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Carlos Hernández · Ricardo Sanz  
Jaime Gómez-Ramirez · Leslie S. Smith  
Amir Hussain · Antonio Chella  
Igor Aleksander *Editors*

# From Brains to Systems

Brain-Inspired Cognitive Systems 2010

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# **Advances in Experimental Medicine and Biology**

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Editors

# From Brains to Systems

Brain-Inspired Cognitive Systems 2010

 Springer

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*To our beloved families and caring friends.*

# Preface

The chapters included in this book are extended versions of the most relevant works presented at the *Brain-inspired Cognitive Systems Conference* held in July 2010 in Madrid, during mild estival days. BICS 2010 was a multitrack conference organised around four strongly related symposia:

- The *Sixth International Symposium on Neural Computation* (NC 2010)
- The *Fifth International Symposium on Biologically Inspired Systems* (BIS 2010)
- The *Fourth International Symposium on Cognitive Neuroscience* (CNS 2010)
- The *Third International Symposium on Models of Consciousness* (MoC 2010)

BICS 2010 was the fourth of a series of BICS events taking place biennially. The three previous BICS conferences were BICS 2008 (Sao Luis, Brazil), BICS 2006 (Lesbos, Greece) and BICS 2004 (Stirling, UK).

The Brain Inspired Cognitive Systems Conference in Madrid brought together a group of leading scientists and engineers who use analytic and synthetic methods both to understand the astonishing cognitive processing properties of biological systems, and specifically those of the living brain, and to exploit such knowledge to advance engineering methods for building artificial systems with higher levels of cognitive competence.

The four BICS 2010 Conference Symposia were closely connected events around different aspects of the relation between brain science and the engineering of cognitive systems. The scientific program tried to encourage cross-fertilization across the many symposia topics. This emphasized the role of BICS as a major meeting point for researchers and practitioners in the areas of biological and artificial cognitive systems, encouraging debates across disciplines so as to enrich researchers with complementary perspectives from the diverse scientific fields:

NC 2010 presented realistic neural network models and applications. In particular, the symposium focussed on pattern onset learning, structural analyses on Spike-Timing-Dependent Plasticity (STDP) and computational implementations of the Continuum Neural Field Theory.

BIS 2010 was mainly devoted to neuromorphic systems and neurophysiologically inspired models.

The symposium explored biologically inspired architectures for simulation of object perception, decision making, attention, language or emotions in autonomous agents.

CNS 2010 covered both computational models of the brain and brain-inspired algorithms and artifacts. This symposium presented a wide-ranging set of empirical and theoretical papers on key topics in the field of cognitive neuroscience such as, perception, attention, memory or cognitive impairment.

MoC 2010 shed light on both philosophical and neurological basis of consciousness. Machine Consciousness focusses on both aspects by investigating how to build self-aware machines. The symposium focused on Machine Consciousness and presented papers such as a metric of visual qualia in ar-

tificial cognitive architectures, and design and implementation principles for self-conscious robots or machine free will.

BICS 2010 gathered cognitive systems engineers and brain scientists in sessions where cross-domain ideas were fostered in the hope of getting new emerging insights on the nature, operation and extractable capabilities of brains. This multiple perspective approach is necessary in complex cognitive systems engineering because the progressively more accurate data about brains is producing a growing need of both a quantitative and theoretical understanding and an associated capacity to manipulate this data and translate it into engineering applications rooted in sound theories.

The conference hosted both researchers that aim to build brain inspired systems with higher cognitive competences, and as well as life scientists who use and develop mathematical and engineering approaches for a better understanding of complex biological systems like the brain. All them trying to meet at the point of rigorous theorising necessary both to understand biology and support engineering.

The four symposia and this resulting book—a collection of selected and extended papers—is an attempt to provide a broader perspective on these issues which are at the core of XXI century science: the discovery of the organisational principles governing the neural dynamics that mediate in cognition and the potential application of these principles into technical systems.

Madrid, Spain

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This book would not have been possible without the dedicated effort of many people to whom we can but express our gratitude here. First and foremost, these are the authors of the chapters, who put a thorough application into adapting the extraordinary work they presented at the BICS 2010 Conference that gave birth to this book. We acknowledge the support provided by the Autonomous Systems Laboratory, the Escuela Técnica Superior de Ingenieros Industriales of the Universidad Politécnica de Madrid and the Ministerio de Ciencia y Tecnología for the organisation of the BICS 2010 Conference. We also owe our gratitude to all the people that collaborated in the celebration of the BICS conference, the organisation, reviewers and specially the contributing participants. Finally very special thanks to Julia Bermejo, whose dedicated help in the revision of the material has ensured the quality of this publication, and to Ann Avouris, the Springer Publishing Editor, whose support has made this book possible.

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# Chapter 1

## Introduction

### From Brains to the Machines of the Future

Ricardo Sanz, Carlos Hernández, and Jaime Gómez-Ramirez

#### 1.1 Introduction

Real-world, optimally performant, mission-flexible robots in open-ended environments have been predicted to arrive on a short time by many technologists. Indeed, they have been arriving in 25 years at least during the last 30 years [11].

