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MODELISATION DES PROPRIETES DU CORTEX CEREBRAL

Comparaison entre aires visuelles, motrices et préfrontales

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Introduction

Traditional views of cortical function define the postero-anterior dimension of the cortex as a substrate for the gradual transition from perceptual to motor processes, and then to organizational functions. Simple behavioral tasks have been used to assess this organization. A subject (rat, monkey, human) is asked to discriminate between or recognize visual, auditory or somatosensory stimuli (*sensory integration*), to perform arm, eye or body movements (*motor performance*), and more generally to produce a series of actions in response to environmental stimuli (*temporal organization of behavior*).

Although much remains to be understood, the mechanisms and cortical networks involved in *sensory integration* and *motor performance* have begun to be well characterized (Maunsell and Newsome, 1987; Johnson, 1992). Experimental studies of these functions also benefit from invaluable theoretical support, which defines the nature of the problems that must be solved by the brain.

The *temporal organization of behavior* has been far more difficult to deal with. Although convergent experimental evidence has demonstrated the critical role of the prefrontal cortex (PFC) in the acquisition and expression of complex behaviors (Goldman-Rakic, 1987; Fuster, 1988), the underlying information processing principles have not been identified. They may be related to short-term memory, expectation of forthcoming events, preparation for response (Fuster 1973; Niki and Watanabe 1976), and higher-level behavioral processes (Watanabe 1981, 1986a,b; Joseph and Barone 1987; Barone and Joseph 1989; Watanabe 1990, 1992). Theoretical studies have suggested that the PFC is involved in “working memory” (Goldman-Rakic, 1987), in “mediation of cross-temporal contingencies” (Fuster, 1988), in “planning and problem solving” (Shallice, 1988). These definitions are attractive since they provide a formal, overall description of prefrontal functions. However, they provide no information on local mechanisms contributing to prefrontal functions.

These observations give rise to two main questions:

1. What is the specificity of information processing in the prefrontal cortex? The early work of Hubel and Wiesel (1968) described the mechanisms involved in processing sensory information (receptive field). Georgopoulos et al. (1982) recently provided important insights into mechanisms of motor information processing (population code). Although these mechanisms are far from being precisely understood, they can help to understand experimental outcomes. However, no specific mechanisms have been identified, which may be responsible for processing in prefrontal circuits.

2. How are sensory-motor programs represented in a neuronal network? We are now familiar with the ways visual objects may be stored in long-term memory (associative memories; Kohonen, 1988; Rolls, 1990) and with the way direction of movement is coded (Georgopoulos et al., 1986; Caminiti et al., 1991; Burnod et al., 1992). But what is the neuronal representation of a temporal sequence of events?

3. Do similar mechanisms contribute to simple and complex cognitive functions? Since the prefrontal cortex reaches its maximum phylogenetic development in humans, in parallel with acquisition of the language, one can wonder whether development of the prefrontal cortex corresponds to acquisition of new processing mechanisms or whether it corresponds simply to greater processing and memorization capacities.

The goal of the present work is to address these issues through a series of computational models.

Information-processing models of brain functions

When facing a complex system, a valuable approach is to attempt to approximate its organization and/or its function by a model. In recent years, numerous information-processing models have attempted to address issues on brain functions. The main characteristic of these models is the great diversity of levels of representation, underlying assumptions and expected outcomes.

A classical approach in brain modeling is to study the computational problems that must be solved, independently of underlying biological constraints (Marr and Poggio 1977; Marr 1982). Emphasis is on representation of information, algorithms, symbolic description. For example, Artificial Intelligence models assume that brain circuits manipulate symbolic information according to production rules (Pylyshyn 1984). These models are well suited for representing abstract and logical aspects of behavior but far less efficient for perceptual and motor problems. Computational vision is another typical example of this approach (Marr 1982; Feldman 1985; Poggio et al. 1985).

Churchland and Sejnowski (1988) have stressed the limitation of Marr's approach for understanding complex information processing systems (in particular brain systems). Dissociation between hardware and software may be misleading since neurobiological data provide essential constraints on computational theories (Churchland and Sejnowski 1988; Douglas and Martin 1991).

Connectionist models provide implementation of biological functions in terms of synaptic interactions (McCulloch and Pitts 1943; Hebb 1949; Rosenblatt 1958) and are thus likely to resolve elegantly the software/hardware dissociation. Furthermore, they are susceptible to learn through the modification of synaptic efficacy. This property has greatly contributed to the popularity of these models. Recently, Rumelhart and McClelland (1986) have described "ready-to-use" techniques to build connectionist models, including a powerful algorithm to train neural networks (back-propagation of error; Rumelhart et al. 1986 LeCun 1987). Subsequently, back-propagation-based models were shown to capture biological (Zipser and Andersen 1988; Lehky and Sejnowski 1988; Lockery et al. 1989; Pouget et al. 1993) as well as psychological (Hinton and Shallice 1991; Cohen and Servan-Schreiber 1992) features of information processing in the brain.

Constraints on models of brain functions

Great care has been taken to justify the validity of models based on the back-propagation algorithm, and to assess their predictive value (Rumelhart and McClelland 1986). However, Crick (1989) has stressed that these models can merely be considered as demonstrations[1] since they result from an optimization-based training process which is not likely to be implemented in brain circuits. Going further along the critic, Reeke and Edelman (1988) have argued that neurobiological foundations of a model are still not sufficient to ensure the predictive value of the model and to avoid errors of interpretation.

To assess the actual relevance of a model, one should ask about assumptions underlying the model and about explanations and predictions produced by the model (Reeke and Sporns 1993). We can summarize the modeling requirements in 4 "quality criteria":

1. Assumptions concerning neuronal processing, adaptive properties, representation of information and neural architecture must be consistent with experimental data.

2. Learning must occur through natural interactions, corresponding either to a conditioning protocol or to a developmental stage.

3. Outcomes of the model must be consistent with experimental results available at the level(s) of representation used in the model (neuronal activity, behavior).

4. The model must make testable predictions.

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[1] Models demonstrate that it is not impossible to a find a neural network, which performs a given function. However, they do not prove that brain circuits performing the same function have similar structure or similar internal mechanisms.

[2] Models demonstrate that it is not impossible to a find a neural network, which performs a given function. However, they do not prove that brain circuits performing the same function have similar structure or similar internal mechanisms.

Modeling cortical functions

Since the claim of many models addressing issues on brain functions would probably impinge on the severe requirements for successful theories (Reeke and Sporns 1993), the development of models should follow carefully selected principles. In this regard, **an objective of this work** is to **provide a modeling framework which allows the quality criteria to be fulfilled**. The modeling framework is based on the architectural and processing characteristics of the cerebral cortex (Burnod 1988). Its key features are: (*i*) a multicellular processing unit (*cortical column*) reflecting the modular nature of cortical organization and function; (*ii*) a group of units (*area*) corresponding to the parcellation of the cortical surface according to the regional variations of cytoarchitectonics, connectivity, and integrative and registering properties of cortical circuits; (*iii*) a network of areas corresponding to the architecture of intracortical pathways.

Within this framework, models for *visual integration* and *motor performance* have been developed in the group NEUROSCIENCES & MODELISATION at Institut des Neurosciences (Paris, France) under the direction of Yves Burnod. They correspond to two types of transformation of retinal information, either toward an object-centered reference frame: (*1*) model of *perceptual grouping* developed by Jean-Luc Anton and Patrick Marchal (Anton 1992); (*2*) model of *invariant pattern recognition* developed by Isabelle Otto (Otto et al. 1992), or toward an arm-centered reference frame: (*3*) model of *coordinates transformation for 3D arm reaching movements* developed by Philippe Grandguillaume and Yves Burnod (Burnod et al. 1992) in collaboration with Roberto Caminiti (Roma, Italy); (*4*) model of acquisition of *context/reinforcement motor behavior* developed in collaboration with Yves Burnod (Guigon and Burnod 1993).

Model of prefrontal functions

These models have allowed the neuronal processes involved in *visual integration* and *motor performance* to be characterized. The **goal of the present work** is (*1*) to describe the computational properties of a neural network involved in the acquisition and execution of tasks, which use temporal delays for structuring behavioral reactions to environmental stimuli (delayed tasks); (*2*) to characterize the neural representation of these tasks in prefrontal circuits; (*3*) to provide a comparison between information processing principles underlying *visual integration*, *motor performance*, and *temporal organization of behavior*.

A neural network model has been designed in close relation to the properties of the prefrontal cortex and has been trained to execute a spatial delayed response task. This task has been chosen for the following reasons: (*i*) It has been well documented in non-human primates by a number of neurophysiological and neuropsychological studies; (*ii*) It appears to strongly challenge prefrontal functions for both learning and execution of the task (Jacobsen 1935); (*iii*) It involves integration of visual cues and production of movements and thus provides a basis for the comparison of different information processing mechanisms.

Methodology

The presentation of the models during the course of this document, follows the same logical order. First, we give an overview of anatomical, physiological, and behavioral data which are relevant for building the model. Then we present the model through the description of its main components, following the principles of cortical modeling. Evaluation of by computer simulations illustrates outcomes and limitations of the model. Results are discussed in relation to biological data.

We have tried to keep the same (simple and classical) mathematical notations across all models. Equations describing temporal evolution of variables (neuronal activity, synaptic efficacies) are quantized time difference equation with terms ensuring convergence and stability.

Plan of work

This document is organized in 3 PARTS (I, II and III) and 6 **chapters** (1 to 6). PART I consists of two chapters (**chapter 1**: *Neural Modeling Principles* and **chapter 2**: *Framework for Modeling Cortical Functions*).

Chapter 1 gives an overview of neural modeling principles derived from connectionist models. A modeling framework based on principles of cortical organization and operation is exposed in **chapter 2**. The goal of this chapter is to provide a formal description of these principles for the use of modeling. In particular, mathematical equations corresponding to computational properties of cortical circuits are given. A short summary of models described in following **chapters 3**, **4**, and **5** terminates this chapter, and illustrates "cortical solutions" to important information processing problems.

The following PART II (**chapters 3**, **4**, and **5**) provides detailed descriptions of models concerning *visual integration*, *motor performance*, and *temporal organization of behavior*. **Chapter 3** (*From Retinal to Object-centered Reference Frame*) illustrates transformations of retinal information for object recognition and **chapter 4** (*From Retinal to Arm-centered Reference Frame*) transformations of retinal information for arm movement. **Chapter 5** (*Modeling Prefrontal Functions*) begins by a review on prefrontal functions and then presents a neural network model for the acquisition of the delayed response task.

PART III contains the **chapter 6** (*Learning Rules and Biological Substrate*). In this chapter, we first present recent results on neuronal processing and synaptic plasticity. Then we discuss the biological and computational properties of a number of synaptic plasticity rules used in neural models. A tentative theory relating synaptic plasticity rules, anatomical brain regions and learning behavior is presented, which is a synthesis of the results of this work.

Collaborations

Studies by other related groups have influenced the present work: theoretical and applied studies on cortical column-based networks by Frédéric Alexandre and Frédéric Guyot (Alexandre 1990; Guyot 1990; Alexandre et al. 1991) at CRIN-INRIA (Nancy, France); models of cerebellar functions by Michel Dufossé, Sandrine Allemand and François Blanc at IMT (Marseille, France).

The model of prefrontal functions (**chapter 5**) has profited from several collaborations:

- with Bernadette Dorizzi at Institut National des Télécommunications (Evry, France): we have worked out formal aspects of time in neural networks (Dorizzi et al. 1991).

- with Wolfram Schultz at Institut de Physiologie, University of Fribourg (Switzerland): we have discussed the assumptions and the predictions of the model in relation to current knowledge on frontal lobe functions (Guigon et al. 1993).

- with Xavier Mondon, June Hirsch and Francis Crépel at Laboratoire de Neurobiologie et Neuropharmacologie du Développement (Orsay, France): we have discussed the properties of channels and the form of plasticity found in the prefrontal cortex (Mondon 1991; Guigon et al. 1991).

- with Bruno Delord and Arno Klaassen at LIMSI (Orsay, France): we have begun the simulation of analogue models of neurons in order to investigate the contribution of currents and modulators in the temporal integrative properties of prefrontal neurons (Klaassen 1992; Burnod et al. 1993).

Part I

Frameworks for modeling

CHAPTER 1

Neural Modeling Principles

Contents

Summary

This chapter gives an overview of neural modeling principles derived from connectionist and PDP models. We describe the classical notions of neural processing, learning rules, architecture of neural networks, and representation of information. We discuss outcomes and limitations of these principles.

1 INTRODUCTION

Information processing models of brain systems have a long historical tradition (McCulloch and Pitts 1943; Hebb 1949). However, only recent developments within cognitive science have provided a set of consistent modeling principles, which capture biological features of information processing in the brain (connectionism, Feldman and Ballard 1982; Parallel Distributed Processing models, Rumelhart and McClelland 1986). These principles have been drawn from the main aspects of brain organization and operations, and allow **computer simulation models** of transformations performed by brain circuits to be built.

In these models, the basic processing unit is a neuron-like element which receives a set of inputs from other units and adjusts its output in response to inputs. In relation to real neurons, unit output can be seen as a firing frequency. Units can be grouped in subsets (such as layers, maps) and connected according to some given rules (random connections, full or partial connections between subsets, ...) to form a network. A network usually contains input and output units, which define a processing pathway and provide a way to put constraints on the network. The ability of such a network is given by the set of modifiable connection weights[3] between units, which shape unit activation. During a training session where inputs and/or outputs of the network are constrained to particular values, connection weights are modified according to a learning rule. Initially, the network has a random behavior defined by random values of connection weights. The training results in functional changes, which reflect the adaptation of the network to external constraints. Such network models can help to explore the relation between local properties of neurons and global performance of large-scale neural networks.

The goal of this chapter is to provide an overview of the basic aspects of neural modeling. However, since good textbooks on neural modeling are now available (Hertz et al. 1991), we focus on main concepts, which will be used in the following chapters.

2 BASIC ASPECTS OF NEURAL MODELING

Neural processing

Neural processing relies on a mathematical model of the neuron. Choosing a model of neuron mainly depends on the intended goal. When one is concerned with the cooperative behavior of an assembly of neuron-like elements, binary devices performing a simple logical operation should provide a correct approximation of real neurons (McCulloch and Pitts 1943; Rosenblatt 1958). Hopfield (1982, 1984) has shown that the emergent properties of a large network of interconnected neurons are rather insensitive to the details of the neuron model.

On the other hand, complex processors based on the functional role of membrane currents, synaptic receptors, transmitters and modulators of real neurons can be designed to investigate the behavior of small neuronal networks (Buonomano et al. 1990).

Although the two approaches have different goals, the former may benefit from the latter. In fact the input/output function of a simple unit can be designed from the repertory of possible transformations observed in real neurons (Sheperd and Koch 1989). For instance, Koch et al. (1983) have shown that nonlinear interactions in a dendrite may result in an analog AND-NOT operation. Accordingly, units performing products instead of summation have been proposed as computing elements (Feldman and Ballard 1982;

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[3] Different terms are equivalently used in neural modeling to describe the connection between two neurons: synaptic efficacy, learning coefficient, learning weight, ...

Williams 1986; Burnod 1988; Durbin and Rumelhart 1989). In the following, we describe some classical computing elements.

The formal neuron. Since McCulloch and Pitts (1943), a popular neuron-like adaptive element has been the formal neuron (Fig. 1.1). It has several weighted input pathways $\{x_i(w_i) \quad 1 \le i \le n\}$ and an output y. Activation is generally modeled by a thresholded-convolution:

$$y(t) = \begin{cases} 1 & \text{if } \sum_{i=1}^{n} w_i(t) x_i(t) > \theta \\ 0 & \text{else} \end{cases} \qquad (1.1)$$

where θ is a positive constant determining the threshold of the neuron and t a quantized time. This rule reflects the fact that neurons display all-or-none responses (action potentials) when they are depolarized above a threshold. Other models of neuron use a graded output (for instance, between 0 and 1), which may represent the average spike rate of the neuron. Formulation by first-order differential equations has also been proposed, to allow continuous time description of neural dynamics (Amari 1980).

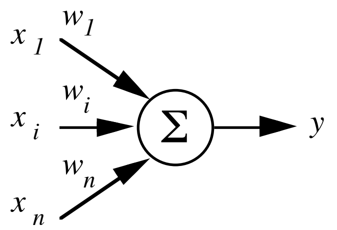

Figure 1.1. The formal neuron has n input pathways (x_i) and an output pathway y. A connection weight (w_i) is associated with each input pathway.

A more realistic model (stochastic neuron) approximates the stochastic behavior of a neuron (Sejnowski 1986). The principle is to compute the weighted sum of the inputs as in Equation 1.1, to convert the result to obtain a value p between 0 and 1 and to use p as the probability of having an output equal to 1. It reflects the equivalence between firing rate of neuron and its probability of firing.

Sigma-pi unit. Most neural models used formal neurons. Williams (1986) has proposed a more general processing element, the sigma-pi unit (Fig. 1.2):

$$y(t) = f[\sum_{S_j \in P} w_j(t) \prod_{i \in S_j} x_i(t)] \qquad (1.2)$$

where P is the power set of [1, .., n], n the degree, and f a non-decreasing function in [0,1]. The sigma-pi unit computes a sum of contributions from multiplicative clusters of input. Mel (1991) has stressed the computational interest of such a unit to represent multidimensional receptive fields or higher-order feature detectors.

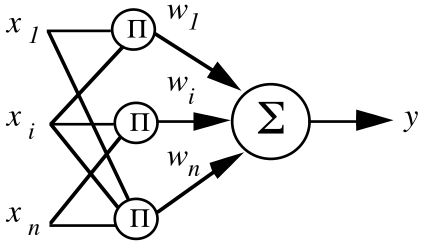

Figure 1.2. The sigma-pi unit has n input pathways (x_i) and an output pathway y. Processing is performed in two steps (product ∏ and weighted summation ∑).

Temporal processing. Neural processing has been mainly described in terms of spatial integration. Another important dimension is defined by the temporal integrative properties of neurons. It has been recently stressed that the dynamics of a real neuronal network may depend not only on synaptic current flow, but also on intrinsic electroresponsive properties of single neurons in the network (see review in Llinás 1988). These properties are determined by the ionic currents present in the cell and by the sensitivity of these currents to neurotransmitters. Interactions between currents and neurotransmitters may generate complex temporal patterns of activity (Sheperd and Koch 1989), which may have computational functions. These aspects have not been frequently used in models (Sutton and Barto 1981; Lisberger and Sejnowski 1992).

Adaptive properties

Modifications of connection weights modulate neural processing and are thus responsible for adaptation of neural networks. The rule governing changes in synaptic weights is called a learning rule and can be formally described by the following equation

$$w_i(t+1) = w_i(t) + \rho_i(t)$$

where ρ_i is the quantity defining the time and direction of change. This quantity ρ_i should depend on past and/or present values of $\{x_j\}$, y, $\{w_j\}$, and ρ_i . A number of rules have been so far designed. Some provide activity-dependent changes in connection weights [Hebbian rule (Hebb 1949), reinforcement rule (Widrow et al. 1973); for a review, see Levine 1991]; others, such as the well known and widely used back propagation algorithm (Rumelhart et al. 1986) or the delta rule (Widrow and Hoff 1960) are global procedures, which minimize network error through gradient descent. A detailed description of learning rules is given in **chapter 6**.

The functional properties of a neural network are defined both by adaptive properties of its component processing units, and by a training set and a training protocol. The training set contains examples, which will be presented to the network. The training protocol defines the order of presentation and the number of repetitions.

A general way to train a network is to form a mapping from examples. In this method (supervised learning), a “teacher” provides for each input the desired output (error-correction method) or a reinforcement that characterizes whether the output generated was correct or not (reinforcement method). On the other hand, unsupervised methods exploit the statistical regularities of the raw input to form a more meaningful internal representation (Kohonen 1982; Barlow 1989).

Neural architecture

Neural architectures are classically defined in terms of layers organized in a hierarchical fashion (multilayered perceptrons; Rosenblatt 1958; Rumelhart and McClelland 1986). These architectures are defined by an input and output layer, which interact with the external world, and some hidden layers, which learn internal representations (Rumelhart et al. 1986). Such architectures are particularly suitable and somewhat consistent with anatomical data for the modeling of sensory systems. Several aspects of the visual system have been addressed using such networks (Lehky and Sejnowski 1988; Zipser and Andersen 1988). Hierarchically organized layers are also well-suited for models of motor system, for example coordinate transformations (Massone and Bizzi 1989) or computation of kinematic and dynamic transformations (Kawato et al. 1987).

Layer organization is implicitly related to hierarchical information processing. In most models, there are no reverse or sideways connections. The flow of information is one way and corresponds to a progressive integration and the creation of higher order representations. Such an architecture reflects the general organization of sensory systems

(De Yoe and Van Essen 1988). The limitation of hierarchical architectures is related to advances in the description of anatomical pathways in the brain. For instance the visual system has as many feedback projections as forward ones and is made of different pathways laterally interconnected (Mishkin et al. 1983). As a correlate, it becomes difficult to define the different processing steps by a “levels of processing”.

Network organization has also been proposed in terms of maps, which reflect variations in the value of a parameter across one or more dimensions of the biological substratum (Knudsen et al. 1987). It has been used for invariant pattern recognition (Fukushima 1988; Otto et al. 1992), coordinate transformations (Burnod et al. 1992), learning arm kinematics and dynamics (Ritter et al. 1989).

The main difference between layer and map organization is related to the spatial arrangement of units in a map. Neighboring relationships within a map contribute to neural processing (Kohonen 1982), while layer codes may reflect any property of incoming information, without metric or order, using arbitrary coding schemes.

Representation of information

The question of the representation of information in networks of neurons is a fundamental issue in neural modeling (see review in Thorpe 1989). The main debate is between *local* and *distributed* coding, i.e. whether each unit codes for particular attribute of information or whether information is coded by a large subset of non specialized units.

Directly derived from the labelled line hypothesis of Müller and from the feature-detector theory (Hubel and Wiesel 1962), the local coding theory (Barlow 1972) makes the assumption that each unit stands for a particular feature or concept (“grand-mother cell”). This kind of storage is very limited in the number of discriminable input states that can be coded (as many as neurons if using a binary code), as well as in its ability to generalize.

Using distributed coding allow each input state to be coded by a set of active units, each unit representing one component of the pattern. The representational capacity in a distributed code is higher due to the combinatorial use of units (for n neurons, 2^n if using a binary code). On the other hand, the mapping becomes more complex (Kohonen et al. 1981). Coarse coding is a form of distributed coding frequently used to represent continuous variables. The principle is that units have broad overlapping receptive fields whose peak sensitivities vary systematically from unit to unit across the population.

The advantages of local and distributed coding can be combined by sparse coding. In this case, input patterns are represented by a small proportion of the available units. This proportion defines a trade-off, on the one hand, between representation capacity (large capacity for a high proportion) and memory capacity (large capacity for a low proportion), and on the other hand, between generalization ability and complexity of mapping (no unit carries explicit information). Note that sparse coding may correspond to a semi-local code (each stimulus is coded by several units, each unit being related to a particular attribute of the stimulus) or to semi-distributed code (each attribute is coded separately, but no unit carries explicit information).

Original coding schemes have been proposed. We can mention the representation by correlation graphs (Bienenstock and von der Malsburg 1987) and code carried by the temporal pattern of activity (Strehler and Lestienne 1986; Lestienne and Strehler 1988; Eskandar et al. 1992).

3 DISCUSSION

In this chapter, we have pointed to a set of basic principles, which allow features of brain organization and operation to be incorporated into models. In this framework, spectacular models have been built, concerning sensory (Lehky and Sejnowski 1988) and sensory-motor transformations (Kuperstein 1988; Zipser and Andersen 1988; Pouget et al. 1993), as well as cognitive functions (Sejnowski and Rosenberg 1987; Dehaene and Changeux 1989; Servan-Schreiber et al. 1990; Dehaene and Changeux 1991; Cohen and Servan-Schreiber 1992).

However, the most promising results have been provided by modeling studies using back-propagation algorithm (Zipser and Andersen 1988; Lehky and Sejnowski 1988; Pouget et al. 1993). This algorithm approximates learning in real neural networks in the sense that, after learning, similar properties can be seen in both systems. But “trajectories” followed by models and by brain networks to reach a particular final state may be quite different (Crick 1989; Reeke and Sporns 1993). The effective outcomes provided by such network models, are thus more likely to be interpreted in terms of statistical analysis rather than in terms of neuronal processing. Another difficulty arises from the fact that learning corresponds to an accurate tuning of each unit in the network. As a consequence, learning new features would most surely erase the previous experiences. This drawback emphasizes that the back-propagation-based modeling method should be unpromising at addressing many problems solved by the brain, in particular, problems related to ontogenetic development, in which a progressive maturation occurs through successive refinement of neuronal networks.

CHAPTER 2

Framework for Modeling Cortical Functions

Contents

Summary

The organization and operation principles of the neocortex are described. On this basis, computational constraints on representation of information, connectivity, neural processing, and adaptive properties in cortical circuits are proposed as a modeling framework. The key feature of this framework is a multicellular processing unit reflecting the modular nature of cortical organization and function. The mathematical equations corresponding to the computational properties of cortical circuits are given. A short summary of the models described in following chapters terminates this chapter, and illustrates "cortical solutions" to important information processing problems.

1 INTRODUCTION

In the previous chapter, we have described a set of modeling principles, which form a basis for the development of information processing models of brain functions. This approach may be defined as "top-down", since a restricted number of hypothesis are made on biological features, and outcomes are mainly derived from algorithmic constraints. However, we have stressed that these hypothesis may not provide enough biological constraints to build successful models (Crick 1989; Reeke and Sporns 1993).

A complementary approach is to ask how the brain is likely to solve problems (Ballard 1986). This "bottom-up" approach focuses on the structural and functional characteristics of brain circuits and their involvement in the implementation of problem-solving algorithms. The goal is not to take into account the greatest number of brain properties, but to point to the critical aspects, which contribute to appropriate computation. The main difficulty of "bottom-up" modeling is to choose the appropriate levels of organization (Churchland and Sejnowski 1988), and at these levels, to face the great diversity of biological components and processes.

Recent works (Ballard 1986; Burnod 1988; Alexandre 1990; Guyot 1990) have proposed a consistent "bottom-up" modeling theory based on the architectural and processing characteristics of the cerebral cortex. The appeal of the neocortex relies on the following facts: (*i*) Great regularity is observed in its organization; (*ii*) Cortical circuits process any set of data with a single format, whatever the modality; (*iii*) The phylogenetic development of the cortex is correlated with the acquisition of higher level behavior structures. However, to focus on the cerebral cortex does not deny the contribution of subcortical systems, such as basal ganglia, cerebellum, or medial temporal lobe structures. It is a mean to describe the computational principles underlying various brain functions within one and the same framework.

Modeling principles are constructed from the modular organization of the cortex (Szentágothai 1975; Mountcastle 1978; Eccles 1981) and concern cortical representation of information, architecture of cortical networks, cytoarchitectonics, input/output and intrinsic connectivity, columnar processing and adaptive properties of cortical circuits. In continuity with previous works (Ballard 1986; Burnod 1988; Alexandre 1990; Guyot 1990), this chapter describes a computational framework based on the properties of the cerebral cortex. The main novelty in this framework is to combine two approaches: (*1*) We describe organizational and operating principles common to different cortical areas; (*2*) We address issues concerning the regional specialization of the cortical surface. To this end, we introduce three modes of operation and three modes of adaptation (termed *tuning*, *gating*, and *timing*). In **chapters 3**, **4**, and **5**, we will show that these operation and adaptation modes are sufficient to solve problems of *visual integration*, *motor performance*, and *temporal organization of behavior*.

2 MODULAR ORGANIZATION OF THE CORTEX

The modular organization of the neocortex is now referred as an organizing principle for cortical functions (Szentágothai 1975; Mountcastle 1978; Eccles 1981). However, this organization does not correspond to a unique and absolute concept, but can be related to six aspects of cortical organization and operation: (*1*) Representation of information; (*2*) Architecture of cortical networks; (*3*) Local circuits and intrinsic neuronal organization of the cortex; (*4*) Intrinsic connectivity and input/output organization; (*5*) Nature of cortical processing, and (*6*) Adaptive properties of cortical circuits.

These aspects are exposed and discussed in the following. For each point, we have selected a restricted number of considerations which appear to be relevant from the point of view of modeling. For more exhaustive presentations, the reader is referred to the literature (Mountcastle 1978; Rakic and Singer 1988; Burnod 1988).

Representation of information - Mapping of multidimensional parameters

Principles. The organization of sensory cortex is defined by the simultaneous mapping of different modalities on the cortical surface. This mapping has the following characteristics: (*i*) Neurons recorded in penetrations normal to the cortical surface share similar properties such as place, modality, dynamic response characteristics, abstracted features (Powell and Mountcastle 1959); (*ii*) The neighboring relationships at the level of the peripheral receptor are preserved (retinotopy, tonotopy, body surface representation); (*iii*) The cortical surface is shared in interdigitated clusters each corresponding to a specific modality. Sharp transitions are observed when passing from one column to the next.

There are numerous experimental illustrations of these principles. In the somatosensory cortex, the place parameter is the location of the receptive field on the body surface and modalities are muscle and joint afferents. Segments of the body surface are mapped into stripes extending along the rostrocaudal axis through areas 3a, 3b, 1 and 2 (Werner and Whitsel 1968). In the visual cortex, the corresponding parameters, derived from geniculate projections, are the location of the receptive field in the visual space and information concerning color, luminance, spatial frequency, motion (Hubel and Wiesel 1977). The thalamic inputs are segregated in different laminar terminations (Hubel and Wiesel 1972) as well as segregated within layers for the ocular dominance (stripes; Hubel and Wiesel 1969).

Cortical maps. A fundamental feature of cortical organization is the map, which can be described with different structures (Knudsen et al. 1987; Stryker et al. 1987): (*i*) *Topographical maps* are groups of neurons in which the place parameter corresponds to the topography of the projected sensory surface, according to a given metric; (*ii*) *Computational maps* provide an ordered representation of parameters obtained by transformation of sensory inputs or motor outputs (direction of motion in middle temporal area; Albright et al. 1984); (*iii*) *Interdigitated maps* have several levels of organization (fine-grain and coarse-grain). The primate primary visual area is a topographic map at a large scale and an interdigitated map at lower scale (low spatial frequency and color-sensitive map intercalated into the cytochrome oxidase blobs; Hubel and Wiesel 1974a,b).

The mapping also concerns output representation. Asanuma et al. (1968) have shown that efferent zones of the motor cortex are organized in vertically oriented arrays of cells, which elicit movement of a single muscle or muscle group. The XY dimensions correspond to location in the pattern of body musculature. Similarly, systematic variations of the direction of eye movements are represented topographically across the superior colliculus (Wurtz and Albano 1980).

Tuning properties. An important property of the mapping is that neurons have a broad tuning, i.e. a large subset of neurons is activated by a given stimulus (for orientation, see Schiller et al. 1976; Albright 1984). Neurons can also be tuned for several parameters. However, tuning curves are peaked and allow a high resolution representation of inputs through relative responses of neurons. Two complementary vectorial methods have been proposed to describe the tuning of neurons. On the one hand, broad tuning has been associated with the notion of population code (Georgopoulos et al. 1986). In this case, each neuron is associated with a vector and neuronal activity is interpreted as the projection of this vector on a population vector (Fig. 2.1A). On the other hand, vectorial coding allows the tuning of a neuron for several parameters to be described (Fig. 2.1B). The sensitivity of a neuron to a given parameter is defined by the projection on the corresponding axis.

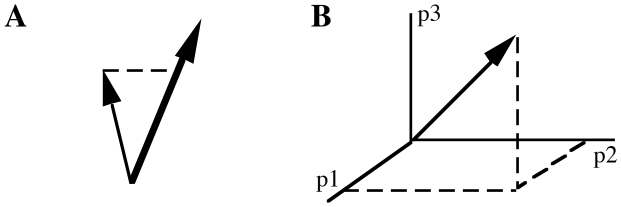

Figure 2.1. Cortical representation of information. A vector is associated to a neuron (thin arrow). **A**. Population coding: activity of the neuron is obtained as the projection of the vector on a population vector (thick arrow). **B**. Vectorial coding: sensitivity of the neuron to a given parameter (p1, p2, p3) is defined by the projection on the corresponding axis.

Efficient representation and computation. From a computational point of view, mapping has numerous advantages (Kohonen 1982), and among them: (*i*) Information can be easily accessed by other neuronal systems with simple schemes of connectivity; (*ii*) Processing is rapid since information is accessed in parallel; (*iii*) Local continuity defines a metric in the parameter space in relation to anatomical distance.

The fact that the same representation mode is used in different modalities (auditory, somatosensory, visual) argues for a single processing mode, whatever the nature of the incoming information.

In summary, the mapping provides a natural interface between the physical dimensions of parameters and the anatomical dimensions of the cortex. Furthermore, it contributes to optimal representation, computation and connectivity in neuronal circuits. Vectorial and population coding are complementary ways to extract information from a map. In the following chapters, we will show that the mapping of information may be an essential component in the acquisition and expression of cortical functions.

Architecture of cortical networks

The anatomical basis of the modular organization is related to the *nonrandom* form of the terminations of thalamo-cortical and cortico-cortical projections. Terminations may be organized in horizontal or vertical patterns of different characteristic forms such as layers, patches, stripes, slabs, columns.

Laminar distribution of connections. In this case, the termination is restricted to a subset of layers. Laminar terminations have been characterized as feedforward or feedback patterns (Maunsell and Van Essen 1983). Feedforward projections terminate mainly in layer IV and III. On the other hand feedback projections terminate in layers I and VI, sparing layer IV. Such a pattern is observed in the successive connections between areas

17, 18, 19 and TE of the primate visual cortex. The form of the termination has been proposed as a way to characterize the level of processing of a cortical area. Comparative processing complexity between two areas is defined by the nature (feedforward or feedback) of their interactions.

Columnar distribution of connections. Projections can terminate in vertically oriented columns extending throughout the depth of the cortical surface. Generally, labelled columns alternate with columns of similar size and devoid of labelling. Note that input columns are also output columns (Schwartz and Goldman-Rakic 1984)

Interestingly, regular organization of connections is not restricted to cortico-cortical networks, but is also observed in cortico-subcortical projections. For instance, cortico-striatal projections terminate in an intricate pattern of irregularly shaped patches separated by free areas (Goldman and Nauta 1977a). This observation stresses that the modular nature of cortical interaction may be a general principle in the definition of cortical interacting networks (Goldman-Rakic 1988).

In summary, cortical interconnections are regularly organized in either the horizontal dimension or the vertical dimension of the cortex. Patterns of connectivity define different modes of interaction between cortical structures, which are compatible with the modular representation of information. The models described in the following chapters illustrate the functional role of the types of interactions.

Cytoarchitectonics

A number of anatomical studies have shown that the cerebral cortex is not to be seen as an uniform lattice of neurons, but is made of local circuits of cooperative neurons arranged throughout the depth of the six cortical layers (column; Szentágothai 1975). A column can be characterized by (*i*) a small group of closely related pyramidal neurons and (*ii*) a set of local-circuit interneurons (Marín-Padilla 1990). The longitudinal size of a column is 30 to 50 μm.

These stereotyped neuronal circuits (about 100 neurons) are repeated, with local variations (for example cytoarchitectony features such as layer IV thickness), throughout the cortical sheet (Szentágothai 1975; Mountcastle 1978). Consistency across cortical areas and across species has been demonstrated, excepted in area 17 of the primate (Rockel et al. 1980).

The architecture of the columns is related to the distribution of neuronal types in the cortical layers. The cortical neurons show great morphological diversity (Ramón y Cajal

1922; Lorente de Nó 1922). However, one classically distinguishes two types of cortical neurons, according to the presence or absence of dendritic spines.

Spiny neurons. The main type of spiny neurons is the pyramidal neuron. Pyramidal neuron is characterized by its specific developmental, structural and functional features (see Marín-Padilla 1990). Four types of pyramidal cell can be distinguished: giant cells of layer V, large cells of layer V and lower layer III, medium cells of upper layer III, small cells of layer II. Whatever their size and laminar position, pyramidal cells have a characteristic apical dendrite extending vertically toward the pial surface and shorter basal dendrites remaining within a single layer. Apical dendrite increases pyramidal neuron inputs in a specific and restricted fashion to only certain layers by emitting a number of side branches in these layers only (Lund and Boothe 1975). Axons of almost all pyramidal cells leaves the cortex (Lund et al. 1975).

Nonpyramidal spiny neurons have been termed spiny stellate neurons and are distinguished of the pyramidal type by their uniform dendritic length. In the visual cortex, they are found in layer IV and receive thalamic excitatory inputs (Lund 1984; White 1981). They send an excitatory projection vertically, toward the supragranular pyramidal neurons. Note that axons of nonpyramidal cells generally remain within the cortex. High density of spiny stellate neurons is found in sensory areas (granular layer).

Non-spiny cells. These neurons have smooth or sparsely spined dendrites. It has been observed that (*i*) the lateral extend of axon terminal fields of these neurons does not exceed the lateral extend of the dendrites, and (*ii*) very few non spiny cells have axons that spread horizontally within a layer. Several classes have been distinguished, mainly on the basis of the morphology of the axon arborization (Jones 1975; Szentágothai 1975; Jones 1981): chandelier cells, basket cells, double bouquet cells, bipolar cells. Description of the neuronal types can be found in Peters and Jones (Peters and Jones 1984).

Properties of neocortical neurons. The role of the types of cells is defined not only by their anatomical location, but also by their intrinsic properties. Neocortical neurons have various electrical properties due to membrane properties. Prince and Huguenard (1988) have discussed the comparative electrophysiological behavior of neurons in relation to ionic conductances. Particularly they have emphasized the great diversity of ionic channels found in neocortical neurons. Classical sodium and potassium currents responsible for the generation of action potentials interact with a great variety of ionic channels sensitive to voltage, transmitters, modulators, and generate a rich repertory of membrane behavior (Connors and Gutnik 1990).

A simple illustration is given by the properties of GABAergic interneurons (basket, chandelier and double bouquet cells) and pyramidal cells. The former have a linear relation between spike frequency and thus respond faithfully to inputs. The latter have nonlinear membrane properties and have thus a more integrative role.

In summary, local cortical circuits are made of neurons with different laminar distributions, orientations, and integrative properties. They have a large repertory of operations both in the horizontal and vertical directions. Modeling will use such units as basic computing elements, which are more likely to approximate cortical processing than a single prototypic neuron.

Input/output organization and intrinsic connectivity of a cortical column

Cortical columns are units which receive convergent inputs from other units, process incoming information, and project divergently to many other units. The integrative function of a column is determined both by input/output connectivity and intrinsic connections.

Input/output organization. The connections of a column are related to the its layer organization in the vertical dimension of the cortex. The intermediate layer IV (which contains granular cells) divide two subsets of pyramidal neurons, the upper division (supragranular cortical layers I, II and III) and the lower division (infragranular cortical layers V and VI). The supragranular layers are mainly specialized in cortico-cortical connections, toward adjacent cortical zones or toward more distant cortical areas (Szentágothai 1975; Jones 1981; Feldman 1984).

The infragranular layers project outside the cortex toward other neural structures or participate to feedback connections (Van Essen and Maunsell 1983; Zeki and Shipp 1988). Cortico-thalamic projections arise from layer VI (Gilbert and Kelly 1975; Lund et al. 1975; Jones and Wise 1977) and cortico-subcortical projections from layer V (Jones and Wise 1977).

Intrinsic connectivity. The cortical column is mainly defined by vertically oriented interactions which occur between layers and link neurons in different layers. Three systems of vertical interactions have been identified: (*i*) an excitatory spiny system based on stellate cells; (*ii*) an inhibitory non-spiny system based on different interneurons (basket, chandelier, double bouquet); (*iii*) a system based on collaterals of pyramidal cell axons.

Interlaminar interactions have been well characterized in the primary visual cortex (Lund and Boothe 1975; Fitzpatrick et al. 1985; Blasdel et al. 1985). Each layer establishes elaborate sets of projections to other layers, either with a point-to-point organization, or with lateral spread, or with a periodic termination (Blasdel et al. 1985). These modes of projection are generally reflected in the differential properties of two interconnected layers. If the two layers have a similar topographical organization, their interconnections are precise with little lateral spread.

The role of vertical interaction is illustrated by the role of interlaminar connections in the formation of receptive field properties. Thalamic-receiving cells have simple receptive fields while those in deeper and in more superficial layers have more complex one.

In summary, the organization of cortico-cortical connectivity allows transformations on different flows of inputs to be performed and different information to be conveyed selectively to different targets. These transformations are a combination of operations within each layer, and operations between layers. The form of the processing may be similar in all cortical areas, but the functional differences come from the differences in the sources and terminations of their connections.

Columnar processing

The columnar organization of neocortical circuits results in specific operations. The term “columnar processing” reflects the fact that (*i*) processing is not determined by the properties of a single neuron, but by a whole circuit; (*ii*) the dynamics of cortical circuits tend to preserve the modular mode of representation.

Feature extraction. Feature extraction processes allow the construction of an ordered representation of abstract parameters. It corresponds to the tuning of the sensitivity of neurons to a particular combination of afferent signals that depicts a stimulus attribute not specifically encoded by any single set of primary afferent fibers, but which is reconstructed from combinations. These operations have been well characterized in thalamic-receiving neurons in sensory areas (visual, somatosensory, auditory).

Typical examples are orientation columns in V1 (Hubel and Wiesel 1977), axis of motion columns in the middle temporal area (Albright et al. 1984). Higher level columnar processing has also been observed in the primate middle temporal (MT) area in the form of a band-like segregation of local and global motion processing (Born and Tootell 1992). Columnar processing is also observed in motor areas. A peripheral input from a particular body part is relayed through the sensory cortex to the discrete region of the motor cortex that produces movement of that body part (Waters et al. 1982).

