incorporated the superior colliculus into his model of saccade generation. The position of the target together with the direction of gaze determine the pattern of retinal activity which is transmitted to the cerebrum for visual processing, yielding activity in the frontal eye fields which combines in the superior colliculus with direct retinal input. Outflow thence to midbrain and pons projects to the horizontal and vertical motor systems, thus in turn affecting gaze direction. Robinson's model was a high-gain position servo, discretely sampling visual cortex. The estimated difference between

target and foveal angle drives rapid eye movement via a burst discharge. The saccade loses velocity rapidly where the error falls to zero. A neural integrator holds the eye at its new position despite the elasticity of eye muscles. van Gisbergen et al gave 2 models extending this to 2D saccades. In model A, the error vector is decomposed into vertical and horizontal dimensions, each driving a pulse generator for its respective direction. In model B, the error vector drives a pulse generator whose vector is then decomposed. The problem with A is that if both systems saturate, one gets saccade starting in fixed direction — and this doesn't happen. B yields correct saccades. Fujita thus incorporates superior colliculus in a B-type model.

Eric Schwartz showed that the projection to visual cortex is described by the complex log z. Fujita assumes the same differential distribution of nerve fibres in deep layers of superior colliculus. He codes saccade size by the number of excited nerve fibres projecting from given spot in superior colliculus to long-lead burst neurons in brainstem — which form what he calls the "LLBN plane." He assumes a rectangular dendritic tree for LLBN neurons, and assumes a uniform distribution of size and location of the rectangles. He then gives a circuit diagram for the reticular formation. The model has gain variables for the projection of superior colliculus to the various populations of LLBNs. Fujita has a model for how the olivocerebellar system might adjust the gains, in line with Ito's ideas on the corticonuclear microcomplex. The model simulates them well, including the long-term change in the gain.

A more abstract, mathematical view of the role of the cerebellum is provided by Michael G. Paulin's Kalman Filter Theory of the Cerebellum. Under certain conditions a Kalman filter is the optimal estimator for the state variables of a dynamical system. The hypothesis put forward here is that the cerebellum is a neural analog of a Kalman filter, providing optimal state variable estimates for reflex control. In particular it is hypothesized that interactions between the cerebellar cortex and the intracerebellar nuclei are described by the matrix Riccati equations of the Kalman filter. The Vestibulo-Ocular Reflex (VOR) affords a unique opportunity for developing and testing a model of cerebellar function based on the Kalman filter hypothesis. The vestibulocerebellum and vestibular nuclei can be regarded as prototypes of the cerebellar neocortex and intracerebellar nuclei. The VOR can be modelled as a Kalman filter which estimates head rotational velocity from sense data. This model parsimoniously describes known VOR dynamics and predicts new observable phenomena. Its specific predictions include time-varying VOR dynamic parameters during head movements, frequency selectivity, autocorrelogram storage and predictive feedforward in the VOR.

According to the model, the vestibulocerebellum provides optimizing time-variation (context sensitivity) of VOR dynamic parameters. Therefore the model predicts that the VOR will become time-invariant when the relevant regions of the vestibulocerebellum are disabled. It predicts dysmetria due to the inability to regulate movements along trajectories. Segmentation of maneuvers ("loss of coordination") is a consequence of dysmetria. Decreased ability to perform