This is a similar scenario to what has been happening with controlled nuclear fusion. Like fusion reactors, the promised robots are not yet here. The machines of the future are still inside the movies.

Commercial robots—the robots that people will pay-for today—are still only able to operate in controlled or semi-controlled environments doing quite simple tasks: welding car parts in factories or cleaning bathroom floors. The complexities of dwelling in the real world, performing heterogeneous tasks in open-ended, dynamic environments, have proven too difficult for the control technologies available these days.

However, the minute animals in our environment are perfectly able to manage in these conditions. They prove that the problems of real-world activity can be solved in economic ways.

The bio-inspired systems research programme is guided by the idea that the solution can be found in their senses, legs or brains. It should be possible to leverage the technologies produced by Darwinian evolution to improve the behavior of our machines.

#### 1.2 Going From Brains to Machines

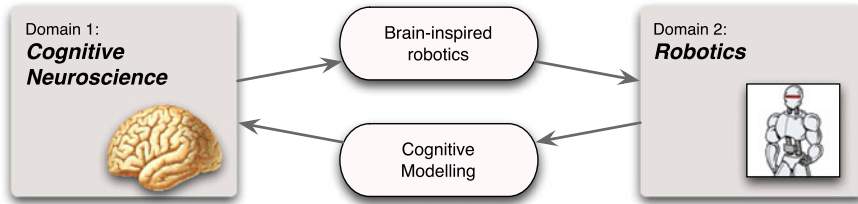
The behavior of a machine is determined by the interaction between its internal dynamics and the environment it is coupled to. The design process of machines starts in the identification of the desired environmental changes—e.g. moving water from here to there—and goes into the design of a structure for the machine that will bring forth such an effect by the emerging machine-environment interaction dynamics.

When the desired behavior is complex the design of the machine structure is divided into two parts: a physical subsystem capable of producing the environment changes and an informational subsystem

---

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**Fig. 1.1** Brain-inspired robotics serve both as an engineering method and as a experimental testbed for biological theories. Theories of brain function can be tested in robot-based controllers implementing transferred theoretical models

that forces the machine behave in a certain way. The term *controller* is used for the informational subsystem in charge of forcing behavior.

There are different strategies to build controllers. The conventional engineering strategy is to build the controller in such a way that the machine will necessarily behave as desired. Let's call this strategy the *design and build* strategy for artificial minds. This is done using first principles and classic engineering strategies for design [9]. However, when behavior or environment is way too complicated, the design strategy does not cope well.

An alternative strategy is used when the task requirements and its constraints are so complex that we cannot apply the design-build strategy. This strategy is based on reverse-engineering systems that manifest the desired behaviour and copy their functional organisations. This second strategy—let's call it *reverse-engineer and copy*—is what is addressed in this volume, taking the brain as a source of design inspiration.

The study of the brain as source of design knowledge for more effective machines offers the possibility of addressing extremely complex, real-world tasks than only animals can perform so far.

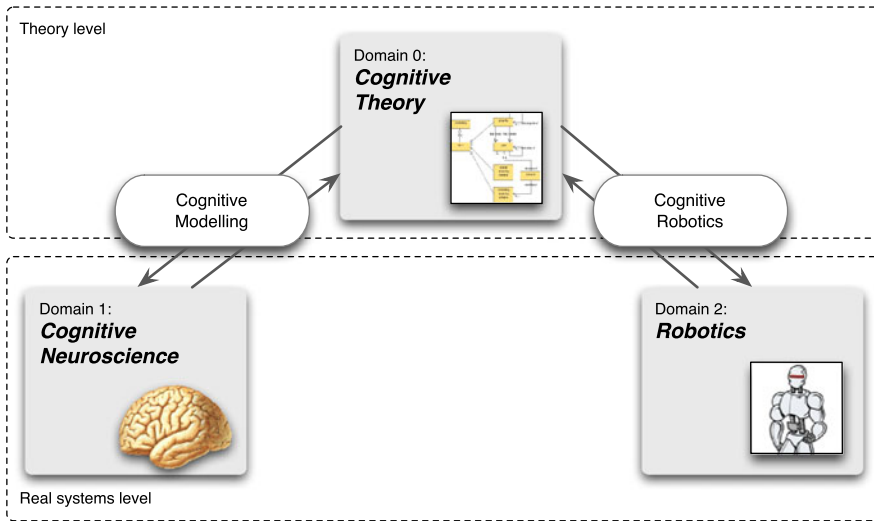
Consider for example the apparently simple task of going around, picking some waste objects to dispose of them into the recycling bin. This is a task that can be done by a toddler or a trained dog. This is also easily done by a robot when the objects and the recycling bin fit certain predefined perceptual categories and the environment conditions are kept in a narrow operative band (e.g. illumination is broadly uniform and sufficient, or the ground is even enough and uncluttered).