Gating. Experimental studies have suggested that cortical inputs have a *gating* (multiplicative) effect on other inputs. Cortico-cortical projections from somatosensory to motor areas in the cat have been shown to influence motor activity only when combined with other inputs to the motor cortex (Asanuma et al. 1982). Sandell and Schiller (1982) have shown that, during reversible cooling of area 18 in the cat, activity in infragranular layers of area 17 is depressed. Note that infragranular layers of 17 are the recipient of feedback projections from area 18. More specifically, Alonso et al. (1993) have observed that local blockade of layer V in area 18 locally and retinotopically suppresses responses of area 17 V1 to high-velocity stimuli. Nonlinear interactions have also been observed in the posterior parietal cortex, between eye position and retinal position (Andersen et al. 1987), and in motor and premotor cortical areas between arm position and visual target (Caminiti et al. 1991; Burnod et al. 1992). All these results support the idea of a gating effect of cortical inputs.

Timing. Generation of oscillatory neuronal responses has been proposed as a form of columnar processing. Gray and Singer (1989) have shown that intracolumnar processing may result in 40Hz oscillation responses to optimally oriented stimuli. Moreover, stimulus-specific synchronous oscillations were observed both within functional columns (Gray and Singer 1989), and between spatially separate columns (Gray et al. 1989).

More generally, sustained activities have been reported in several cortical areas. There are no experimental demonstrations that sustained activities may result from columnar processing. However, neurons with different patterns of discharge have been found with differential laminar distributions in the prefrontal cortex (Sakai and Hamada 1981): (*i*) Neurons with sustained activity have their soma in layers III and VI; (*ii*) Transient neurons related to visual stimuli are found in supragranular layers; (*iii*) Neuronal activity related to motor performance is distributed preferentially in the infragranular layers (V and VI) (Sawaguchi et al. 1989a). Furthermore, this laminar distribution of neurons is functionally related to the laminar organization of connectivity: (*i*) Projections from the inferotemporal cortex to the PFC terminate in lower layer III and layer IV (Barbas and Mesulam 1981); (*ii*) Deep layers of the PFC projects to the thalamus, caudate nucleus, and superior colliculus, and are thus likely to participate to initiation or preparation of a motor command. These arguments support the idea that vertical processes may be involved in the construction of these neuronal responses, in particular the sustained ones.

In summary, cortical processing is strongly related to the way information is mapped in cortical circuit and to architecture of local cortical circuits ("columnar processing").

Columnar processing results both in spatial anatomical reordering of topography and functional changes. It can be characterized by functionally well defined mechanisms such as *tuning*, *gating*, and *timing*.

Adaptive properties

There is now a great deal of evidence that neocortical neurons can express long lasting modifications of synaptic transmission such as long-term potentiation (LTP) and long-term depression (LTD) (Tsumoto 1992). These phenomena have been observed in the visual cortex (Artola and Singer 1987; Artola et al. 1990), in the motor cortex (Baranyi and Féher 1981), in the prefrontal cortex (Hirsch and Crépel 1991) and have been related to the presence of NMDA receptors.

These cellular mechanisms may form the basis of cortical plasticity. In the visual cortex, Frégnac et al. (1988) have demonstrated that the development of functional properties such as orientation, ocular dominance, disparity may result from activity-dependent modulations of synaptic transmission following a Hebbian rule (*adaptive tuning*). Plasticity of somatosensory maps has been observed following peripheral lesions (Merzenich 1987). Ahissar et al. (1992) have shown that functional connections between neurons in the auditory cortex change with the behavioral relevance of external stimuli, following a generalized Hebbian rule.

An hypothesis about the mechanism of plasticity is that experience-dependent synaptic changes depend on correlations between pre- and postsynaptic activity (Hebbian rule). However, the Hebbian paradigm may not be efficient in all cortical areas (such as premotor and prefrontal cortex).

In summary, adaptive properties of cortical circuits may reflect activity-dependent modifications of synaptic transmission. The rule governing modifications is of Hebbian-type in sensory areas, but may be different in other cortical areas.

Conclusion

These principles reflect the computational properties of cortical circuits resulting from the columnar organization of neocortex. They are not at all sufficient to characterize the diversity and the complexity of cortical functions. However, they provide a framework for describing cortical networks and expressing computational constraints on cortical processing. Formal description, based on principles of Parallel Distributed Processing models (see **chapter 1**) is given in the following section.

3 A UNIT FOR CORTICAL PROCESSING

Several functional circuits have been proposed as a model of the cortical column (Szentágothai 1975; Eccles 1981). These models provide a simplified description of the intrinsic organization of the column. On this basis, Burnod (1988) has designed a model including possible and plausible processing and adaptive mechanisms of the cortical column. Alexandre and Guyot (Alexandre 1990; Guyot 1990; Alexandre et al. 1991) have demonstrated the computational properties of the model of Burnod (1988) on artificial problems such as pattern recognition and speech recognition.

In this section, we describe a generic cortical column-like processing unit for the use of neural modeling. The unit does not reflect the exact arrangement of layers, interneurons and pyramidal cells in a column. It is drawn from the following organizational and computational principles of cortical columns: (*1*) Inputs and outputs are segregated by layers according to their source and target structures, respectively; (*2*) Horizontal and vertical integrative processes participate to the functional properties of the unit; (*3*) The columnar circuits have adaptive properties.

This section is organized following the plan of the previous section (representation of information, connectivity, processing unit, columnar operations, adaptive properties). The goal is to provide correspondences between biological data and modeling principles. The biological basis of the mechanisms (Equations 2.1 to 2.6) are discussed in **chapter 6**.

Representation of information

Ballard (1986) has proposed a formal way to characterize the layout of cortical maps when multiple parameters are simultaneously represented. The two dimensions of the cortical surface are *primary indices*, generally related to the coordinates system of a peripheral structure. *Secondary indices* are characteristic parameters within the modality of afferent information (Fig. 2.2A). In the visual system, primary indices are retinal coordinates and secondary indices are orientation, color, motion, or spatial frequency.

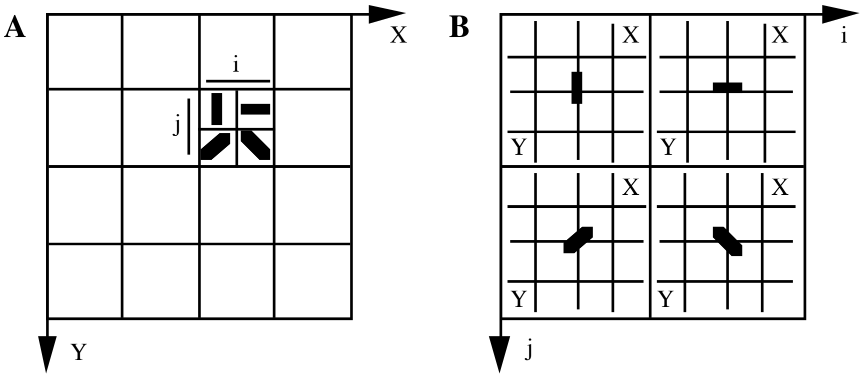

Figure 2.2. Primary and secondary indices. Primary indices are the XY dimensions of a two-dimensional maps. Secondary indices (i,j) are related to different orientations found at each position (**A**). In **B**, a reordering of primary and secondary indices has been performed.

In **chapter 3**, we illustrate the role of primary and secondary indices in the interaction between two flows of information. Reordering of indices, as shown in Fig. 2.2B, allows the transition from a retinal reference frame to an object-centered reference frame (see Fig. 3.4).

Connectivity in cortico-cortical circuits

On the basis of laminar terminations, anatomical studies have characterized patterns of connectivity, such as feedforward, feedback, and lateral pattern (Van Essen and Maunsell 1983; Zeki and Shipp 1988). Furthermore, a functional role has been proposed for the patterns related to the level of processing. Accordingly, we can give the following formal description of cortical connectivity (Fig. 2.3): (*i*) *Feedforward* connections carry information from lower to higher-level processing steps; (*ii*) *Feedback* connections carry information in the opposite direction; (*iii*) *Lateral* connections carry information at one level of processing either locally within an area or between two areas. Intrareal connections are defined either by topographic proximity (with close primary indices) or by topologic proximity (same primary indices, but different secondary indices).

Figure 2.3 summarizes the types of connections, which are found in a cortical network. In the following, we will frequently use the terms *feedforward*, *feedback*, and *lateral* to characterize the flow of information in a network.

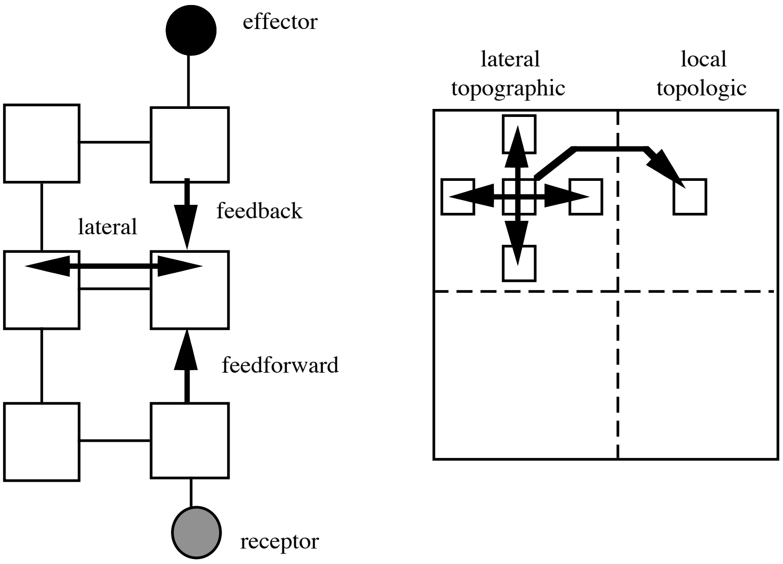

Figure 2.3. Model of cortico-cortical connectivity. The types of connection found in a cortical network are illustrated (see Text).

Column-like processing unit

In the previous section, we have stressed that cortical columns are multicellular circuits organized around a small set of pyramidal cells and local-circuit interneurons. Following this description, the main components of a plausible column-like unit must be the following: (*i*) a layered organization corresponding to the selective processing of different types of inputs; (*ii*) a set of laminar interactions corresponding to the filtering operation performed on columnar inputs; (*iii*) a set of interlaminar interactions corresponding to the vertical integrative role of pyramidal cells within a column; (*iv*) a set of registration coefficients defining the adaptive properties of the column. These components are summarized in Fig. 2.4. The laminar organization of the column is represented by a set of input/output divisions[4] $\{D^i, 1 \le i \le N\}$. A division D^i receives a subset of inputs (x_j^i, $1 \le j \le n_i$) sharing a common origin or a common modality. Each division provides a specific output y^i, computed from the contribution of each division (u^j, $1 \le j \le N$), to a particular target. Adaptive properties are provided by a set a modifiable *columnar registration coefficients*, both within a division and between divisions (see below). Note that the unit is a generic processing element. A division is functionally equivalent to a cortical layer, but does not correspond a priori to one particular layer. However, once the

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[4] We call them "divisions" and not "layers" to avoid the confusion with the classical use of "layers". In the framework of neural networks, the term "layer" refers to a set of neurons with similar connectivity.

unit is embedded in a network, a correspondence can be drawn from the integrative properties of the division and its input/output connections.

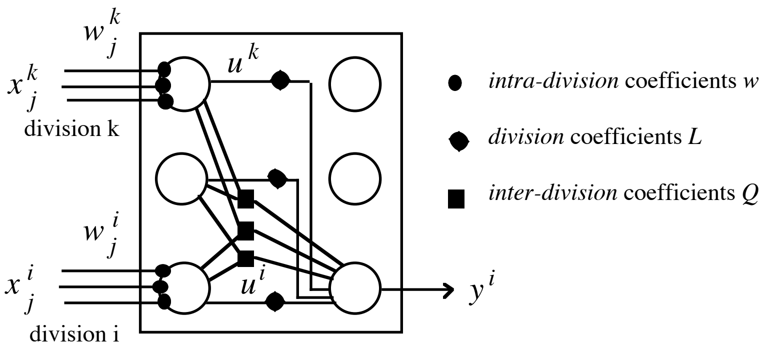

Figure 2.4. Model of the cortical column. The column-like unit is represented as a multicellular circuit. Each circle corresponds to an operation. The unit is made up of several input/output divisions (separated by horizontal hatched lines). Each division has two parts separated by the vertical hatched line. It corresponds to the two processing steps of the unit: (*1*) Each input-division receives a subset of inputs, which are integrated independently; (*2*) The second step is a polynomial (sum-product) combination within each output-division of input-divisions activities. It produces an output per division. Each symbol refers to a particular coefficient.

"Columnar" operations

According to the architecture of the cortical column, processing is performed in two steps (Fig. 2.4): (*i*) first within each division (feature extraction), and (*ii*) then between divisions (gating, timing).

Within a division: feature extraction operation. This operation reflects the properties of cortical neurons receiving thalamic inputs. Distributed incoming signals are integrated through a weighted convolution-like operation:

$$u^i(t) = F\left(\sum_{j=1}^{n_i} w_j^i(t)\, x_j^i(t) \right) \qquad (2.1)$$

where the "intra-division" coefficients $\{w\} = \{w_j^i \in [0,1],\ 1 \leq j \leq n_i\}$ define the "tuning" properties of the division D^i, $u^i \in [0,1]$ is the filtering outcome, t a quantized time, which describes the course of processing[5], and F a nonlinear non-decreasing function in [0,1]. Note that the processing within a division is similar to that of most of the neural units in

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[5] Neuronal dynamics can described either by discrete time equation or by continuous time differential equation.

the classical neural networks. The set of coefficients define the receptive field of the division. Activity-dependent modification of the coefficients $\{w\}$ is termed *adaptive tuning* and is described below (Equation 2.4).

Between divisions: vertical integrative process. Each division D^i provides an output activity y^i resulting from the division-specific filtering contributions (u^i, $1 \leq i \leq N$; Equation 2.1). The output activity y^i depends upon the combination of two terms: the first term expresses the influence of each division D^j ($1 \leq j \leq N$) independently, with a "division" coefficient L^i_j, and the second one expresses the nonlinear interaction between pairs of divisions (D^j and D^k), with an "inter-division" coefficient (Q^i_{jk}). We have stressed that the integrative function of a column should result in two processing modes, namely *gating* and *timing*.

1. *Gating*. The formulation of the gating effect is the following:

$$y^i(t) = F\left[\sum_{j=1}^{N} \sum_{k=j+1}^{N} Q^i_{jk}(t)\, u^j(t)\, u^k(t) + \sum_{j=1}^{N} L^i_j(t)\, u^j(t) \right] \qquad (2.2)$$

This equation expresses that the division D^i can perform adaptive linear and bilinear combinations on incoming information flows. The modification rules for coefficients $\{L\}$ and $\{Q\}$ are collectively termed *adaptive gating*, and are described below (Equation 2.5). The computational properties associated with Equations 2.2 and 2.5 are efficient for solving problems of *visual integration* and *motor performance*, as illustrated in the following **chapters 3** and **4**.

2. *Timing*. This mechanism is related to the production of long-lasting activities. and is defined by

$$\begin{cases} A^i(t) = MAX_{j=1..N}\, \{L^i_j(t) u^j(t)\} \\ A'^i(t) = MAX_{j=1..N}\, \{u^j(t)\} \end{cases}$$

and

$$y^i(t) = \begin{cases} g[A^i(t)] \ \ if \ y^i(t-1) = 0 \\ else \ \begin{cases} g[A'^i(t)] \ \ if \ A'^i(t) \neq 0 \\ else \ \ g[\eta y^i(t-1)] \end{cases} \end{cases} \qquad (2.3)$$

where g is the function defined by

$$g(z) = \begin{cases} 1 \text{ with prob } z \\ 0 \text{ with prob } 1 - z \end{cases}$$

Equation 2.3 expresses that the division D^i is likely to become active ($y^i(t) = 1$) for an incoming activation (A^i), to stay active for a while (with a probability $\eta y^i(t-1)$) and then to return to rest ($y^i(t) = 0$) for a new activation (A'^i). Transitions between rest and sustained states depend on the coefficients L_j^i. which can change with learning according to Equation 2.6 (*adaptive timing*, below). In **chapter 5**, we will show that Equations 2.3 and 2.6 provide explications and predictions on the role of the prefrontal cortex in the *temporal organization of behavior*.

Adaptive properties

In the previous section, we have shown that the cortical columns have a large repertory of adaptations corresponding to intrinsic properties of neocortical neurons and intrinsic connectivity. Here, we make the proposal that three types of adaptation should reflect major adaptive properties of the cortical column: *adaptive tuning*, *adaptive gating*, and *adaptive timing*. In a column-like unit, the adaptations are related to activity-dependent modifications of columnar registration coefficients (w, Q, L) according to a learning rule (see **chapter 1**). More details on learning rules are given in **chapter 6**.

Adaptive tuning. It corresponds to associative modifications of coefficients $\{w\}$ related to receptive field properties. This phenomenon can be described by

$$\Delta w_j^i(t, t+1) = \lambda [\sigma x_j^i(t) - w_j^i(t)] y^i(t-1) u^i(t) \qquad (2.4)$$

where λ is a positive constant determining the rate of learning and σ a positive constant. This rule is derived from the Hebbian rule and expresses that (*1*) the coefficient w_j^i increases toward σ with the coincidence of pre- and postsynaptic activity when the column has been previously active, and (*2*) decreases toward 0 with postsynaptic activity alone in the same condition. In this way, coefficients can be tuned around values that correspond to the most probable input within division D^i when this division has been active.

Adaptive gating. Coefficients $\{Q\}$ and $\{L\}$ involved in gating effects can change according to

$$\begin{cases} \Delta Q^{i}_{jk}(t,t+1) = y^{i}(t-1)[-\lambda u^{k}(t-1) + \mu u^{k}(t-1)u^{j}(t)] \\ \Delta L^{i}_{j}(t,t+1) = y^{i}(t-1)[-\lambda u^{j}(t-1) + \mu u^{j}(t)] \end{cases} \tag{2.5}$$

where λ and μ are parameters. The logic of the modification is that of operant conditioning. When the activation of the division D^i is always followed by the same afferent input in division D^j, the division coefficient L^{i}_{j} increases toward a maximal value, which reflects an unconditional coupling (independent of any other conditions) between the two divisions. On the other hand, when the afferent input occurs only sometimes, it means that another condition is required and may be represented by input in another division, say D^k. If the conjunction of the two inputs in D^j and D^k has an higher probability of being related to the activation of D^i, then the inter-division coefficient Q^{i}_{jk} increases and the incoming information in one of the divisions acts as a gating signal (AND gate) or a gain signal (product) on the other input. The rule defined by Equation 2.5 is an original proposal of this work and will be termed R1 in the following.

Adaptive timing. The control of long-lasting activities can be obtained by modifications of division coefficient according to

$$\begin{cases} \Delta^{i-}_{jk}(t) = u^{k}(t)y^{i}(t-1) \\ \Delta^{i+}_{jk}(t) = \bar{u}^{k}(t)\bar{y}^{i}(t)r(t) \\ \Delta L^{i}_{j}(t,t+1) = e^{j}(t)\{ \sum_{k=1,\, k\neq j}^{N} [-\alpha\Delta^{i-}_{jk}(t) + \beta\Delta^{i+}_{jk}(t)]\} \end{cases} \tag{2.6}$$

where α and β are parameters. Equation 2.6 is coupled with Equation 2.3 and its functioning is explained in **chapter 5**. Basically, Equation 2.6 allow the relation between two temporally non simultaneous inputs and a reinforcement signal to be learned. The rule defined by (2.6) is another original proposal and will be termed R2.

Summary

Principles of cortical organization and computation have been translated into modeling principles. On this basis, models can be constructed formally, and then tested by computer simulations, in order to assess their actual behavior in conditions, which resemble a real environment (**chapters 3**, **4**, and **5**).

4 CORTICAL NETWORK ORGANIZATION AND SENSORY-MOTOR PROGRAMS

Investigations of cortical functions are generally based upon studies of subjects (monkeys, humans) performing sensory-motor tasks. These tasks generally require the integration of processes such as discrimination, recognition, reaching, into a coherent behavior, defined by some internal or external contingencies. A classical example is the delayed-response task (Fig. 2.5). In this task, the monkey is asked to touch a lever indicated by an instruction given for some time before.

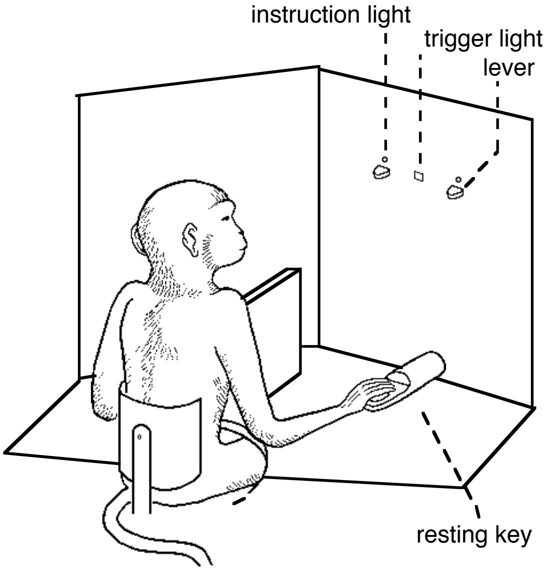

Figure 2.5. An example for the basic form of a spatial delayed response task. A monkey installed in a primate chair faces a panel containing at least two instruction lights mounted directly above two horizontally arranged levers and a trigger light of different color and form. While the animal sits with its arm relaxed on a resting key, one of the two instruction lights comes up for a short period, e.g. 1s. A few seconds after the instruction is extinguished, the trigger light comes up and the animal reaches and touches the lever indicated by the instruction and receives a drop of liquid as reward.

To perform this task, at least three fundamental processes must be carried out by the cerebral cortex: (*i*) in order to recognize the target object, the cortex has to transform the pattern of excitation on the retina from a retinotopic coordinate system to a coordinate system centered on the object itself; (*ii*) in order to bring the hand to the desired position in space, the cortex must transform the visual information related to the target location (relative to the hand) into an appropriate motor command of the reaching hand; (*iii*) in order to control the temporal order of behavioral actions, the cortical circuits must contribute to processes such as short-term memory, expectation of forthcoming events, and preparation for response.

The functional cortical networks subserving such perceptual and motor transformations can be described using the principles of cortical organization and operation exposed in the previous section (Burnod 1988; Burnod et al. 1991). Basically, these transformation can be defined by the nature of representations used, the nature of neuronal processing, and the repertory of adaptive properties (Table 2.1). Following this principle, we give in this section a general view of cortical networks involved in *visual integration*, *motor performance*, and *temporal integration of behavior*. This presentation introduces the following **chapters** (**3**, **4**, **5**).

Table 2.1. Characteristics of the models.

	chapter 3		**chapter 4**		**chapter 5**
	Perceptual grouping	Invariant recognition	Coordinate transformation	Context/ reinforcement	Temporal sequences
topographic maps	x	x	x	x	
non topographic maps		x			x
population code	x	x	x	x	
feedforward/lateral	x				
feedforward/feedback		x			
feedforward/feedforward			x	x	
multiple interactions					x
tuning	x	x	x		
gating	x (3.1)	x (3.2)	x (4.2)	x (4.6)	x (5.1)
timing					x (5.2)
adaptive tuning			x (4.3)		
adaptive gating		x (3.3)	x (4.4)	x (4.8)	
adaptive timing					x (5.3)

Notes. References to equations are in parenthesis.

Cortical network architecture: Circular representation

Cortical networks involved in *visual integration*, *motor performance*, and *temporal integration of behavior* can be described by a circular representation (Burnod 1988; Morel and Bullier 1990; Young 1992). Figure 2.6 provides a simplified view of the circular network, with four input-output poles and reference frames: (*1*) External sensory inputs such as visual inputs in a retinal centered reference frame; (*2*) Sensory interoceptive inputs and motor commands: for example, this input represents the position of the arm in body centered reference frame; (*3*) Information relative to the objects, stored in an object centered reference frame, with an input specifying their significance; (*4*) Internal coding of sensory-motor programs in a time related reference frame.

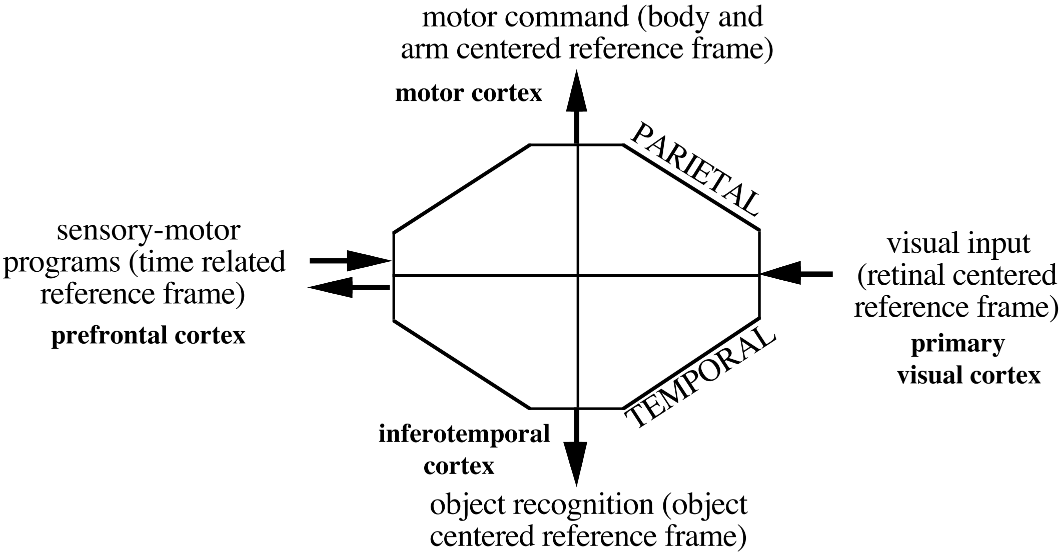

Figure 2.6. Circular multilayered network for sensory-motor transformations with reference frames and corresponding cortical maps.

From retinal to object-centered reference frame

Two important transformations are performed by the visual system: (*1*) a low level transformation resulting in the perceptual grouping of textured surfaces; (*2*) a higher level transformation resulting in invariant recognition of objects. Neurobiological data give some insights in the nature of these transformations. Low-level processing is probably performed at early stages of the visual system. Responses to textured stimuli have been found in the primary visual cortex (Knierim and Van Essen 1992). Visual information is then processed at least in two parallel streams (Fig. 2.7), the dorsal stream to the parietal lobe for target location (the WHERE pathway) and the ventral stream to temporal lobe for target identification (the WHAT pathway) (Ungerleider and Mishkin 1982). The more anterior portions of the temporal lobe tend to be critical for storing prototypes of visual objects in a form that is accessible even with large variations in texture, position, orientation, size. The posterior regions are more concerned with addressing transforms of the retinal images to the stored prototypes (Weizkrantz and Saunders 1984) and receive projections from the parietal stream which can be involved in geometrical transformations necessary to match the incoming signal with the stored prototypes. The main constraint of visual processing is to capture the diversity in the flow of visual information and to form invariant internal representations.

Perceptual grouping of textured surfaces can be obtained in two processing steps combining *tuning* and *gating* (Anton 1992; Table 2.1, **chapter 3**): *feedforward* retinotopically organized primary indices and *lateral* secondary indices related to feature extraction (*tuning*) are combined through *gating*. Following a relaxation process and without any adaptation, the neurons, which perform the same filtering and which have their receptive fields in a textured surface, tend to have the same response. Accordingly, each population of filtering cells becomes sensitive to uniform surfaces.

The architecture of the model for invariant recognition is a double-branched multilayered network (Fig. 2.7), with one input (in retinal coordinates) and two outputs: form identification in the temporal branch and form location in the parietal branch (Otto et al. 1992; **chapter 3**). After learning, the temporal branch shows significant size-invariance and shift-invariance which are both related to the anatomical convergence pattern of the network. The parietal branch computes in parallel both direction and distance of the target from the center of the retina. When the temporal branch fails to directly recognize the pattern, it can trigger the parietal branch output which drive an eye movement which reset the eccentric pattern to the central zone where it is then successfully recognized. The two processing streams interact and the processing units in the temporal branch can combine: (*i*) feedforward information from the retina; (*ii*) positional information from the parietal branch; (*iii*) feedback information which indicates success or failure of the recognition process. The main components of this model are (Table 2.1): *feedforward* retinotopically organized primary indices and secondary indices related to feature extraction (*tuning*), *feedback* nonretinotopically organized indices related to prototype coding, *adaptive gating* between *feedforward* and *feedback* flows of information, semi-distributed population code.

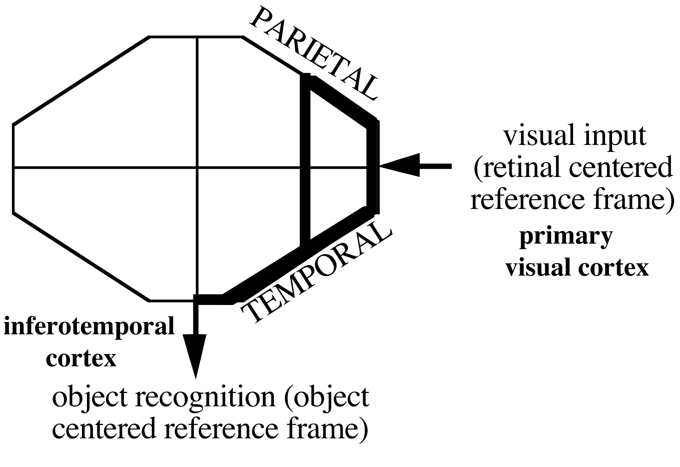

Figure 2.7. Cortical circuit for visual transformations (perceptual grouping, object recognition).

From retinal to arm-centered reference frame

Following integration through the visual system, visual information arising from retinal stimulation can be used to guide visual reaching movement toward targets in space. Cortical areas involved in the control of reaching behavior in the primate are the primary motor cortex (M1), the premotor cortex (PM), the supplementary motor area (SMA), and the posterior parietal cortex areas 5 and 7 (Fig. 2.8; review in Johnson 1992). Studies on neuronal activity within the motor cortex (Georgopoulos et al. 1982) have shown that the activity of individual arm-related neurons is broadly tuned around a preferred direction of movement in 3D space. Recent data demonstrate that these cells preferred directions rotate with the initial position of the arm and the rotation of the population of preferred directions predicts the rotation of the arm in space (Caminiti et al. 1991). The population vector, which sums all the cell preferred directions weighted by their own activities, always predicts the direction of movement even if the initial position of the arm is changed. The control of an output map organized around a continuous parameter puts strong constraints on neuronal processing underlying computation of the direction of the movement.

Visual reaching can be modeled by a neural network, which computes the appropriate motor command corresponding to the ballistic phase of the movement (Burnod et al. 1992; **chapter 4**). In this network, processing units combine: (*i*) Feedforward visual information on the desired trajectory; (*ii*) Kinesthetic information concerning the orientation of the arm in space and (*iii*) Feedback information from areas which command the effective movement (efferent copy of the motor command). The input-output operations which are learned by these units during spontaneous movements can be approximated by a bilinear combination which is sufficient to predict the cortical activity before reaching both at the level of single neurons and at the level of the whole neuronal population. In this model, the neural circuits converging toward a single neuron in the motor cortex learn to predict the vectorial effect of the synergistic contraction of muscles on the hand trajectory by generalizing the result of few trials in 2D subspaces, but not in the whole 3D space. The population of cortical neurons can compute the appropriate command in the whole 3D space thanks to the fact that the distribution of cell preferred directions is uniform in this population (Caminiti et al. 1991). Critical features of this model are summarized in Table 2.1: mapping of input and output parameters, *adaptive tuning* and *adaptive gating* in two *feedforward* information flows, population code.

A movement can be driven by a target to reach, but also by a goal corresponding to the delivery of a reward (context/reinforcement behavior). Burnod et al. (1982) have described the relationships between neuronal activity of movement-related cells in the motor cortex and movement changed with the performance rate during a context/reinforcement behavior. They found the neuronal activity became more closely time-locked with the onset of the movement, as the performance improved. This modification reflects an increase in the conditional probability of discharge of neurons in relation to the beginning of the movement. Reward-related cells also change their activity with learning in such a way that, after learning, termination of activity strongly predicts a new movement.

A network model has been proposed which illustrates the neural computation underlying acquisition of context/reinforcement behavior (Guigon and Burnod 1993; **chapter 4**). The network is made of units, which are broadly tuned around a preferred direction of movement. Each unit combines two flows of information: one carries a contextual signal and the other a drive/reinforcement signal. The combination results in a movement determined by the population activity over all the units of the network. The model shows that efficient control of the movement is obtained through acquisition of conditional relations between the two flows of information. Table 2.1 indicates the main components of this model: mapping of output parameter, *adaptive gating* in two *feedforward* information flows, population code.

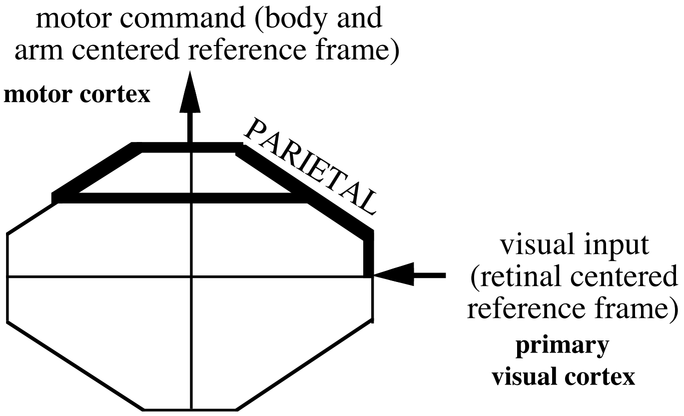

Figure 2.8. Cortical circuit for motor performance (visual reaching, context/reinforcement behavior).

Time integration in prefrontal circuits

Complex sensory-motor sequences are learned and produced by a cortical network (Fig. 2.9) which relates temporal, parietal and motor areas with the prefrontal cortex (Goldman-Rakic 1988). Neuronal activities recorded in PFC during the delayed tasks in behaving monkeys appear to be a striking correlate of behavior (Fuster 1973, 1988). For example, neurophysiological studies have demonstrated sustained neuronal activity during the delay between an instruction cue and the final permission to use the information contained therein for a spatial reaching movement (Fuster and Alexander 1971; Kubota and Niki 1971). The delay related activity may reflect short-term mnemonic aspects related to the instruction cue, the expectation of forthcoming signals and the preparation of the behavioral reaction.

A model of prefrontal circuits has been proposed (Guigon et al. 1993; **chapter 5**). The model indicates that the main characteristics of prefrontal neuronal activities, both during acquisition and execution of a task by behaving monkey, can be explained as the product of two factors: a learning rule based on the control of sustained activities, which is proposed as the main property of prefrontal neuronal circuits, and a specific step-by-step conditioning program. A simulated neural network illustrates the abilities of the model: (*i*) to learn, via a natural step-by-step training protocol, the paradigmatic task (delayed response) used for testing prefrontal neurons in primates, (*ii*) to display the same categories of neuronal activities, and (*iii*) to predict how they change during learning. In agreement with experimental data, two main types of activity contribute to the adaptive properties of the network. The first is transient activity time-locked to events of the task and its profile remains constant during successive training stages. The second is sustained activity that undergoes non-monotonic changes with changes in reward contingency that occur during the transition between stages. The characteristics of this model are (Table 2.1): non-topographical representations, *gating* and *adaptive timing* in multiple information flows.

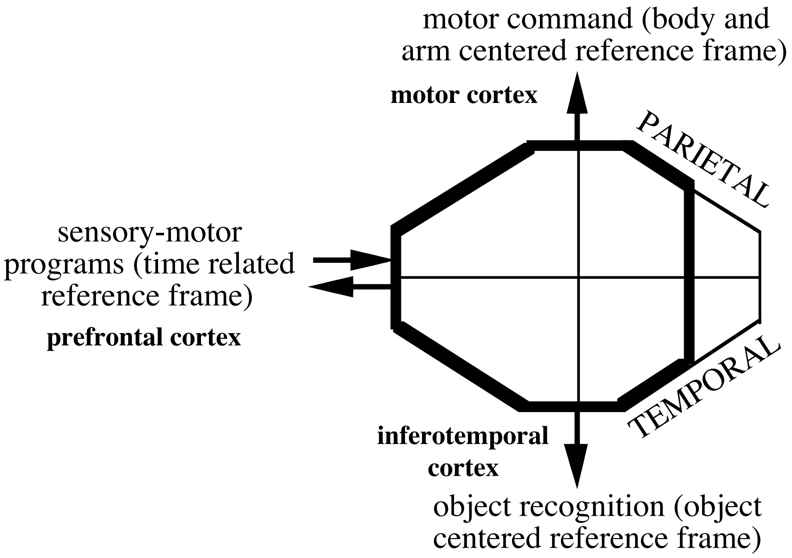

Figure 2.9. Cortical circuit for sensory-motor programs. Higher-level visual and motor transformations are integrated in programs.

5 DISCUSSION

Most neural models of brain functions have been constructed using some or other principles of cortical organization. However, in many cases, biological principles were mixed with "alien" principles and models became complex hybrid systems, which give rise to strong criticism (see **chapter 1**). Ballard (1986) has addressed more directly the computational properties of cortical circuits, but made no reference to possible adaptive properties. Global consideration of the architectural and processing characteristics of the cerebral cortex has been worked out by Burnod (1988), Alexandre (1990), Guyot (1990). The novelty of the present work is to propose a set of cortical mechanisms, which are sufficient to solve problems of *visual integration*, *motor performance*, and *temporal organization of behavior* (see following chapters for details). The main interest relies in the fact the same set of principles underlies the expression of rather different problems, which have been generally solved using specific principles.

The modeling principles encompass several levels of brain organization, including synapses, neurons, networks, and maps. It allows multiple the constraints in the construction of models of cortical functions to be taken into account. A central, original component of the framework is a multicellular processing unit (cortical column), reflecting the layered organization of the cortex and the differential laminar distribution of cell types. The architecture of unit allows various processing and learning modes to be embed as a basis for regional variations. Furthermore, the layered structure of the unit facilitates the construction of neuronal networks with various patterns of connectivity.

The unit implements two levels of processing (feature extraction and vertical integration). In this way, there is a dissociation between the specific operation performed by cortical circuits and the nature of data on which they act. It means that processing is independent of particular input codes since feature extraction provides an unique format, whatever the modalities. This unit resembles the sigma-pi unit (**chapter 1**). However, it is different for the following reasons: (*i*) The cortical unit has several independent input pathways (divisions) and several output pathways; (*ii*) Nonlinear interactions are not performed directly on the inputs, but only after a filtering process. The computational interest of sigma-pi units is to represent multidimensional receptive fields or higher-order feature detectors. However, there is no easy way to set the coefficients of the unit. Durbin and Rumelhart (1989) have proposed a method to train networks of sigma-pi units, but the method was based on the backpropagation algorithm.

Part II

Models of cortical functions

CHAPTER 3

From Retinal to Object-centered Reference Frame

Contents

Summary

This chapter presents two models, which illustrate cortical computation in the visual system. The goal of both models is to extract information from a retinal image. In the first model, a perceptual grouping of textured surfaces is obtained by filtering and multiplicative combinations between *feedforward* retinotopically organized primary indices and *lateral* secondary indices related to feature extraction. The second model shows that invariant pattern recognition can result from filtering and multiplicative combinations between *feedforward* retinotopically organized indices and *feedback* secondary indices related to semantic representations. These models illustrate the fact that similar cortical mechanisms may be involved in different functions of the visual system.

1 INTRODUCTION

Visual processing aims at transforming the retinal image into successive representational stages (representation of local properties of the image, representation of properties of visible surfaces in a viewer-centered coordinate, object-centered representation of the shape; Marr 1982). Many models of the visual system have proposed many solutions to explain various aspects of its function (Bienenstock et al. 1982; Frohn et al. 1987; Fukushima 1988; Lehky and Sejnowski 1988). The goal of this chapter is to show that the same set of computational and organizational properties of the visual cortex is likely to contribute to the solution of different visual problems at different representational stages.

The visual system performs two main transformations: (*1*) a low level transformation resulting in the perceptual grouping of textured surfaces; (*2*) a higher level transformation resulting in invariant recognition of objects. Following the principles exposed in the previous chapter (**chapter 2**), models have been constructed taking into account issues concerning representation of information, architecture of cortical networks, cortical processing and adaptive properties.

2 PERCEPTUAL GROUPING

Visual mechanisms have been studied using mainly simple stimuli such as spots and bars (Hubel and Wiesel 1965). However, visual stimuli in the natural world have complex properties such as texture. A texture is made of a great number of interdigitated patterns, the form and arrangement of which characterize the texture. Perception and discrimination of textures should provide an important contribution to object discrimination and recognition. For instance, it allows the borders between objects to be recognized, which are similar for other parameters. The present model developed by Anton (1992) investigates the possible neurobiological basis of texture discrimination.

The main characteristics of this model are: *feedforward* retinotopically organized primary indices, *lateral* secondary indices related to feature extraction (*tuning*), *gating* between *feedforward* and *lateral* flows of information.

Description of the model

Anton (1992) has proposed a model of texture discrimination based on computational principles of cortical processing (see **chapter 2**). A major hypothesis of this model is that texture information is processed at early stages of visual processing. The model has two processing steps:

Tuning. The retinal image is transformed in 10 new images as a result of 10 filtering operations. If retinal coordinates are primary indices, the 10 filtering outputs $V_{\alpha\beta} = (A^1_{\alpha\beta}, .., A^{10}_{\alpha\beta})$ at a point (α,β) can be considered as secondary indices (Fig. 3.1).

Gating. Activity of filtering cells are modulated by neighboring cells performing similar filtering (same secondary indice). When considering the 4 neighboring cells, the output activity $y^i_{\alpha\beta}$ of the neuron at position (α,β) with secondary indice i ($1 \leq i \leq 10$) at time t is given by

$$y^{i}_{\alpha\beta}(t) = \lambda y^{i}_{\alpha\beta}(t-1) + \sum_{\alpha'\beta'} \varphi(V_{\alpha\beta}, V_{\alpha'\beta'}) y^{i}_{\alpha'\beta'}(t-1) \qquad (3.1)$$

where $\{y^{i}_{\alpha'\beta'}\}_{\alpha'\beta'}$ are the inputs from neighboring neurons for the same secondary indice i, λ a parameter, and φ a coupling function between two populations of filtering cells $V_{\alpha\beta}$ and $V_{\alpha'\beta'}$. Equation 3.1 expressed a *gating* effect of lateral interactions related to the coupling between secondary indices, on the feedforward flow of information derived from filtering processes.

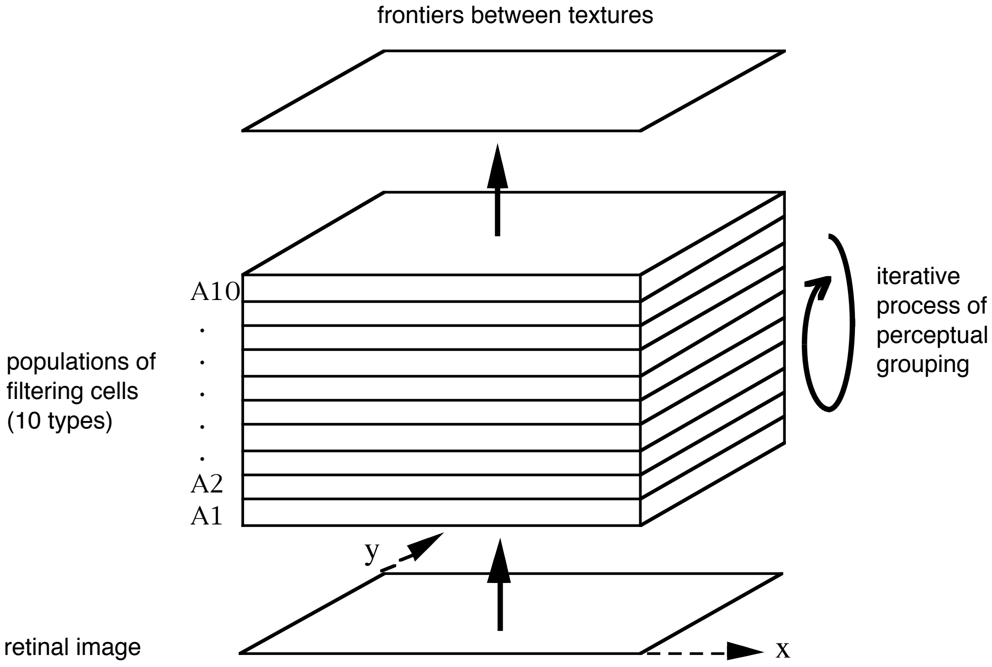

Figure 3.1. Architecture of network for perceptual grouping of textured surfaces (From Anton 1992).

Behavior of the model

Initially, filtering cells are inactive. When a retinal image is presented, neuronal responses are defined by receptive field properties. Equation 3.1 defines an iterative process which gives the temporal evolution of neuronal responses. Within a few iterations, neurons which perform the same filtering and which have their receptive fields in a textured surface tend to have the same response. Accordingly, each population of filtering cells becomes sensitive to uniform surfaces.

Choosing the coupling function φ defines three types of perceptual grouping (Anton 1992). The model shows that the coupling between primary indices (retinotopic proximity) alone ($\varphi = \text{constant}$) produces fuzzy frontiers between textures (*non differential grouping*). On the other hand, coupling between secondary indices greatly enhance the discriminating capacities of the network (*similarity* and *similarity/homogeneity grouping*).

Discussion

This model illustrates a mechanism of local columnar interactions in a topographical map which produces perceptual grouping of textured surfaces. Emergent properties of the network are strongly related to the underlying organization since performance depends on (*i*) filtering of retinotopically organized incoming information (*tuning*); (*ii*) intercolumnar interactions: primary indices are connected following neighboring relationships, and (*iii*) intracolumnar interactions: activities related to neighboring primary and secondary indices are combined multiplicatively (*gating*; Equation 3.1).

Hence the model demonstrates the adequation between the organization of the primary visual cortex (Hubel and Wiesel 1977), a simple form of columnar processing based on local correlations (Gray and Singer 1989) and the texture discrimination (Knierim and Van Essen 1992).

3 INVARIANT RECOGNITION

A particular object can correspond to an infinite number of possible retinal images. A bottle, for example, can be seen at different distances, in different positions and with different shapes and colors. However, we can always recognize it. This is what we call invariant visual recognition (IVR). This property is of very great interest for both neuroscientists and engineers. From a neurobiological point of view, IVR raises the question of what kinds of processes operate on the retinal image to allow the previously stored “internal representation(s)” necessary for recognition to be retrieved. From a traditional engineering point of view, it would be extremely useful to design computers and robots that would be able to recognize objects in naturally varying perspectives and contexts.

In this section, we describe a neural network which models specific biological properties which could be responsible for the invariant visual recognition capabilities of the brain. We first expose relevant biological data and previous modeling approaches. Then we turn to the presentation of the model. Computer simulations illustrate the properties of the model. A more detailed description of this model can be found in Otto et al. (1992).

The main components of this model are: *feedforward* retinotopically organized primary indices and secondary indices related to feature extraction (*tuning*), *feedback* nonretinotopically organized indices related to prototype coding, *adaptive gating* between *feedforward* and *feedback* flows of information, semi-distributed population code.

References

1. The primary visual cortex (V1) is the source of two major cortical pathways (Ungerleider and Mishkin 1982). The ventral pathway coursing through striate (V1), extrastriate (V2, V4), and inferotemporal (TEO, TEp, TEa) cortex, is involved in 3D form identification, surface properties, color extraction, and, in a more general way, in object discrimination and recognition. The dorsal pathway leads to the posterior parietal cortex. It is involved in motion detection, spatial location, three-dimensional relationships (visuomotor performance, visuospatial perception, spatial attention).

2. VENTRAL PATHWAY. The physical properties of a visual object (shape, color, size, texture) are analyzed in the successive processing steps of the dorsolateral system. Integration proceeds through foveal receptive fields of increasing size (Maunsell and Newsome 1987). Cortical neurons exhibit differential selective properties along the processing pathway. Neurons are selective: (*i*) to simple features like oriented edges, color, direction of movement of moving patterns in the first steps; (*ii*) to complex patterns in the highest steps (and not to their component features; Miyashita 1990); and (*iii*) to both in intermediate associative levels (Tanaka et al. 1991). No clear visuotopic organization is found in area TE, at the cortical extremity of this stream (Desimone and Gross 1979), and neuronal responses become invariant with respect to stimulus size, orientation or color (Miyashita 1990).

Functionally the inferotemporal cortex can be divided in two distinct areas: (*i*) the anterior portion (area TE) involved in mnemonic functions which is hypothesized not only to synthesize the analyzed attributes into a unique configuration, but also to work as the storehouse for central representations of the objects (Miyashita 1990) and (*ii*) the posterior portion (area TEO) which seems to be responsible for linking the object reference frame (in TE) to the retinal reference frame (in striate and extrastriate areas; Weiskrantz 1990). Lesions in the lower part of IT (TE) lead to lasting deficits in the learning of new visual discriminations and the recollection of previously learned memories (Dean 1976) while lesions of intermediate temporal cortex (TEO) impair the visual discrimination of objects per se whether the discriminanda differ in color, orientation, brightness, pattern or shape (Ungerleider and Mishkin 1982; Mishkin et al. 1983).

3. DORSAL PATHWAY. The dorsal pathway can be subdivided into two streams: (*i*) a dorsomedial stream involving the parieto-occipital visual area (PO) and area PG (or 7a) in the inferior parietal lobule (IPL), and (*ii*) a dorsolateral stream involving areas MT and MST as well as the lateral intraparietal areas. Neurophysiological explorations of the parietal areas (Mountcastle et al. 1975) have shown that they process complementary aspects of space. The dorsolateral pathway processes visual motion (MT), with more and more integrated aspects (MST). The dorsomedial pathway seems to be involved in coding the location of visual stimuli for spatial orientation, spatial perception (Lamotte and Acuna 1978) and visual guidance of hand movements (Ungerleider and Mishkin 1984; Weiskrantz and Saunders 1984). For example, in area 7a, neurons can combine information on the retinal location of visual stimuli and on the position of the eyes in the orbits possibly to locate visual targets in a head-centered space (Andersen and Mountcastle 1983; Andersen et al. 1985). The two subsystems can contribute to the control of eye movements: MST neurons for smooth pursuit, 7a neurons for fixation and area LIP for programming saccadic eye movements (neurons can hold in short-term memory the metrics of planned eye movements in motor coordinates) (Hyvarinen 1981; Andersen et al. 1985).

4. Computer-based studies of pattern recognition (particularly alphanumeric patterns) has focused on methods such as: (*1*) Template matching: the simplest way to recognize patterns would be to match each incoming pattern against the set of stored templates. Not only does this method need a previous “cleaning up” of the image to normalize the patterns in size, angle ..., but also it is not satisfactory for generalization processes; (*2*) Feature analysis: it would be more efficient to discriminate patterns by dealing with the combination of local features which can distinguish one from another. But descriptions of patterns in terms of a set of mini-templates, such as a Pandemonium system adapted from Selfridge (1958), will fail on capturing overall structural relations. It will confuse patterns built up from common local features, but globally organized in a different spatial arrangement (like a “T” and a “L”); (*3*) A more flexible representation of patterns is provided in humans by language: a set of symbolic propositions can describe the components of a pattern, making explicit the structural arrangements of these primitives. This symbolic approach has often been attempted in Artificial Intelligence, but the main problem lies in the necessity for human to make an a priori cognitive description of what is pertinent to recognize a particular pattern and what is not.

More recently, neural network approaches have tried to get rid of these top-down inferences. It is the network itself which provides, by learning from examples, the adequate configuration of local primitives to discriminate each pattern from the others. Various global properties such as parallel data processing, noise suppression and associative recall can be used to improve performance. However, Invariant Visual Recognition is typically not an emergent property of these networks and thus particular models have been proposed to improve Invariant Visual capabilities: combination of AND/OR functions with increasing receptive field size (Fukushima 1988), graph matching with short-term plasticity (Bienenstock and Von der Malsburg 1987), networks with Sigma-Pi units allowing autocorrelations (Glünder 1987).

5. Mathematical studies have stressed the interesting properties of distributed representations of information as synaptic weight in a group of neurons (Kohonen 1988). Information about visual images can be represented by the distribution of active neurons in a form of associative memory (Rolls 1990). Associative memories have nice computational properties such as completion of novel patterns, content addressability, resistance to noise and degradation, and generalization.

Description of the model

Network architecture. The architecture is a Y-like multi-layered network organized in six maps along four sequential processing stages which model the main functional steps of the actual cortical areas (Fig. 3.2). The two low-level stages are learning-independent and the two high-level stages are learning dependent: (*i*) Primary areas perform low-level processing, such as elementary feature extraction, on the retinal information; (*ii*) Secondary areas perform more elaborated processing using larger receptive fields, but still with a retinal reference frame; (*iii*) Associative intermediate areas relate the resulting pattern of activity with the (*iv*) highest-level steps which store the learned prototypes.

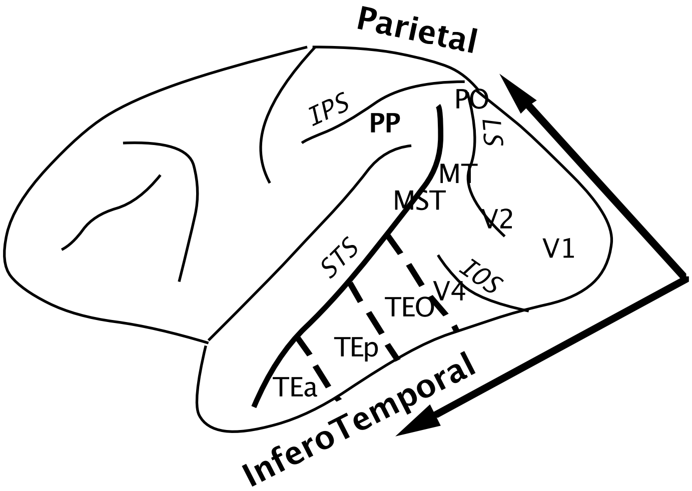

Figure 3.2. Visual areas of the primate. Visual information is first processed by V1 and V2 and then by two major pathways: a ventral pathway toward the inferotemporal lobe rather involved in object recognition and the dorsal pathway toward the parietal lobe rather involved in localization and motion detection. The figure shows some important functional steps in each stream: V4 and IT subdivisions (TEO, TEp, TEa) in the ventral pathway, PO and PP (including 7a and LIP) in the dorso-medial pathway and MT and MST in the dorso-lateral pathway (From Otto et al. 1992).

All the units in a given map perform the same type of local processing on the afferent information flow. They are classified according to three kinds of indice (which correspond to the dimensions of the processing maps in Fig. 3.3: (*1*) topographic (*X*,*Y*) (*2*) local indice *l* and (*3*) global indice *g*:

- The topographic indice defines the ordered relations between the successive maps: two neighboring units in a given map have two neighboring receptive fields in the afferent map. This topography becomes less precise along the processing hierarchy. This index corresponds to the two planar coordinates (*X*,*Y*) labelling the relative location of each unit in its respective map and consequently the location of its retinal receptive field.

- The local feedforward indice (*l*) labels the specific filtering process that each unit performs on the sensory information. For each topographic indice (*X*,*Y*), four units ($l = 4$) of the Primary Sensory Area (PSA) detect four orientations of edges modeling the tuning properties of the cortical columns in striate and extrastriate cortices: horizontal (H), vertical (V) and the two diagonals (D1,D2). Units of the Secondary Sensory Area (SSA) detect six combinations of orientations ($l = 6$) with larger receptive fields: (HH), (VV), (D1D1), (D2D2), (HV) and (D1D2). Such extraction evokes simplified models of complex and hypercomplex cells found in the striate and extrastriate cortices. This organization with 3 indices is maintained in the Associative areas.

- The global feedback index *g*, found only in the Associative maps tAA and pAA, characterizes units receiving feedback links from groups coding a given prototype *g* in the Semantic maps. These feedback links will allow the association between a configuration of local features (*l*, through feedforward links) and a given prototype (*g*, through feedback links) within the associative map to be learned. After learning, a pattern presented on the retina will activate a configuration of local features *l* and this ascending information will be matched with the stored internal representations.

- The first three dimensions (*X*, *Y*, *l*) are maintained in groups of neurons coding for different prototypes (*g*) in the Semantic maps (semi-distributed coding), but with still larger receptive field sizes (less precision on *X* and *Y*). In these maps, a pattern (for example, a particular view of a given prototype) is thus not encoded in a single unit, but is encoded by a population, i.e. is reflected in the pattern of activity across this population of units coding for different relative positions, orientations and other characteristics of the same prototype. The summed population activity will be the same for various views of a prototype, even if at the level of the single cells (or automata) the pattern of activation can be different and reflects the particular characteristics of each view. Recognition of a prototype corresponds to a strong population activity in the corresponding cell cluster, and if several groups are simultaneously active, the discrimination is made through a winner-take-all mechanism.

The response in the WHERE branch is also the result of a population code. The units vote for a given position (upper left / upper right / lower left / lower right) with a strength proportional to their activation. Since they model populations of neurons in the parietal stream which project to structures commanding eye movements, a vectorial sum of the activities can be interpreted as a shift command to reset a pattern on the fovea.

Processing units, neural processing, and learning rule. The processing unit is a column-like units with 3 divisions, corresponding to the classical division of vertical dimension of the cortex: supragranular (layers II and III), granular (layer IV), and infragranular (layer V and VI) divisions. The unit combines three types of inputs:

- Feedforward (or bottom-up) inputs, in the intermediate division (modeling cortical granular layer IV), from previous stage units, providing sensory information from the outside world that has already been subject to selective filtering through previous processing steps;

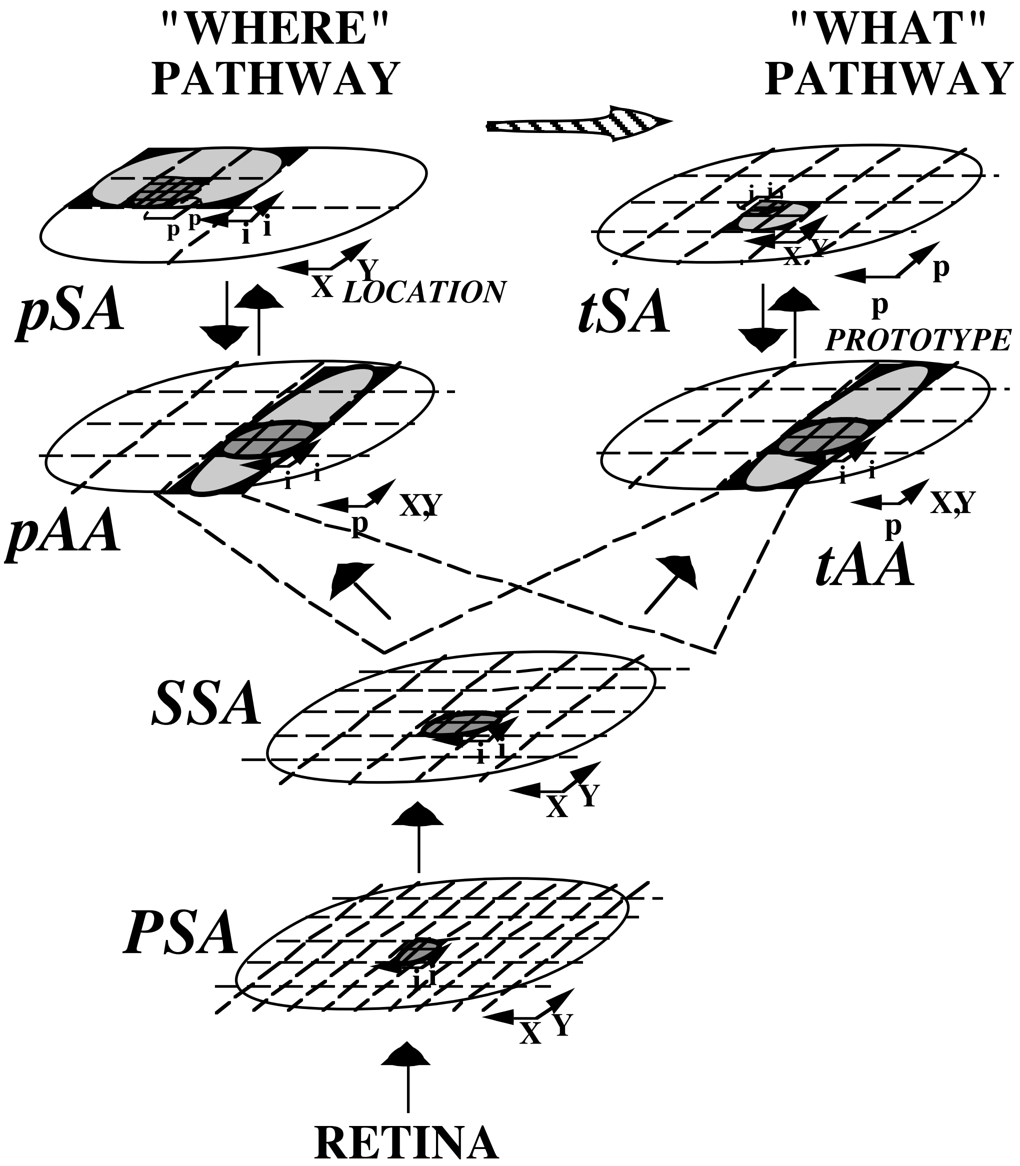

Figure 3.3. Architecture for invariant pattern recognition. The global architecture of the network is Y-like shaped with a WHAT pathway performing pattern recognition and a WHERE pathway encoding the location of the pattern (From Otto et al. 1992).

- Feedback inputs from higher stage units (modeling top-down effects), in the upper division, which control the ascending flow of information by a gating or an inhibitory effect which is determined by both previous learning and the internal state of expectation of the system;

- Lateral inputs provided by neighboring units, in the upper division, which can become either excitatory or inhibitory, depending upon the differential activities of the units, modeling the intracortical balance between columns.

The processing unit produces two kinds of outputs:

- The upper division (modeling the supragranular cortical layers) makes local connections with surrounding units of the same map and long-range connections to other maps;

- The lower division (infragranular cortical layers) projects outside the network to other structures involved in oculo-motor commands or generates the feedback connections for selective control of the incoming information provided by lower maps.

Interactions between feedforward and feedback connections through reciprocal connections between the Associative map and the Semantic map in both WHAT and WHERE pathways (i.e. between tAA and tSA and between pAA and pSA), are used for learning. Connections between RETINA and PSA, between PSA and SSA, between SSA and the two Associative Areas (tAA and pAA) involve only feedforward connections and are thus not influenced by learning. Local connections are not used in this model.

Each unit in each area combines information entering in its divisions i $(1 \leq i \leq 3)$ according to

$$u^i(t) = F\Big[\sum_{j=1}^{n_i} w_j^i(t)\; x_j^i(t) \Big]$$

and

$$y^i(t) = F\Big[\sum_{j=1}^{N} \sum_{k=j+1}^{N} Q_{jk}^i(t)\; u^j(t)\; u^k(t) + \sum_{j=1}^{N} L_j^i(t)\; u^j(t) \Big] \qquad (3.2)$$

This two-step transformation has been described in **chapter 2** (Equations 2.1 and 2.2).

Initially, receptive field weights are pretuned as described in the previous paragraph. All linear interaction coefficients are equal to 1, excepted the feedforward coefficients in associative maps (tAA and pAA), which are chosen randomly and vary according to

$$\begin{cases} \Delta Q_{jk}^i(t,t+1) = y^i(t-1)[-\lambda u^k(t-1) + \mu u^k(t-1) u^j(t)] \\ \Delta L_j^i(t,t+1) = y^i(t-1)[-\lambda u^j(t-1) + \mu u^j(t)] \end{cases} \qquad (3.3)$$

where λ and μ are parameters. This rule expresses that the feedforward coefficient would (*i*) increase when a feedforward output is followed by a feedback input; (*ii*) decrease when a feedforward output is not followed by a feedback input. Practically, it means that associative units will change their transmission to the semantic maps with an increase when a positive association occurs (feedforward activation followed by a feedback input), a decrease when a negative association occurs (no feedforward activation followed by a feedback input).

Behavior of the model

Training set. The learning corpus is constituted of a set of 28 binary patterns digitized in a 12x12 grid (the 26 capital letters of the alphabet plus two geometrical figures: triangle and diamond). During the learning session, a given pattern is presented once on the central part of the retina. At the same time, all the units in both Semantic Areas are inactive excepted those corresponding to the adequate prototype (uniform population activation over all the local indices l of the prototype g) and its location (uniform activation corresponding to a centered position), which are forced at an active state. Information propagates in the whole network according to the connectivity and the functional rules both in the bottom-up direction (through *feedforward* connections) from the retina to the two associative areas and in the top-down direction (through *feedback* connections) from Semantic Areas down to Associative Areas. At the level of the Associative Areas, the two flows interact and build up by learning the excitatory or inhibitory learning coefficients which correspond to the internal representations of the external pattern. In accordance with the differences in the receptive field size between the two branches of the network, two schemes of internal representations (Fig. 3.4) are obtained at the end of the learning session:

- in the Temporal Associative Area (tAA), the model has associated each prototype with a set of local features with their relative spatial arrangement. This maintained configuration of local features will allow patterns to be differentiated during the recognition session;

- in the Parietal Associative Area (pAA), although the local features of each pattern have been detected as well, their relative positions have been mixed by wider receptive fields: the local features have been spread and thus learned everywhere in the Associative Map. Ambiguous patterns built up with the same local features, but in a different spatial configuration (like a square and the letter 'H') will thus be confused. However, they will always be localized, whatever their position on the retina.

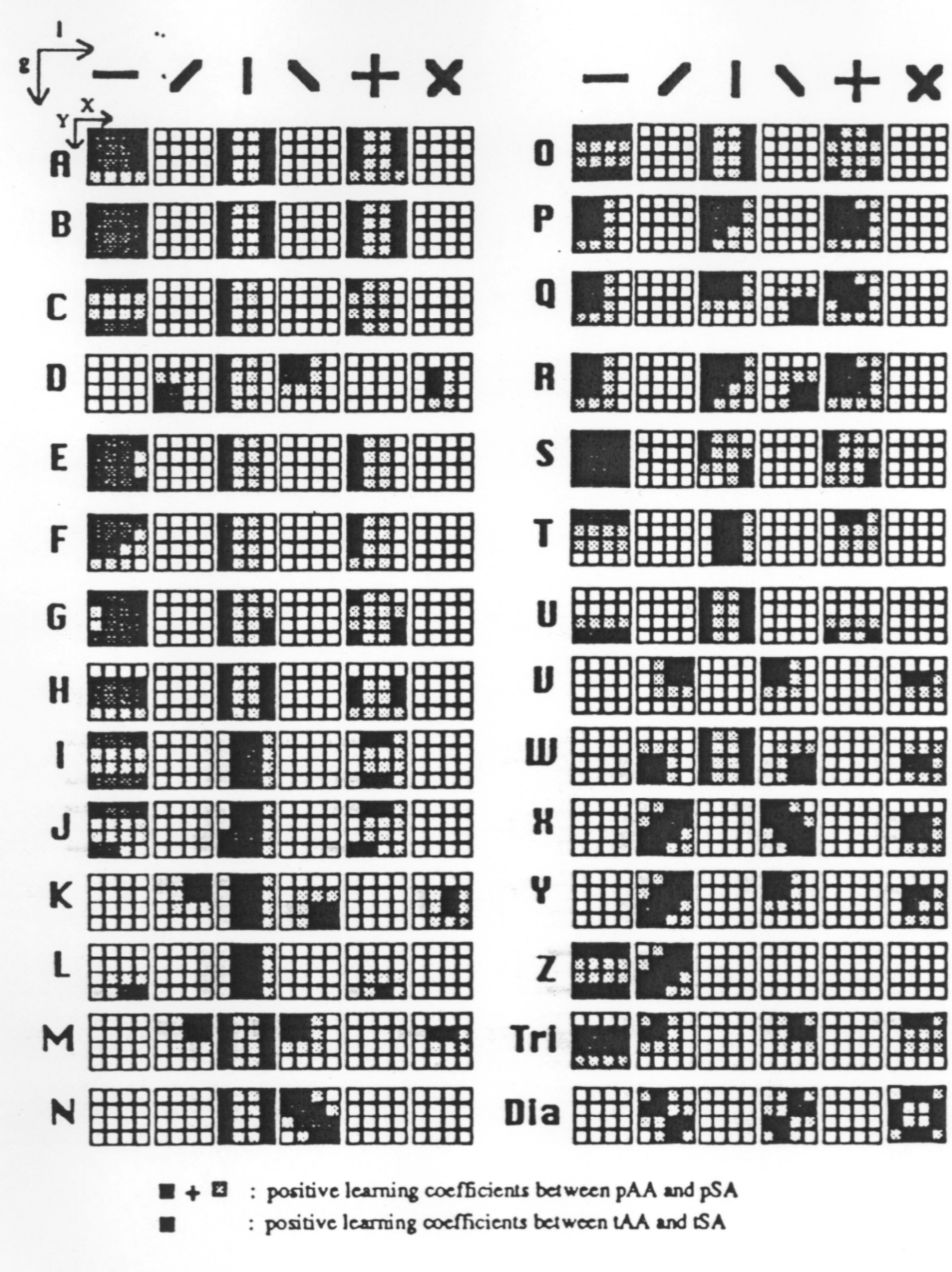

Figure 3.4. Learning coefficients in temporal and parietal associative areas. This figure compares the two sets of learning coefficients stored in the feedback connections from the Semantic areas down to the corresponding Associative ones: they store two "internal representations" (represented within the same map: dark squares only for the temporal coefficients and dark squares plus grey ones for the parietal ones) of the 28 learned prototypes. Each prototype (p) is coded in a cluster of 4(X)x4(Y)x6(i) processing units (semi-distributed coding, with 6 blocks of 16 units for 6 features HH, D1D1, VV, D2D2, HV, D1D2 in 16 positions). Black squares signal for both (i) the basic features componing each learned prototype and their topographical location (X,Y). Notice that an adequate set of features is extracted in both the WHAT and WHERE pathways, but their relative positions (spatial configuration) is maintained only in the Temporal Associative map (From Otto et al. 1992).

Size invariance. During the recognition session, the network reaches its stable state in one time step and gives a response in the two Semantic Areas. Figure 3.5 shows that the model has a recognition rate of 100% when the patterns are presented in the same conditions as in the learning set (size 12, at the center). Figure 3.5 also shows that, when the size is decreased by 25% (from size 13 down to size 9), the network also responds with a very satisfactory rate (superior to 70%) for varying sizes. Other investigations using smaller sizes for the learning set show that the recognition rates for patterns with increasing or decreasing sizes are roughly symmetrical with respect to the learned one. Thus moderate size invariant properties are obtained in the temporal branch.

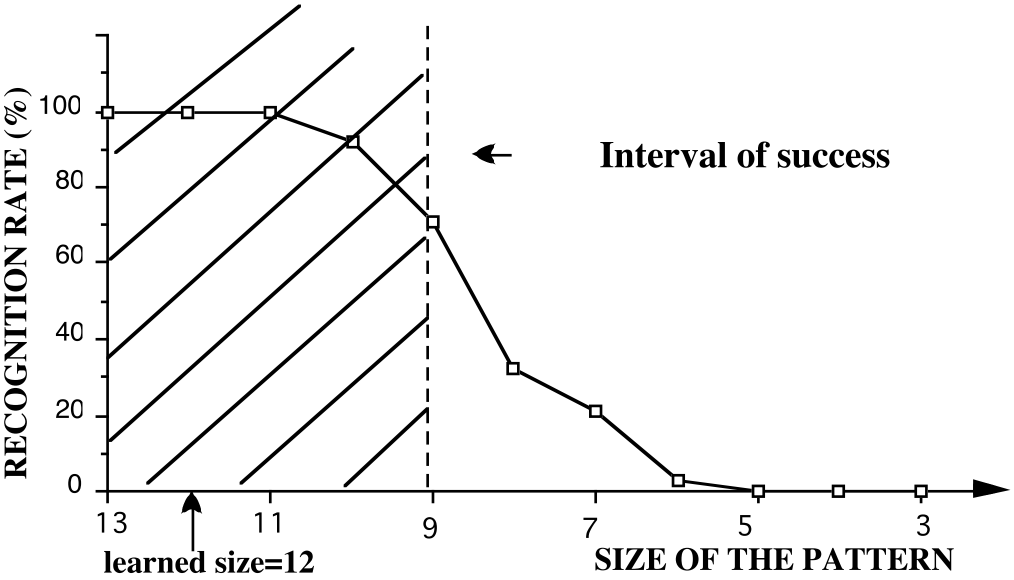

Figure 3.5. Performances of the temporal pathway: effect of changing size only. After the 28 patterns have been learned at one size (size 12, 24x24 pixels) and in the central position, they are presented, during the recognition session, in the central position, but with varying sizes: from a size 13 (26x26 pixels) down to a size 3 (9x9 pixels). Notice that the recognition rate remains above 70% despite decreases from the learned size of up to 33% (From Otto et al. 1992).

Shift invariance. The pattern, with the learned size (size 12 = 24x24 pixels) is allowed to vary in location, from one side to the other of the retina, on both the vertical and horizontal axes (corresponding to a shift up to 6 pixels on each axis and in the two directions). The model shows a very interesting invariant recognition rate: it remains superior to 70% for a translation on RETINA corresponding to the size of the receptive fields of the Temporal Associative Area ($|\delta x| = 4$ and $|\delta y| = 4$ pixels on RETINA). This effect is due to the convergent connectivity. Thus moderate shift invariant properties are obtained without ocular movement.

Parieto-temporal cooperation. Figure 3.6 shows the behavior of the Y-like network when both size and location of the presented pattern are changed (for each size from 13 to 3, the pattern is presented in all the locations over the retina). When the pattern is not too small, the WHAT branch can perform direct recognition at different locations, mainly around the center of RETINA: the positions of the patterns where this direct recognition is satisfactory are represented in Fig. 3.6 by the darkened squares. In this case (temporal satisfaction), the WHERE computation is performed in parallel in the parietal branch, but is not used for recognition. A recognized pattern finally results in a well-contrasted pattern of activity in the Temporal Semantic area (tSA). We consider that the overall effect of this Temporal activity is inhibitory on the output from the WHERE branch (driving the ocular command).

By contrast, failure of recognition corresponds to spread of activities within the Temporal Semantic map (tSA), without any emergent well-contrasted pattern. The overall effect on the WHERE branch is considered as an excitatory gating effect on its oculomotor output. The WHERE branch has already extracted a global location of the pattern displayed on the retina (population coding). The output effect of the Parietal areas toward the structures that command the extraocular muscles (colliculus, FEF) is modeled by a vector: the population code is transformed into a motor command (vectors shown in Fig. 3.6) which drives the movement to be performed to reset the pattern in the foveal region.

Figure 3.6 shows that the WHERE branch not only computes the good direction, from the target location toward the center of the visual field, but also calculates an amplitude which increases, in a step-like fashion, with the eccentricity of the target: the greater the eccentricity of the target, the larger the amplitude of the resetting vector.

Discussion

This model proposes a computational solution to the invariant recognition problem - invariance in size, invariance in position - which is based on neurobiological knowledge. The invariance property in the whole visual field mainly comes from the cooperation between two regions which are known to extract two different information, one which has limited invariant capacities for object recognition in the center of the visual field and the other which can extract object locations in the periphery and drive eye movements to reset the pattern in the central region.

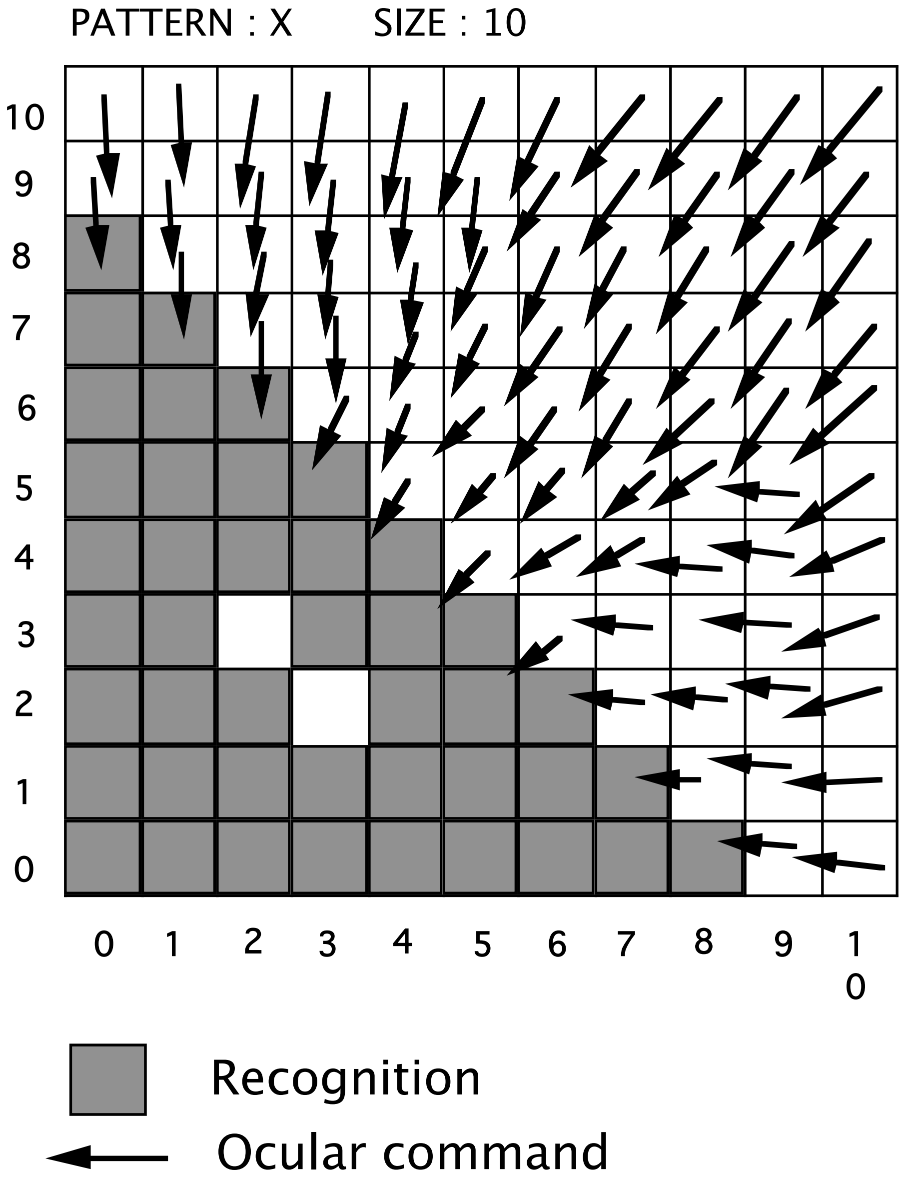

Figure 3.6. Cooperation between temporal and parietal pathways. With the same learning paradigm as in Fig. 3.4 and Fig. 3.5, a pattern is presented during the recognition session with varying sizes and position shifts on the retina of up to -10/+10 "pixels". This figure shows the behavior of the double-branched network for a prototype (here the capital letter "X") presented with one size (size 10, 20x20 pixels) in all the positions (in the upper quarter of the retina, the other quarters can be deduced by symmetry). Dark squares represent the positions where the pattern is directly recognized by the WHAT branch. Arrows represent the vectorial population coding of an ocular movement performed in the WHERE branch when the WHAT branch fails to recognize the pattern. Notice that these vectors contain the directional information needed to reset the pattern closer to the positions where it is directly recognized (dark squares). Furthermore, the amplitude of the vector increases with the distance of the pattern from the center (From Otto et al. 1992)

A Y-like double branched network allows these two aspects (form and location) to be extracted, with an optimal trade-off between precision of recognition and invariant capabilities in each branch which is due to a differential distribution of receptive field sizes and visual field representation in the two streams. Invariant capabilities in the central part of the visual field are due to the increase in the receptive field size along the successive steps of the WHAT pathway. These steps have clearly different functional roles since only the associative area has the optimal trade-off between the size of the receptive fields and the maintenance of spatial configuration of features to learn patterns efficiently. A semi-distributed coding of information allows a limited number of prototypes to be represented in the network by independent neuronal groups: each neuron can optimally learn a specific feature of a given prototype and different views of the same prototype are represented by different patterns of activation within the same neuronal group. The lamination of the local cortical circuits in input-output divisions allow information along each stream to be integrated (through feedforward processing), local features and prototypes in the associative areas to be associated (through feedforward and feedback interactions), and the functional cooperation between the two branches to be achieved (through lateral interactions). The learning rules of these units are based on conditional probabilities (consequence of a multicellular circuit) which allow immediate learning.

As in other models (Rumelhart et al. 1986), the learning signal is provided by a feedback flow of information. But in this model, the feedback connections do not send an abstract error signal, but rather neuronal activities representing the top-down expectations of the system. Furthermore, these feedback projections are modifiable by learning, providing a semi-distributed storage of the learned prototypes which will be matched during the recognition session with the incoming patterns.

The only adaptive connections in this model are feed-back connections that are modifiable in either excitatory or inhibitory direction. Lateral and long range connections could also be adaptable with similar learning rules (Bouthkil and Burnod 1992). They could introduce supplementary controls on the recognition process.

This model illustrates the importance of several features of cortical organization for solving a difficult computational problem (invariant recognition): (*i*) The columnar organization allows distributed interactions between two flows of information (*feedforward* and *feedback*) and the construction of a distributed long-term memory for objects; (*ii*) Packing of information in terms of primary and secondary indices provides of efficient and economical mean for neuronal processing and neuronal storage; (*iii*) *Adaptive gating* (Equations 3.2 and 3.3) is an efficient mechanism for the formation of long-term memory representations.

4 GENERAL DISCUSSION

This chapter illustrates the consistent relationships between principles of cortical organization and emergent properties of cortical networks in the visual system. Starting from a common retinal input, different functions are expressed depending on the nature of primary and secondary indices.

At early stages of visual processing, primary indices corresponding to retinotopic mapping are predominantly represented and secondary indices correspond to parallel processing of submodalities (for instance different filtering processes). Information flow has two components: a feedforward and a lateral one. Neuronal interactions can be viewed as local correlations within or between indices, as in perceptual grouping process. Transformations result in a spatial anatomical reordering of topography and in a function change. However, the reordering is respectful of retinotopic coordinates, which remain the primary indices.

Higher level functions, such as recognition, are related to combinations between several flows of information and to the use of non-retinotopic representations. In this case, functional changes are correlated with a transition from retinotopic to object coordinates. In these new coordinates, computation cannot be described in terms of filtering processes, since neighboring relations are no longer significant. At this level, receptive fields can correspond to the convergence toward a grand-mother cell, which computes the "population" code over the field (as in the WHAT branch). In the WHERE branch, the population code is not related to object coordinates, but to local retinotopic indices within object representation, which carry coarse-coded information on spatial location. In the following chapter, another type of population code is presented based on the vectorial contribution of each neuron to the direction of the movement (Georgopoulos et al. 1986).

It is important to note that the population code is informative on the behavior of a group of neurons, but may not be explicitly computed, i.e. no single neuron responds as the whole population. It means that the representations derived from a transformation are used for successive processing steps keeping with the simultaneous and parallel mapping of parameters and operations.