However, when these operational conditions are not met, the *designed-built* robot, designed departing from now no longer holding assumptions, will fail in performing the task. Do not try to find articles about robots failing in the scholarly journals of the field. From time to time they appear in funny videos in YouTube but nobody is willing to publish about failures—neither authors nor editors. But failures are there: robots are not functionally robust enough except in performing simple tasks. There is a strong need of improving mission-level robustness if the robots are going to be able to provide their services in open-ended conditions.

It is in this context when we revert to the second strategy: copying brains. Bioinspired cognitive architectures offer the promise of solving this kind of problems because the original architectures—those of brains—are already solving them. There are plenty of threads in this research strategy. Some of them are focused in physical competences of agents but most of them are related to mental competences. Current trends tend to depart from the exploration of the abstractions about the mind and intelligence (as embraced by AI of the sixties), turning to the insights gained exploring the brain [14].

Some will argue that by focusing in the brain we are losing the necessary holistic picture of biological agents. Beyond discussions about embodiment and disembodiment [1, 6] there is a clear need of focusing on the cognitive organisation of the agent (that obviously encompasses the body [12]). While the body is enormously relevant in cognitive processes [2, 10], the role of the brain in higher level cognition is indubitable. The flow from brain knowledge to robotics is a potential source of technological assets. Also, while brain-inspired robotics is a very promising engineering method it is also well settled as an experimental testbed for biological theories (see Fig. 1.1).





**Fig. 1.2** Brain-inspired robotics will be a technology *sensu stricto* when biological implementation details are abstracted out and only systemic aspects prevail. This implies rendering the theories in cognitive neuroscience in a form that is devoid of biological ties (the abstract *Theory level* shown in the figure above)

Building robot controllers by implementing theories about the brain will serve two basic purposes: (i) controlling the robots and (ii) exploring the implications of the theories and, in a sense, validating them in their ecological contexts [4].

However, systematic cognitive systems engineering requires solid theories and not just a collection of inexplicable designs. It is necessary to transition from a catalog of *ad-hoc* cognitive mechanisms to a rigorous cognitive science; this science may later be applied in the requirements-driven, design process necessary for attaining pre-specified performance levels (see Fig. 1.2).

In bioinspired cognitive systems' engineering it is necessary to extract basic design principles [7, 8]. It is not enough to copy the organisations of animals' brains or bodies [13, 17]. This is the fundamental methodological doctrine behind the several works included in this book: all they try to go beyond the shallow analysis of biological structures, trying to offer more profound, rigorous visions on cognitive systems operation.

### 1.3 Book Contents

The book contains eighteen chapters that cover the whole spectrum of the conference. From models of biological aspects at molecular levels to philosophical considerations about the most abstract aspects of minds.

**Coath et al.**—*Emergent Feature Sensitivity in a Model of the Auditory Thalamocortical System*—investigate plasticity of the brain auditory system. They address the question of whether a recurrently connected thalamocortical model exhibiting spike time dependent plasticity can be tuned to specific features of a stimulus. This is of relevance to the understanding of post-natal—and beyond—construction of cortical and thalamic representations of the features of auditory stimulus that will be available for the cortex-related auditory processing. This work is relevant for the understanding of continuous, post-developmental plasticity that may be critical for robust autonomous systems in changing environments.

**Humble et al.**—*STDP Pattern Onset Learning Depends on Background Activity*—study to what extent the well-known spike-timing dependent plasticity [5] depends on background activity leading

even to instabilities. From their results the authors present preliminary insights into the neuron's encoding of temporal patterns of coincidence of spikes and how the temporal precision of the onset response depends on the background activity.

**Basalyga et al.**—*Emergence of Small-World Structure in Networks of Spiking Neurons Through STDP Plasticity*—investigate how a neural network structure changes under synaptic plasticity. They use complex networks of conductance-based, single-compartment integrate-and-fire excitatory and inhibitory neurons showing that under certain conditions, a nontrivial small-world<sup>1</sup> structure can emerge from a random initial network by learning.

**Lefort et al.**—*Coupling BCM and Neural Fields for the Emergence of Self-organization Consensus*—focus on the integration of multimodal perception. They propose a cortex-inspired models for multi-modality association. The model integrates modality maps using an associative map to raise a consistent multimodal perception of the environment. They couple the BCM learning rule and neural maps to obtain a decentralized and unsupervised self-organization.

**Bhattacharya et al.**—*Alpha and Theta Rhythm Abnormality in Alzheimer's Disease: A Study Using a Computational Model*—address theoretical model construction towards solving clinical issues of disease. Their models—of thalamocortical circuitry which exhibits oscillation within the theta and the alpha bands—are aimed at gaining a better understanding of the neuronal mechanisms underlying EEG band power changes. Their work shows how the change in model oscillatory behaviour is related to changes in the connectivity parameters in the thalamocortical as well as sensory input pathways. This understanding of the mechanics under the disease symptomatology may in the future provide useful biomarkers towards early detection of the Alzheimer's disease and for neuropharmaceutical investigations.