CHAPTER 4

From Retinal to Arm-centered Reference Frame

Contents

Summary

This chapter presents two models, which illustrate cortical computation in an arm-centered reference frame. The goal of both models is to control a set a broadly tuned neurons indicating the direction of the movement. In the first model, the movement is aimed at a visual target and the neural network learns sensory-motor correspondences between vision, arm position and movement toward the target, through spontaneous movements. The operation which is learned by the network can be approximated by a bilinear combination, which can be interpreted as a projection of the visual information on a reference frame which rotates with the arm. In the second model, the movement is oriented toward a goal arbitrarily defined by a reward. Learning the correct movement depends on the acquisition of conditional relations between incoming signals and results in a multiplicative transformations. Both models rely on multiplicative neuronal interactions, but for different reasons. They show that learning of visually guided movement and goal-directed movement can result from similar adaptive processes, and illustrate the generality of cortical processing.

1 INTRODUCTION

Following integration through the visual system, visual information arising from retinal stimulation can be used to guide movement toward targets in space. Cortical networks and mechanisms involved in this transformation are not fully identified and are under intensive investigations (review in Caminiti et al. 1992). However, an important computational constraint has been clearly identified: the direction of movement is represented by a population code in a set of broadly tuned neurons (Georgopoulos et al. 1986; Caminiti et al. 1991). Accordingly, controlling the direction of the movement requires the acquisition of the relationship between behavior of single neurons and behavior of a population.

This chapter describes two models corresponding to two modes of control of movement: (*1*) A model for the computation of the direction of a movement toward a target (Burnod et al. 1992); (*2*) A model for the operant learning of the direction of a goal-directed movement (Guigon and Burnod 1993). In both cases, the training follows the logic of operant conditioning: spontaneous behaviors, which modify the environment, are used to discover the correct sensory-motor correspondences.

These models illustrate interactions between incoming flows of information for the control of an output map organized around a continuous parameter (direction of movement). Following the principles exposed in **chapter 2** and used in the previous chapter, transformations are characterized by a neuronal network with a specific organization and specific processing and adaptive columnar properties.

2 COORDINATES TRANSFORMATION

In order to bring the hand to a desired position in space, the cortex must transform visual information related to the target location and kinesthetic information related to arm position into an appropriate motor command of the reaching hand. Cortical areas involved in the control of reaching behavior in the primate are the primary motor cortex (M1), the premotor cortex (PM), the supplementary motor area (SMA), and the posterior parietal cortex areas 5 and 7 (review in Johnson 1992). Neurophysiological studies on arm movement direction toward visual targets have shown that neural activity in the motor (Georgopoulos et al. 1986; Caminiti et al. 1991), premotor (Caminiti et al. 1991) and parietal cortices (Kalaska et al. 1990) is broadly tuned around a particular direction of movement, the cell's preferred direction. Furthermore, the direction of the movement is precisely predicted by a population vector constructed from the vectorial contribution of each neuron along its preferred direction. Recently Caminiti et al. (1991) have shown that the cell’s preferred direction changes with the position of the arm. However, the population vector computed from the preferred direction vectors over a group of cells always predicts the direction of the movement, whatever the position of the arm in space.

On the basis of these data and of principles of cortical computation (**chapter 2**), Burnod et al. (1992) have proposed a neural network model to perform coordinates transformations. The main characteristics of this model are: mapping of input and output parameters, *adaptive tuning* and *adaptive gating* in two *feedforward* information flows, population code.

Description of model

The network (Fig. 4.1) is made of two maps (*matching* and *synergy*). Matching units are cortical column-like units with 3 input/output divisions, which receive three kinds of input: (*i*) a visual input representing the direction of the desired trajectory toward the visual target; (*ii*) a somatic input representing the current initial arm position; (iii) a feedback input composed of the outputs of the synergy units. Each synergy unit also receives three kinds of inputs in three divisions: (*i*) a feedforward input from the matching units; (*ii*) a lateral input from other synergy units, and (*iii*) a feedback input from somesthetic receptors activated by the movement. Synergy units project to "motor output units" modeling motor units in the spinal cord.

Following Equations 2.1 and 2.2 (see **chapter 2**), neural processing is performed in two steps, for each division *i*:

$$u^i(t) = F\left(\sum_{j=1}^{n_i} w_j^i(t)\, x_j^i(t) \right) \qquad (4.1)$$

and then

$$y^i(t) = F\left[\sum_{j=1}^{N} \sum_{k=j+1}^{N} Q_{jk}^i(t)\, u^j(t)\, u^k(t) + \sum_{j=1}^{N} L_j^i(t)\, u^j(t) \right] \qquad (4.2)$$

where u^i is the result of the filtering process in channel *i* and y^i the output of the channel *i*. Rules for modifications of registration coefficients are the following:

1. Coefficients *w* are modified by *adaptive tuning* according to

$$\Delta w_j^i(t,t+1) = \lambda[\sigma x_j^i(t) - w_j^i(t)]\, y^i(t-1)\, u^i(t) \qquad (4.3)$$

where λ and σ are parameters. This rule allows the coefficients to be adjusted around values that correspond to the most probable input within division D^i when this division has been previously active.

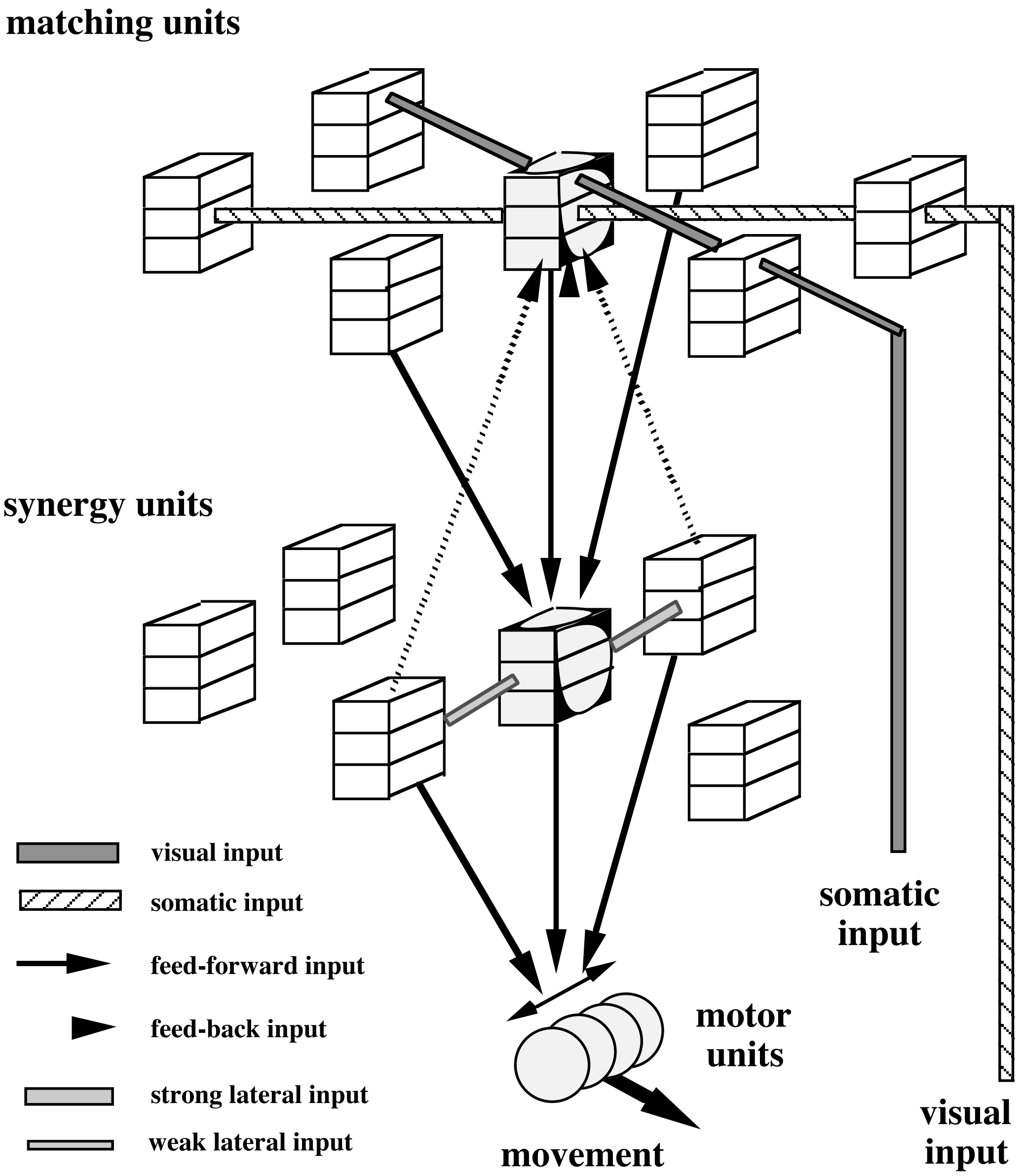

Figure 4.1. Architecture of the neural network modelling the operations performed by the cerebral cortex for visuomotor transformations. The processing units model the cortical column, with inputs and outputs organized in layers. A set of synergy units and a set of matching units are reciprocally connected. Each synergy unit addresses a motor command to a subset of motor units, whose contraction produces a vectorial effect on the hand position. A matching unit receives sensory information from two sources: a somatic input (on its somatic layer-division) which encodes the initial arm position, a visual input (on the visual layer-division) which codes for the desired trajectory and feedback information (on the feedback layer-division) from active synergy units. Each matching unit projects to synergy units. Synergy units receive a feedforward input from matching units a lateral input from other synergy units and a feedback input from peripheral receptors (not shown in the figure). Input connections to synergy and matching units are adaptive and are tuned by the feedback loop produced by spontaneous movements. (From Burnod et al. 1992).

2. Coefficients L and Q are modified by *adaptive gating* according to

$$\begin{cases} \Delta Q_{jk}^{i}(t,t+1) = y^{i}(t-1)[-\lambda u^{k}(t-1) + \mu u^{k}(t-1)u^{j}(t)] \\ \Delta L_{j}^{i}(t,t+1) = y^{i}(t-1)[-\lambda u^{j}(t-1) + \mu u^{j}(t)] \end{cases} \qquad (4.4)$$

Equation 4.4 allows conditional interactions between incoming information flow to be captured. Accordingly, the division coefficient L_j^i becomes maximal when division D^j has an unconditional influence on division D^i (see **chapter 2**) . On the other hand, the inter-division coefficient Q_{jk}^i increases when interactions between D^i and D^j are conditional to activation of another division D^k . Different values of L and Q coefficients correspond to different processing operations such as AND and OR operations.

Behavior of the model

The network learns self-consistency between sensory and motor signals through spontaneous movements (Kuperstein and Rubinstein 1989). Associations between synergy signal (output), kinesthetic signal (arm position), and reafferent visual signal following a spontaneous movement are stored in filtering (w), linear (L), and bilinear coefficients (Q) in a distributed fashion (Equations 4.3 and 4.4).

After training, visual inputs (corresponding to a target in space) are able to trigger synergy units activation that produce a population vector indicating the direction of the movement, taking into account the initial position of the arm. The operation which is learned by the network can be approximated by a bilinear combination, which can be interpreted as a projection of the visual information on a reference frame which rotates with the arm. The bilinear combination is sufficient to predict the cortical activity before reaching both at the level of single neurons and at the level of the whole neuronal population. Neural circuits converging toward a single neuron in the motor cortex learn to predict the vectorial effect of the synergistic contraction of muscles on the hand trajectory by generalizing the result of few trials in 2D subspaces, but not in the whole 3D space. The population of cortical neurons can compute the appropriate command in the whole 3D space thanks to the fact that the distribution of cell preferred directions is uniform in this population

Discussion

This model illustrates a "cortical" solution to a problem of coordinates transformation. The solution corresponds to an internal representation of sensory-motor self-consistency and is produced by emergent properties of a network of cortical column-like units. Appropriate control of the neuronal population results from two columnar adaptive mechanisms: (*1*) *Adaptive tuning* (Equation 4.3) allows the filtering properties of matching units on incoming signals to be adjusted; (*2*) *Adaptive gating* (Equation 4.4) is responsible for the acquisition of a bilinear operation in matching units.

Besides its explicative and predictive value (discussion in Burnod et al. 1992), this model points to a general form of multimodal neuronal combination. When two independent flows of information can be related by a third one through self-consistency, the fusion of the two flow can be obtained by extracting the geometrical properties of the self-consistency relation. The same type of model can thus be used for other types of coordinates transformation, such as coordinates transformation for saccadic eye movements in the superior colliculus (Gazeres 1993).

3 OPERANT LEARNING OF THE DIRECTION OF A MOVEMENT

Output maps can be controlled either through self-consistency of visuo-motor input/output relationships as shown in the previous section, or through arbitrary consistency defined by a goal. In the latter case, learning occurs by progressive adjustments to external requirements. In this section, we first review recent studies describing quantitative variations in brain activity during acquisition of simple behavior or change of behavior. It concerns mainly primates (monkeys and humans) and comes from different recording techniques (brain potentials, cortical fields, single unit recordings). Then we describe a model of a simple task, which illustrates a way to control the direction of a population vector (and thus of a movement) by local adaptations in each neuron of the population (Guigon and Burnod 1993). The main components of this model are: mapping of output parameter, *adaptive gating* in two *feedforward* information flows, population code (Table 2.2).

References

1. Burnod et al. (1982) have described the short-term changes in neuronal activity in motor and parietal areas during the operant acquisition of self-initiated flexion movements.

Monkeys were trained to perform a flexion movement from a starting position to a final predetermined angular sector without visual control. The size of the sector was progressively reduced in order to increase the precision of the movement. During the training session, the manner in which the movements were performed gradually changes. At the beginning, movements were made by progressive adjustments until the correct angular position was reached. As learning proceeded, the movement amplitude became more precise, the intervals between movements more regular. The performance rate (number of rewarded movements per unit of time) increased with training. The relationships between neuronal activity of movement-related cells and movement changed with the performance rate: as the performance improved, the neuronal activity became more closely time-locked with the onset of the movement. This modification reflects an increase in the conditional probability of discharge of neurons in relation to the beginning of the movement. Reward-related cells also change their activity with learning in such a way that, after learning, termination of activity strongly predicts a new movement.

2. Using a different technique, Sasaki and Gemba (1982; Gemba and Sasaki 1984) have described cerebral field potentials in various areas during the acquisition of a skilled conditioned movement. Monkeys were instructed to lift a lever by wrist extension within the duration of a light stimulus, duration which depends on the stage of the learning process. Premovement potentials in the different areas were found to develop with learning. At early stages of learning, monkeys lifted the lever randomly and short-latency responses to the stimulus were found in striate, prestriate, premotor and prefrontal cortices. Early premovement potentials (s-P, d-N) appeared in the motor cortex once the monkey started to perform correctly. As the performance improved, late premovement potentials (s-N, d-P) developed in the motor cortex. Steady responses were observed in the final stages of training. Sasaki and Gemba have shown that the late premovement activity in the monkey motor cortex is related to cerebello-thalamo-cortical connections.

3. Long-lasting, learning-dependent changes in brain activity are thus observed in different cortical structures when an animal is operantly trained to execute a skilled movement. Correlates of the performance of skilled movements have also been found in humans, using movement related brain macropotentials (MRBMs; Papakostopoulos 1978; Chiarenza et al. 1983, 1990). These potentials were recorded when subjects perform self-initiated skilled movements and received visual feedback on the performance (Papakostopoulos 1978). Different potentials have been characterized corresponding to ongoing behavior: (*i*) The Bereischaftpotential (BP; Kornhuber and Deecke 1965) is observed in precentral regions well before the movement (~1s). It precedes the muscular activity and reflects preparatory processes of the movement; (*ii*) The motor cortex potential

(MCP; Papakostopoulos et al. 1975) appears in the precentral regions with EMG activity. It may be regarded as an index of sensory reafferent activity (Papakostopoulos et al. 1975); (*iii*) The skilled performance positivity (SPP; Papakostopoulos 1978) is a postmotor potential observed mainly in parietal regions. It appears during skilled activity in relation to a feedback on the behavioral efficiency.

4. Developmental studies have shown that MRBMs undergo age-dependent changes. In one study (Chiarenza et al. 1983), the MRBM correlates of motor performance of 6 to 13 year-old subjects were analyzed. Although EMG activity was independent of age, brain potentials were found to vary significantly with age. Whereas characteristic potentials (BP, MCP, SPP) were present in older subjects, younger subjects lacked BP and showed a smaller SPP.

Description of the model

The following task is used to illustrate the acquisition of a simple goal-directed behavior. A monkey is operantly trained to perform arm movements in the horizontal plane from an initial central position to the periphery in such a way that the final hand position is in a given angular sector (Fig. 4.2A). We have chosen a task in which the controlled variable is the direction of the movement since simple representation of movement direction has been found in motor cortical areas of the monkey (Georgopoulos et al. 1982). For a sake of simplicity, we do not consider the amplitude of movement.

We consider a network of n units ($N^a ,1 \leq a \leq n$) each tuned for a preferred direction $\boldsymbol{p}^a$ (**bold** characters are used for vectors) in such a way that the vectors $\boldsymbol{p}^a$ are uniformly distributed in the 2D horizontal space (Fig. 4.2B). At each time t, each unit N^a contributes to the direction of the movement in proportion of its activity ${}^a y(t)$ along its preferred direction $\boldsymbol{p}^a$. The resulting movement is characterized by the direction $\boldsymbol{d(t)}$ according to

$$\boldsymbol{d}(t) = \frac{1}{n} \sum_{a=1}^{n} {}^a y(t) \boldsymbol{p}^a \qquad (4.5)$$

Each unit N^a in the network has two input pathways, which enter in two divisions (the left index is used for the unit, the right index for the division):

- One for a contextual signal, indexed 1 (${}^a x^1$). This signal is different at each time and for each unit. It corresponds to the ability of the network to generate all possible behaviors (all directions of movement).

- One for a drive/reinforcement signal, indexed 2 ($^a x^2$). We have assumed that the same pathway can convey both the neural correlate of an internal motivational state related to the expectation of a reward (Toates 1986) and the effective reward. The drive/reinforcement signal is the same for all units (Fig. 4.2B).

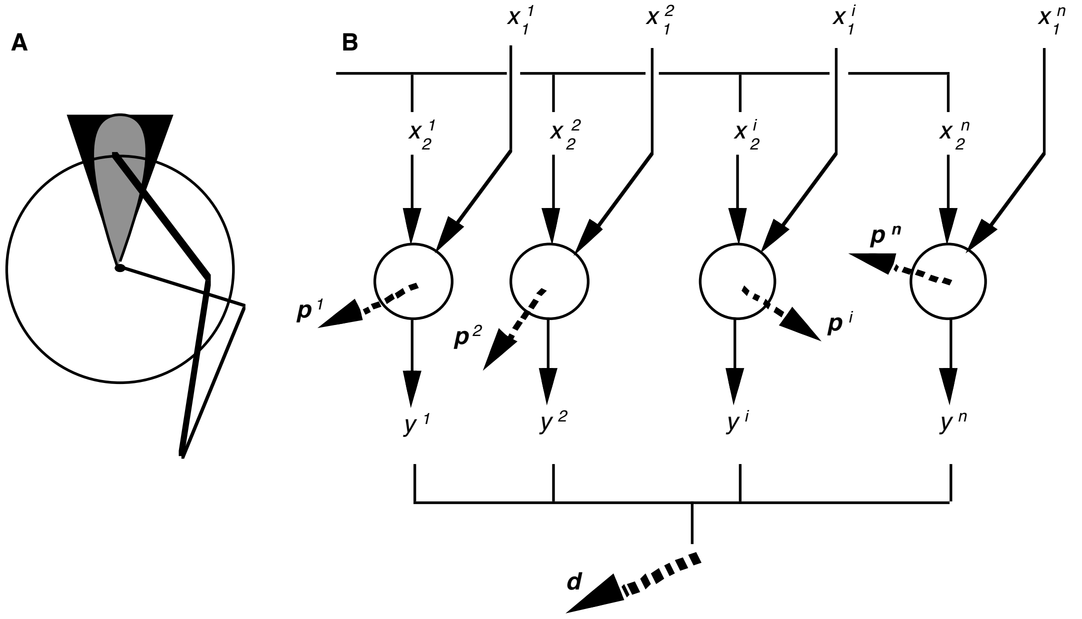

Figure 4.2. Neural network model for the acquisition of a goal-directed behavior. **A**. The drawing is a schematic description the task used to illustrate acquisition of a goal-directed behavior. The goal of the task is to move the arm (represented by two connected lines) between an initial central position (*thin line*) to a peripheral position (*thick line*) in the shaded angular sector. **B**. The neuronal network used to model the acquisition of the task is shown. Each neuron has two input pathways (x), indexed 1 and 2, and one output pathway (y). *Thin dashed arrow* at the center of a neuron represents the preferred direction of the neuron (see Text). *Thick dashed arrow* is the population vector.

The pathways are either active or inactive, the corresponding signal being 1 or 0, respectively. Following principles of **chapter 2**, cortical processing can be approximated by weighted additive contributions of each input and weighted multiplicative contributions of pairs of inputs. The unit N^a is thus activated according to

$$y(t) = F[L_1(t)\, x^1(t) + L_2(t)\, x^2(t) + Q_{12}(t)\, x^1(t)\, x^2(t)\,]Z(t) \quad (4.6)$$

where L_1 and L_2 are the additive coefficients of pathways 1 and 2, respectively, Q_{12} the multiplicative coefficient between pathways 1 and 2 (we have omitted the right index in reference to the unit), and F the stochastic output function defined by

$$F(u) = \begin{cases} 1 \text{ with probability } g(u) \\ 0 \text{ with probability } 1-g(u) \end{cases} \qquad g(u) = \frac{1}{1+e^{-\gamma(u-\phi)}}$$

where γ and ϕ are parameters. The term $Z(t)$ corresponds to the influence of the population of units on unit N^a through lateral interactions, and is defined by

$$Z(t) = \cos(\mathbf{p}^a, \mathbf{d(t)})$$

(cosine of the angle between vectors $\mathbf{p}^a$ and $\mathbf{d(t)}$). Note that Equation 4.6 corresponds to Equation 2.2. Learning coefficients are likely to change between time t and t + 1 according to

$$\begin{cases} L_1(t+1) = L_1(t) + g_1(x^1,y,t) \\ L_2(t+1) = L_2(t) + g_2(x^2,y,t) \\ Q_{12}(t+1) = Q_{12}(t) + g_{12}(x^1,x^2,y,t) \end{cases} \qquad (4.7)$$

where g_1, g_2, and g_{12} are functions which define coefficient variations, and with the initial values $L_1(0)$, $L_2(0)$, $Q_{12}(0)$. These relations express that additive coefficients are specific to one pathway, whereas the multiplicative coefficient is related to the two pathways. The behavior of the network is fully described by Equations 4.6 and 4.7. Arbitrary activation of the input pathways 1 and 2 at time t produces a movement in the direction $\mathbf{d(t)}$ predicted by Equations 4.5 and 4.6. If the movement is in the intended angular sector, the drive/reinforcement pathway is activated at time t+1. Learning coefficients in the network are then modified according to Equation 4.7. The contribution of each unit to the correct movement is measured by the quantity $y(t)x^2(t+1)$, which is non-zero if activation of the neuron ($y(t)$) has been followed by a reward ($x^2(t+1)$). Similarly, the contribution of the neuron to an incorrect movement is measured by $y(t)[1 - x^2(t+1)]$. In order to be efficient for the acquisition of the task, modification of learning coefficients must depend on both quantities. The consequences are the following:

1. The additive contributions (L_1, L_2) do not provide efficient adaptation since the context pathway (indexed 1) has an unconditional influence on the network (which does not depend on the reward). However, the contribution of the drive/reinforcement pathway alone (indexed 2) is likely to produce adaptation if the learning coefficient is changed according to

$$\Delta L_2(t,t+1) = y(t)\{\lambda x^2(t+1) - \mu[1-x^2(t+1)]\}$$

where λ and μ are parameters. It predicts that the coefficient would increase by λ for correct movements and decrease by μ for incorrect movements. A steady increase occurs when the neuron frequently contributes to the movement in the correct direction.

2. The multiplicative contribution provides the most efficient adaptation, since the multiplication coefficient can register the probability of occurrence of the reward conditionally to a specific context according to

$$\Delta Q_{12}(t,t+1) = x^{1}(t)\ y(t)\{\lambda x^{2}(t+1) - \mu[1-x^{2}(t+1)]\} \qquad (4.8)$$

where λ and μ are parameters. Equation 4.8 states that the multiplicative coefficient would increase by λ if the context pathway has contributed to a rewarded movement and would decrease by μ if it has contributed to a non-rewarded movement. Before learning, all contexts can equally contribute to the production of a movement. After learning, only those which have been repeatedly involved in correct movements can still contribute to the network response. Acquisition of the task occurs with repetitive pairing of some randomly selected context pathways and the drive/reinforcement pathway. Since each direction of movement is related to a specific context input (Fig. 4.2B), multiplicative coefficients can store precise conditional relations between the context and the reward. Equation 4.8 is a form of *adaptive gating* derived from Equation 2.5.

Behavior of the model - Simulations, results and predictions

Figure 4.3 depicts results obtained by computer simulations. We have chosen $N = 16$, and an the intended angular sector (60°, 115°). All learning coefficients were initially at 0.5. The training consisted of 30 blocks of 10 trials, where a trial corresponds to the activation of the network, the measure of direction of the resulting movement and the delivery of a reward for a correct movement. For each trial, we noted whether it was correct or not and we recorded the activity and the variation in learning coefficients in each neuron. The performance rate was computed using the percentage of correct responses in successive blocks of 10 trials (trials with no movement were not taken into account). For each neuron, individual trial activity and variation in the learning coefficients were average by block of 10 trials. Figure 4.3 illustrates the results for the case of multiplicative contribution of the two input pathways. The monotonic increase in the performance (*open circles*) rate reflects progressive acquisition of the correct behavior (Fig. 4.3A). Variations in activity and learning coefficient in two neurons are displayed in Fig. 4.3B and 4.3C:

- A neuron whose preferred direction is in the intended angular sector (Fig. 4.3B) displays a learning-dependent increase in activity (*crosses*) correlated with the increase in the learning coefficient (*solid circles*).

- No development of activity is observed in a neuron whose preferred direction is not directed toward the correct sector (Fig. 4.3C).

The model emphasizes the following characteristics of the acquisition of a goal-directed behavior:

- The observed behavior of the network can be quite similar at early and late phases of training. The network can produce the correct response at the beginning of the training. The difference between early and late training period is not a matter of ability to succeed in a given trial, but rather of ability to reach a good performance criterion. This interpretation is consistent with the surprising experimental observations that show that the development of performance seems to precede the development of activity (Watanabe 1990; Mitz et al. 1991). Sasaki and Gemba (1982) observed that some activity became differentiated earlier than the performance. It was true for sensory processes, but not for activity related to the production of the response (early and late precentral potentials) which appeared only when the monkey starts to perform correctly (Sasaki and Gemba 1982).

- Increasing activity in network occurs in parallel with the acquisition of the task (Fig. 4.3B). The model suggests that the changes in neuronal activity are likely to be described by changes in conditional probability encoded in learning coefficients of the network (Fig. 4.3B). This interpretation provides a simple way to relate distributed information processing in a neuronal network and execution of a global action. Changes observed in motor areas of the cortex during learning are likely to be explained in this way (see *References*).

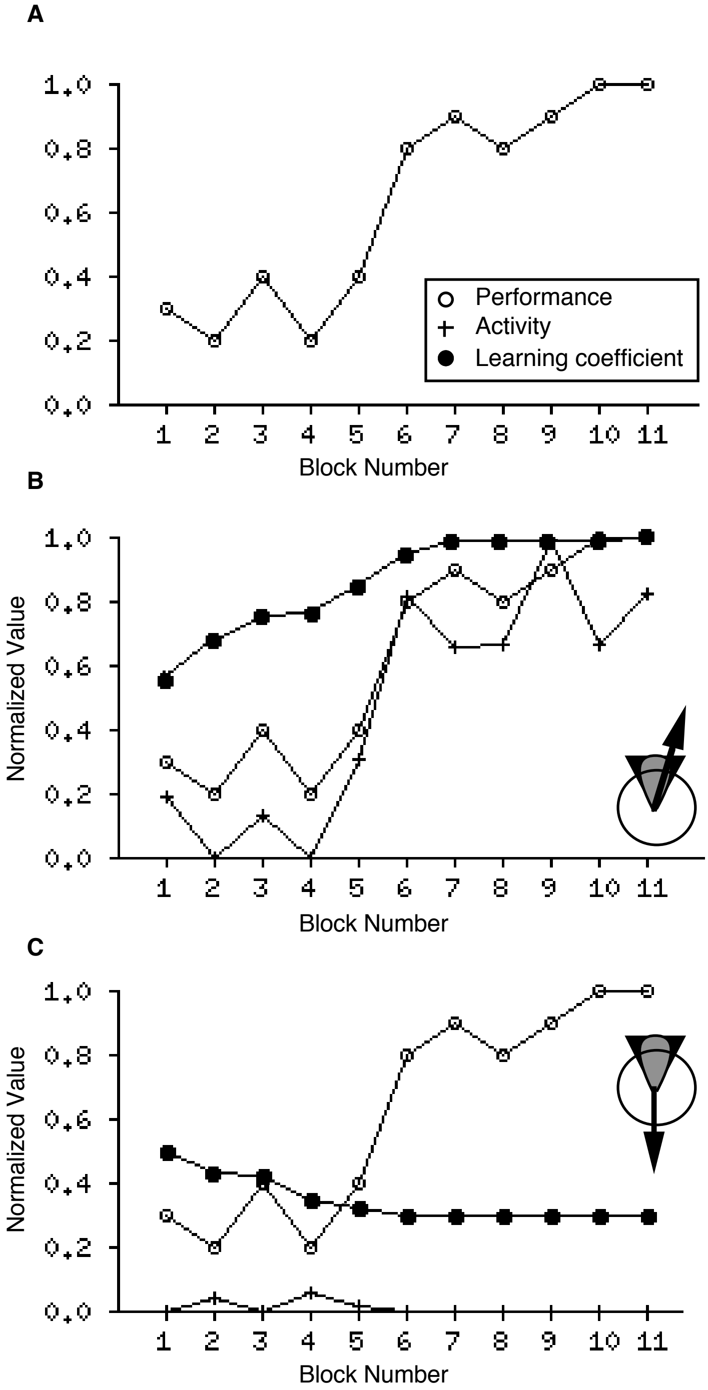

Figure 4.3. Acquisition of a goal-directed behavior. Quantitative variations in the level of performance (**A**), in normalized neuronal activity and in normalized learning coefficients (**B** and **C**) for the neuronal network described in Fig. 4.2A. **B** and **C** are the results for two neurons, whose preferred direction is indicated by the thick arrow at the right of the graph. A block = 10 trials. The parameters are the following: $\lambda = 0.5$, $\mu = 0.15$, $\gamma = 8.0$, $\phi = 0.5$, $L_1(0) = L_2(0) = Q_{12}(0) = 0.5$.

Discussion

This model shows that a goal-directed behavior can be stored in a set of neurons using a mechanism based on *operant conditioning*. However, acquisition is not likely to occur when considering only unconditional contribution of input pathways. Successful learning is observed when conditional interactions between incoming signals are stored. In this case, a memory is constructed which contains a statistical approximation of conditional probabilities related to the production of the behavior (for instance, movement followed by a reward).

It is important to note that Equations 4.4 and 4.8 do not give a specific role to the reward. Any signal following a neuron's activation can be used as a reward. This observation stresses that conditioning can operantly occur on any reafferent signal matching the intended effect of an action. Similar "self-consistency" constraints have been used in the model described in the previous section (see also Burnod et al. 1992): the desired hand trajectory was operantly learned as the sensory effect (visual trajectory) of a motor command. This property is interesting regard to the ability of humans to learn with the expected effect of their action rather than with an absolute reward (Chiarenza et al. 1990).

4 GENERAL DISCUSSION

In the previous chapter, processing was driven by incoming visual information in a retinal reference frame. The main constraint was to capture the diversity of input activity and to form invariant internal representations. On the other hand, network models of the present chapter are characterized by the constraint on their output organization. These models are based on the broad directional tuning properties of motor cortex neurons and on the property of the population vector to predict the direction of the movement. In both cases, computational solutions are based on principles of cortical computation exposed in **chapter 2**. This observation is important since it means that vision problems and motor performance problems may be solved using similar neural computation on adequate neural architectures.

Both models are trained using natural sensory-motor correspondences. In one case, these correspondences are related to consistency in visuo-motor transformations and may be found during spontaneous movement under visual control in critical periods of infancy (Hay 1984). The other case makes use of a conditioning protocol, which defines arbitrary correspondences. Similar adaptive mechanisms are used in both models, based on a neural analog of operant conditioning (Equations 4.4 and 4.8). The fact that the same rule of plasticity may be used during development and conditioning is an interesting property, which recalls results in the visual cortex (Singer 1987).

A novelty provided by these models is the training protocol. Generally, neural networks are trained following the logic of classical conditioning: learning can occur even when the output of the network is incorrect, the output being unconditionally given by the teacher. On the other, the present networks learn the consequences of their action on the environment (visual reafference or reinforcement). Practically, the mechanism of *adaptive gating* allows the excitability of neurons which have been involved in the production of the intended response to be modified in such a way as to increase their involvement in future responses. In the same way, neurons involved in the production of incorrect responses may be depressed. After modification, the correct response is more surely and more frequently evoked, reflecting the conditioning process. As a correlate, neurons involved in the response undergo learning-dependent increase in activity.

CHAPTER 5

Modeling Prefrontal Functions

Contents

Summary

We investigate and compare the computational properties of neuronal circuits in the network linking the prefrontal cortex with sensory, motor and limbic structures, in order to address the issue of the role of the prefrontal cortex in the temporal organization of behavior. The main characteristics of prefrontal neuronal activities, both during acquisition and execution of a task by behaving monkey, can be explained as the product of two factors: (*i*) a *learning rule* based on the control of sustained activities, which is proposed as the main property of prefrontal neuronal circuits; (*ii*) and a specific *stage-by-stage* conditioning program. A simulated neural network illustrates the abilities of the model: (*i*) to learn, with a natural stage-by-stage training protocol, the paradigmatic task (delayed response) used for testing the prefrontal neurons in primates (*ii*) to display the same categories of neuronal activities and to predict how they change during the acquisition of the task. Consistently with experimental data, two main types of activity (1 and 2) contribute to the adaptive properties of the network. Type 1 units display transient activity time-locked to events of the task and their profile keeps constant in the successive training stages. In Type 2 units, sustained activity undergoes non monotonic changes and decreases with changes in reward contingency that occur during transition between stages.

1 INTRODUCTION

In the present chapter, we address issues concerning the involvement of the prefrontal cortex and connected sensory and motor structures in the acquisition and the execution of sequential behaviors by the means of a computational model. After reviewing recent data on the prefrontal cortex, we describe a set of neurobiological and psychological data which emphasize the properties of prefrontal circuits and those of circuits in connected sensory and motor cortices (inferotemporal cortex, posterior parietal cortex, frontal motor areas). This characterization is taken as the basis to define modeling constraints (indexed 1 and 2, for sensory-motor circuits and prefrontal circuits, respectively). The constraints concern **representation of information**, **connectivity** and **neural processing** in these cortical structures. They are expressed following the principles of **chapter 2**, and are used to the construction of a neuronal network, which allows to explore and simulate the functions of these brain structures.

The properties of the model are illustrated by computer simulations which show the behavior of the neuronal network when it is trained to execute a typical sequential behavior (delayed response task). This task has been chosen because it has been well documented in non-human primates by a number of neurophysiological and neuropsychological studies and because it appears to strongly challenge prefrontal functions for both learning and execution of the task (Jacobsen 1935). Results concern both the execution of the task and the learning session (modulation of activity). The model suggests that involvement of the prefrontal cortex in the temporal organization of behavior can be related to the ability of prefrontal circuits to learn the control of a pattern of sustained activity, and allows precise predictions on learning-dependent changes in neuronal activity in the prefrontal cortex. We discuss these points in relation to experimental observations and current theories of prefrontal functions.

Although we address a restricted range of prefrontal functions from a restricted point a view (a specific behavioral task), we suggest that the model effectively captures a class of intrinsic properties of prefrontal circuits, which would help to define involvement of the prefrontal cortex in more complex or more “cognitive” behaviors.

To our knowledge, no models have provided computational accounts of the adaptive properties of prefrontal circuits related to the acquisition of behavioral tasks. The aim of this model is to describe a way to *store* and *retrieve* sensory-motor sequences in a neuronal network, which is consistent with anatomical and physiological properties of the prefrontal cortex and connected sensory and motor structures. The model will allow to address issues on the contribution of the prefrontal cortex to temporal organization of behavior. It will also provide a basis to compare the participation of several anatomical structures to the acquisition and execution of complex behaviors.

2 PREFRONTAL CORTEX

The goal of this section is to present some recent experimental results and theoretical issues concerning the organization and the role of the prefrontal cortex. Since there is a great amount of data, no exhaustive review is provided. For complete reviews, the reader is referred to the more recent synthesis works (Goldman-Rakic 1987; Fuster 1988).

Anatomical organization

The prefrontal cortex (PFC, or frontal agranular cortex, frontal association cortex) is defined as the part of the cerebral cortex which receives projections from the mediodorsal nucleus of the thalamus. In the monkey, it is limited by the arcuate sulcus in the dorsolateral surface and by the anterior extremity of the cingulate sulcus in the medial surface.

The PFC has been described as a region of cross-modal integration (Jones 1969; Barbas and Mesulam 1985; for a review, see Fuster 1988). It receives projections from higher-order, modality-specific sensory cortices and from polysensory cortex in the superior temporal sulcus. Since the prefrontal cortex cannot be considered as a uniform entity and is connected to a great number of cortical and subcortical structures, we will focus on some functionally important interactions.

Connections to the posterior parietal cortex. Parcellation of the prefrontal cortex by parieto-prefrontal projections can be described in the following way (Cavada and Goldman-Rakic 1989; Neal et al. 1990; Tanila et al. 1993): (*i*) Area 7a, which is involved in visual and visuomotor functions is connected to the fundus of the principal sulcus and the superior convexity of area 46; (*ii*) Somatosensory area 7b projects to the inferior bank of the principal sulcus; (*iii*) Area 7m has both somatosensory and visual functions and is connected to superior bank of the principal sulcus; (*iv*) Oculomotor area 7ip is connected to the caudal part of the principal sulcus. Schwartz and Goldman-Rakic (1984) have shown that parieto-prefrontal projections terminate in a feedforward pattern (i.e. in layers I, IV, and VI) while reciprocal connections are feedback projections (layers I and VI). The role of these parieto-prefrontal connections may be to provide the prefrontal cortex with visual and visuospatial information. Goldman-Rakic (1988) has argued that the parieto-prefrontal pathway is an important pathway for the guidance of hand and eye movements.

Connections to the inferotemporal cortex. Inferotemporal projections have been shown to terminate in the inferior parts of the prefrontal cortex, including the inferior bank of the principal sulcus, the cortex inferior to the principal sulcus, and the orbital surface (Barbas and Mesulam 1981; Barbas and Mesulam 1985; Ungerleider et al. 1989). Ungerleider et al. (1989) have noted that all inferotemporal fibers projecting to the prefrontal cortex course via the uncinate fascicle. Functionally, integrated information concerning properties of visual stimuli are thus likely to be provided to PFC circuits.

Connections to cortical motor structures. The prefrontal cortex can influence the motor cortex through projections from the ventral bank of the principal sulcus to the inferior area 6 (Matelli et al. 1986), which is itself strongly connected to M1 (Muakkassa and Strick 1979). On the other hand, superior area 6 where most recordings have been made (Caminiti et al. 1991; Mitz et al. 1991) is only indirectly linked with prefrontal and motor cortices (Barbas and Pandya 1987).

Connections to basal ganglia. Indirect influence on motor structures is provided by cortico-subcortical projections. Alexander et al. (1986) have proposed a functional description of interactions between frontal lobe areas and basal ganglia structures in terms of loops. Each loop connects a cortical area to itself through striatum, pallidum or substantia nigra, and thalamus back to the cortex. Such an organization appears as a substrat for parallel processing of cortical information through segregated pathways.

Other connections. The prefrontal cortex receives important projections from the hypothalamus, the amygdala and several brain stem structures, directly or indirectly through the thalamus (review in Fuster 1988). These structures have been shown to be involved in the control of behavior (McGinty and Szymusiak 1988) and should inform the PFC about processes of arousal, attention, feeding, reward.

Columnar organization. Cortico-prefrontal connections have been shown to terminate in vertically oriented columns (Goldman and Nauta 1977a; Goldman-Rakic and Schwartz 1982). Columns were labelled across all cortical layers and labelled columns alternate with free columns on the cortical surface. This finding is surprising since columnar organization is generally associated with the topographical mapping of a peripheral receptor such as in visual and somatosensory cortex.

Regional distribution of function. A strong correspondence between afference distribution and functional properties of dorsolateral prefrontal neurons has been recently demonstrated (Bruce 1988; Tanila et al. 1993). Visual, auditory and somatosensory responses are distributed in respect to the parcellation of the dorsolateral surface by associative cortical afferents.

Visual responses are broadly distributed in the prefrontal cortex, but a topographical organization can be recognized: foveal visual field is represented below the principal sulcus whereas the peripheral visual field is represented above (Suzuki and Azuma 1983). This organization reflects the underlying anatomical relationships since (*i*) the dorsomedial part of the periprincipal area is strongly connected to the posterior parietal cortex which is specialized for spatial processing; (*ii*) the ventrolateral part is the recipient of IT inputs, specialized for foveal form/pattern processing. Oculomotor (eye position-, fixation-, and saccade-related) responses are found in both banks and caudal part of the principal sulcus, and in the dorsal convexity. These regions are known to be connected to parietal areas 7a and 7ip.

The preferential distribution of auditory responses in the cortex superior to the principal sulcus (Azuma and Suzuki 1984; Vaadia et al. 1986) is consistent the projections from the auditory association cortex (Pandya et al. 1969) and the polysensory cortex of the superior temporal sulcus. However, neurons are unselective for particular sounds.