**Raiko and Valpola**—*Oscillatory Neural Network for Image Segmentation with Biased Competition for Attention*—study the emergent properties of a cortex-inspired artificial neural network for image segmentation. They combine segmentation by oscillations and biased competition for perceptual processing. They show encouraging results of experiments using artificial image data.

**Johnsson and Gil**—*Internal Simulation of Perceptions and Actions*—address the architectural aspects of neural network architectures based on associative self-organising maps to be able to internally simulate perceptions and actions. They present several topologies—mostly recurrently connected—as e.g. a bimodal perceptual architecture and action neural networks adapted by the delta rule. They show simulation tests that show encouraging experimental results.

**Woodman et al.**—*Building Neurocognitive Networks with a Distributed Functional Architecture*—suggest that the very possibility of successful modeling human behavior with reduced-dimensionality models is a key point in understanding the implementation of cognitive processes in general. They suggest that this is due to a separation in the time scales of the dynamics guiding neural processes and the overall behavioral expression, offering a distributed model based on structured flows on manifolds to understand the organization of this class of behavioral dynamics. They demonstrate this model in a functional architecture of handwriting showing hierarchical sequencing of behavioral processes.

**Schierwagen**—*Reverse Engineering for Biologically Inspired Cognitive Architectures: A Critical Analysis*—analyses methodological and theoretical issues in the development of biologically inspired cognitive systems. He is concerned about the very possibility of reverse-engineering brains by conventional decompositional analysis. Schierwagen concludes that this approach is a no go, discussing the implications for investigations of organisms and behavior as sources of engineering knowledge.

**Quinton et al.**—*Competition in High Dimensional Spaces Using a Sparse Approximation of Neural Fields*—address the computational tractability of implementations of the continuum neural field

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<sup>1</sup>A small-world network is a type of mathematical graph in which most nodes are not neighbors of one another, but most nodes can be reached from every other by a small number of hops or steps.

theory when an adaptive resolution or an arbitrary number of input dimensions is required. They propose a more economic alternative to self-organizing maps using a sparse implementation based on Gaussian mixture models. They test the proposed algorithm in a reactive color tracking application, using spatially distributed color features.

**Aleksander and Gamez**—*Informational Theories of Consciousness: A Review and Extension*—analyse recent theories that establish a systematic link between conscious experience and the flow of information—differentiation and integration—in certain areas of the brain. They analyse measures of information integration [15, 16] and some related algorithms for providing quantitative measures of information integration or causal density; hopefully to be used to make predictions about consciousness. They analyse the computational complexity of these algorithms, which limit their application to just small datasets—networks of around a dozen neurons—implementing one of the better known algorithms in the SpikeStream neural simulator to carry out some experimental comparisons.

**Gómez and Sanz**—*Hippocampal Categories: A Mathematical Foundation for Navigation and Memory*—address the theoretical tools necessary for capturing the theories of cognition that span from neurons to psychological aspects. The mathematical theory of categories is proposed as a valid foundational framework for theoretical modeling in brain sciences, and demonstrated presenting a category-based formal model of grid cells and place cells in hippocampus.

**Dura-Bernal et al.**—*The Role of Feedback in a Hierarchical Model of Object Perception*—address the question of robust object recognition—including occluded and illusory images, or position and size invariances. They propose a model derived from the HMAX model showing how this feedforward system can include feedback, by means of an architecture which reconciles biased competition and predictive coding approaches. This work provides a biologically plausible model of the interaction between top-down global feedback and bottom-up local evidence in the context of hierarchical object perception.

**Manzotti**—*Machine Free Will: Is Free Will a Necessary Ingredient of Machine Consciousness?*—addresses the elusive concept of free will in a mechanistic context. Manzotti analyses whether freedom and consciousness are independent aspects of the human mind or by-product of the same underlying structure; this analysis leads to the author outlining a proposal for an architecture sustaining machine free will.

**Jändel**—*Natural Evolution of Neural Support Vector Machines*—describe two different neural implementations of support vector machines for one-shot trainable pattern recognition. One is based on oscillating associative memory—inspired in the olfactory system—and the second is founded on competitive queuing memory—originally employed for generating motor action sequences in the brain. For both support vector machine models they show that there is a plausible evolutionary path showing that they can apparently emerge by natural processes.

**Chella et al.**—*Self-Conscious Robotic System Design Process—from Analysis to Implementation*—address some of the engineering issues concerning the development of robots endowed with self-conscious capabilities. They analyse the whole engineering lifecycle (from analysis to implementation) focusing on aspects that are specific to the development of self-conscious robotic systems. They propose a new design process—PASSIC—offering custom software engineering techniques for realizing the complex sub-systems needed. This work binds the studies of consciousness with the necessary engineering methods to apply them.