Somatosensory responses (passive stimulation of skin and mouth, compression of muscle, passive movements of joints) are found mainly in the region ventral to the principal sulcus, which is connected to somatosensory and motor areas (Preuss and Goldman-Rakic 1989). However, no somatotopy is observed (Tanila et al. 1993).

These results are consistent with anatomical pathways converging to the prefrontal cortex. Such a correspondence between anatomical and physiological properties suggest that prefrontal neuronal activity can be explained in part by the characteristics of afferent information to the frontal lobe. However, one should not forget the difficulty to reconcile anatomico-physiological and lesion-induced functional parcellation (Rosenkilde 1979).

Neurophysiological studies

Most of the single unit recordings in the prefrontal cortex have focused on the role of this cortex in temporal integration of sensory and motor events. The pioneering studies have investigated the area of the principal sulcus in monkeys performing delayed-response tasks (Fuster and Alexander 1971; Fuster 1973; Kubota et al. 1974; Niki 1974c) and delayed-alternation task (Kubota and Niki 1971; Niki 1974a; Niki 1974b). The main result of these studies was that neuron firing is related to more than one event of the task. Since, a wide variety of paradigms have been used [delayed-matching to sample (Rosenkilde et al. 1981; Fuster et al. 1982; Fuster et al. 1985; Quintana et al. 1988; Yajeya et al. 1988; Quintana et al. 1989; di Pellegrino and Wise 1991), go/no-go tasks (Komatsu 1982; Thorpe et al. 1983; Watanabe 1986; Bakay Pragay et al. 1987; Niki et al. 1990), delayed conditional position discrimination (Niki and Watanabe 1976; Quintana et al. 1988; Yajeya et al. 1988; Quintana et al. 1989), reaction time procedures (Sakai 1974; Sawaguchi 1987), visual tracking task (Kubota and Funahashi 1982), oculomotor tasks (Joseph and Barone 1987; Barone and Joseph 1989; Funahashi et al. 1989, 1990, 1991)].

Classical results on delayed response tasks. Fuster (1973) has proposed a descriptive classification of patterns of activity. This classification reflects the temporal relationships between task event occurrences and neuronal activity. Two other aspects are of importance for understanding neuronal discharge: the relation to the characteristics of events (color, form, position of cues, kinematic and dynamic parameters of responses) and the relation to behavioral patterns (anticipation, expectation, preparation, memory). Following this classification, cue-related (Fuster 1973; Niki 1974c; Kubota et al. 1980; Fuster et al. 1982; Watanabe 1986a, 1990), delay-related (Fuster 1973; Niki and Watanabe 1976a,b; Fuster et al. 1982; Kojima and Goldman-Rakic 1982; Watanabe 1986a), response-related (Kubota and Niki 1971; Kubota et al. 1974; Niki 1974a,b,c; Niki and Watanabe 1979; Kubota and Funahashi 1982; Ono et al. 1984; Watanabe 1986b; Quintana et al. 1988; see also Watanabe 1986b for activity during no-go response), and reward-related (Niki et al. 1972; Rosenkilde et al. 1981; Fuster et al. 1982; Inoue et al. 1985) activities have been characterized in the PFC (see review in Fuster 1988). Color selectivity has also been also found (Fuster et al. 1982; Kubota et al. 1980; di Pellegrino and Wise 1991; Quintana and Fuster 1992).

Involvement in delayed oculomotor responses. The involvement of prefrontal neurons in memory guided responses has been shown to extend to oculomotor behaviors. Joseph and Barone (1987) have first proposed that prefrontal neurons should be studied during oculomotor behaviors, in which eye movements are programmed. They have shown that the dorsolateral prefrontal cortex is active during oculomotor delayed responses (Joseph and Barone 1987), and that some neurons may be involved in spatial short-term memory. Using an 8-choice spatial oculomotor delayed-response task, Funahashi et al. (1989, 1990, 1991) have demonstrated that: (*i*) Prefrontal neurons have memory fields, i.e. they display a selective delayed activity for the position of the instructive stimulus in the visual space (Funahashi et al. 1990). This result extends the classical results obtained with two-choice paradigms; (*ii*) Prefrontal neurons display directionally specific phasic visual responses to cues, in register with the memory field. The visual input to the PFC participates to the directional selectivity of memory fields, but delay-related activity is not a simple continuation of cue-related activity (Funahashi et al. 1989); (*iii*) Prefrontal neurons exhibit directionally pre- and post-saccadic activity. Post-saccadic activity is context-dependent and is thus not likely to be related to a corollary discharge (Funahashi et al. 1991). These results are of importance since they emphasize that similar mechanisms seem to underlie the expression of different types of memory-guided behavior (manual and oculomotor).

Information code in prefrontal neurons. In the prefrontal cortex, some neurons respond to complex visual stimuli (Pigarev et al. 1979), other to a simple spot of light (Mikami et al. 1982; Suzuki and Azuma 1983); furthermore, neurons have been found to be insensitive to changes in the physical characteristics of a visual stimulus: color (Kojima 1980), size, intensity, position (Suzuki and Azuma 1977). Moreover, some prefrontal neurons exhibit differential responses to relevant vs. irrelevant stimuli (Yajeya et al. 1988). It means that operations performed by prefrontal circuits seem to reflect more the integration of visual information in the behavior than a specific visual operation (like filtering, for example). When neurons are studied in two tasks involving similar stimuli (DMS and DR in Fuster et al. 1982; DMS and DCPD in Quintana et al. 1988) very few neurons give similar response to the same stimulus in the two tasks.

These results have lead to the conclusion that some prefrontal neurons code the **meaning** of a stimulus independent of its physical properties. The meaning may be spatial (Watanabe 1981), non-spatial (Watanabe 1986a). This meaning reflects either: (*i*) an association with a behavioral response (which response is instructed by the stimulus?). It determines the “behavioral significance”of the stimulus; or (*ii*) an association with the predictive value of the stimulus concerning the reinforcement (will it be followed by a reward?). It is the “associative significance” of the stimulus. Neural correlates of “behavioral significance” have been reported by Watanabe (Watanabe 1981; Watanabe 1986a).

Thorpe et al. (1983) first reported units in the orbitofrontal cortex related to the appetitive or aversive nature of a visual stimulus. Watanabe (1990) found strong neuronal correlate of associative significance. In this study, monkeys were involved simultaneously in two tasks: a direct task and the corresponding reversal task. Some neurons (Type M) responded differentially to the same first stimulus (thus no local context could help to determine the response) if the monkey was currently executing a block of direct or reversal trials (Watanabe 1990). Watanabe (1990) also found more complex units (type MP) which were neither solely related to the physical properties of the stimulus nor solely to its meaning.

Post-trial activities. Studies of prefrontal neurons have generally reported "intra-trial" activities (i.e. related to cue, delay, movement, ...). "Inter-trial" activities, occurring before the instruction or after the behavioral responses, are also of interest since they should reflect more general aspects related to the control of the behavior. Different types of post-trial activity have been observed: (*1*) *Juice-related activity.* Such a response is observed in some neurons whenever juice was delivered, irrespective of whether it was given as reward or not (free reward; Inoue et al. 1985; Kubota and Komatsu 1985; Niki et al. 1972; Niki and Watanabe 1979; Rosenkilde et al. 1981; Thorpe et al. 1983). Since activity disappears with aversive food, it should be related to sensory properties of the reward; (*2*) *Reinforcement-related activity.* A reinforcement-related unit responds only when the reward is given for the correct response and does not respond to free reward (Inoue et al. 1985; Thorpe et al. 1983). It corresponds to reinforcing properties of the reward per se; (*3*) *Error-omission-related activity.* In this case, neuronal activity is observed during erroneous trials. Interestingly, the same activity is observed during correct trials when the reinforcement is omitted (Niki and Watanabe 1979; Rosenkilde et al. 1981; Komatsu 1982); (*4*) *Reinforcement-error-related activity.* The response is observed after both correct and erroneous responses and show differential activity after correct and erroneous trials (Kubota and Komatsu 1985; Niki and Watanabe 1979; Rosenkilde et al. 1981; Thorpe et al. 1983). This activity may be involved in coding the consequence of the response; (*5*) *End-of-trial-related Activity.* Activity changes whenever the trial ended, irrespective of whether it was correct or not, and irrespective of whether the reward was given or not (Kubota and Komatsu 1985; Rosenkilde et al. 1981).

These patterns should very likely be involved in behavioral control since they closely reflect important behavioral state (error, omission, termination) of the monkey.

Multimodal neurons. Polysensory units have been found in the prefrontal cortex (Benevento et al. 1977; Wolberg and Sela 1980; Bruce and Goldberg 1985). These units are similar to units found in the cortex of the superior temporal sulcus (Benevento et al. 1977; Desimone and Gross 1979; Bruce et al. 1981; Baylis et al. 1987; Hikosaka et al. 1988). Benevento et al. (1977) reported more than half bimodal units in the lateral orbitofrontal cortex. Thorpe et al. (1983) confirmed these results in the awake monkey (neurons selective for the same food in visual and gustatory modalities). Vaadia et al. (1986) found in pre- and postarcuate areas with a similar tuning for auditory and visual localization. Using visual and auditory association tasks, Watanabe (Watanabe 1992) has shown that prefrontal neurons are likely to code for the associative significance of a stimulus. Some prefrontal and premotor neurons display cue-differential activity which was specific for rewarded trials in both visual and auditory modalities. It means that neurons respond to stimuli of different modalities, but which have the same associative significance. On the other, no neurons were found related to the physical properties of the stimulus whatever their modality. These units are found both: (*i*) in the region the lower arcuate sulcus (area 45) and in the inferior convexity which are known to receive visual and auditory association inputs (Chavis and Pandya 1976); (*ii*) in the region of the principal sulcus and in the premotor cortex where no direct visual and auditory inputs have been reported. The existence of multimodal units in the prefrontal cortex may be related to the cross-modal aspect of prefrontal functions.

Learning-dependent changes in neuronal activities. Several forms of change have been studied: (*1*) New learning experiments: the subject is required to adapt its behavior to unknown new conditions. This learning scheme may be a learning-set paradigm, when the task is defined by a rule (Harlow 1949); (*2*) Reversal experiments: the subject is first trained to perform a conditional task (for instance, a GO/NO-GO discrimination task). After a given performance level is reached, the discrimination is reversed (the GO signal becomes a NO-GO signal) without warning the subject.

Niki et al. (1990) have described variations of neuronal activity in prefrontal and premotor cortex during learning of new discriminations (new visual stimuli) and reversal learning (see below). Monkeys were trained on a GO/NO-GO discrimination task with several pairs of stimuli. Long-lasting alterations of activity were found when new stimuli were used: activity increased for one stimulus whereas it did not change for the other stimulus. These changes were evenly found in prefrontal and premotor tested areas. Niki et al. (1990) observed that such learning-dependent changes occurred in neurons whose activity was related to the forthcoming movement.

Neural correlates of reversal learning have been described in several neurophysiological studies. Thorpe et al. (1983) trained monkeys to perform a visual GO/NO-GO discrimination task and reversal. Three types of learning-dependent changes in neuronal activity were observed in the orbitofrontal cortex (Thorpe et al. 1983): (*1*) Some neurons reverse their response to visual stimuli when the monkey reversed his behavioral response, reflecting the significance of the stimuli (rewarded or not rewarded); (*2*) Some neurons kept responding in the same way, indicating a relation with physical properties of the stimuli; (*3*) Some neurons stopped responding in the reversal condition. Since the reversal task involves the same stimuli as the direct task, this modulation reflects a complex interaction of physical properties and meaning of the stimuli.

During reversal learning, Niki et al. (1990) observed two characteristic patterns of variation: (*1*) Neurons which showed opposite discharge patterns for correct and incorrect trials (Type 1) keep the same level of activity when the behavioral responses are reversed; (*2*) Neurons which showed the same discharge patterns for correct and incorrect trials (Type 2) reversed their activity with the reversal. Type 1 reflects a dependence on the impending response whereas Type 2 is related to stimulus-response association. Consistent results were obtained by Watanabe (1990). Indeed, Watanabe (1990) observed that changing the "associative" significance of a visual cue (i.e., is it predictive of a reward?) elicits learning-dependent decrease of neuronal activity in the small number of units examined in prefrontal and premotor cortices.

Distribution. A majority of neurophysiological studies have reported a general lack of topographical organization in prefrontal cortical areas. Furthermore, authors frequently stressed that no clear regional differences in the distribution of cells types can be observed. We have previously stressed that activity in prefrontal neurons is likely to be defined by the underlying anatomical organization. However, such a proposal appears correct for passive, but not for active neuronal responses. A possible reason of this discrepancy may be related to the strong influence of behavioral context on prefrontal neuronal activity.

Laminar distribution of task-related neurons has not been frequently reported. Sakai and Hamada (1981) have shown that neurons displaying sustained activity have their soma in layers III and VI while transient neurons are found in supragranular layers. Sawaguchi et al. (1989a) have shown that neuronal activity related to motor performance is distributed preferentially in the infragranular layers (V and VI) whereas activity related to visual reception is distributed predominantly in superficial and middle layers (II-IV). These results are in keeping with anatomical organization since: (*i*) Barbas and Mesulam (1981) have shown that projections from the inferotemporal cortex to the PFC terminate in lower layer III and layer IV; (*ii*) Deep layers of the PFC projects to the thalamus, caudate nucleus, and superior colliculus, and are thus likely to participate to initiation or preparation of a motor command.

Pharmacological tests

The relationship between anatomical locus and expression of delayed response behavior has been studied with injections of pharmacological products. Sawaguchi et al. (1989b) have shown that injections of bicuculline (antagonist of GABA) at different locus in the periprincipal region during a spatial delayed response task lead to different patterns of error: (*i*) Injection in the dorso-caudal region. An increased frequency of directional error is observed. The deficit is the same for both direction of response; (*ii*) Injection in the bottom region of the middle part of the principal sulcus. Selective directional errors are observed, probably related to a deficit in motor performance; (*iii*) Injection in the dorsal region of the caudal principal sulcus. The deficit is characterized by omission errors, i.e. a failure to respond during the go period; (*iv*) Injection in the dorsal bank of central caudal principal sulcus. Prolonged intertrial intervals are observed. This study shows that the processes involved in the correct execution of a DR tasks (detection of the spatial cue, memory, detection of the go-signal, response) are likely to be disturb independently.

The action of several neuromodulators have been tested. Sawaguchi et al. (1990a,b) have show that application of dopamine augments the activity of prefrontal neurons involved in temporal integration of visual cues and motor performance based on short-term memory (Cue, Delay, Go), whereas noradrenaline modulates activity of PFC neurons that may be related to visual reception and behavioral states (Precue, non differential Delay).

Local injections of selective antagonists of D1 dopamine receptors in PFC induced error and increased latency in the performance of a memory-guided oculomotor task (Sawaguchi and Goldman-Rakic 1991). The deficit was dose-dependent and sensitive to the duration of the delay. No effect was observed on the performance of a control task (visually-guided oculomotor task) stressing the specific role of dopamine receptor in mnemonic processes.

Aou et al. (1983a) have shown that reward-related activity in the prefrontal cortex is likely to be regulated by catecholamines (noradrenaline, dopamine). In contrast to catecholamines, acetylcholine non specifically influences neuronal activity, whether related to stimulus, bar press or reward (Aou et al. 1983b).

Metabolic studies

Recent studies with PET have shown a parcellation of the human prefrontal cortex similar to that observed in non-human primates (Petrides et al. 1993a). Normal subjects were tested in three tasks involving a series of cards with the same eight designs at various positions: (*1*) a control task requiring to point to a given prespecified design on each card presented; (*2*) a self-ordered task requiring to point to a different design on each card without repetition; (*3*) a conditional task requiring to point to a design on each card according to a previously learned association rule. A significant increase in activation was observed in the right mid-dorsolateral frontal cortex (areas 46 and 9) during the performance of the self-ordered task whereas a more posterior region of the prefrontal cortex (area 8) was active during the conditional task. These results are consistent with lesions effects in monkeys. Lesion of the periarcuate region (area 8 and rostral area 6) strongly impairs the performance of visual conditional tasks (Halsband and Passingham 1982; Petrides 1982), but has no effects on working memory tasks (Petrides 1991).

Working memory tasks activate the prefrontal cortex, unilaterally when it involves stimuli (Jonides et al. 1993; Petrides et al. 1993a) or bilaterally with verbal material (Petrides et al. 1993b).

Theoretical views

Goldman-Rakic (1987) has proposed that the prefrontal cortex is necessary for expression of behaviors guided by representation or internalized models and not when the behavior is guided by external stimuli. The mechanism of the prefrontal cortex is related to a distributed system of interconnected neural networks. Specific functions would thus come from dynamics of the system and interactions between independent networks, rather than from a strictly hierarchical processing based on the convergence through association regions. In a such a system, the “working memory” appears as a relevant concept which characterizes the specificity of prefrontal functions (Goldman-Rakic 1988).

A theory of a supra-ordinate prefrontal function has been proposed by Fuster (1988) to correlate a variety of anatomical, physiological and neurophysiological data. This supra-ordinate function is the integration of temporally separate events into a purposive behavioral structure (temporal contingencies). It necessitates at least two temporally symmetrical functions: (*i*) a provisional or short-term memory which permits referring to any event in a behavioral sequence to preceding events and to the original scheme of action; (*ii*) a prospective function which is an anticipation of events and the preparation for them (anticipatory set or preparation). The complementary function, proposed by Fuster, is the control of interference.

Shallice (1988) has proposed that the central function of the frontal lobe is a supervisory attention (SAS, Supervisory Attentional System) which allows to compete with distractions. It can be seen as a general and hierarchically structured planning program. Damasio (Damasio et al. 1990) has argued that the competence of the PFC is related social behavior. Grafman (1989) has introduced a model of frontal-lobe knowledge representation. In this model, managerial knowledge units (MKUs) are large-scale conceptual units, similar to those described for handling information in the framework of Artificial Intelligence (script; Schank 1982). MKUs contain an overlearned sequence of events that is retrieved automatically. When activated, MKUs manage the behavior by executing or responding to a series of event under attentional control.

Modeling studies

Dehaene and Changeux (1989) have proposed a model of prefrontal circuits for the acquisition of elementary rules of behavior. The network model has two levels of organization (Dehaene and Changeux 1989): (*1*) Level 1 is a one-to-one input/output network allowing correspondences between sensory inputs (object position, color) and motor output (orientation toward the object). Synapses at level 1 are modified according to the Hebbian/Anti-Hebbian rule; (*2*) Level 2 is made of a memory layer, with one-to-one afferent and efferent connections with sensory and motor layers, respectively, and a rule-coding layer, which modulates modality-specific (object position, color) afferent connections to memory units. Input-to-memory synapses undergo Hebbian-like activity-dependent changes, but are influenced by rule-to-memory modulation.

The behavior of the network with Level 1 only is strongly biased toward always choosing the same response, whatever the correctness of the choice (in DR task). Due to the anti-Hebbian component of the learning rule, the behavior reverses in a few trials and develops a bias toward the other response The network performs at chance on DR and DMS tasks. Activation of rule-coding units (Level 1+2) allows the selective extraction of sensory features (position, color). Selective memorization is thus obtained by input-to-memory connections and sustained activity due to excitatory self-connections. Active memory units gate input-output relations for the choice. Learning consists in a search for the correct pattern of activation of the rule-coding layer (through frequent random modifications). The performance of the network is compared to the performance of human babies and monkeys. With Level 1, the network performs in the same way as 7 1/2-9-month-old babies and 1 1/2-2 1/2-month-old monkeys or prefrontal monkeys. On the other hand Level 1+2 network is comparable to 12-month-old babies and 4-month-old monkeys.

An interesting feature of this model is the use of a learning rule which allows to learn sequences of events (triad synaptic; Dehaene et al. 1987). However, an important limitation is related to the use of rule-coding units, which appear not very realistic at the neuronal level.

Dehaene and Changeux (1991) continued their modeling of prefrontal functions with focus on the Wisconsin Card Sorting Test. Both theoretical analysis and neural modeling are provided. An analysis in terms of rule-selecting machines allows to characterize the way to succeed in WCST: (*i*) the ability to change the current rule rapidly when a negative reward occurs; (*ii*) the ability to memorize previously tested rules and to avoid testing them twice; (*iii*) the ability to reject some rules a priori by reasoning on the possible outcomes of using one rule or the other. The network model has quite the same architecture as in the model for the DR task, excepted that: (*i*) memory units do not directly activate output units, but activate "intention" units, each coding for the choice of a reference card; (*ii*) memory-to-intention connections are modulated by rule-coding units specifying the sorting rule (color, form, number); (*iii*) the network is supervised by an "error" cluster which becomes active when a negative reward is obtained and then transform the rule-coding units into a "generator of diversity". Negative reward leads to a short-term depression of the connections of the currently active rule-coding unit.

This model extends the previous one (Dehaene and Changeux 1989) to a more complex task. It is interesting to note that quite similar local mechanisms are used in both models, but with different architectures. It argues for the fact that complex tasks do not require more complex mechanisms than simple ones, but only more complex interactions, in particular between internally generated signals.

Cohen and Servan-Schreiber (1992; see also Servan-Schreiber et al. 1990) have developed a series of models, which address issues on the prefrontal functions in relation to internal representation of contextual information and the role of the dopaminergic system. Models of three psychological tests (Stroop task, continuous performance test, lexical disambiguation) have been constructed using back-propagation-based neuronal networks and rule-coding units. The effect of dopamine on neurons was modeled by an action on the excitability function (modification of the relation between depolarization and firing frequency) and results in specific disturbing effects resembling schizophrenic performance. On the basis of these models, Cohen and Servan-Schreiber (1992) have argued that schizophrenic behavioral deficits are likely to arise from a disturbance of the dopaminergic neuromodulatory effect in the prefrontal cortex.

Of related interest are models concerning the generation of sustained activity as observed in prefrontal neurons during delay tasks. Dehaene and Changeux (1989, 1991) have proposed a solution based on neuronal circuits with recurrent excitatory connections forming reverberant circuits. Units in a fully recurrent perceptron learn to produce sustained activities of the type recorded in cortical neurons (Zipser 1991).

General neural network models have been developed to address problems where processing is critically linked to time. The simpler approach is to turn temporal sequences into spatial patterns through delay-lines and to train the network with a standard backpropagation algorithm (time-delay neural networks, Waibel 1989). Another approach is provided by recurrent networks (Williams and Zipser 1989; Elman 1990). These back-propagation-based networks can encode and retrieve on-line complex temporal sequences. In order to have an on-line recognition, *recurrent networks* have been proposed, where outputs are fed-back to the input layers: partially recurrent networks, with context units (Elman 1990) or fully recurrent networks (Williams and Zipser 1989). However, these networks have difficulties with variable delays between successive inputs, since they are fed at clock times dependent on the internal dynamic of the network. Dynamic associative memories have also been proposed (Amit 1988) for sequence retrieval. But their storage abilities are related to a fixed delay and long sequences cannot be learned. Greater flexibility is possible in guided propagation networks where units learn to predict the next events from previous ones and from a dynamic context (Béroule 1988). In the model introduced by Ans (1990) for learning of temporal sequences, recall of a sequence can be evoked by the occurrence of a contextual item, and its reproduction can be driven according to a varying rhythm.

3 DESCRIPTION OF THE MODEL

In this section, we first summarize a set of anatomical, physiological, and psychological data on the prefrontal cortex and connected sensory and motor structures, in the form of 3 assertions. Each assertion reflects a major constraint to build a plausible model and concerns (*C0*) **training protocols for the acquisition of goal-directed behaviors**; (*C1*) **sensory and motor structures connected to the prefrontal cortex**; (*C2*) the **prefrontal cortex** itself. Then, we give an interpretation of these constraints in the framework of cortical modeling (**chapter 2**), in order to build a neural network model.

Modeling constraints

The three constraints are the following:

(*C0*) *The training protocols used for the acquisition of sensory-motor sequences are progressive stage-by stage procedures. Learning does not occur in a single stage, but with a series of successive stages approaching the final performance.*

When animals are trained to perform complex sensory-motor sequences, their behavior is progressively shaped by successive changes in reward contingencies. Once a given behavior is established (as measured by the performance rate), changing the task rule is responsible for the development of a new behavior, since the reward becomes contingent to a new goal. Thus at each stage, a new behavior is built on the basis of previous abilities.

(*C1*) *The prefrontal cortex receives integrated information from major sensory, motor and limbic structures. Information in these structures connected to the prefrontal cortex can be represented by a* ***position code****, along primary or secondary indices or behavioral sensory or motor parameters within specific modalities, in direct relation to sensory inputs or motor outputs. Processing in these structures should allow the modulation of sensory inputs or motor outputs by behavioral conditions.*

(*C2*) *Connectivity of prefrontal circuits allow large interactions between sensory, motor, and internal signals such as drive and reinforcement. The basic processing property of prefrontal circuits is* ***the control of a sustained activation*** *as a basis of time integration. The active character of prefrontal functions is related to a drive which determines the ability to form new behavioral structures. The prefrontal cortex is sensitive to reinforcement contingencies.*

Representation of the external world

The constraint *C1* stresses that sensory and motor variables can be organized in maps, which reflect variations of the value of a parameter (form features, direction of movement) across one or more dimensions of the biological substratum (Knudsen et al. 1987). As a result units in sensory and motor structures (*SM* units) can be grouped in a one-dimensional map along sensory or motor parameters. Information is represented by a position code.

It has been frequently suggested that the same anatomical pathway is used for an intended action and the effective realization of the action. For instance, a desired trajectory can be represented in a body reference frame by the same group of neurons that code the motor command. This property allows to give a simple role to *SM* units. The input of a *SM* unit corresponds to the intended effect of the action resulting from the unit activation. If the unit is related to the production of an arm movement, its input is the target of the movement as defined by the inverse relation between the target and the movement. If the unit is tuned for a sensory pattern, the unit’s output can be considered as an action which centered the pattern on the receptor (for instance an ocular movement).

In this model, we will not consider the detail of such sensory-motor transformations (Burnod et al. 1992; Otto et al. 1992; **chapters 3** and **4**), but rather the way to integrate them in a goal-directed behavior.

Network architecture

SM units are directly connected to the input and output pathways (*I* and *O*). On the other hand, units in the prefrontal cortex (*PF* units) do not code a priori for specific patterns (constraint *C2*). *PF* units have no direct relations with the external world, but interact with it through *SM* units. In this sense, a set of *PF* units can be viewed, in the words of PDP, as a hidden layer. The constraint *C2* also stresses that *PF* units are connected to two specific pathways: (*i*) a drive pathway *D* which is made active at the beginning of each behavior of the network; (*ii*) a reinforcement pathway *R*, which is activated when a correct behavior is produced by the network.

We can give the following formal description of a network of *SM* and *PF* units: (*i*) Each *SM* unit is connected to a unit in the input pathway *I* and to a unit in the output pathway *O*; (*ii*) Each *PF* unit is connected to the drive pathway *D* and the reinforcement pathway *R*; (*iii*) Each *PF* unit projects to a subset of *SM* units; (iv) Each *SM* unit projects to a subset of *PF* units.

This architecture allows general interactions between sensory and motor events. Sensory events can activate a subset of *SM* units through the input pathway *I*, which activate a subset of *PF* units. Activated *PF* units can in turn activate a subset of *SM* units, producing for instance a motor event through the output pathway *O*. The range of possible behaviors depends on: (*i*) The information available to *SM* units through input and output pathways *I* and *O*; (*ii*) The ability of *PF* units to relate sensory and motor activations. The function of such network is defined by the dynamics of processing units and the adjustable connection coefficients between processing units. This is the object of the next paragraph.

Rules for neural processing

In this paragraph, we describe the processing rules of *SM* and *PF* units, respectively. These rules should not be chosen arbitrarily, but should be designed in close relation to constraints *C1* and *C2*. For a sake of simplicity, equations are written in relation to the implementation of the network and we have omitted the terms related to the stability and the convergence. A complete description is given in Appendix.

Rule for SM units. Each *SM* unit combines information from an input pathway *I* and some *PF* pathways and provides it to the output pathway *O*. The constraint *C1* stresses that activity of *SM* units is related to sensory or motor parameters (through *I* or *O*), but can also be modulated by behavioral conditions (through *PF*). To allow such modulation, we assume that *SM* units perform multiplicative combinations between inputs of different origins. A unit with to two afferent pathways x_I and x_{PF} is controlled by the following equation

$$y(t) = F(x_I(t)\ x_{PF}(t)\ ) \qquad (5.1)$$

where *y* the output signal and *F* a binary stochastic function (see Appendix). Note that *t* is a quantized time which describes the course of processing. We assume that the interaction between the two pathways is not modifiable (no learning coefficient). Equation 5.1 is a simplified form of *gating* (Equation 2.2).

Rule for PF units. The constraint *C2* gives the characteristics of *PF* units. These units differ from *SM* units for the following reasons: (*i*) They receives inputs from the drive pathway *D* and from some *SM* units; (*ii*) They display sustained activations; (*iii*) They are sensitive to a reinforcement signal. Figure 5.1A shows a unit with two input pathways x_1 and x_2 , and a reinforcement pathway *r*, where pathways *1* and *2* can correspond either to *D* or to *SM*. Activation is described by Equation 5.2:

$$\begin{cases} A(t) = MAX[L_1(t)x_1(t),\ L_2(t)x_2(t)] \\ A'(t) = MAX[x_1(t),\ x_2(t)] \end{cases}$$

and

$$y(t) = \begin{cases} g[A(t)] \text{ if } y(t-1)=0 \\ else \begin{cases} g[A'(t)] \text{ if } A'(t)\neq 0 \\ else\ g[\eta y(t-1)] \end{cases} \end{cases} \qquad (5.2)$$

where *g* is the function defined by

$$g(z) = \begin{cases} 1 \text{ with prob } z \\ 0 \text{ with prob } 1 - z \end{cases}$$

where x_1 , x_2 are the input signals, L_1 , L_2 the learning coefficients, *y* the output signal and η a parameter. Equation 5.2 is a similar to Equation 2.3, but it is written for two input pathways. It expresses that the unit is likely to become active ($y(t) = 1$) for an incoming activation (A), to stay active for a while (with a probability $\eta y(t-1)$) and then to return to rest ($y(t)=0$) for a new activation (A'). Transitions between rest and sustained states depend on the learning coefficients which are modified according to Equation 5.3, derived from Equation 2.6 (*adaptive timing*):

$$\begin{cases} L_1(t=0) = L_0 \\ \Delta L_1(t,t+1) = e_1(t)[-\alpha x_2(t)y(t-1)+\beta\bar{x}_2(t)\bar{y}(t)r(t)] \\ L_2(t=0) = L_0 \\ \Delta L_2(t,t+1) = e_2(t)[-\alpha x_1(t)y(t-1)+\beta\bar{x}_1(t)\bar{y}(t)r(t)] \end{cases} \qquad (5.3)$$

where α and β are parameters and L_0 the initial value of learning coefficients, $\bar{x}_1$, $\bar{x}_2$ and e_1 , e_2 are non conditional and conditional input traces, respectively, and $\bar{y}$ the output trace (Sutton and Barto 1981; see Appendix). A trace allows to keep a non-zero value for some period of time after the occurrence of a signal (see Fig. 5.1B; Sutton and Barto 1981). Figure 5.1B illustrates the behavior of the Equations 5.2 and 5.3. Equation 5.3 predicts that the learning coefficient L_1 would successively (Fig. 5.1B): (*1*) decrease by α when the sustained activation of the unit by the pathway *1* is terminated by activation of the pathway *2* ($e_1(t)\ x_2(t)\ y(t-1)$); (*2*) increase by β when a reinforcement signal occurs ($e_1(t)\bar{x}_2(t)\bar{y}(t)\ r(t)$). The index $I=\alpha/\beta$ characterizes the comparative influence of reinforced and non-reinforced behaviors. Before learning, coefficients are assumed to have a low value. According to Equation 5.2, the unit has a low probability of becoming activated (sustained activity). Repetitive presentations of a reinforced sequence lead to an increasing learning coefficient. Thus, after learning, the unit becomes surely activated when the first event of the sequence is presented, predicting the occurrence of a reinforcement. In this formulation, we have assumed that only the transition to the active state (sustained activity) is controlled by a learning coefficient. Equations 5.2 and 5.3 define the rule R2, which models operation and adaptation in prefrontal circuits.

This process is quite different from Hebbian learning since, in this case, Hebbian conditions alone (pre- and postsynaptic activation) are ineffective in modulating the learning coefficient. While the Hebbian rule is sensitive to temporal coincidence, the present rule allows to store relations between non simultaneous events (through the sustained activity and the traces). This rule defines the ability of *PF* units to mediate of cross-temporal contingencies.

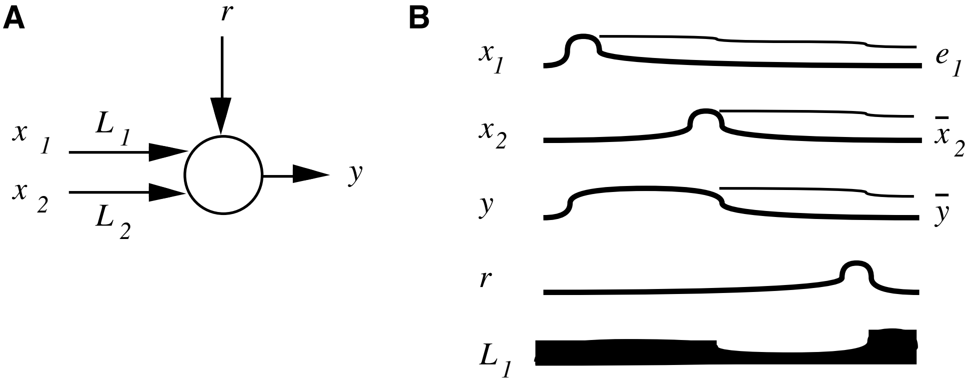

Figure 5.1. Activation and learning rules for prefrontal units. Illustration of the properties of Equations 5.2 and 5.3 (rule R2). **A**. The unit has two weighted input pathways x_1 (L_1) and x_2 (L_2) , a reinforcement pathway *r*, and an output pathway *y*. **B**. Qualitative variations of the learning coefficient L_1 when input, output and reinforcement pathways are activated as shown in the tracings (*thick lines*). The input and output traces (see Text) are shown on the same tracing that inputs and output respectively, with *thin lines*. Note the conditions which elicit change in the learning coefficient: decrease with the end of the sustained activity and increase with the reinforcement.

Training protocol - Example of the delayed-response task

Using the constraints *C1* and *C2*, we have described a neuronal network and its dynamics which allows: (*i*) the production of behaviors (Equations 5.1 and 5.2); (*ii*) the storage of information (Equation 5.3). The main characteristic of neural network models is the ability to learn with examples by modifying the values of connections coefficients between processing units of the network (Rumelhart and McClelland 1986). Which examples are given to the network, in what order they are given are questions which must be answered using the constraint *C0*.

The constraint *C0* emphasizes that stage-by-stage training protocols are used for the acquisition of goal-directed behaviors. In the following, we will take the example of the delayed-response task for illustration (see Fig. 2.5). Animals learn a delayed response task by a protocol, which may be illustrated by at least three stages. 1) Initially, they would learn to reach one of the two levers (*movement*) whenever they wish to and receive a drop of liquid (*reinforcement*). Through learning, the lever becomes associated with primary liquid reward and constitutes a conditioned incentive stimulus (*drive*) which, on the basis of the thirst drive of the fluid-deprived animal, creates an internal motivational state eliciting the movement (Toates 1986). 2) In the next stage, the animal is only allowed to reach toward a lever after a trigger light (*go signal*) has come up. This light now constitutes the incentive stimulus and determines the time of reaching. 3) In the final stage, the instruction light (*instruction stimulus*) comes up before the trigger light and determines which lever needs to be touched after the trigger light. Thus, there is the initial acquisition of the task contingency for stage 1, and there are two changes in reward contingency when advancing to stages 2 and 3. Within each task, the task contingency remains constant, but performance increases according to the respective learning requirements. Although this three-stage protocol is greatly simplified in comparison to real experimental training, it provides a functional description of major behavioral changes which occur during the training of the monkey.

The successive learning stages can be described by a tree, as shown in Fig. 5.2. The top of the tree is the *drive* and the leaves are the successive events of the sequence. The rule to traverse the tree is to start at the top (*drive*) and to take the left branches before the right one. Embedded boxes represent the sub-sequences built at each training stage. For each box, there is a specific training set, involving the drive, the reinforcement and the events proper to the box. The training set is repeatedly presented until a given performance rate (reinforcement rate) is reached. Then the box is included in a bigger one corresponding to the following training stage.

Such a training protocol is quite different from the protocols classically used for neural networks. Generally, networks are trained using pairs of associated patterns (input/output associations). The logic is that of classical conditioning: learning can occur even when the output of the network is incorrect, the output being unconditionally given by the teacher. Protocols used to train monkeys are more suitably described in the framework of reinforcement procedures (Hinton 1987). In these procedures, the network is supervised by a scalar signal corresponding to correct or incorrect behavior (for instance, 1 or 0, respectively). In this case, the network must be able to produce sometimes the correct behavior before any training (logic of operant conditioning).

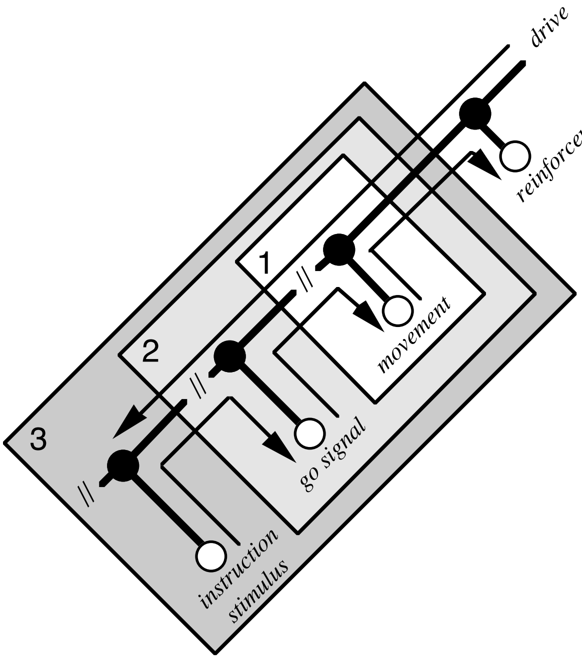

Figure 5.2. Tree representation of a sequence made of the successive following events: *drive*, *instruction stimulus*, *go signal*, *movement*, *reinforcement.* The black circles are the nodes of the tree, the white circles the leaves. The tree is first traversed from the right to the left (leftward arrow) until a leaf is found. Different subsequences corresponding to the successive training stages (1, 2, 3) are embedded in the tree when different terminations (symbol //) are used (embedded boxes; 1. *drive*, *movement*, *reinforcement*; 2. *drive*, *go signal*, *movement*, *reinforcement*; 3. *drive*, *instruction stimulus*, *go signal*, *movement*, *reinforcement*).

4 BEHAVIOR OF THE MODEL - SIMULATIONS, RESULTS AND PREDICTIONS

In this section, we present a quantitative evaluation of our model. We have performed computer simulations of a neural network designed as explained in the previous section. The network was trained to execute a delayed response task using a stage-by-stage protocol. The results concern: (*i*) The global behavior of the network (as measured by the performance rate); (*ii*) The behavior of units in the network (measured by units output activation) both during the training and once the training is completed. While the behavior of the network can be compared with the behavior of the monkey, unit activations can be compared with available data on neuronal activity in the cortex of behaving monkeys.

Computer simulations - Methods

Network architecture and representation of events. We have used a network architecture corresponding to the general description of the previous section. The network is shown in Fig. 5.3:

- The set of *SM* units is made of 8 units. Each unit (*circle* in Fig. 5.3) allows the representation of an event through its afference from the input pathway *I* and its efference to the output pathway *O*. Events may be redundantly represented.

- The set of *PF* units is made of 32 units, shared into 8 classes (*squares* in Fig. 5.3).

- Each class of *PF* units is reciprocally connected to one *SM* unit and receives non reciprocal projections from two other *SM* units (the connection between a class and a unit corresponds to connections to each unit of the class).

The events corresponding to a delayed response task trial are represented in input or output pathways of the network (dashed boxes *I* and *O*; Fig. 5.3). The notations for the task events are the following: (*i*) *l-left* and *l-right*: positions of left and right levers; (*ii*) *m-left* and *m-right*: movements toward the levers; (*iii*) *gs*: go signal; (*iv*) *i-left* and *i-right*: instruction stimuli. For a sake of clarity, events (and thus processing units) have been grouped according to their order of appearance in the training protocol.

We have made the following assumptions: (*i*) A redundant representation is used when the same event occurs in different situations (go signal); (*ii*) All the units in a given *PF* class have the same relationships with *SM* units; (*iii*) There are no interfering events excepted during the first training stage, where movements (*m-left*, *m-right*, *m-3*, *m-4*) toward four levers (*l-left*, *l-right*, *l-3*, *l-4*) are possible (but only two are corrects). These assumptions are discussed at the end of the section.

Training protocol. The training protocol was as shown in Fig. 5.4. It was made of three stages (1, 1'+2, 2'+3) where stages 1, 2 and 3 correspond to those described in the previous section and stages 1' and 2' are intermediary stages which allow the transition between successive behaviors. Note that each trial began with the delivery of a drive signal *d* and ended with a reinforcement signal *r* when the behavior is correct. A delay of length δ (measured in relation to the quantized time step used in Equations 5.1, 5.2, and 5.3) was introduced between the instruction stimulus and the go signal in the stage 3. The training at each stage was performed until a correct and stable level of performance was reached.