**Arrabales et al.**—*Simulating Visual Qualia in the CERA-CRANIUM Cognitive Architecture*—touch upon the elusive problem of hard consciousness in robots. They attack qualia by a complementary study building “artificial visual qualia” using their cognitive architecture CERA-CRANIUM based on Baars [3] global workspace theory. They study artificial qualia as simulated, synthetic visual experience. The inspection of the dynamics and transient inner states of the cognitive artificial system let them discuss the possible existence of similar mechanisms in human brains.

**Thomsen**—*The Ouroboros Model, Selected Facets*—describes some fundamental aspects of the Ouroboros cognitive architecture: self-referential recursive processes, schema-based memory organi-

sation, feature-driven expectations, etc. Thomsen shows how the Ouroboros Model can address biological cognitive system aspects like attention, emotion, priming, masking, learning, sleep and consciousness.

## 1.4 Value and Perspectives

Science moves in little steps, but also makes its progress with revolutionary discoveries and concepts that sweep away whole and entire edifices of thinking and replace them with new theories that explain more with less. However, there is a constant in this march, the strive for mathematisation and unification.

The extent to which reverse-engineering of brains will help with technological advance in the engineering of more robust autonomous systems is yet to be clear. Nevertheless, the different approaches offered in this book show a steady progress toward more rigorous methods of analysis and synthesis. This rigour implies that they may eventually converge into a single, unified theory of cognition: the very holy grail of cognitive science and engineering.

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## Chapter 2

# Emergent Feature Sensitivity in a Model of the Auditory Thalamocortical System

Martin Coath, Robert Mill, Susan L. Denham, and Thomas Wennekers

**Abstract** If, as is widely believed, perception is based upon the responses of neurons that are tuned to stimulus features, then precisely what features are encoded and how do neurons in the system come to be sensitive to those features? Here we show differential responses to ripple stimuli can arise through exposure to formative stimuli in a recurrently connected model of the thalamocortical system which exhibits delays, lateral and recurrent connections, and learning in the form of spike timing dependent plasticity.

### 2.1 Introduction

Since Hubel and Wiesel [11] showed that, for neurons in visual cortex there were ‘preferred stimuli’ which evoked a more vigorous response than all other stimuli, it has become commonplace to think of neurons, or clusters of neurons, as having stimulus preferences—or alternatively as responding to ‘features’ of the stimulus.

Although it is widely believed that auditory perception is based on the responses of neurons that are tuned to features of the stimulus it is not clear what these features are or how they might come in to existence. There is, however, evidence that cortical responses develop to reflect the nature of stimuli in the early post-natal period [12, 24, 25] and that this plasticity persists beyond early development [20]. In addition it has been shown that excitatory corticofugal projections to the thalamus are likely to be crucial in thalamic plasticity and hence in the representation of the stimulus that is available to the cortex [7].

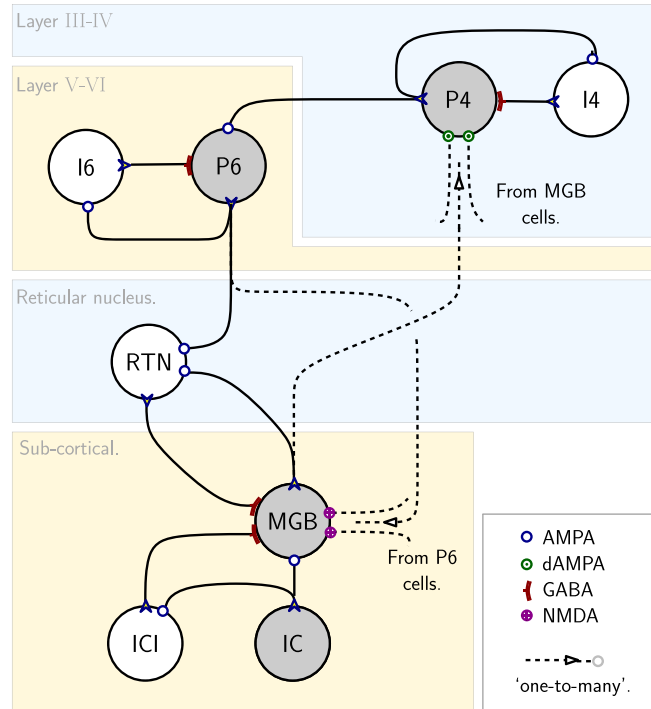
The work presented here is motivated by the desire to investigate whether a recurrently connected thalamocortical model exhibiting spike time dependent plasticity (STDP) can be sensitized to specific features of a stimulus by exposure. Modelling studies have suggested [4, 5] that the spectro-temporal patterns found in a limited number of stimuli, which reflect some putative early auditory environment, may bootstrap the formation of neural responses and that unsupervised, correlation based learning leads to a range of responses with features similar to those reported from measurements *in vivo*. However in this previously reported work the model of STDP adopted, mostly for reasons of computational efficiency, was based on average activity over a period of time rather than the times of the spikes themselves. In addition this model also led to some synaptic weights increasing without limit and hence an arbitrary cut-off in the time used for training.

Here we employ a model of plasticity that depends on times of pre-synaptic spikes and a variable representing the post-synaptic activity [2] and avoids the problem of unlimited weights by using synapses that are bi-stable, that is, over time the weights of all synapses tend to one or zero. We

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**Fig. 2.1** Each vertical sub-unit of the network consists of eight neurons. The sub-cortical section receives input from one stimulus channel representing a position on the tonotopic axis. Each thalamic (MGB) cell is connected to a number of cortical cells representing layer IV, the principal receiving layer. Layer VI cells recurrently connect the cortex to the thalamus *via* NMDA synapses which exhibit STDP and thus are the loci of the correlation-based learning in the network



show that a model of auditory cortex incorporating lateral spread of excitation with associated delays, recurrent connections between layers, and exhibiting STDP (learning) adapts during exposure to training patterns (stimuli) in a way that is determined partly by the stimuli themselves, and the resulting network exhibits ‘feature preferences’ that could support the representation of the input in a high dimensional feature space.

## 2.2 Methods

### 2.2.1 The Network

#### 2.2.1.1 Network Architecture

The model auditory cortex consists of five hundred repeating units each consisting of eight neurons arranged in layers, as illustrated in Fig. 2.1. The lower, sub-cortical, section represents the junction of the inferior-colliculus (IC) with the medial geniculate body of the thalamus (MGB). The upper section represents a two-layer cortical structure consisting of a receiving layer (layer IV [22] marked simply as P<sub>4</sub> in Fig. 2.1) and a second layer (marked as P<sub>6</sub> in the figure) providing a recurrent excitatory connection to the thalamus [10], and recurrent inhibitory connection to the thalamus via the thalamic reticular nucleus (RTN) [9, 10]. Inhibitory inputs to the thalamus also come from the IC, in this case via a GABA-type interneuron, although there is evidence for direct connections from GABAergic cells in IC [14, 21].

The recurrent excitatory connections from P<sub>6</sub> to MGB are mediated by NMDA type synapses that are the loci of the STDP (see Sect. 2.2.2). This approach reflects the belief that the principle role of such corticofugal connections is to modulate thalamocortical transmission and that “corticofugal

modulation is an important mechanism for learning induced or experience-dependent auditory plasticity” [17, 26]. Although it is clear that some of the changes associated with this plasticity must be located in the cortex, there is recent evidence that corticothalamic synapses are regulated by cortical activity during the early developmental period [23].

### 2.2.1.2 Neurons

The neurons used are linear integrate-and-fire units and use a stimulation paradigm not of current injection, but of conductance injection which moves integrate-and-fire models closer to a situation that cortical neurons would experience in vivo [6]. This modification also allows the use of conductance-based synapses as described in Sect. 2.2.1.3 below.

The behaviour of the neurons can be described by:

$$\tau \frac{dV}{dt} = -(V(t) - E_L) - \sum_i w_i \cdot (V(t) - E_{Ri})$$

$$\text{if } V > V_T \quad \text{then } V \rightarrow E_L : Z(t) \rightarrow 1 \text{ else } Z(t) \rightarrow 0 \quad (2.1)$$

where  $\tau$  is the membrane time constant,  $V$  the membrane potential,  $E_L = 0$  the leak reversal potential,  $w_i(t)$  is the weight of the  $i$ th synapse—this is a function of time because the value of  $w$  subsumes not only the weight constant but also the time varying conductance of the synapse (see Sect. 2.2.1.3),  $V_T = 1$  is the firing threshold potential, and  $Z(t)$  is the output of the neuron expressed as delta functions at firing times. Values for  $\tau$  were assigned identically and independently randomly from an equal distribution (i.i.d.) in the range 9–11 ms. The value  $E_{Ri}$  is the reversal potential of the  $i$ th synapse.

In addition all neurons received i.i.d. current injections representing the sum of non-stimulus-specific activity. This has the effect of bringing the neurons closer to threshold and the range of values was chosen such that a low level (<1 Hz) of spontaneous action potentials was evoked.

### 2.2.1.3 Synapses

There are four types of synapse present in the model. Each exhibits a time dependent conductance which is derived from the train of spikes (delta functions) originating in the pre-synaptic neuron. The conductance is the output of a second-order low-pass filter and the resulting temporal response function for a single spike is an alpha-function characterised by two parameters: the rise-time  $\tau_r$  and the decay-time  $\tau_d$ .

The majority of excitatory synapses have fast rise and fall times and are designated AMPA types. Other excitatory synapses in the thalamocortical projections have longer rise and fall times and are designated as NMDA synapses. Inhibitory synapses are all of the same type which have very fast rise times and intermediate fall time and these are designated as GABA. The time constants are given in Table 2.1 [8].