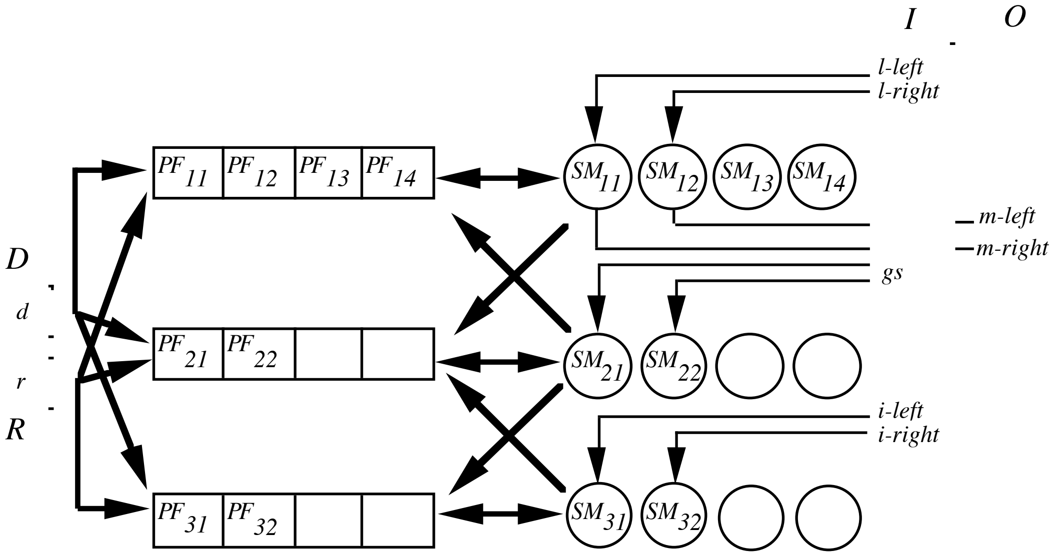

Figure 5.3. Architecture of the network for the acquisition of a delayed response task, used for computer simulations. Circles correspond to processing units, squares to classes of processing units (each class in made of 4 units). *Thin arrows* are for one-to-one connections (between pathway *I* and *SM* units, between *SM* units and pathway *O*). *Thick arrows* are for one-to-many and many-to-one connections. Arrows between *SM* units and *PF* classes indicates that each unit SM_{ij} is reciprocally connected to each unit of the class PF_{ij} , and projects non reciprocally to each unit of the class PF_{kj} with k = i - 1 and k = i + 1. Arrows between *D* and *PF* classes indicates projections from *D* to all units in all *PF* classes (idem for *R*).

Data collection. The results were collected as follows:

- At each training stage (1, 1'+2, 2'+3), we examined the network during the execution of a trial. We noted whether the trial was correct or not and recorded the neuronal activities during the trial (units' output).

- For each stage, individual trial data were collected by block of correct or erroneous trials to compute cumulative histograms of activity.

- Individual trial data were collected by block of trials to compute the performance rate during the acquisition of the task.

- Cumulative histograms were collected to compute the variation of block activity during the acquisition of the task.

Details concerning simulations are given in Appendix.

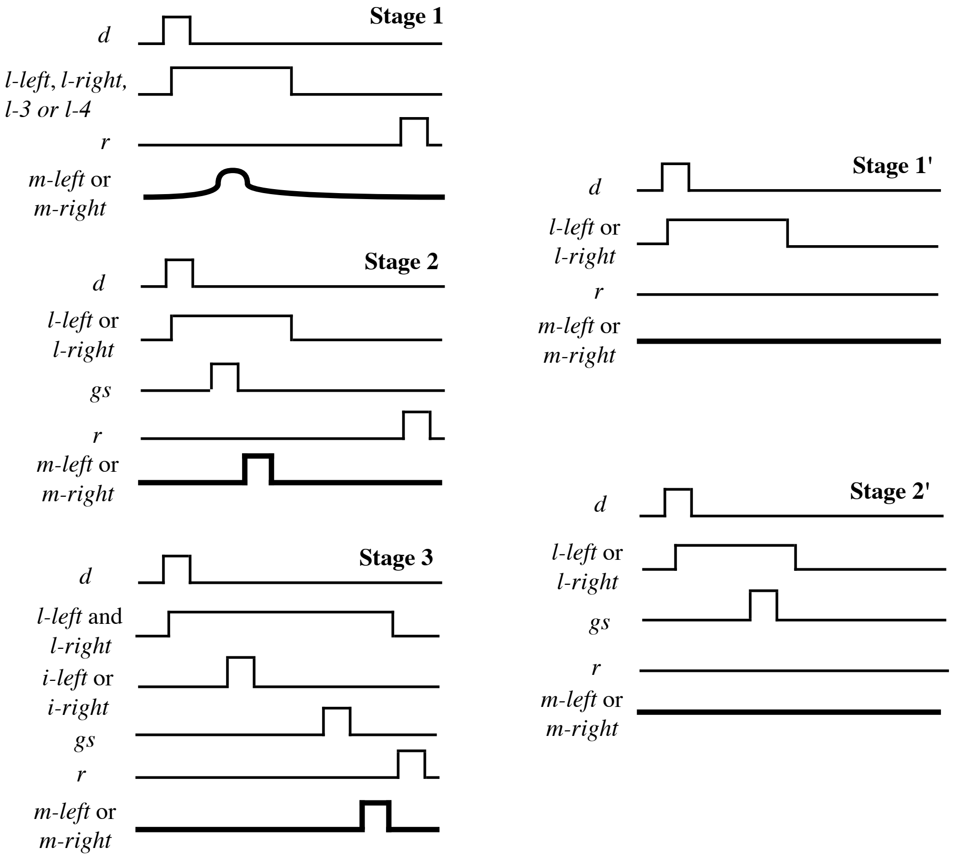

Figure 5.4. Stage-by-stage training protocol for the acquisition of the delayed response task, used in computer simulations. At each stage, input pathways of the network depicted in Fig. 5.3 are activated in a given temporal order as shown by the tracings (*thin lines*). The expected behavior is shown with *thick lines*. The stages are executed in the following order (left to right and top to bottom): 1, 1’, 2, 2’, and 3.

General behavior of the network

The network was trained in successive stages. At each stage, the network was presented with a number of trials, until the required behavior is reached (see Fig. 5.4). The performance rate of the network, as obtained by computer simulations, is shown in Fig. 5.5: the rate increases during the acquisition of a particular behavior and decreases when changing behavior. After completing the training, the network is able to produce the correct behavior when presented with a set of events corresponding to a DR task trial. The global behavior of the network thus reflects qualitatively the behavior of a monkey during similar training.

Note that the variations of the performance as depicted in Fig. 5.5 depend on the rate of changes of learning coefficients (Equation 5.3). Thus only qualitative comparisons with experimental results are possible.

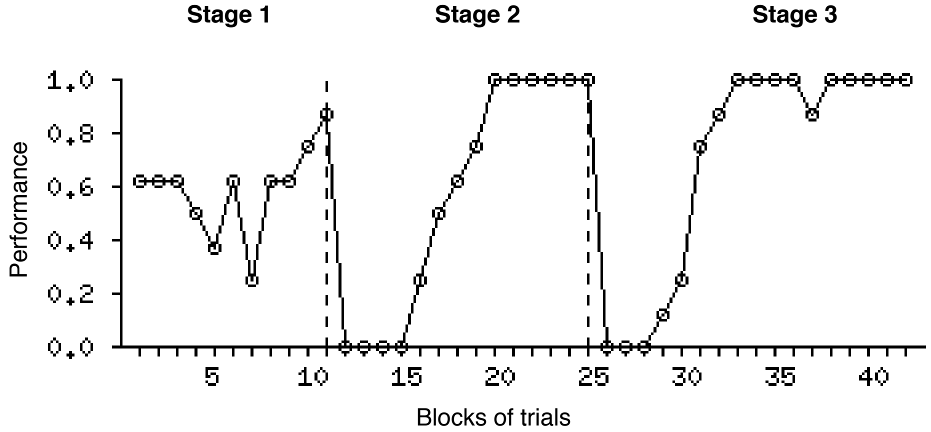

Figure 5.5. Performance rate of the network as obtained by computer simulations. Vertical dashed lines delimit training stages (1, 1'+2, 2'+3). Each horizontal division corresponds to a block of 8 successive trials. The corresponding ordinate value is the proportion of reinforced trials in the block. Parameter values are given in Appendix.

Activities after learning

Figures 5.6 to 5.11 illustrate activities of units in the network (Fig. 5.3) during the successive stages of training. Patterns of activity can be classified in several categories, according to the temporal relationships between task events and peaks of activity: anticipatory, stimulus-related, delay-related, preparation of movement, movement-related. Several patterns are observed in *SM* and *PF* units.

SM units. *SM* units display transient activities time-locked to the onset of events (Figs. 5.6, 5.7, 5.8). Unit SM_{11} (Fig. 5.6A) is active just before the movement, and is differentially active for left vs right movements. Similar results are observed in units SM_{12} , which is preferentially related to rightward trials. Units in Fig. 5.7 (SM_{21} , SM_{22}) are active following the occurrence of the go signal. Figure 5.8 shows *SM* units related to the instruction stimuli. These types of activity have been observed experimentally. Transient activities have been found in the inferotemporal cortex, related to instruction stimuli or go signal (Mikami and Kubota 1980; Fuster et al. 1985), in motor and premotor areas, related to instruction stimuli, go signal, or movements (Alexander and Crutcher 1990; di Pellegrino and Wise 1991).

PF units. Within each *PF* class, all the units display similar patterns of activity (not shown). *PF* units of different classes provide different patterns of activity, according to their relation to *SM* units (Figs. 5.9, 5.10, 5.11). The most interesting one is the differential delay activity, that is a sustained activity between the onset of the instruction stimulus and the onset of the go signal specific for right vs left trials (classes PF_{21} and

PF_{22} ; Fig. 5.10A and 5.10B, stage 3). Other patterns are found such as differential anticipatory activity before the movement (classes PF_{11} and PF_{12} ; Fig. 5.9A and 5.9B, stage 3) and before the instruction (classes PF_{31} and PF_{32} ; Fig. 5.11A and 5.11B, stage 3).

All these patterns have been described in the prefrontal cortex during the delayed response task (Fuster 1973; Niki and Watanabe 1976; Komatsu 1982; see also for oculomotor paradigms, Funahashi et al. 1990). These results appear thus consistent with experimental data. Further results concern learning-dependent changes of activity in the processing units. Since there are few studies on neuronal activities during learning, these results can merely be considered as predictions of the model.

Modulation of activity during learning

The model predicts the changes of neuronal activities in the course of learning. Unit outputs are modulated according to the dynamics of processing (Equations 5.1 and 5.2), and activity-dependent variations of learning coefficients (Equation 5.3). Changes concern not only the level of activity, but also the temporal pattern and the relation to external events.

General considerations on learning-dependent changes of neuronal discharges. Since processing units are progressively involved during the course of learning, the number of task-related units increase as the learning proceeds. Moreover activities in task-related units are lower during the early phase of learning, reflecting the initial low value of learning weights. These findings are consistent with those of Kubota and Komatsu (1985) who studied evolution of learning related activity during a go/no-go discrimination task.

SM units. Figures 5.6, 5.7 and 5.8 show the evolution of the pattern of activity for 6 *SM* units. The following characteristics are observed: (*i*) Units display transient activity (1 time step of the simulation) time-locked to sensory or motor events (movement in Fig. 5.6, go signal in Fig. 5.7, and instruction stimulus in Fig. 5.8); (*ii*) Units become active when a given sensory or motor event is introduced (at stage 1 in Fig. 5.6, at stage 2 in Fig. 5.7, and at stage 3 in Fig. 5.8); (*iii*) Once a unit becomes active, it keeps the same pattern of activity and the same relation with task events in the following training stages.

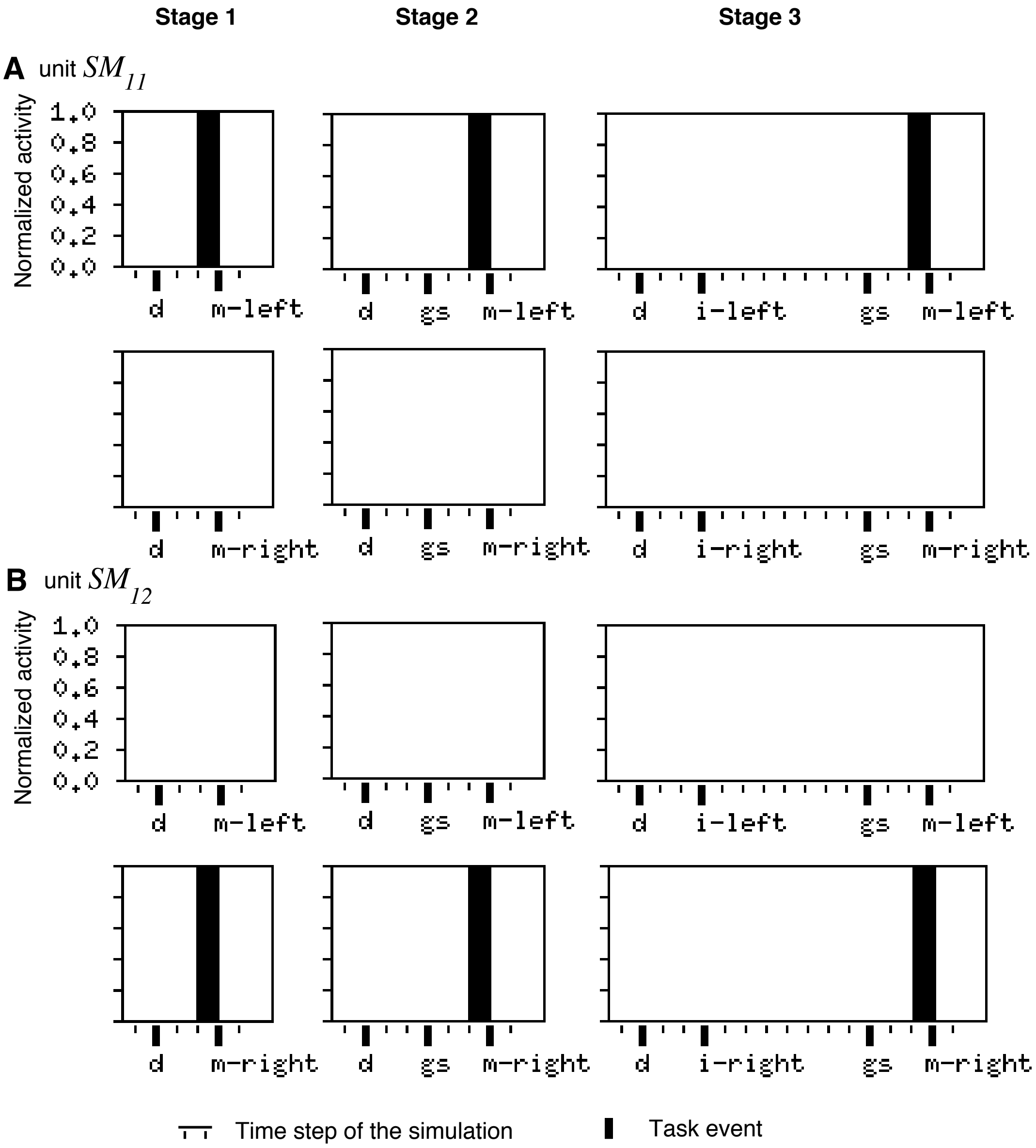

Figure 5.6. Evolution of output activity of 2 *SM* units (top to bottom; **A**, **B**) during the training stages (left to right; 1, 2, 3). Units SM_{11} (**A**) and SM_{12} (**B**) display a transient activity (1 time step) before the leftward and rightward movements, respectively, in the 3 training stages. Each histogram shows the mean activity of the unit in 15 successive reinforced (LEFT or RIGHT) trials, from just before the drive to just after the movement. The horizontal axis is the time axis. Horizontal divisions (*thin vertical lines*) correspond to the time step of the simulation (1 division = 1 iteration). Task events are indicated with *thick vertical lines*. The reinforcement event is not shown. The mean normalized activity (percentage of trials during which the unit is active) is displayed on the vertical axis.

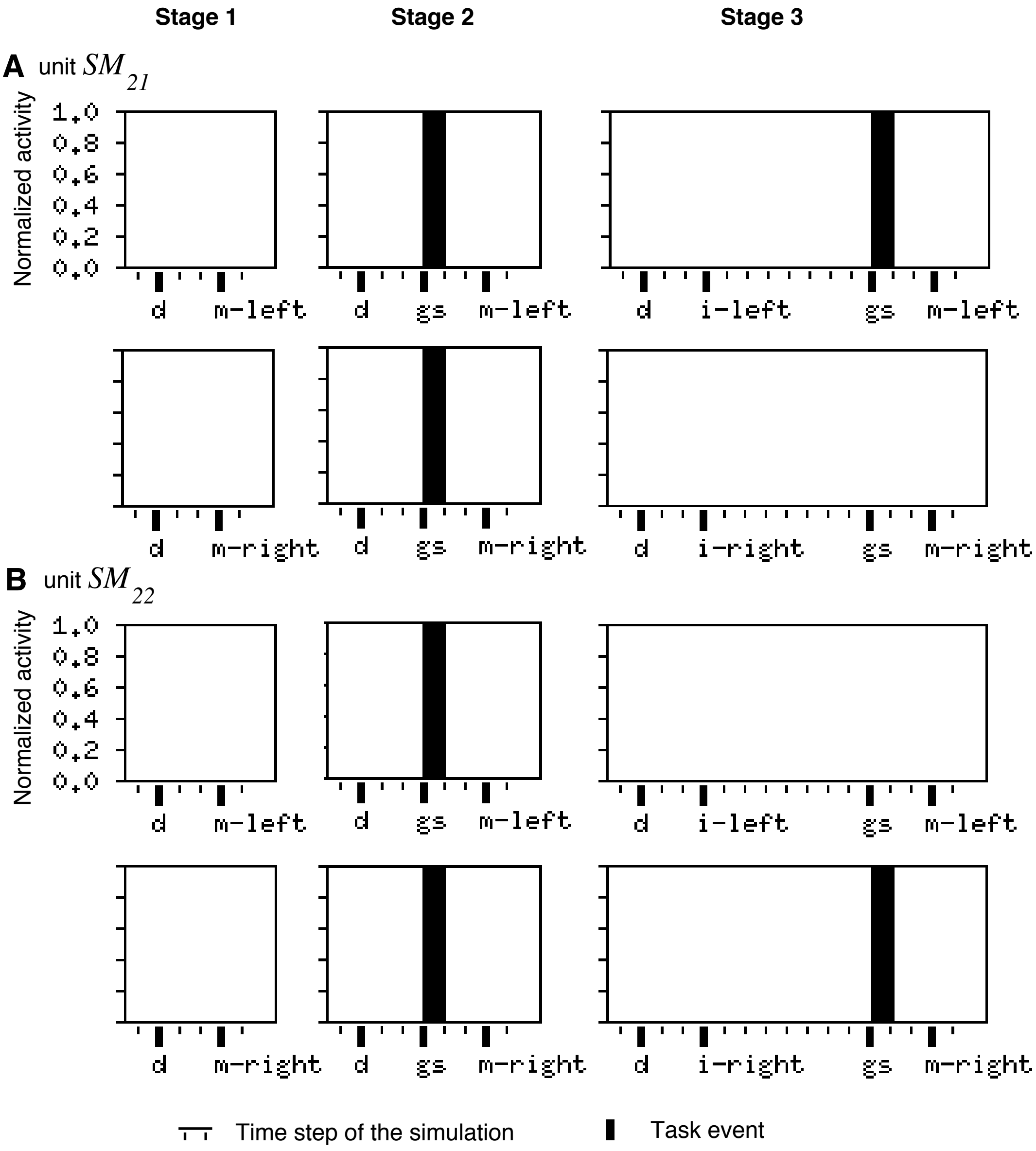

Figure 5.7. Same as Fig. 5.6 for units SM_{21} (**A**) and SM_{22} (**B**). Both units are active with the go signal (*gs*) at stage 2, and are preferentially for LEFT or RIGHT trials at stage 3.

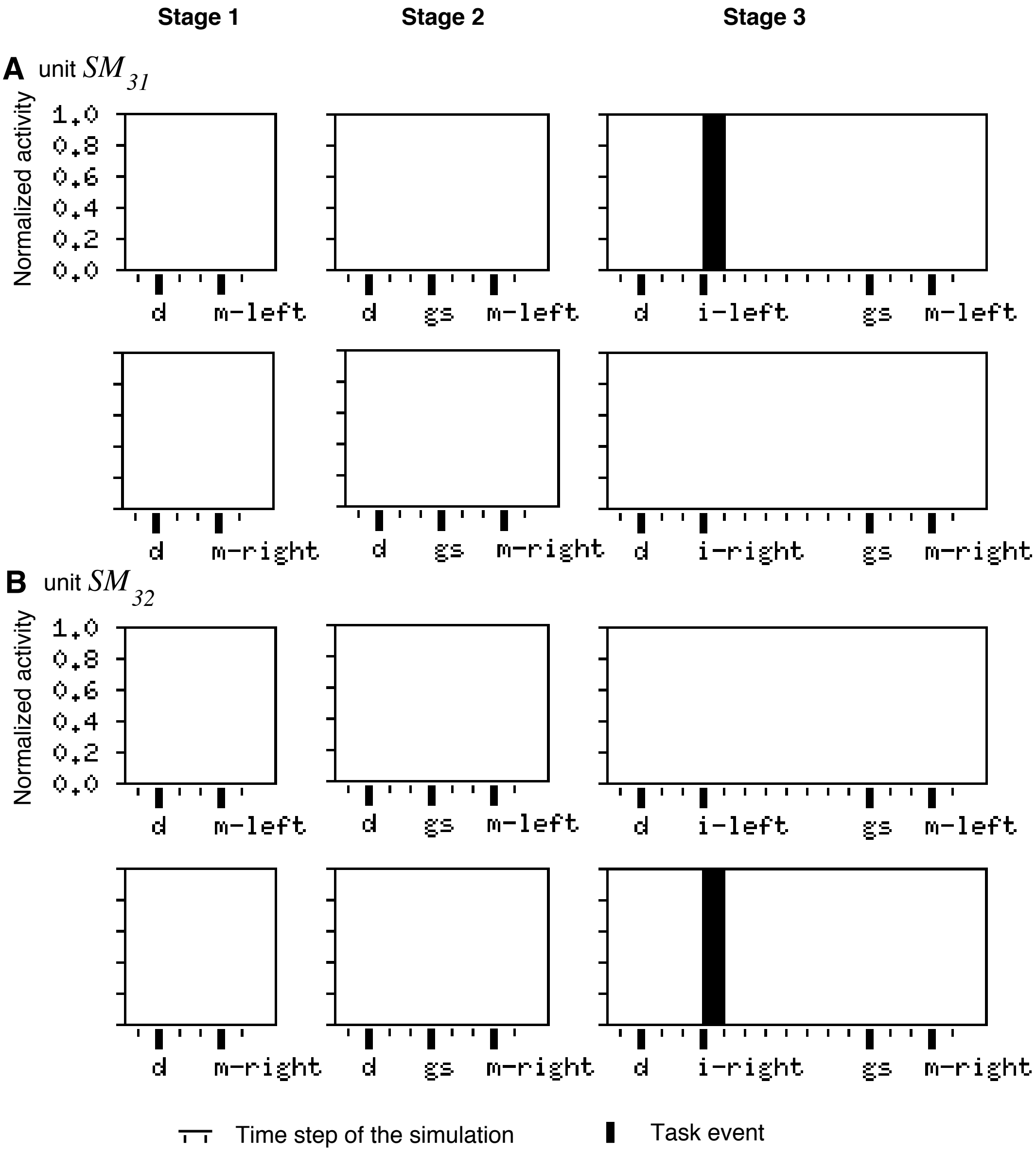

Figure 5.8. Same as Fig. 5.6 for units SM_{31} (**A**) and SM_{32} (**B**) . Units become active at stage 3 and display differential activity for left and right instruction stimuli.

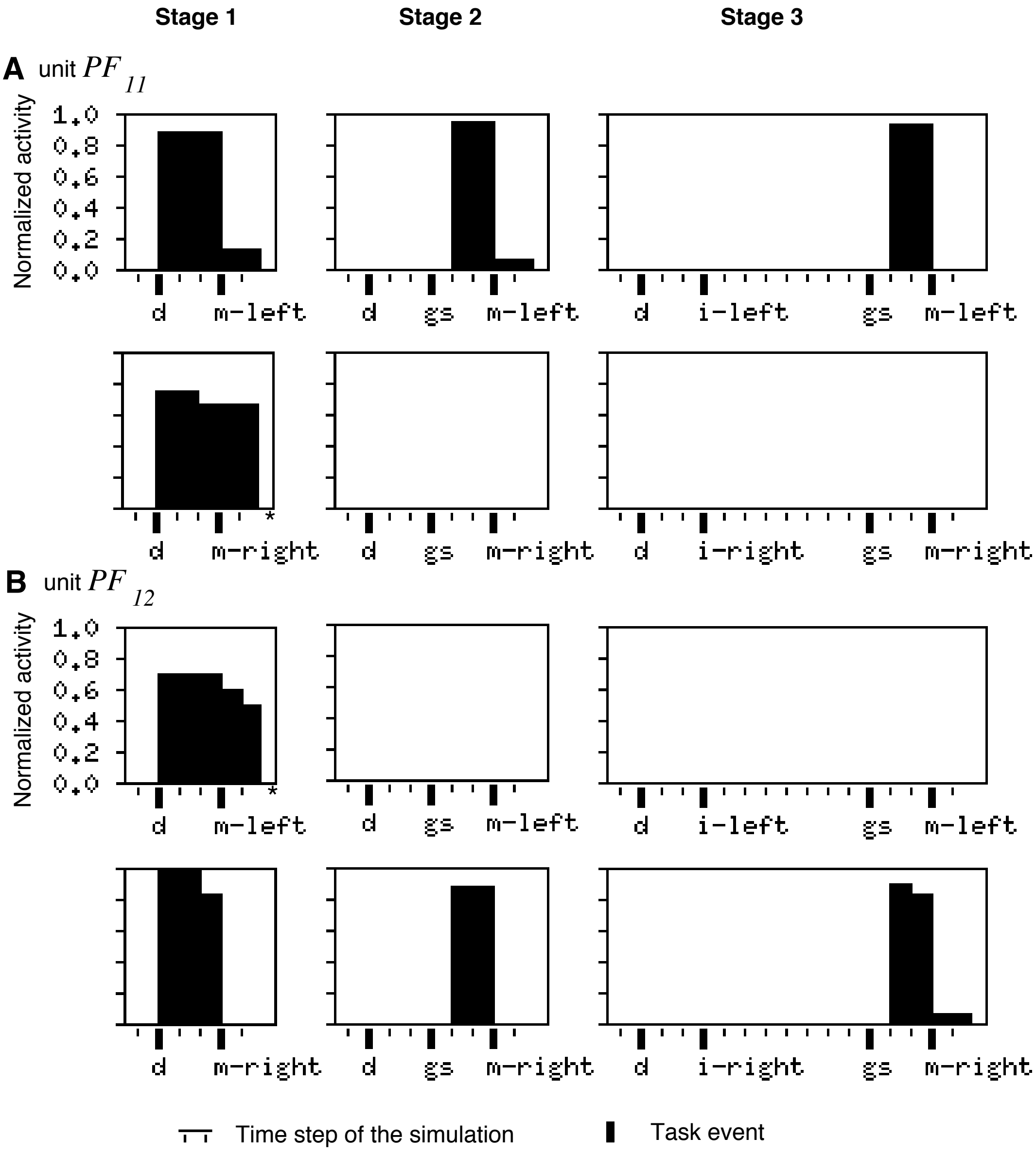

Figure 5.9. Evolution of output activity of 2 *PF* units (top to bottom; **A**, **B**) during the training stages (left to right; 1, 2, 3). Units PF_{11} (**A**) and PF_{12} (**B**) are sustainedly active (>1 time step) before LEFT and RIGHT movements, respectively, in the 3 training stages. Note that activity always ends with the movement. Histograms are the same as in Fig. 5.6. The symbol (*) indicates that sustained activity continues after the movement, but is not shown on the histogram.

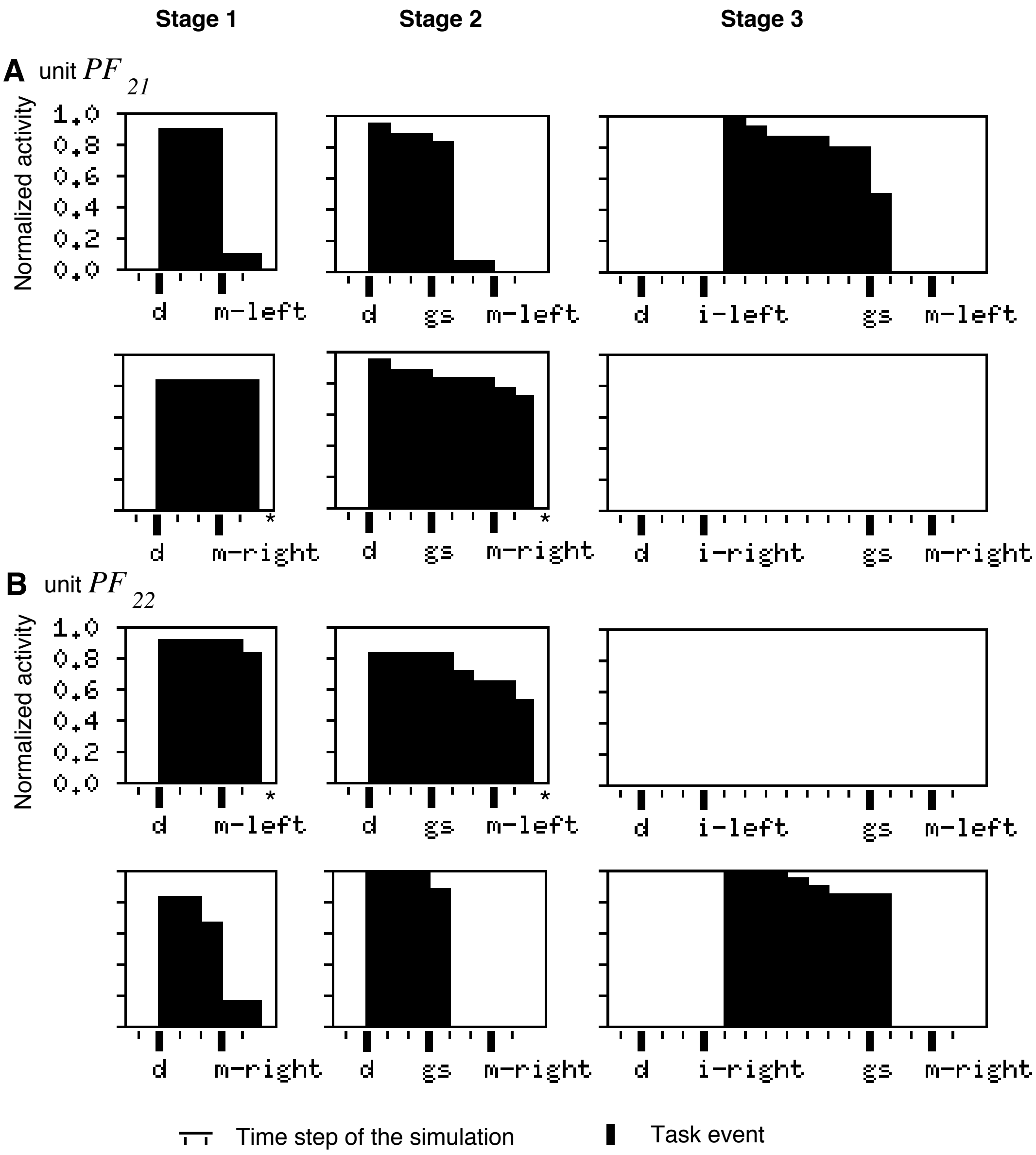

Figure 5.10. Same as Fig. 5.9 for units PF_{21} (**A**) and PF_{22} (**B**) . These units are sustainedly active in the 3 training stages: between the drive and the movement at stage 1, between the drive and the go signal at stage 2, and during the delay between the instruction stimulus and the go signal at stage 3. Activities are different for LEFT and RIGHT trials.

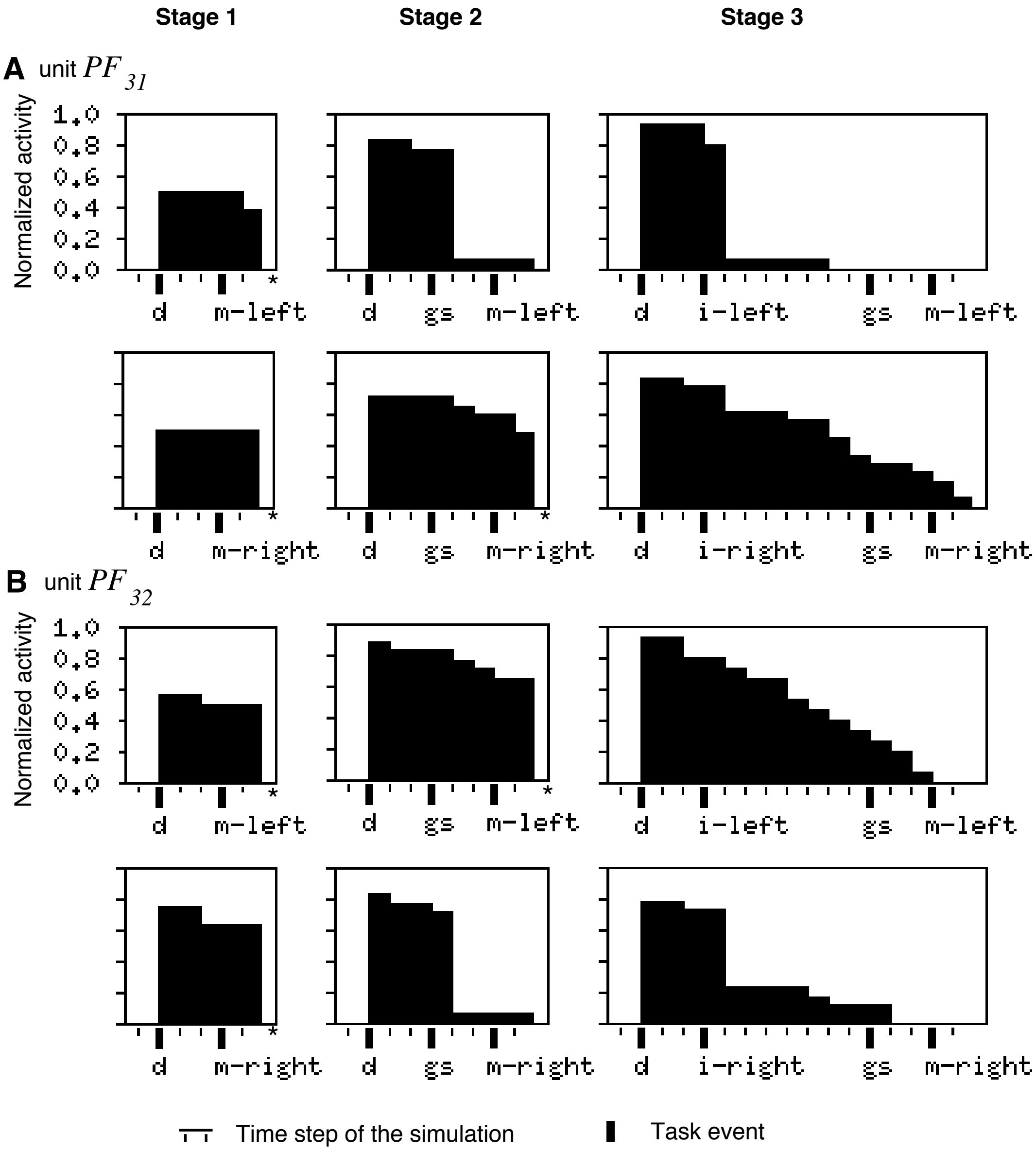

Figure 5.11. Same as Fig. 5.9 for units PF_{31} (**A**) and PF_{32} (**B**) . At stage 2 and 3, these units are sustainedly active in anticipation of task events, differentially for LEFT and RIGHT trials. Activity always starts with the drive, but stops with the go signal at stage 2 and with the instruction stimulus at stage 3.

Figure 5.6 illustrates the changes of activity in units SM_{11} and SM_{12} related to the movement toward the left and right levers, respectively. An activity is seen before the onset of the movement in the three training stages. These units keep the same temporal pattern of activity and the same relations with external events in the stages of learning. Units SM_{21} and SM_{22} (Fig. 5.7A and 5.7B) become active when the go signal is introduced in the second training stage. Note that units are non differentially activated by the go signal at stage 2 and respond preferentially to the go signal in left vs right trials at stage 3. Activities related to the instruction stimuli are shown in Fig. 5.8.

Units similar to SM_{11} and SM_{12} have been found experimentally. In fact, Okano and Tanji (1987), and Romo and Schultz (1987) have observed that, in some units, similar activity precedes self-initiated and visually-triggered arm movements in the motor, premotor, and supplementary cortex.

Premovement activity has been frequently observed in the frontal lobe: in the motor cortex (Caminiti et al. 1991), the premotor cortex (Weinrich and Wise 1982; Caminiti et al. 1991), the supplementary motor area (Tanji et al. 1980) and the prefrontal cortex (Kubota et al. 1980; Watanabe 1981). By construction of the model, motor elements, which show premovement activity, reflect properties of motor and premotor cortical neurons (Caminiti et al. 1991; Burnod et al. 1992). These element are tuned for a preferred direction in space. In both studies (Caminiti et al. 1991; Mitz et al. 1991), recording have been made in the dorsorostral part of the premotor cortex, a region which has reciprocal connections to the prefrontal cortex (Barbas and Pandya 1987). These units are thus likely to belong the same population, to receive prefrontal modulation and to participate to learning of arm reaching movements in a delayed response task.

PF units. Changes in *PF* units are shown in Figs. 5.9, 5.10 and 5.11. The following characteristics are observed: (*i*) Units display sustained activities (>2 time steps of the simulation); (*ii*) Units become differentially active for left vs right trials when a particular sensory or motor event is introduced (movement in Fig. 5.9 and 5.10, go signal in Fig. 5.11); (*iii*) A great heterogeneity of activity is found.

Units in Fig. 5.9 have quite the same behavior as units shown in Fig. 5.6. They are active before the movement in the 3 training stages and are selective for right vs left trials (compare 5.9A and 5.9B). Figure 5.10 shows the evolution of activity in delay related units. Note that these units change their time of activation with learning (Fig. 5.10A, left trials; Fig. 5.10B, right trials). In the first stage, they start their activity with the drive and stop it with the movement. At stage 2, activity starts with the drive, but ends with go signal. During the last stage, activity starts with the instruction stimulus and ends with the go signal. Units in Fig. 5.11 always start their activity with the drive, but change the time of return to rest (with the go signal at stage 2, and with the instruction stimulus at stage 3).

The role of *PF* and *SM* units in the acquisition and execution of the task is illustrated in Fig. 5.12. Each histogram in Fig. 5.12 is the superposition of three histograms (3 units) at a given training stage (taken from Figs. 5.6, 5.7, 5.8, 5.9, 5.10, and 5.11). Figure 5.12A is for *PF* units. It shows: (*i*) that, at each training stage, each unit is active between two successive task events; (*ii*) that this relation changes from stage to stage; (*iii*) that units become progressively specialized for different successions of events. At stage 3, each unit is related to a specific succession of events (drive/instruction stimulus in PF_{31}, instruction stimulus/go signal in PF_{21}, go signal/movement in PF_{11}). Note the changing role of unit PF_{21} in the course of learning. For a sake of comparison, the same results are shown for *SM* units in Fig. 5.12B.

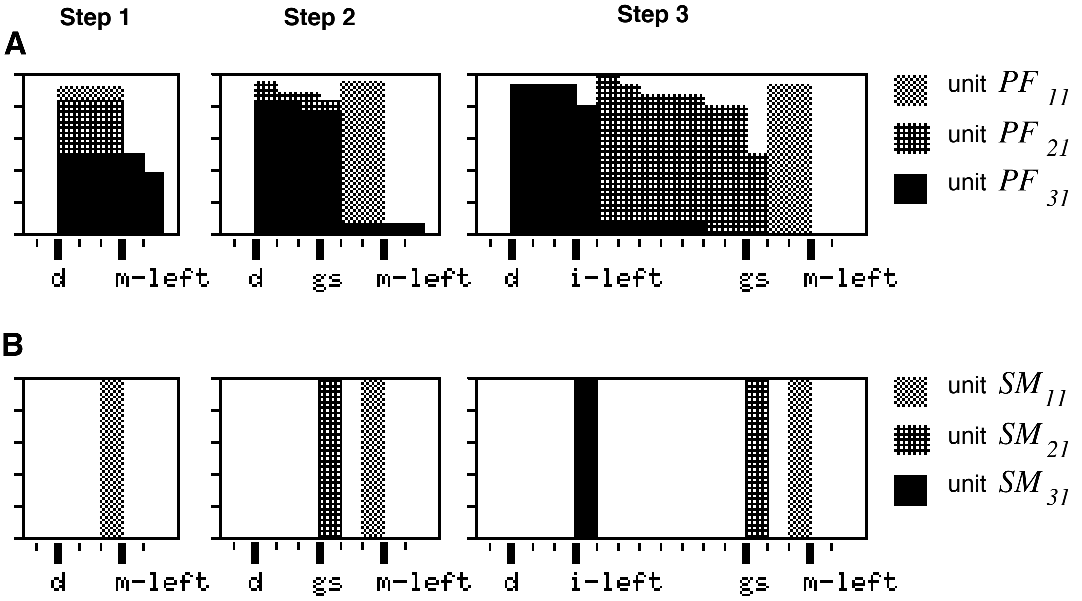

Figure 5.12. Superposition of activity histograms for some *PF* units (**A**) and some *SM* units (**B**), during the training stages (left to right; 1, 2, 3). **A**. Activity of units PF_{11} (*light shaded pattern*), PF_{21} (*dark shaded pattern*), and PF_{31} (*plain pattern*) during left trials is superposed. Note the progressive differentiation of activity in the successive stages. **B**. Same as **A** with units SM_{11}, SM_{21}, and SM_{31}. Activities in *SM* units are correlated with end of activity in *PF* units.

Changes in level of activity in *PF* classes are shown in Fig. 5.13. Modulations are correlated with the changes of reinforcement contingency, depending on variations of the reinforcement rate. When changing from stage 1 to stage 2, two behaviors are alternatively performed by the network, in a way similar to that observed in monkeys: the previous correct behavior (self-initiated movements) and the new correct behavior (stimulus-triggered movements). Mean activity during reinforced trials in class PF_{11} increased for leftward self-initiated movements during the first stage (*open circles*; Fig. 5.13A). During the transition between stage 1 and stage 2, activity first decreased and increased again (*crosses*; Fig. 5.13A) with the increase of the performance rate (see Fig. 5.5). The same phenomenon is observed between stage 2 and stage 3 (*closed circles*; Fig. 5.13A).

Variations of activity in class PF_{21} are shown in Fig. 5.13B. These variations are quite similar to those observed in Fig. 5.13A, with monotonic (increase) changes at each stage and non-monotonic changes (decrease and increase) at the transition between two stages. Figure 5.13C illustrates the variations in class PF_{31} units. In this case, variations start at stage 2, but still follow the same principle.

During reversal learning in a go/no go discrimination task, Niki et al. (1990) found some neurons that reverse their activity with the change in reward contingency (Type 2) and some that keep the same activity (Type 1). The *SM* units of this model resembles the Type 1 units since both are related to the impending behavioral response and do not change their activity with change in reward contingency. Type 2 units (Niki et al. 1990) reverse their activity with the change in reward contingency as do *PF* units in the network. Although few units were studied, it is interesting to note that Type 2 units were not likely to be found in premotor cortex while the prefrontal cortex contained both types of units in similar proportions (Niki et al. 1990). It supports our hypothesis that some units (*PF* units) are specific to the prefrontal cortex. Modifications of activity in *PF* units can also be compared with those found by Thorpe et al. (1983). Neurons in the orbitofrontal cortex decrease or increase their activity in relation to the learning of the associative significance of a visual stimulus. The results are also consistent with observations of Watanabe (1990) who found decreasing activity when changing the significance of a stimulus without changing the required behavioral response. Modulations of activity in *PF* units may thus be related to the change in the associative significance of the current behavior (will it lead to a reward?) (Thorpe et al. 1983; Watanabe 1990).

Non-monotonic changes found in prefrontal units subserve both the development of new behaviors and the transition between two behaviors on the basis of changes in reward contingency. Decreasing activity related to unrewarded behavioral actions is responsible for the suppression of these actions. Subsequent increases in neuronal activity reflect the construction of a new rewarded behavior (for example, the integration of new environmental cues). This view is consistent with the proposals of Fuster (1988). Indeed, Fuster (1988) suggested that newness and complexity are the main challenges to prefrontal functions. The properties of prefrontal units in the model reflect both the ability to take into account changing environmental demands and the ability to integrate a set of sensory, motor and more complex events in a coherent goal-directed behavior.

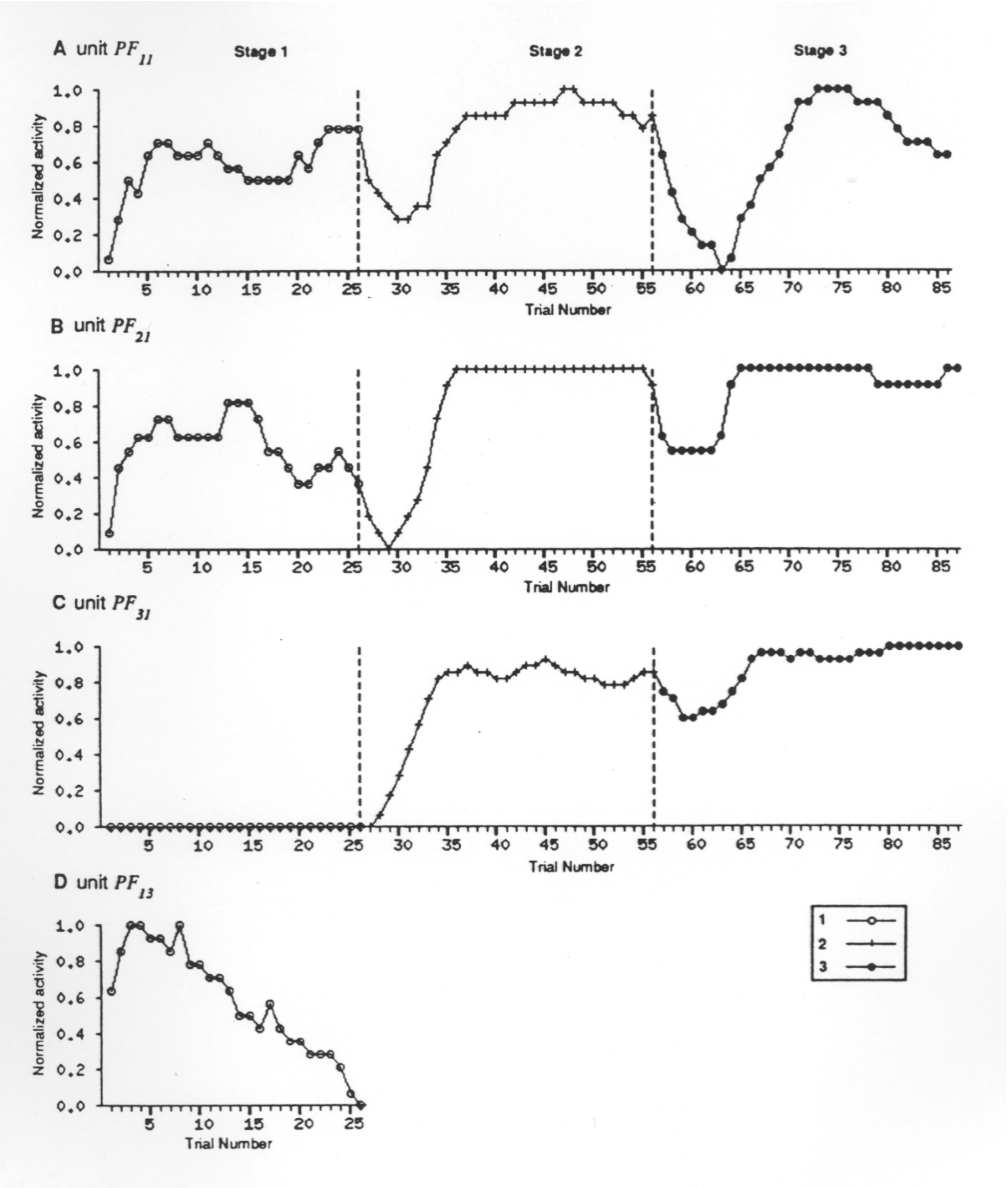

Figure 5.13. Variation of the level of activity in *PF* classes (**A**, **B**, **C**, **D**) during the training period. Graphs **A**, **B** and **C** are constructed from the activity during reinforced LEFT trials of all the unit in a class (4 units per class). Trial activity is computed in the following way: (*i*) For each unit, the unit trial activity is 1 if the unit has been made active with a probability different from 0.5 during the trial, 0 else; (*ii*) Trial class activity is the average unit trial activity of all the units; (*iii*) Trial activity is obtained as the five-point left moving averages of trial class activities and normalized. Each horizontal division corresponds to a trial. *Vertical dashed lines* indicate the transitions between training stages. Note the combination of increasing and decreasing activity (**A**, **B**, **C**): activity decreases at the transition between two stages and increases after the transition. In **D**, decreasing activity related to incorrect movement during the first training stage is shown.

Internal representation of sensory-motor sequences

These results illustrate a process which allows to store and retrieve sequences of sensory and motor events in a neuronal substrat. The DR task is composed of two sequences of 3 events. According to the model, the task can be stored using 6 classes of *PF* units and 6 *SM* units. Each *SM* unit is dedicated to the representation of an event and each *PF* class to the representation of the succession of two events. In the following, we address issues concerning the generality of this process.

There are no a priori representations of sequences in the network. The representation of sequences is an important issue since it would be quite different if sequences are selected among pre-existing sequences or if sequences are constructed in relation to external constraints. In the present model, the network stores sequences specified by a training set and a training protocol. The nature of sequences which can be stored in the network is defined by the information available in input and output pathways (Which stimuli will be involved? Which actions will be elicited?), and the connectivity between processing units. In this sense, sequences do not exist a priori in the network, but are stored by changing the efficiency of transmission between processing units (learning coefficients).

Interferences can be suppressed provided they are actually made active. In the network of Fig. 5.4, we have assumed that interferences occurred only during the first training stage. The suppression of the interfering events is learnt by the network, as shown by the decreasing activity in *PF* units related to these events (PF_{13} ; Fig. 5.13D). The network is thus able to suppress irrelevant events provided these events are actually introduced in the training protocol. In the same way, interferences could have been introduced and suppressed in the following training stages (using for instance several go signals).

Generality of network architecture. The network of Fig. 5.4 is constructed according to general principles of interaction between the prefrontal cortex and connected sensory and motor structures. Interaction is defined by connections between *PF* and *SM* units. Both reciprocal and non-reciprocal connections are used. Their role is related to processing rules. At the level of a *PF* unit, reciprocal connections correspond to a strong selectivity to a specific sensory or motor event. Two interconnected *PF* and *SM* units display strongly related activities. Compare Fig. 5.6A and 5.9A for left trials: activity ends with movement to the left in units SM_{11} and PF_{11} . On the other hand, non-reciprocal connections define a non specific selectivity to other events and are responsible for eliciting sustained activities in *PF* units. Since *PF* units are adaptive devices which learn the control of their input pathways and their sustained activation, the ability of the network to learn a task does not depend on its particular and unique set of connections between *PF* and *SM* units. Several networks with different patterns of interconnections can learn the same task and reach the same level of performance. The differences between these networks will be found at the level of single unit activity. However, the variations of activity corresponding to the stage-by-stage acquisition of the task will follow the principle shown in Fig. 5.13 (that is a combination of monotonic and non-monotonic variations related to the training stages).

Redundant representations in SM units are necessary to allow the acquisition of conditional sequences. We have assumed that a redundant representation in *SM* units is used when the same event occurs in different situations. A *SM* unit combines two types of information (one concerns the external world, through pathways *I* and *O*; the other is related to the internal state of the network, through *PF* inputs) to produce a new information which is distributed to *PF* units. If the unit is involved in two behaviors, it may be required to carry a differential information when one or the other is executed. For instance, the unit SM_{21} related to the go signal (Fig. 5.4) should be active only after one of the two instruction stimuli. Unless, the conditional information given by the instruction is lost at the time to execute the movement.

On the other hand, the same *SM* unit is likely to be used in different behaviors if it does not carry critical conditional information. For instance, the unit SM_{21} (which relates *i-left* to *m-left*) can be used when a new stimulus (*i1-left*) is introduced before the go signal to instruct the same final response (*m-left*). In the same way, *SM* units related to movements (SM_{11} , SM_{12}) can be involved in several behaviors when the same movement is executed in different contexts.

Redundant representations in PF units are necessary to allow the formation of new behaviors. There are two forms of redundancy in *PF* units: (*i*) *PF* units are grouped into classes corresponding to uniform input/output relations with *SM* units (all *PF* units in a class are connected to the same *SM* units); (*ii*) some *PF* classes are connected to redundant *SM* representations.

The first case corresponds to a complete redundancy since all units of a given class behave in a similar fashion at any time. This form of redundancy is used to compensate the variability due to the stochastic behavior of processing units (Equations 5.1 and 5.2).

In the second case, the redundancy is related to the ability to construct new behaviors. Consider units responding in anticipation of the go signal in the second training stage (PF_{21} , PF_{22} ; Fig. 5.7B). These units become differentially responsive to the instruction stimuli during the third stage. Note that the differentiation is dependent on the connections of the units with *SM* units. The repertory of possible new behaviors is defined by the number of redundant representations and by the sensory-motor functioning range of corresponding neurons (in the model, relations with *SM* units).

Sensitivity to parameters

The ability of the network depends on the value of the parameters of the model. In the following, we describe the effects of the variation of some parameters on the behavior of the network:

- Decay rate of sustained activity (η). It defines the mean duration of the sustained activity. A strong decay rate will mainly impairs the stage 3 of the training protocol, when a delay is introduced between the instruction stimulus and the go signal. However, the real effect is dependent on the redundancy of *PF* units.

- Learning rule parameters (α and β). The ratio $I = \alpha/\beta$ defines the respective importance of non reinforced and reinforced behaviors, respectively. If I is low, learning coefficients change mainly in relation to correct behaviors. In this case, incorrect behaviors slowly disappear. On the other hand, if I is high, incorrect behavior rapidly extinguish.

- Trace parameters (see Appendix). They define the amplitude and the duration of activation of variables used in the learning rule. If traces are too short, the behavior of the network will stay at or near random since units will not benefit from the reinforcement.

5 DISCUSSION

We began by discussing the respective constraints for a model of prefrontal and connected sensory-motor structures. We addressed these constraints at several levels of brain organization, and in close relation to available biological knowledge. We then described two processing modes, which characterize two types of processing units (*SM* and *PF*), within the framework of cortical modeling (**chapter 2**). Quantitative evaluations were presented: the model appeared to be consistent with available experimental data and made predictions about neural correlates of learning. The model thus provides insights into several fundamental issues regarding the prefrontal functions. These issues as well as the limitations of the model are discussed in this section.

The delayed response task and prefrontal functions

This work has focused on the functional properties of prefrontal circuits which enable to learn a delayed response task. Since Jacobsen (1935) the delayed response task has been widely used to test cognitive aspects of prefrontal functions. Although there are still strong discrepancies on the critical parameters which actually tap the prefrontal cortex during delayed tasks (Rosenkilde 1979), lesion studies have emphasized the importance of the temporal factor. Monkeys with bilateral prefrontal lesions are severely impaired when long intratrial delays are used (Fuster 1988). As a general rule, a frontal monkey would fail to execute a behavior determined by some recent events. Convincing evidence for the involvement of PFC in DR task arise also from electrophysiological studies. Recordings of single-cell activity have shown that neuronal discharges are strongly correlated with task events and delays (Fuster 1973; see review in Fuster 1988). Thus the DR task appears to be well-suited and attractive to access to prefrontal functions. As a consequence, a model of the DR task offers a direct way to assess computational processes in regard to available data on the prefrontal cortex.

Modeling others tasks

A number of tasks have been used to study the prefrontal cortical areas in behaving monkeys. The most classical are the delayed response task (DR), the delayed alternation task (DA), the delayed matching to sample (DMS), and GO/NO-GO response tasks. Do all these tasks tap similar prefrontal functions? Several remarks can help to provide a response:

- Electrophysiological properties of prefrontal neurons are relatively constant through the protocols used, in the sense that the same set of stereotyped activities are found (Komatsu 1982). This result is probably related to the fact that a set of common elementary processes underlie the execution of each task: expectation of environmental stimuli, short-term memorization, preparation of response, reward integration. This response is not completely satisfactory since it does not take into account behavioral aspects related to these mechanisms. For instance, delayed response and delayed alternation tasks are somewhat different since one is controlled by external cues whereas the other depends on internal cues. However, similar activities are observed in both tasks (Kubota and Niki 1971; Niki and Watanabe 1976). The model predicts that in both cases, a single function may be used. This function could be a general ability to determine “behavioral significance” (which response?) and “associative significance” (will it lead to a reward?)

of a situation. In this form, the function is independent of particular modalities: it works evenly with visual or auditory signals, with internal or external signals. Neuronal activities reflecting behavioral significance have been frequently observed, for example differential delay activity (Niki and Watanabe 1976) or differential activity on GO and NO-GO trials (Komatsu 1982). Watanabe (1990) found strong neuronal correlate of associative significance. In this study, monkeys were involved simultaneously in two tasks: a direct task and the corresponding reversal task. Some neurons responded differentially to the same first stimulus (thus no local context could help to determine the response) if the monkey was currently executing a block of direct or reversal trials (Watanabe 1990).

- Lesions studies provide a parcellation of the prefrontal cortex related to the behavioral tasks (Rosenkilde 1979). A prediction of the model is that anatomical specializations are related to the same set of mechanisms expressed on different architectural substrats (different patterns of cortico-cortical and subcortical connections). We can thus reliably assume that “more” complex tasks would rely on more integrated signals or combinations of signals rather than on more complex functional mechanisms. Such signals have been found experimentally in several studies (Rosenkilde et al. 1981; Watanabe 1989, 1990). For example, Watanabe (1989) described post-trial neuronal responses related to the correct execution of a trial, independent of external assessment (reward). In the same way that the model is able to capture temporal relationships between sensory and motor signals, it can capture relationships between more “abstract” signals.

Rule-coding units - Higher-level modeling

This model relies on the fact that the task requirements (memorization, behavioral responses) are acquired by a set of processing units through sensorimotor experiences. Although the model exhibits correct behavior in the task, it does not predict a relation between the two component programs of the task (left and right). This relation has been observed experimentally: when the monkey fails to execute the correct behavior (for example, it goes left after the right instruction stimulus), activity before the response allows to predict the failure (Niki and Watanabe 1976). Computationally, it may be explained by the fact that two signals may be combined when the instruction stimulus is given: the first corresponds to the stimulus itself and the second to the prediction of the reward in the current situation. Since there are two ways to obtained the reward, failure to predict one way leads to the prediction of the other. A proposal, related to what have been said in the previous paragraph, is that temporal relationships between some complex signals [for example, post-trial signals reflecting error, reinforcement, omission of reinforcement, observed by Rosenkilde et al. (1981) and Watanabe (1989)] are likely to express prediction of the reward. Alternatively, some models propose a direct representation of task requirements by providing “rule-coding” units (Dehaene and Changeux 1989, 1991). Dehaene and Changeux (1989) showed that the rule which guides the correct behavior of a network can be selected by learning. After learning, the activity of rule-coding units thus reflects the effective rule which leads to the reward. Incorrect rule selection leads to failure of the behavior. Cohen and Servan-Schreiber (1992) used similar units to learn psychological tasks in a recurrent neural network. This approach clearly simplifies computational processes since the network is directly supervised by high-level representations of modality or programs.

Although rule-coding units are attractive for modeling of “cognitive” tasks, rules such as “choose color”, “choose position” (Dehaene and Changeux 1989, 1991; Cohen and Servan-Schreiber 1992) appear to be not very realistic at the neuronal level. More likely, activity of rule-coding units would express relationships such as “choose this program because it is surely rewarded” (see, Watanabe 1989, 1990). Although it is not a direct concern, the present model proposes a way to construct such rule-coding units by learning.

A rule for prefrontal units

The main hypothesis of the model is that the involvement of the prefrontal cortex in the mediation of cross-temporal contingencies (Fuster 1988) is subserved by patterns of sustained activity. This hypothesis has two aspects. The first concerns the effective importance of sustained activation in the execution of behavior. The second aspect is somewhat new, since it postulates that learning at the level of prefrontal neurons is related to sustained activation of these neurons.

Mechanisms of sustained activation. Sustained activations may come from different mechanisms at different levels of brain organization:

- Local recurrent circuits of excitatory and inhibitory neurons are likely to produce a sustained activity (recurrent excitatory pathways) and to stop it (inhibitory pathways) (Dehaene and Changeux 1991; Zipser 1991).

- Neuronal pathways including one or more structures can lead to the same results, provided there exist point-to-point loops. Reciprocal connections between the dorsolateral prefrontal cortex (DLC) and the mediodorsal nucleus (MD) of the thalamus have been proposed as a possible pathway (Fuster 1988). It has been shown that cooling of a large portion of DLC results in a diminution of the firing frequency (during the delay) of neurons in the parvocellular portion of the nucleus MD (Fuster and Alexander 1973). An alternative pathway is the cortico-striato-pallido-thalamo-cortical loop (Alexander et al. 1986). Sustained activations during delays occur throughout major parts of cortico-basal ganglia loops, such as the supplementary motor area (Tanji et al. 1980), postolateral putamen (Alexander and Crutcher 1990), pallidum (Nambu et al. 1990) and pars reticulata of substantia nigra (Hikosaka and Wurtz 1983; Schultz 1986). Although these activations begin slightly earlier in the supplementary motor area, as compared to the striatum, the large overlap suggests their largely simultaneous occurrence (Romo and Schultz 1987). Thus delay-related activations could be built up through successive reverberations in loops linking the cortex and the basal ganglia.

- An hypothesis, which is not incompatible with the previous ones, is that the sustained activity is due to properties of neuron membrane channels. At the level of individual neurons, the development of activations lasting over several seconds may be facilitated by the action of slow Na^+ and K^+ channels. In the spinal cord, specific ionic channels can generate a bistable state of activity as demonstrated in motoneurons, with a state ON resulting in long lasting activities (Hounsgaard et al. 1984). In the striatum, spiny neurons giving rise to prolonged excitatory post-synaptic potentials, slowly depolarizing ramps and slowly inactivating K^+ conductances (Calabresi et al. 1987; Kawaguchi et al. 1989; Pennartz et al. 1991; Surmeier et al. 1991). In this respect, an important candidate current to control a bistable mechanism and learning of sequences could be the I_{Ks} potassium current which has been shown to exist in prefrontal neurons (Hammond and Crépel 1992): (*i*) it slowly inactivates, giving more sensitivity to sequential stimulation; (*ii*) it inactivates for repetitive, sequential stimulations. Inactivation of this current could result in steady firing. Such channel properties could give very strong and robust regulatory properties to the temporal processing in prefrontal circuits (see **chapter 6**).

Learning to control sustained activation. Adaptive changes related to the sustained activation are described by Equation 5.3. According to this equation, learning coefficients of a *PF* unit are modulated in relation to the state of activity. The learning mechanism implies both activity-dependent decreases (LTD) and increases (LTP) of synaptic efficacy. Colocalization of LTP and LTD has been demonstrated in the prefrontal cortex of the rat (Hirsch and Crépel 1991). Artola et al. (1990) have observed that induction of LTP and LTD in the visual cortex depends on different voltage-dependent thresholds. Stimulations occurring at different levels of post-synaptic depolarization are likely to have different actions (LTP or LTD). A prediction of the model is that combined LTP and LTD processes should modify the temporal integration of inputs, due to specific membrane properties, such as I_{Ks} current (see **chapter 6**).

Reinforcement

Modulations of learning coefficients also depend on an absolute reinforcement signal related to the execution of a correct behavior. We have assumed that such a signal could be provided to each *PF* unit through a specialized pathway. This hypothesis can be related to the following facts:

- Neurons responding to the reward have been found to be widely distributed in the prefrontal cortex (Fuster 1988), although more common in the rostral part (rostral dorsolateral PFC, orbitofrontal cortex). This difference may reflect the density of fiber connections from limbic structures (amygdala, hypothalamus). These neurons are likely to relay information concerning reinforcement all over the prefrontal areas.

- Aou et al. (1983a) have shown that reward-related activity in the prefrontal cortex is likely to be regulated by catecholamines (noradrenaline, dopamine). The diffuse effect of modulators can be a way to provide a large-scale unconditional influence related to the reinforcing value of external events.

Sustained activities

Sustained activity and short-term (working) memory. Some authors have proposed that sustained activities observed in the prefrontal cortex of behaving monkeys are neural correlates of short-term memory (Fuster 1973, 1988; Goldman-Rakic 1988). Although effective involvement of the prefrontal cortex in a generic short-term mnemonic process is still matter of debate (Passingham 1985), long-lasting activities have been shown to reflect short-term memorization of instruction cues, expectation of forthcoming signals and preparation of a behavioral reaction (Fuster 1973; Niki and Watanabe 1976). Sustained activities in the prefrontal cortex have three important characteristics: (*i*) They are found during the delay interposed between a cue and a response, whatever the modalities used; (*ii*) The duration of the activity is linked to the duration of the delay. Increasing the delay length leads to an increased duration of the activity (Kojima and Goldman-Rakic 1982; Batuev et al. 1985); (*iii*) Recording in untrained animals, Fuster (1973) found less delay related activities than in trained monkeys in similar behavioral conditions. Furthermore, there appears to be a relationship between the level of performance and the amount of delay activation (Fuster 1973; Watanabe 1986).

Mediation of cross-temporal contingencies. An alternative interpretation is to consider sustained activities as a mean to mediate of cross-temporal contingencies. Quintana and Fuster (1992) trained a monkey to perform 3 tasks: (*1*) a delayed matching to sample (Red-Green); (*2*) a delayed conditional position discrimination with Red-Left and Green-Right combinations; (*3*) a delayed conditional position discrimination with Yellow-Right and Blue-Left combinations. In this way, yellow and blue unconditionally predict the direction of the response whereas red and green predict a response with a probability of 75%. Results show that, during the mediation of cross-temporal contingency, sensory-coupled neurons tend to decrease their discharge with intratrial time while motor-coupled neurons accelerate their response. Furthermore they demonstrate that anticipatory activity can be related to the predictability of the forthcoming response.

The present model assumes that the control of sustained activation in a unit is related to a subset of learning coefficients. The value of these coefficients defines the probability of the unit to become sustainedly active. This mechanism is consistent with the characteristics of sustained activity in the prefrontal cortex.

A rule for sensory-motor units

Neural modeling generally uses a threshold summing device (formal neuron; McCulloch and Pitts 1943) as a simple, but correct approximation of real neurons. Weight coefficients reflect the tuning properties of the neuron, found, for example, in the orientation-selective cells in the primary visual cortex (Hubel and Wiesel 1968). The tuning curve can be adjust through learning by a Hebbian rule. The ability to perform multiplicative combinations (Equation 5.1) reflect the behavior of neurons combining two sources of information and performing non-linear interactions between them. It has been observed in the posterior parietal cortex where interaction of eye position and retinal position was found to be multiplicative (Andersen et al. 1987). Similar interactions between arm position and visual trajectory can explain quantitative patterns of activity observed in premotor and motor areas during 3D arm reaching movements (Caminiti et al. 1991; Burnod et al. 1992; **chapter 4**). Recently, Eskandar et al. (1992) have shown that the operation performed by inferotemporal neurons in a sequential matching task is likely to be described by a product between two sources of information (vision and memory).

From a computational point of view, additive and multiplicative contributions can subserve different functions. In the first case, a thresholded-convolution operation is performed. It corresponds to the filtering properties of the neuron. The second case (multiplicative) appears at a higher level of processing since it measures interactions between input signals. This rule is useful when inputs come from independent sources (different modalities). Biologically, the multiplicative rule may be related to the voltage properties of NMDA receptors (Nowak et al. 1984; Collingridge and Bliss 1987).

Prefrontal vs. sensory-motor processing

One way to compare the two types of processing is to ask what kind of code is used in the different regions. Georgopoulos et al. (1982) have shown that neurons in the motor cortex are active preferentially for a given direction of arm movement (with a broad tuning around the preferred direction) and that the direction of an instructed forthcoming movement is predicted by a population code. Similarly, graded neuronal responses have been observed for saccade representations in the superior colliculus (Lee et al. 1988), for faces representations in the inferotemporal cortex (Young and Yamane 1992). On the other hand, no simple code has been found in prefrontal neurons. The types of neuronal activity described in the prefrontal cortex are diffusely distributed and intermixed. Why such a redundant representation? Due to neuronal variability, no individual neuron can perform as well as a monkey during a given task (for instance, be active every time the monkey performs a given action). However, the average response of a few cells may reduce the variability of responses and provide a reliable prediction of the behavior. The present model allows to propose a different (but not incompatible) view. According to the model, two *PF* units which show similar responses at a given training stage are likely to become differentiated at the following stage when the behavior becomes dependent on new conditions. In this case, the redundant representation is related to the ability to form new behaviors.

It is important to note that the two processing modes are not necessarily specific to some given anatomical regions. Both can coexist in the same region. What defines the expression of the rule is the type of signals locally available, for example in relation to local primary and secondary indices, or reinforcement signals.

Procedural vs. declarative: different memory systems

There remain aspects that cannot be taken into account by the model. Learning a delayed response task provide rather inflexible representations, since it can be expressed only within the restricted environment defined by the training protocol (a set of lights and levers, and a fixed ordered succession of events). Learning occurs with the repetition of sensorimotor associations in order to access to a given performance rate. At the opposite, several tasks such as delayed non matching to sample, Konorski task, rely for some aspects on elementary processes previously described, but also involve flexible representations not provided by the model. Recently, two memory systems have been described (Mishkin and Appenzeler 1987): one subserves fixed inflexible representations (procedural learning) while the other is involved in flexible representations (declarative learning) (Eichenbaum et al. 1992). Different anatomical substrats appear to mediate these aspects: the cortico-striatal system and the medial temporal lobe (Saint-Cyr et al. 1988).

Part III

Synthesis

CHAPTER 6

Learning Rules and Biological Substrate

Contents

Summary

In this chapter, we first present recent results on neuronal processing and synaptic plasticity. Then we discuss the biological and computational properties of a number of synaptic plasticity rules used in neural models. A tentative theory relating synaptic plasticity rules, cortical areas, and cortical functions is presented, which is a synthesis of the results of this work.

1 INTRODUCTION

It is now well admitted that long-lasting modifications of synaptic transmission should contribute to adaptive properties of vertebrate neuronal networks. However, the problem of the relation between modifications at the level of a single neuron and the behavior of neuronal networks and of entire organisms has withstood experimental tests, and there is no unambiguous demonstration of it at this time (see Eichenbaum and Otto 1993).

A convenient approach to address this problem is to build a computational model. The synaptic plasticity is described by a “learning rule” (Hebb 1949), which governs the modification of a large scale neural network. The resulting behavior of the network allows the contribution and the form of the learning rule to be questioned. In this way, several studies have demonstrated that large scale networks of neural elements using simple plasticity rule exhibit powerful forms of learning (Linsker 1986; Pearson et al. 1987; Kohonen 1988).

The form of the synaptic plasticity rule has been recognized as a fundamental issue. The focus of experimental and theoretical studies has been mainly the Hebbian paradigm (Hebb 1949; Brown et al. 1990), and thus the relation between simultaneity of synaptic events and plasticity. However, Sutton and Barto (1981) have stressed that computational capabilities provided by a plasticity rule based on temporal contiguity should not extend beyond spatial correlations. As a consequence, a network of Hebbian adaptive elements is not likely to learn problems including temporal dependencies. This remark does not mean that the principle of temporal contiguity is inappropriate to address issues on synaptic plasticity and activity-dependent adaptation of neural networks. In fact, Bienenstock et al. (1982) have shown in a model, that Hebbian modifications combined with a time-varying threshold between increase and decrease produce a temporal competition rather than a spatial one. This theoretical prediction has received support from recent experimental studies. These studies have shown that the direction of synaptic modification (increase or decrease) can be controlled in the temporal domain (see **Long-lasting changes in synaptic efficacy**, below).

The main consequence of these observations is that Hebbian conditions are important to drive synaptic plasticity, but may be modulated by time-varying variables. We have illustrated this idea in the previous **chapters 3**, **4**, and **5**. We have shown that learning rules including temporal modulation of Hebbian conditions (rule R1, **chapters 3** and **4**; rule R2, **chapter 5**) provide efficient solutions to problems of *visual integration*, *motor performance*, and *temporal organization of behavior*. On the basis of these models, the goal of this chapter is provided a theory, which tries to relate synaptic plasticity rules, cortical regions, and cortical functions. To introduce the basis of this theory, the first section presents recent results on mechanisms of synaptic plasticity and membrane channels properties. In the second section, we describe a number of synaptic plasticity rules used in computational models. Starting from Hebbian rules, we illustrate the progressive introduction of more complex conditions of plasticity. Rules have been assigned in one of 3 categories, which characterize their preferred temporal pattern of synaptic activation. Possible biological implementations of the rules are discussed in relation to observations of the first section. A tentative theory is then proposed in the third section, which provides a framework for assessing the contribution of cortical structures to brain functions.

2 NEURONAL PROCESSING AND SYNAPTIC PLASTICITY

Two fundamental issues in neural modeling methods are operation modes (activation rules) and adaptation modes (learning rules) of neurons. Activation rules indicate how neurons respond to the synaptic flow of information. Learning rules describe long-lasting activity-dependent modifications of synaptic transmission. The goal of the section is not to provide an exhaustive description of these phenomena, but rather to discuss a set of mechanisms, which are likely to subserve the different forms of activation and learning rules encountered in modeling studies.

We first address issues on the integrative properties of neurons. In particular, nonlinear and temporal. membrane channels. Then, we present recent results concerning conditions of induction of classical forms of plasticity (long-term potentiation and long-term depression).

Neuronal processing

Classical theories on synaptic mechanisms involve linear summation of excitatory postsynaptic potential (Eccles 1964). However, in most neurons, classical sodium and potassium currents responsible for the generation of action potentials interact with a great variety of ionic channels sensitive to voltage, transmitters, modulators, and generate a rich repertory of membrane responsiveness (Llinás 1988) and membrane behavior (Connors and Gutnik 1990).

For instance, it has been proposed that the voltage sensitivity of a particular class of excitatory amino acids receptors (NMDA receptor; Nowak et al. 1984) may result in nonlinear neuronal processing. Fox et al. (1990) have shown that NMDA receptors provide a multiplicative gain control mechanism in cat visual cortex. Similarly, Matsumura et al. (1992) have shown that suppression of GABAergic inhibition may enhance neuronal activity by revealing subthreshold excitatory inputs. This effect is similar to an AND function.

Another important property is the temporal dimension of neuronal processing. Integration of synaptic inputs over a long time, exceeding the time span of classical temporal summation, has been demonstrated in hippocampus (Storm 1988) and the prefrontal cortex (Hammond and Crépel 1992). This membrane behavior is due to a slowly inactivating potassium current (I_D in the hippocampus, I_{Ks} in the prefrontal cortex).

Prolonged near-threshold depolarizing stimuli activate these currents, which initially inhibits spike firing since it overwhelms inward currents. Delayed firing is then observed which can last for several seconds (Storm 1988). Inactivation allows sodium-mediated inward currents to be unmasked and thus the discharge of the neuron. Since these currents are partly inactivated a steady-state potential, hyperpolarizing or depolarizing the neuron changes the availability of the channel and allow the firing mode of the neuron to be controlled (Hammond and Crépel 1992). Repetitive long depolarizing pulses induce a progressive reduction of the delayed activation and can favor spontaneous plateau depolarization lasting for several seconds.

Long-lasting changes in synaptic efficacy

LTP and LTD. Current knowledge on long-term potentiation (LTP) encompasses a broad range of findings. The reader is thus referred to the literature for a complete review (Madison et al. 1991; Ben-Ari et al. 1992; Tsumoto 1992; Colley and Routtenberg 1993). We will just emphasize a few important points. LTP is a long-lasting enhancement of the synaptic transmission following brief repetitive stimulation of afferent pathways, which can last for a few weeks. It has been first demonstrated in the hippocampus (Bliss and Lomo 1973), and after in various areas of the neocortex. Different forms of LTP have been observed (Fig. 6.1A), such as homosynaptic LTP, and associative LTP.

Unlike LTP, long-term depression (LTD) has not been studied systematically in the brain (Tsumoto 1992; Malenka 1993). Figure 6.1B illustrate the different forms of LTD observed in the neocortex and in the hippocampus: homosynaptic LTD, heterosynaptic LTD, associative LTD.

Threshold for depression and potentiation. On theoretical basis, Bienenstock et al. (1982) have proposed that the direction of synaptic modification should depend on the level of postsynaptic activity (Fig. 6.2A). Recent experimental evidences have supported this proposal (Fig. 6.2B; Artola et al. 1990), but have also described other possible “threshold” variables: postsynaptic potential, intracellular calcium, stimulation frequency.

Artola et al. (1990) have reported that activation of cortical neurons above a critical threshold of postsynaptic activity leads to long-term depression in the stimulated pathway. Above the threshold, a long-term potentiation is observed.

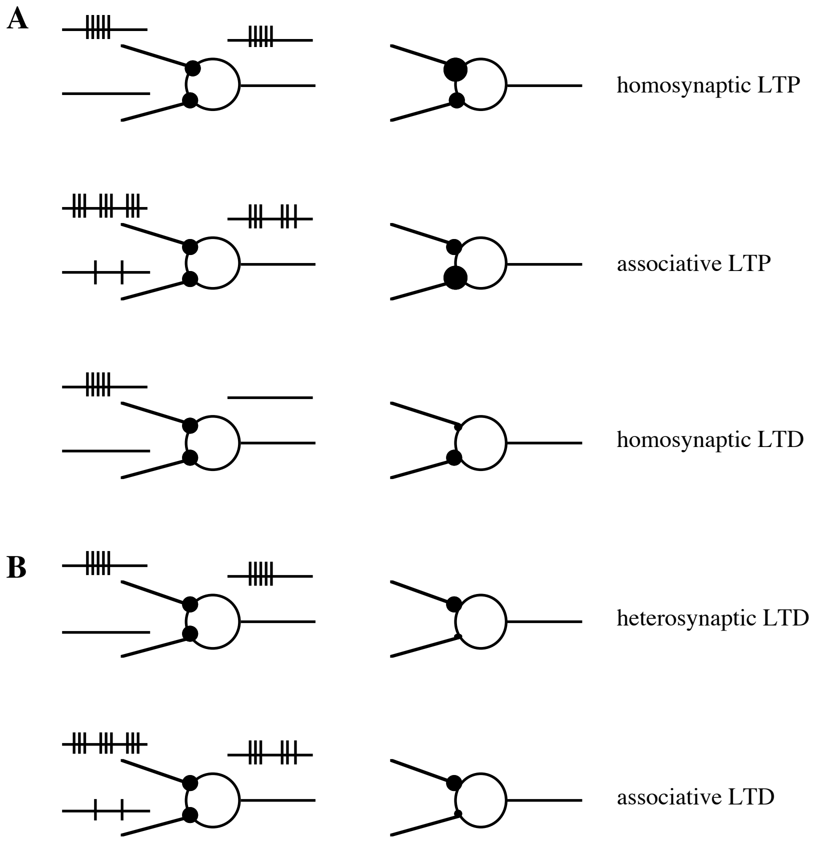

Figure 6.1. Different forms of long-term potentiation (**A**), and long-term depression (**B**), taken from Tsumoto (1992). Changes in synaptic efficacy are indicated by the size of the circles: depressed (•), normal (●), and potentiated (⬤).

As illustrated in Fig. 6.2B, two thresholds for synaptic modifications exist, depending on the postsynaptic potential. The first threshold is not dependent on NMDA receptors (Artola et al. 1990), while the second corresponds probably to the threshold of NMDA conductances. A corresponding view is provided by the results of Hirsch and Crépel in the prefrontal cortex (Hirsch and Crépel 1991). They have shown that mechanisms leading to LTP and LTD may be localized in the same cell and that blockade of LTP by NMDA antagonist unmasks LTD. Lisman (1989) has proposed that Ca2+/calmodulin-dependent protein kinase II within postsynaptic density can store a graded synaptic weight. The quantitative level of the activity-dependent rise in intracellular concentration of postsynaptic calcium (Ca^{2+}) determines whether increase or decrease. Wexler and Stanton (1993) have proposed that Ca^{2+} may be a switch for plasticity while second messengers (diacylglycerol, cAMP) modulate thresholds for LTD, STP, LTP (see below).

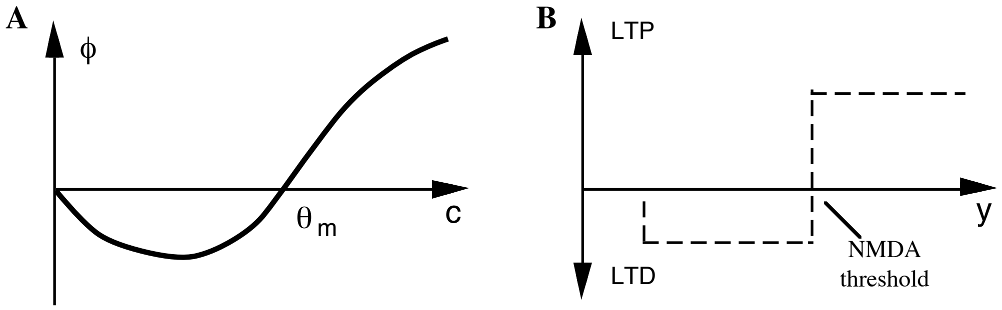

Figure 6.2. A. The relation between postsynaptic activity (c) and variation in synaptic efficacy (ϕ) proposed by Bienenstock et al. (1982). **B**. Experimental curve based on the results of Artola et al. (1990). The threshold θ_m is related to the threshold of NMDA receptors. Note that the size of LTP and LTD has not been defined quantitatively.

Dudek and Bear (1992) have shown that different levels of stimulation frequency lead to LTD (1-3 Hz), no change (10 Hz), or LTP (50 Hz), in the hippocampus. These results are in part confirmed by Mulkey and Malenka (1992). They have observed that repetitive low frequency stimulations (1 Hz) systematically induces LTD. If one assumes that postsynaptic activity is more or less monotonically related to stimulation frequency, these observations fit well the theoretical prediction of Bienenstock et al. (see Fig. 6.2A).

Which of these variables actually define the threshold is not known. However, since there are evidences that they may not independent variables (see below), the threshold is probably not influenced or controlled by a unique factor.

Controlling the threshold. In the previous paragraph, we have shown that the direction of synaptic modification is likely to be a function of some variables in accordance with theoretical predictions (Bienenstock et al. 1982). Another prediction concerns the way to control the threshold variable: Bienenstock et al. have proposed that the threshold is related to the recent history of postsynaptic activity (precisely the mean activity on a past period). This control by previous activity allows the threshold to be adaptively displaced so that it eventually separates one input from others. Different implementations are possible.