**Table 2.1** Time constants used in synapse models

	$\tau_r$	$\tau_d$
AMPA	0.90 ms	1.50 ms
GABA	0.01 ms	5.00 ms
NMDA	3.00 ms	40.00 ms

### 2.2.1.4 Depressing Synapses

The axons that project from MGB to layer IV of the cortex have the same time constants as other AMPA synapses but exhibit synaptic depression and are referred to as dAMPA. The dynamical properties of cortical synapses can influence the temporal sensitivity of cortical circuitry. Here we use a model of synaptic depression which is characterised by the variable representing the running fraction of available neurotransmitter  $x(t)$  that recovers to unity with a time constant  $\tau_A$  [19].

$$\frac{dx}{dt} = \frac{1-x}{\tau_A} - x \cdot Z(t) \quad (2.2)$$

The time constant  $\tau_A$  was adjusted so as to be consistent with paired pulse ratios reported in in vivo studies of pyramidal neurons [1]. All simulations were run with  $\tau_A = 30$  ms.

### 2.2.1.5 Connections Between Columns

The excitatory afferents from the thalamus to each cell in the cortical receiving layer come from a number of MGB cells as indicated in Fig. 2.1. These are selected based on connection probabilities that vary with the distance between cells as shown in (2.3), i.e. falling as the inter-column distance  $d$  increases. The maximum probability of a connection being made is at  $d = 0$  and this value is controlled by the variable  $C$  and the ‘width’ of the function is determined by  $s$ . All simulations were run with  $C = 0.2$ ,  $s = 20$ .

In a similar way the corticothalamic connections to each MGB cell also come from a number of  $P_6$  cells selected in a similar way. For these connections  $C = 0.1$ ,  $s = 100$ . The probability of connection is given by:

$$P = C \cdot \exp\left(\frac{-0.5 \cdot d^2}{s^2}\right) \quad (2.3)$$

For each of the 500,000 possible connections in the cortico-thalamic and thalamocortical projections a Boolean value was chosen with the probability of TRUE being  $P$  and a synapse created, or not, accordingly.

These ‘fan out’ connections give the opportunity for cortical neurons to integrate information from heterotopic areas of thalamus and also stand as surrogates for the cortico–cortical connections [18] which have no explicit representation in this model. The cortico–thalamic connections are mediated via NMDA type synapses which are the loci of the STDP and hence the correlation-based learning in the network, see Sect. 2.2.2.

### 2.2.1.6 Delays

In order to investigate the role played by the temporal structure of the stimuli in the emergent stimulus preferences of the network, delays were incorporated in to the network. Assumptions were made about the dimensions of the cortical area represented by the model and the range of values for axonal propagation rates. Using these two figures, distance dependent delays were introduced for fan-out connections in the model based on the inter-column distance.

Under the simplifying assumption that the delay increases linearly with  $d$  we have assumed a maximum separation between neurons of 1 cm and values of axonal propagation rate from 0.5–10.0  $\text{ms}^{-1}$ .



### 2.2.2 Synaptic Plasticity

*Spike-timing-dependent plasticity* (STDP) is the modification of synaptic weights based on the correlation between pre- and post-synaptic firing times. Evidence for this has been gathered in vitro, and is beginning to emerge in vivo [13], and it is believed to be a feature of synapses which have NMDA receptors that regulate the genes required for long term maintenance of these changes [15]. In general, if a pre-synaptic spike precedes a post-synaptic spike then the synapse is potentiated; if the timing of the spikes is reversed then the synapse is depressed.

One problem with correlation-based learning is that the weight changes are unstable and additional mechanisms have to be invoked to ensure that weights do not increase in an uncontrolled manner. Our approach in earlier work was to start with very low weights and keep the training short [3]. In this way we see how the pattern of weight changes establishes itself in the early stages of training. Another possibility, the approach that is adopted here, is to implement a form of STDP in which the weights are bi-stable [2].

The learning rule used in the results presented here is summarized in (2.4), (2.5), and (2.6). At the arrival time of each pre-synaptic spike the synaptic efficacy  $X$  is modified based on the post-synaptic neuron membrane potential  $V$  and the post-synaptic neuron internal state variable  $C$ . The variable  $C$  is identified with the calcium concentration [16] and is determined by a leaky integration of post-synaptic spiking activity with a relatively slow time constant  $\tau_C$ :

$$\frac{dC(t)}{dt} = -\frac{1}{\tau_C}C(t) + J_C \sum_i \delta(t - t_i) \quad (2.4)$$

where  $J_C$  is the contribution of a single post-synaptic spike. The synapse is potentiated by a small amount  $a$  if  $V$  is above a pre-determined threshold  $\theta_V$  and  $C$  is within set limits  $\theta_{up}^l$  and  $\theta_{up}^h$ . Similarly the synapse is de-potentiated by an amount  $b$  if  $V$  is less than or equal to  $\theta_V$  and  $C$  is within a different pair of bounds  $\theta_{down}^l$  and  $\theta_{down}^h$ :

$$\begin{aligned} X &\rightarrow X + a && \text{if } V(t_{pre}) > \theta_V && \text{and } \theta_{up}^l < C(t_{pre}) < \theta_{up}^h \\ X &\rightarrow X - b && \text{if } V(t_{pre}) \leq \theta_V && \text{and } \theta_{down}^l < C(t_{pre}) < \theta_{down}^h \end{aligned} \quad (2.5)$$

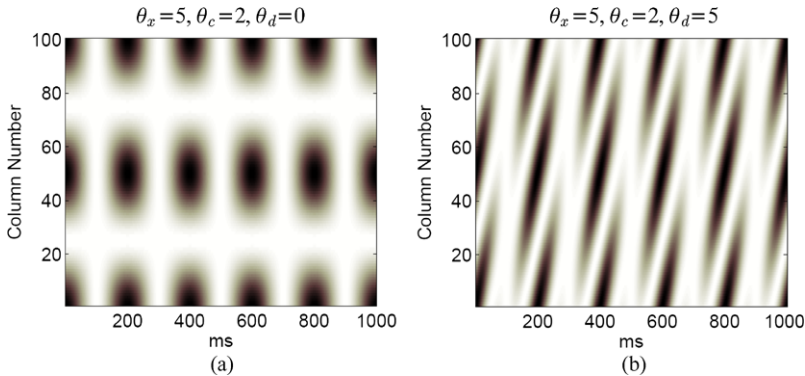
If no modification is triggered by the conditions in (2.5) (including in the absence of pre-synaptic spikes)  $X$  drifts towards one of two stable states depending on whether it is greater than a threshold value  $\theta_X$ :

$$\begin{aligned} \frac{dX}{dt} &= \alpha && \text{if } X > \theta_X \\ \frac{dX}{dt} &= -\beta && \text{if } X \leq \theta_X \end{aligned} \quad (2.6)$$

where  $\alpha$  and  $\beta$  are positive constants.

### 2.2.3 Training

Each of the stimuli used in these experiments consists of a pattern of current injection into the units representing neurons of the inferior colliculus, these are marked IC in Fig. 2.1. Although, for simplicity, these patterns of current injection are not derived from audio files via a cochlear model they can be thought of as time varying patterns of activity across the tonotopic axis represented by the one dimensional array of IC cells.



**Fig. 2.2** Example stimuli used in training the network. Each example, in common with all such stimuli used in the experiments, have a 5 Hz amplitude modulation rate. **(a)** A stimulus with no FM component, and **(b)** a stimulus with a slowly moving *up* FM component (determined by  $\theta_d$ ). In the work reported here stimuli varied only in the value for  $\theta_d$

### 2.2.3.1 Parametric AM/FM Stimuli

The stimuli were all of the form given by (2.7) below:

$$z(t, c) = \frac{(\cos(2\pi t\theta_x) + 1)(\cos(2\pi(c\theta_c + t\theta_d) + 1))}{4} \quad (2.7)$$

where  $z(t, c)$  is the value of the current injection at time  $t$  and in channel  $c$ .

The parameters  $\theta_x$ ,  $\theta_c$  and  $\theta_d$  can be adjusted to give sweeps or gratings that move in the tonotopic axis with time, and also patches of stimulation that have a temporal amplitude modulation (AM) but no frequency modulation (FM) component. Examples of such stimuli are shown below in Fig. 2.2.

The value of  $\theta_x$ , the temporal modulation rate, was fixed at 5 for all experiments. This value was chosen because of the inherent low-pass nature of the thalamocortical projections caused by the depressing synapses, (see Fig. 2.1) hence stimuli with temporal modulation rates much greater than 5 would drive the cortical receiving layer only weakly. In addition rates of temporal modulation around 4–5 Hz are important for communication signals such as the syllable rate for human speech. The value of  $\theta_c$ , the spectral density, was fixed at 2.

For each experiment one value of  $\theta_d$  was chosen as the training stimulus. The network was then exposed to 50 epochs (each 2 seconds) of this stimulus with the learning rule turned on. Between each of these learning phases the response of the network was recorded to 10 other stimuli. These are referred to as test stimuli, with a range of values for  $\theta_d$  both positive and negative. Each test and training stimulus was separated from the previous one by  $\approx 300$  ms of random current injection at the same mean level as the stimuli and the phase of the stimulus advanced by a random value from 0 to  $2\pi$  to ensure that both the training and test stimuli were not presented starting at the same phase in all cases, this process is summarised in Fig. 2.3. In the results section we consider networks trained with the values for  $\theta_d$  of  $-10$ ,  $-5$ ,  $0$ ,  $5$ ,  $10$ . Fixing  $\theta_d$  at integer multiples of  $\theta_x$  produces stimuli with similar temporal characteristics in that the maxima of the current injections occur in the same channels with each presentation.

### 2.2.3.2 Random Chord Stimuli

We also consider results of training with stimuli that consist of injections of current in channels chosen at random ( $P = 0.1$ ) for short periods of time chosen from an equal distribution from 20–60 ms. These noise-like ‘random chord’ stimuli are more suitable than random current injections representing white noise which drive the cortical receiving layer only very weakly.