Chen and Huang (1991) have shown that protein kinase C (PKC) activation modifies the Mg^{2+} block of NMDA channels and may thus indirectly modulate LTP induction since the level of NMDA receptor activation determines the threshold for LTP induction. Such a control has been confirmed by Aniksztejn et al. (1992) who have shown that STP can be transform in a NMDA-dependent and PKC-sensitive LTP when applying metabotropic glutamate (Q_p) receptor agonist. Glutamate is thus likely to modulate LTP induction (see review in Ben-Ari et al. 1992).

Wexler and Stanton (1993) have shown that the amplitude of LTD following low-frequency stimulation (LFS; 1 Hz) is dependent on the previous induction of homosynaptic LTP (and also STP only). This LFS-induced LTD requires the activation of both NMDA and metabotropic receptors. Previously inducing LTP thus increases the likelihood of eliciting LTD with low-frequency stimulation. These results demonstrate the importance of recent history in the direction of synaptic plasticity.

Conclusion

It is frequently claimed that activity-dependent changes in synaptic efficacy are critical for the development of appropriate neural circuits and for many forms of neural plasticity, including learning and memory. Until now studies have mainly focused on very simple conditions of plasticity (temporal contiguity). It is now demonstrated that Hebbian-like synaptic modifications do exist in the brain. However, it should be noted that mechanisms described in this section, including membrane channel properties, are likely to underlie more complex forms of plasticity such as those described in the following section (rule R1, rule R2). In particular, the influence of temporal sequences of synaptic events on plasticity could be profitably studied experimentally.

3 CELLULAR PLASTICITY AND FORMAL LEARNING RULES

Relations between local synaptic changes and learning-dependent adaptations of large scale neural networks have not been successfully assessed experimentally. Fortunately, the emergence of simple neural models exhibiting nontrivial features of information processing in the brain (Rosenblatt 1958; Marr 1969; Kohonen 1988) has encouraged theoretical studies, which allow the relationship between single neuron properties and population behavior to be questioned. However, the actual relevance of theoretical developments depends not only upon the correct explication of the neuron/population relation, but also upon the nature of underlying biological assumptions.

Most theoretical developments on synaptic plasticity rules have concerned the Hebbian rule in its multiple forms (Brown et al. 1990), and there are now experimental evidences that this rule (in one of its form) governs long-term potentiation of synaptic transmission in many brain regions (Brown et al. 1988). Starting from the Hebbian paradigm, we discuss in this section the biological implementation of different learning rules. Rules have been assigned in one of 3 categories, which characterize their preferred temporal pattern of synaptic activation.

For a sake of comparison, all the rules are described using the same notations. Furthermore, rules are presented in a simplified form to allow a direct comparison on qualitative criteria. Basically, we can formally describe a learning rule in the following way. Consider a neuron-like element with n weighted input pathways $\{x_i(w_i)\}$, $1 \le i \le n$ and an output y. For a sake of simplicity, the synaptic modification is described for pathway 1. When needed, other pathways are used, with indices 2 and 3. The synaptic weight w_1 changes according to

$$w_1(t+1) = w_1(t) + \rho_1(t)$$

where ρ_1 is the quantity defining the time and direction of change. This quantity ρ_1 should depend on past and/or present values of $\{x_i\}$, y, $\{w_i\}$, and ρ_1. Input and output are in [0,1]. The weight w_1 has the initial value $w_1(0)$ at time $t = 0$. An important issue in the study of learning rules is the mathematical behavior (convergence, stability) of the equation defining synaptic variations. This is not the concern of the present work. Thus, equations are generally written in order to illustrate the qualitative variation in learning weights, with no reference to corresponding mathematical constraints.

Hebbian rules

Changes in synaptic efficacy are generally described in the framework of classical conditioning. Classical conditioning concepts are based on the principle of temporal contiguity as does the Hebbian rule (Hebb 1949): requirements for efficacy changes are related to the simultaneity of pre- and postsynaptic activity. In a simple form, the modification term for the Hebbian rule is

$$\rho_1^{Hebb}(t) = \lambda[\sigma x_1(t) - w_1(t)]y(t)$$

where λ is a parameter determining the rate of change and σ the maximal value of w_1. In this form, the rule provides a decay term corresponding to associative heterosynaptic depression. Figure 6.3 illustrates this Hebbian paradigm.

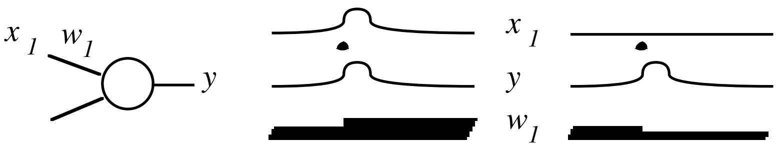

Figure 6.3. Hebbian rule. The learning coefficient w_1 increases for coincident pre- and postsynaptic activities (left), and decreases for postsynaptic activity alone (right).

An interesting form of Hebbian learning has been proposed by Bienenstock et al. (1982) and used for modeling the development of orientation selectivity in the visual cortex. The formulation of the modification term (BCM) is the following (Fig. 6.4):

$$\rho_1^{BCM}(t) = \lambda[\,\phi(y(t))x_1(t) \; - \; \varepsilon w_1(t)\,]$$

where λ and ε are positive parameters, and ϕ the function defined by

$$\phi(y(t)) = \begin{cases} <0 & \text{if } y(t)<\theta_m(t) \\ >0 & y>\theta_m(t) \end{cases}$$

where θ_m is a time-varying threshold such as

$$\theta_m = mean_t\,(y(t))$$

This rule provides a form of temporal integration since the decision threshold of the neuron depends on the recent history of postsynaptic activity (mean over recent time) of the neuron.

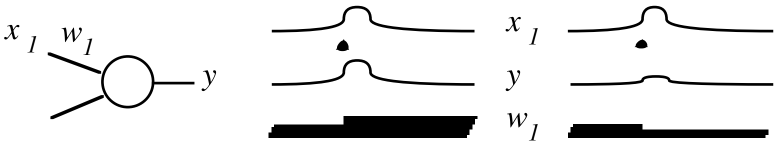

Figure 6.4. Rule BCM (Bienenstock et al. 1982). The learning coefficient w_1 increases for coincident pre- and postsynaptic activities, when postsynaptic activity is above a threshold (left). When postsynaptic activity is below the threshold, the coefficient decreases (right).

Existence of the threshold θ_m is consistent with the findings of Artola et al. (1990; Fig. 6.2 in the previous section). Time-varying threshold is a fundamental feature of this rule (Bienenstock et al. 1982) and also a strong prediction, which may have physiological support, as illustrated in the previous section.

Hebbian rules implement a correlation principle, which allows *adaptive tuning* of learning weights. Adaptation may result from a spatial competition between synapses (Stent 1973): some synapses increase their efficacy while some other decrease it. It may also result from a temporal competition between incoming patterns (Bienenstock et al. 1982). Since theoretical and biological basis of Hebbian learning have been extensively discussed in the literature (see Brown et al. 1990), we will not discuss further this point.

Error-correcting rules

The correlation principle underlying Hebbian rules may not be sufficient to solve problems involving temporal constraints. For instance, Sutton and Barto (1981) have developed a cellular analog of classical conditioning and they have shown that a Hebbian rule was sufficient to explain stimulus substitution, but not to explain more complex properties related to temporal properties of classical conditioning (effect of interstimulus interval length). Sutton and Barto (1981) have stressed that a more successful analog should involve a “prediction” rule, similar the error-correcting rule of Widrow and Hoff (1960).

Hebbian modifications are related to pre- and postsynaptic activity. More powerful learning rules have been proposed, which take into account these two terms, but also a training signal[6] (Widrow and Hoff 1960). The Delta rule designed by Widrow and Hoff allows the weights to be adjusted in proportion to the difference between a desired and computed value. The modification term is

$$\rho_1^{\Delta}(t) = \chi(t)[z(t) - y(t)]x_1(t)$$

where z is the desired output. Practically, the use of this rule for biological modeling is limited by the fact that there are generally no direct quantitative representations of error or desired value at the neuronal level. An exception is the cerebellum (CBM), which has been successfully modeled using this rule (Marr 1969), since an error signal is provided by the inferior olivary (Ito 1984; Kawato and Gomi 1992). In this case, the rule can be written

$$\rho_1^{CBM}(t) = -\lambda x_1(t-1)\ y(t-1)x_2(t)$$

---

[6] Also termed “teaching signal” or “error signal”.

where x_1 can interpreted as the parallel fiber (*context*) signal and x_2 as the climbing fiber (*error*) signal (Fig. 6.5). Synaptic transmission decreases on afferences which were active before the occurrence of an error. Biological support of this rule has been demonstrated in the cerebellum in the form of heterosynaptic long-term depression (Ito 1989).

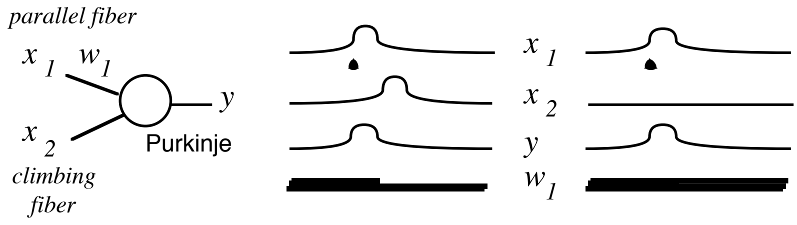

Figure 6.5. CBM rule. The learning coefficient w_1 decreases for coincident pre- and postsynaptic activities followed by stimulation of another pathway 2 (left). No modification is observed when pre- and postsynaptic activities are not followed by stimulation of pathway 2 (right).

The CBM rule makes use of a teaching signal, defined by its afferent pathway (climbing fiber), and which corresponds to an error. In a more general way, the teaching signal may be related to any input/output loop, as proposed in **chapters 3** and **4** (rule R1, Equations 3.3, 4.4, and 4.7; see also Burnod et al. 1992; Otto et al. 1992; Guigon and Burnod 1993). Basically, the modification term (Fig. 6.6) is

$$\rho_1^{R1}(t) = -\mu x_2(t)\, y(t) + (\lambda - \mu) x_2(t-1)\, y(t-1) x_1(t)$$

where λ and μ are parameters, which define the sensitivity of the neuron to error-correction learning (index $I = \mu/\lambda$). The rule is defined by a heterosynaptic depression ($-x_2(t)\ y(t)$) followed by a homosynaptic potentiation ($x_2(t-1)\ y(t-1)x_1(t)$). Both phenomena have been experimentally observed (see previous section) and may be the basis of the rule R1. The successive expression of the two modifications may be related to a control of the threshold between LTP and LTD (see Fig. 6.2), for instance through increase in intracellular calcium concentration following the first activation.

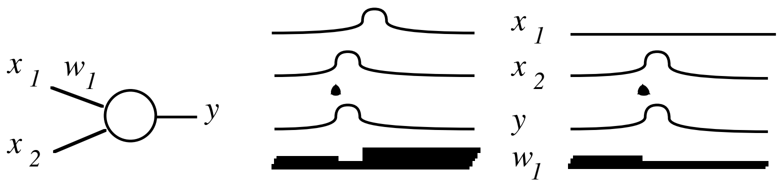

Figure 6.6. Rule R1. The learning coefficient w_1 successively decreases for coincident pre- and postsynaptic activities in pathway 2, and increases for a stimulation of pathway 1 (left). A decrease is observed when pre- and postsynaptic activities are not followed by stimulation of pathway 1 (right).

Formally, error-correcting rules are more efficient than Hebbian rules (Widrow and Hoff 1960; Sutton and Barto 1981). However, these rules should not be seen as competitive. As illustrated in previous chapters, they may subserve different adaptations. Hebbian rules allow *adaptive tuning*, i.e. learning-dependent adjustment of receptive fields. The rule R1 is useful to learn the combination of two independent flows of information, which are related by a self-consistency relation (*adaptive gating*). The contribution of these rules has been illustrated for the acquisition of sensory-motor transformations (visual recognition, **chapter 3**; visually-guided reaching, **chapter 4**) and simple contingent responses (context/reinforcement behavior, **chapter 4**).

Learning temporal sequences

When delays of arbitrary length are introduced between synaptic events, both *adaptive tuning* and *adaptive gating* mechanisms are not able to capture the temporal relationships between the successive events. A mechanism for integration of non-coincident inputs is thus necessary to solve problems including delays.

An original learning rule has been proposed by Dehaene et al. (1987). In a simplified form, the formulation is the following

$$\rho_1^{Triad}(t) = -\lambda \bar{x}_2(t)\, x_2(t)\, x_1(t) + \mu \bar{x}_2(t)\, x_2(t)\, y(t) x_1(t)$$

where x_2 is a modulatory input for pathway 1 (Fig. 6.7). Prolonged activation of the modulatory input (~0.1s) gates both Hebbian ($\bar{x}_2(t)\ x_2(t)\ y(t)x_1(t)$) and anti-Hebbian ($-\bar{x}_2(t)\, x_2(t)\, x_1(t)$) modifications on pathway 1. In this way, the neuron can detect temporal sequences of events not restricted to Hebbian conditions.

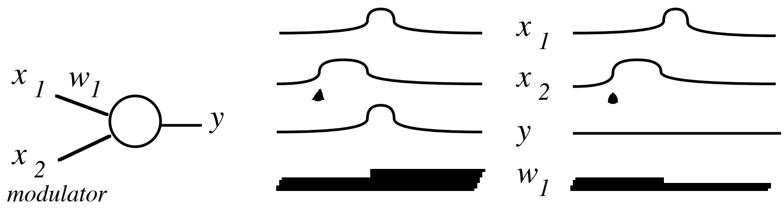

Figure 6.7. Synaptic triad (Dehaene et al. 1987). The learning coefficient w_1 increases for coincident pre- and postsynaptic activities in pathway 1 following prolonged activation of the modulatory input 2. A decrease is observed when the modulatory input is followed by presynaptic activity (right).

Synaptic triad can be implement with allosteric receptors (Dehaene et al. 1987). Using this rule, Dehaene and Changeux (1989, 1991) have constructed models of the delayed response task and Wisconsin Card Sorting test (see **chapter 5**).

In the **chapter 2**, we have proposed a mode of operation and adaptation in cortical columns based on the control of sustained activities (Equation 2.6, rule R2). The modification term is

$$\rho_1^{R2}(t) \;=\; e_1(t)\;[-\mu x_2(t)\; y(t) + (\lambda - \mu)\bar{x}_2(t)\bar{y}(t)\; x_3(t)\;]$$

where x_1 and x_2 are two successive synaptic inputs separated by a delay, and x_3 a reinforcement signal. As illustrated in Fig. 6.8, this rule predicts that the learning coefficient w_1 would successively: (*i*) decrease by μ when the sustained activation of the unit by the pathway 1 is terminated by activation of the pathway 2; (*ii*) increase by λ when a reinforcement signal occurs. In this way, repetitive presentations of a reinforced sequence (x_1 , x_2 , and x_3) lead to an increasing learning coefficient. Thus, the unit becomes surely activated when the first event of the sequence is presented, predicting the occurrence of a reinforcement. As shown in **chapter 5**, the rule R2 allows a neural network to learn sequences of sensory-motor events including delays.

The rule combines activity-dependent decrease and increase in synaptic transmission, which may be related to the colocalization of LTD and LTP in prefrontal neurons (Hirsch and Crépel 1991). Whether the neuron expresses LTP or LTD depends on recent history of postsynaptic activity (sustained activity). Interaction between membrane channels responsible for sustained activity (in particular, the slowly inactivating potassium current I_{Ks}) and LTP/LTD expression should allow activity-dependent modification of the integration of temporally non simultaneous synaptic inputs.

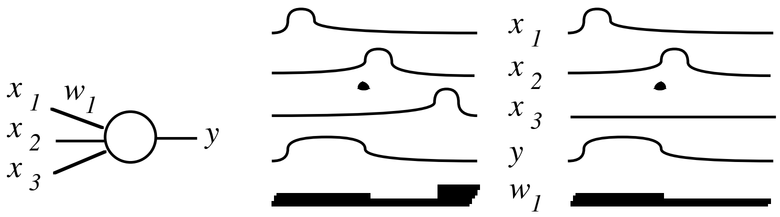

Figure 6.8. Rule R2. The learning coefficient w_1 successively decreases for coincident pre- and end of sustained postsynaptic activities in pathway 2, and increases for a stimulation of pathway 3 (left). A decrease is observed when no stimulation of pathway 3 occurs (right).

Conclusion

Figures 6.3 to 6.8 allow the comparison between learning rules used in neural modeling. Learning rules have been generally compared in the spatial dimension (Brown et al. 1990). The most interesting aspect of the present comparison concerns the temporal dimension. Stimulation paradigms involve not only temporal contiguity between synaptic events, but also interactions between non simultaneous events. At each time, conditions of plasticity seem to follow Hebbian or anti-Hebbian rules, but when considered over an appropriate temporal span, a global logic can be seen corresponding to a preferred mode of stimulation. Accordingly, these rules do not deny the role of Hebbian plasticity, but emphasize that temporal modulations of Hebbian conditions should result in powerful adaptive properties.

4 CORTICAL AREA, CORTICAL FUNCTION, AND LEARNING RULE

In this section, we make a tentative proposal on the relation between a cortical area, a cortical function and a learning rule (Table 6.1). This proposal relies on the data and models of **chapters 3**, **4**, and **5**, and data on behavioral plasticity, when available. We propose that the function of a cortical area can be described by (*i*) a specific input/output connectivity and (*ii*) an operation/adaptation mode. On this basis, an important characteristic is the actual *reinforcement* signal in the cortical area, i.e. the signal, which drives the synaptic plasticity (ρ_1 in the previous section).

Table 6.1. Relation between anatomical substratum and function

	Organization	Rule	Network operation
Visual cortex	topographic maps	vectorial code *adaptive tuning* *gating*	autoorganization perceptual grouping
Inferotemporal cortex	topographic and non topographic maps	population code *tuning* *adaptive gating*	visual discrimination visual recognition
Parietal/premotor/ motor cortex	topologic maps continuous parameters	population code *adaptive tuning* *adaptive gating*	coordinates transformation context/reinforcement behavior
Prefrontal cortex	non topographic maps	*adaptive timing*	temporal sequences

Visual cortex

At early stages of visual processing, maps are primarily organized according to retinotopic indices. The development of functional properties such as orientation, ocular dominance, disparity, occurs during a critical period of postnatal life. Frégnac et al. (1988) have shown that this development may result from activity-dependent modulations of synaptic transmission following a Hebbian rule (*adaptive tuning*). Furthermore, the postsynaptic activation reflecting retinal and non retinal inputs must reach a given level to allow synaptic modification (Singer et al. 1982). It has been proposed that extraretinal signals can have a *gating* effect for synaptic plasticity (Trotter et al. 1987). However, the exact nature of this gating effect has not been firmly established.

The resulting organization takes the form of interdigitated secondary indices corresponding to the parallel and redundant mapping of information and operations. In the normally reared adult visual cortex, plasticity may be prevented by the predominance of inhibitory intracortical networks. In this case, the same *tuning* and *gating* effects observed in the developing brain may result in perceptual grouping as demonstrated by the model of **chapter 3**.

Inferotemporal cortex

As shown by the model of invariant recognition exposed in **chapter 3**, the inferotemporal cortex can be seen as the interface between retinotopic representations derived from retinal inputs (*feedforward*), and non-retinotopic object-related representations (*feedback*). Transformations in the *feedforward* direction are defined by the pre-established tuning properties of neurons at early stages of processing. At higher stages, learning occurs through *adaptive gating* between *feedforward* and *feedback* flows of information. The global transformation results in the storage of learned objects in a semi-distributed fashion, as large collection of coarse retinotopic representations (see Fig. 3.4).

The reinforcement signal is defined by the coincident activation of two independent sources of information (visual and semantic) in two different reference frames (see also Rolls 1990). The distribution of this signal is defined by the pattern of feedback projections carrying semantic information. The logic of this transformation is such that two stimuli (of different categories) should activate different output pathways (discrimination). It is interesting to not that simple principles such as retinotopy, lateral inhibition and Hebbian changes may not be sufficient for invariant recognition (Frohn et al. 1987). Frohn et al. have stressed that a subsystem with nonretinotopical organization should be necessary to gain invariance properties.

Parietal/premotor/motor cortex

In cortical networks involved in the control of reaching movements, an important parameter is the direction of the movement, which is represented in populations of neurons in a distributed fashion. Control of the direction of movement can be obtained by combining visual information related to a target and kinesthetic information related to the position of the arm (Burnod et al. 1992; **chapter 4**). We have stressed that a powerful way to learn the appropriate transformations is to correlate the sensory signals produced by spontaneous movements. In this way, input/output relationships are tuned to allow a consistent correspondence between vision and movement. After learning, a visual target activates the visual map and triggers a movement associated by learning with the visual image of the arm at the place of the target. This movement-dependent matching between sensory maps has been called “self-consistency” (Kuperstein 1988).

The model of coordinate transformation exposed in **chapter 4** shows that input/output relationships can be appropriately modified during the learning period using *adaptive gating* (rule R1, Equation 4.4). The *adaptive gating* rule (Fig. 6.6) allows the combination of two flows of information to be learned using self-consistency as reinforcement. Neurons which have been involved in the production of an intended response (reaching a target) increase their excitability since they are reinforced by the consequences of their activation (reafferent visual input corresponding to the hand on the target), conditionally to the initial position of the arm. In this way, neurons learn to predict the effects of their action.

Prefrontal cortex

In **chapter 5**, we have emphasized that the role of the prefrontal cortex is critically related to the production of goal-directed behaviors. This assertion is related to the following facts: (1) Anatomical constraints in the prefrontal cortex are not in terms of mapping of sensory or motor parameters, but in terms of non-topographically organized representations and multiples interactions between different modalities; (2) Operations performed by prefrontal neurons reflect integration of sensory and motor information in the behavior rather a modality-specific transformation related to intrinsic (physical) properties of events. The mechanism of temporal integration is probably related to sustained activities (see discussion in **chapter 5**). Unlike visual and motor areas (see above), the operating mode cannot be described by vectorial or population schemes. It means that the "preferred events" of neurons (those, which are efficient to drive the neurons) in PFC are not defined only by place, modality, or any reconstructed property mapped in cortical circuits, but also by the particular significance in the behavior, related to temporal and reinforcement contingencies. For instance, prefrontal neurons would respond differentially to the same visual stimulus in two behavioral conditions.

Thus, although prefrontal neurons appear to be involved in simple sensory and motor functions, their activity results mainly from behavioral constraints induced by a training protocol. Self-consistency relationships are not defined by a sensory-motor loop, but by an arbitrary program, indicating the rule to obtain a reinforcement. In this case, the reinforcement signal is an absolute signal defining the correctness of the behavior.

Once a given behavior is established following a given rule, changing the task rule is responsible for the development of a new behavior, since the reward becomes contingent to new goal. Prefrontal neurons seem to contribute to the construction of the new behavior, as observed during performance of reversal learning (Watanabe 1990). The model of **chapter 5** illustrates the behavior of a neural network driven by an arbitrary training protocol. Learning occurs through *adaptive timing* (rule R2, Equation 5.3, Fig. 6.8) and neuronal activities change following variations of the performance rate of the network (Fig. 5.13).

The rule R2 defining the *adaptive timing* can be seen as a neural analog of plasticity in the prefrontal cortex. This rule reflects the ability to "link" successive synaptic events to a reinforcing event. It says that simple associative conditions should not be sufficient to drive synaptic plasticity, unlike in the visual cortex (Frégnac et al. 1988). This observation is consistent with some experimental evidences showing that associative protocols may not efficient to elicit LTP in the prefrontal cortex.

It is interesting to note that internal signals correlated with the reinforcement have been observed experimentally (Watanabe 1989). These signals may provide a basis to the acquisition of programs requiring planning. When one or more actions must be executed before reaching a goal (reinforcement), internal evaluations, related to the resolution of (non reinforced) subgoals, are necessary to guide appropriate actions. Using internal evaluation signals as a reinforcement provide a general mean to learn complex behaviors. In this sense, *adaptive timing* may contribute to acquisition of higher level behavioral structures such as language.

5 DISCUSSION

Starting from the Hebbian rule, we have shown that progressively more powerful rules can be constructed, corresponding to different controls of the relation between LTP and LTD. Unlike the Hebbian rule, most of these rules have not been directly demonstrated experimentally. However, the fact that the Hebbian paradigm is not sufficient to solve problems including temporal dependencies points to existence of non-Hebbian forms of plasticity. These rules rely on experimental evidences related to different forms of plasticity (Fig. 6.1) and to the LTP/LTD curve (Fig. 6.2).

On the basis of these rules, we have made a proposal on the relation between a cortical area, a cortical function, and a learning rule (Table 6.1). According to this proposal, a particular form of anatomical organization (including input/output connectivity and representation of information in afferent and efferent structures), and a particular mode of operation/adaptation should result in a particular function. From a qualitative point of view, this observation is a trivial consequence of the diversity of neural organizations and processes. However, since we have provided a quantitative analysis through computational models (**chapters 3**, **4**, and **5**), nontrivial relations can be drawn, which reflect the regional specialization of the cortical surface.

In particular, we have shown that information processing mechanisms underlying *visual integration*, *motor performance*, and *temporal organization of behavior*, can be consistently described by a restricted number of factors (Table 6.1). However, it is important to note that regional variations should be considered as gradients rather than a precise parcellation delineated by functionally identified cortical areas.

Conclusion

Modeling has been a growing field in recent years. Many models have been designed at various level of representations, in order to confirm or strengthen experimental results. These attempts relied on the correct assumption that modeling is likely to provide a descriptive and predictive representation of transformations in the brain, and can help to understand the relation between different levels of brain organization. Starting from a qualitative description including various anatomical, physiological, and psychological data, a quantitative description can be obtained by translating computational principles into mathematical equations, and then into a computer model.

However, the great majority of neural models have been aimed at explaining a specific set of data (Zipser and Andersen 1988; Lehky and Sejnowski 1988; Lockery et al. 1989). Moreover, most of these models are based on the back-propagation algorithm, which is quite successful for publication, but far less as far as explicative and predictive abilities are concerned (Crick 1989; Reeke and Sporns 1993).

On the other hand, original modeling approaches have been shown to be possible and fruitful (Kawato and Gomi 1992; Edelman 1993; Gluck and Granger 1993; Reeke and Sporns 1993). In this regard, the present document has described, summarized, and we hope, synthesized a systematic work of description and modelization of cortical functions based on carefully selected principles. This work has been undertaken for several years in the laboratory and has provided encouraging results. It has benefited from influential developments within cognitive science in recent years such as connectionism (Feldman and Ballard 1982; Ballard 1986), animal learning models (Sutton and Barto 1981), reinforcement models (Barto et al. 1983), PDP models (Rumelhart and McClelland 1986), guided propagation (Béroule 1988; Blanchet 1992).

An important issue addressed in this work is related to the need of neurobiological constraints for computational theories. In continuity with previous works (Ballard 1986; Burnod 1988; Alexandre 1990; Guyot 1990), we have identified a framework based on the architectural and processing characteristics of the cerebral cortex. Modeling principles have been constructed from the modular organization of the cortex and concern *representation of information*, *connectivity*, *neural processing* and *neural plasticity* in cortical areas. We have argued that columnar processing can be approximated by a combination of convolution (receptive field filtering: *tuning*) and polynomial (interlaminar interactions: *gating* and *timing*) operations. These operations depend upon a set of columnar registration coefficients defining the long-lasting adaptive properties of cortical circuits (*adaptive tuning*, *adaptive gating*, and *adaptive timing*). Note that no explicit algorithm for neural computation is provided. Accordingly, emergent properties are uniquely defined by local operation and adaptation mechanisms and not by finding minima of an "energy" (Hopfield 1982) or "error" function (Rumelhart et al. 1986).

Within this framework, we have described models of *visual integration* (**chapter 3**), *motor performance* (**chapter 4**), and *temporal organization of the behavior* (**chapter 5**). On the basis of these models, the major claim of this work is that the computational properties of different cortical areas can be consistently described both by a set of common principles and by regional variations along two dimensions: (1) the organization of the anatomical substrat in terms of afferent and efferent pathways, and (2) the properties of local neuronal circuits.

Common principles are related to organization and operation in terms of multicellular circuits (cortical columns), which are more likely to approximate cortical processing than a single prototypic neuron. Generally, modeled neurons are considered as threshold automata and the goal of neuronal algorithms is to characterize the relationship between incoming activity and threshold by modifying synaptic weights. Such a tuning defines a linear separation in the input space and is thus sensitive to any further modification of synaptic weights. On the other hand, multicellular circuits implement two levels of processing (filtering, integration), which allow the specific operation performed by a cortical circuit to be dissociated from the nature of data on which it acts.

Regional variations of anatomy have been described in relation to the nature and organization of afferent and efferent flows of information. Characteristics have been derived in terms of feedforward, feedback, or lateral information flows, of primary and secondary indices, of topographic or non-topographic mapping. We have defined the regional variations of columnar properties by a set of operation and adaptation modes (*tuning*, *gating*, and *timing*). Two original operation and adaptation rules (R1 and R2) have been designed, based on the idea that linear properties of neuronal processing and Hebbian forms of plasticity should not be sufficient to solve problems involving temporal dependencies. The novelty of these rules is the activity-dependent on-line priming of long-lasting changes in synaptic strength (**chapter 6**). In the framework of current interest in LTP and LTD, it corresponds to the ability to control the LTD/LTP curve threshold. Another novelty (rule R2) is that the synaptic control is not related to the level of firing frequency, but to the mode of discharge (phasic vs tonic). Bienenstock et al. (1982) have proposed that learning should depend on the recent history of neuronal activity. Here we extend the concept to the activation of the neuron which depends on an internal state (sustained activity). This proposal is in keeping with recent results on the control of neuronal excitability by temporal sequences of synaptic events (Hammond and Crépel

1992). It may be predicted that there exists a coupling between temporal sequences of synaptic events and plasticity. More precisely, specific sequences should allow variations of synaptic efficacy, which do not encode steady state statistics (Levy et al. 1990), but rather predictions of forthcoming events.

Combination of organizational and operational variations have been shown to result in specific functional properties, as shown by models of **chapters 3**, **4**, and **5** (see also Table 6.1). On this basis, we have proposed a theory, which relate cortical areas, cortical functions, and computational properties. This theory allows specific predictions to be made on the form of plasticity, which should be found in different cortical areas. In particular, we have emphasized that the Hebbian paradigm should not be by itself efficient to drive synaptic plasticity in certain cortical regions.

Among the models, the model of prefrontal functions (**chapter 5**) constitutes the main contribution of the present work. To our knowledge, no models have provided computational accounts of the adaptive properties of prefrontal circuits related to the acquisition of behavioral tasks. The model Darwin III of Reeke et al. (1990) is able to perform several sensory-motor transformations (visual tracking, recognition, reaching) and simple contingent responses, such as object-reward associations. However it cannot adapt its behavior to complex changes in its environment. Models of Dehaene and Changeux (1989, 1991) have addressed issues on prefrontal functions (delayed-response task, Wisconsin Card Sorting Test). However, they have not addressed the problem of successive adaptations to external contingencies.

Outcomes of the model in terms of neuronal activity are consistent with experimental data. More interestingly, results become precise predictions as far as learning-dependent variation of activity are concerned. Such predictions are of importance in relation to the interpretation of patterns of neuronal activity in the frontal lobe. In fact, the only consideration of classical descriptive parameters of neuronal activity (latency, phasic/tonic, relation to internal or external events) is not sufficient to assess the message carried out by the activity. In this respect, two solutions have been proposed: (*i*) Using tasks which involve complex sensory-motor contingencies (Watanabe 1986a,b; Joseph and Barone 1987; Barone and Joseph 1989; Watanabe 1990, 1992; di Pellegrino and Wise 1993). In this way, it is possible to dissociate the phenomena that are likely to drive the neurons; (*ii*) Studying variations of activity throughout acquisition or on-line modification of behavioral tasks (Niki et al. 1990). The history of neuronal activity, and in particular correlations between variations of activity and behavioral change, is informative on the specialization and the role of the neuron. In relation to the latter method, the model makes predictions on the relation between patterns of neuronal activity and learning-dependent changes in activity.

It is important to note that the present work does not provide a general theory of brain functions. The modeling framework provides only a guideline and not an a priori guarantee of success. It says that one should ask about neurobiological data and it says how to ask about it. In particular, it stresses that every aspect either physiological, psychological or theoretical should be expressed in neural terms.

Expected outcomes of this work concern two different aspects. On the one hand, a new modeling framework is proposed and should facilitate the development of models. We hope that it will trigger further modeling developments, which go in the sense of explication rather than simple imitation. On the other hand, predictions of the models should provide new insights in the computation performed by the cerebral cortex, in particular for problems which have withstood experimental tests.

Appendix: Model of the delayed-response task

FORMAL DESCRIPTION OF THE MODEL

Notations. $\mathbb{N}$ is the set of integer number, {0,1} the set of 0 and 1, $\mathbb{R}$ the set of real numbers, $\mathbb{R}^{+}$ the set of non-negative real numbers, $\mathbb{R}^{+*}$ the set of strictly non-negative real numbers, and [0,1] the closed real interval.

$n \in \mathbb{N}$ is the number of input pathways

$t \in \mathbb{N}$ is an increasing variable describing the time step of the simulations

For each i, $1 \leq i \leq n$, $x_i(t) \in \{0,1\}$ is the input signal in the pathway i.

For each i, $1 \leq i \leq n$, $w_i(t) \in [0,1]$ is the learning coefficient of the pathway i.

$y(t) \in \{0,1\}$ is the output signal

$r(t) \in \{0,1\}$ is the reinforcement signal

Traces. The non conditional input trace $\bar{x}_i$ is defined by

$$\bar{x}_i(t+1) = \kappa \bar{x}_i(t) + x_i(t)$$

where $\kappa \in [0,1]$.

The conditional input trace e_i is defined by

$$e_i(t+1) = \omega e_i(t) + x_i(t)\, y(t)$$

where $\omega \in [0,1]$.

The output trace $\bar{y}$ is defined by

$$\bar{y}(t+1) = \chi_1 \bar{y}(t) + \chi_2\, y(t)[y(t) - y(t+1)]$$

where χ_1 and $\chi_2 \in [0,1]$.

Stochastic function. The function F is defined by

$$F(u) = \begin{cases} 1 & with\ prob\ f(u) \\ 0 & with\ prob\ 1\text{-}f(u) \end{cases}$$

where f is the function

$$f(u) = \begin{cases} 0 & 0 \leq u \leq \lambda \\ 1 & \mu \leq u \leq 1 \\ u & else \end{cases}$$

where $\lambda \in [0,1]$, $\mu \in [\lambda,1]$, $\theta \in \mathbb{R}^+$ and $\phi \in \mathbb{R}^+$.

Rule R2. Unit is activated according to

$$\begin{cases} A(t) = MAX_{i=1..n}\ \{w_i(t)x_i(t)\} \\ A'(t) = MAX_{i=1..n}\ \{x_i(t)\} \end{cases}$$

and

$$y(t) = \begin{cases} g[A(t)] \ if\ y(t\text{-}1)=0 \\ else \begin{cases} g[A'(t)] \ if\ A'(t) \neq 0 \\ else\ g[\eta y(t\text{-}1)] \end{cases} \end{cases}$$

where

- *MAX* is the function which selects the maximum value between a set of variables
- $\eta \in [0,1]$
- g is the function defined by

$$g(z) = \begin{cases} 1 & with\ prob\ z \\ 0 & with\ prob\ 1 - z \end{cases}$$

Learning coefficients are modified according to

$$\begin{cases} w_i(t=0) = w_0 \\ \Delta_i^-(t) = K_i^-(t)x_j(t)y(t-1) \\ \Delta_i^+(t) = K_i^+(t)\overline{x}_j(t)\overline{y}(t)r(t) \\ \Delta w_i(t,t+1) = e_i(t)\{ \sum\limits_{j=1, j\neq i}^{n} [-\alpha\Delta_i^-(t) + \beta\Delta_i^+(t)]\} \end{cases}$$

where

- $w_0 \in [0,1]$
- $\alpha \in \mathbb{R}^+$ and $\beta \in \mathbb{R}^+$
- K_i^+ and K_i^- are functions which ensure the convergence and the stability of the variations:

$$\begin{cases} K_i^+(t) = \gamma r(t) - w_i(t) \\ K_i^-(t) = w_i(t) \end{cases}$$

DESCRIPTION OF THE SIMULATIONS

Training steps. The number of trials during each step was the following:

- Step 1: 15 blocks of 8 trials
- Steps (1’+2): 15 blocks of 8 trials
- Steps (2’+3): 17 blocks of 8 trials

Parameters. For the simulations, the following parameter values were used: $\delta = 8$ (delay length); $\theta = 0.3$; $\phi = 8.0$; $\lambda = 0.25$; $\mu = 1.0$ (stochastic function); $\kappa = 0.995$; $\omega = 0.995$; $\chi_1 = 0.97$; $\chi_2 = 0.9$ (traces); $\eta = 0.985$; $\alpha = 0.1$; $\beta = 0.35$; $\gamma = 1.0$; $w_0 = 0.5$ (Rule R2).

Abbreviations

ACh, acetylcholine; AMPA, α-amino-3-hydroxy-5-methyl-4-isoxazoleproprionate; APV, 2-amino-5-phosphonovaleric acid; BCM, Bienenstock, Cooper and Murno; BP, Bereischaftpotential ; CBM, cerebellum; CNS, central nervous system; CR, conditioned response; CS, conditioned stimulus; DA, dopamine; EPSP, excitatory postsynaptic potential; GPe, external segment of the globus pallidus; GPi, internal segment of the globus pallidus; IPL, inferior parietal lobule; IPSP, inhibitory postsynaptic potential; IT, inferotemporal cortex; LTD, long-term depression; LTP, long-term potentiation; MCP, motor cortex potential; MRBMs, movement related brain macropotentials; MST, middle superior temporal area; MT, middle temporal area; NA, noradrenaline; NMDA, *N*-methyl-D-aspartate; PDP, parallel distributed processing; PFC, prefrontal cortex; PKC, protein kinase C; PO, parieto-occipital area; SNc, substantia nigra pars compacta; SNr, substantia nigra pars reticulata; SPP, skilled performance positivity; STN, subthalamic nucleus; STP, short-term potentiation; TTX, tetrodotoxin; UCS, unconditioned stimulus; UCR, unconditioned response; V1, primary visual area; WH, Widrow-Hoff

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CONTENTS

Résumé de la thèse - Le présent travail s'inscrit dans le cadre des développements récents des Sciences Cognitives. Le thème central est la modélisation des propriétés et des fonctions du cortex cérébral. Le but de ce travail est de proposer un cadre formel pour la modélisation et, dans ce cadre, de comparer les processus corticaux liés à l'intégration sensorielle (reconnaissance de formes), à la performance motrice (commande du mouvement) et à l'organisation temporelle du comportement (planification).

Le chapitre 1 présente un vue générale des principes de modélisation neuronale venant des modèles connexionnistes. Un cadre de modélisation défini à partir des principes d'organisation du le cortex cérébral est décrit dans le chapitre 2. Le but de ce chapitre est de fournir une description formelle de ces principes pour la modélisation. En particulier, une formulation mathématique des propriétés computationnelles des circuits corticaux est exposée.

Les chapitres 3, 4, et 5 fournissent une description détaillée de modèles d'intégration visuelle, de performance motrice et d'organisation temporelle du comportement. Le chapitre 3 illustre les transformations de l'information rétinienne pour la reconnaissance de formes et le chapitre 4, les transformations pour le contrôle du mouvement du bras. Le chapitre 5 commence par une revue sur le cortex préfrontal et présente un modèle de réseau de neurones construit à partir des propriétés du cortex préfrontal. Ce modèle prédit les activités neuronales pendant l'apprentissage et l'exécution d'une tâche de planification similaire à celle utilisée pour les études chez le primate (tâche de réponse différée).

Le chapitre 6 propose une discussion sur les bases biologiques de la plasticité et sur les règles d'apprentissage utilisées pour modéliser les fonctions corticales. Elle montre que la règle de Hebb n'est pas suffisante pour rendre compte des propriétés adaptatives du cortex. Des extensions de cette règle sont proposées, en particulier pour intégrer le temps dans les phénomènes d'apprentissage synaptique et cellulaire. Une théorie qui relie les règles de plasticité et la spécialisation des régions et des fonctions corticales est exposée comme une synthèse des différents modèles proposés.

Mots clefs - Modélisation, Cortex cérébral, Réseaux de neurones, Règles d'apprentissage

Thesis abstract - The present work is related to recent developments within cognitive science. The main purpose is to model the properties and functions of the cerebral cortex. The goal is to build a modeling framework, and within this framework, to compare cortical processes involved in sensory integration (pattern recognition), motor performance (command of arm movement), and temporal organization of behavior (planning).

Chapter 1 gives an overview of neural modeling principles derived from connectionist models. A modeling framework based on principles of cortical organization and operation is exposed in chapter 2. The goal of this chapter is to provide a formal description of these principles for the use of modeling. In particular, mathematical equations corresponding to computational properties of cortical circuits are given.

Chapters 3, 4, and 5 provide detailed descriptions of models concerning visual integration, motor performance, and temporal organization of behavior. Chapter 3 illustrates transformations of retinal information for object recognition and chapter 4 transformations of retinal information for arm movement. Chapter 5 begins by a review on prefrontal functions and then presents a neural network model built from the properties of the prefrontal cortex. This models predicts neuronal activities during the acquisition and expression of simple planning task, similar to that used in primates (delayed response task).

Chapter 6 contains a discussion on the biological basis of plasticity and on learning rules used in models of cortical functions. It shows that the Hebbian rule is not sufficient to account for the adaptive properties of neocortex. Extensions of this rule are proposed, in particular to introduce the temporal dimension in synaptic and cellular plasticity. A tentative theory relating synaptic plasticity rules and the specialization of cortical regions and function is presented, which is a synthesis of the different models exposed in this work.

Keywords - Modeling, Cerebral cortex, Neural networks, Learning rules