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Constructivist Neural Network Models of Cognitive Development

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Declaration

I have composed this thesis myself and it reports original research that has been conducted by myself unless otherwise indicated.

Edinburgh, 7th May 2000

Gert Westermann

Acknowledgements

My foremost thanks go to my supervisors, David Willshaw and Richard Shillcock. While they gave me the freedom to pursue my own interests, they had an open ear whenever I needed it and I am grateful for many interesting discussions and valuable suggestions throughout the course of my PhD, and for their extensive comments on drafts of this thesis.

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The Centre for Cognitive Science provided the interdisciplinary and stimulating environment without which this thesis would not have been possible. The CNS (later ANC) research group was equally stimulating, and I learned so much from our weekly teas and talks and from discussions especially with Tim Hely, Volker Steuber, Stephen Eglen, Mark Ellison, and Arjen van Ooyen.

Stephen Eglen and Sarah Gingell read the chapter on brain development, and Martina Penke scrutinized the chapters on past tense and agrammatic aphasia simulations, and I am very grateful for their many valuable comments.

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Betty Hughes was always ready to help with many administrative matters and made complicated bureaucracy seem very simple.

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Finally, I want to thank Tomke for her support, patience, and for many wonderful times, and Diane for helping me not to get stressed out at the writing-up stage of this thesis.

Abstract

In this thesis I investigate the modelling of cognitive development with constructivist neural networks. I argue that the constructivist nature of development, that is, the building of a cognitive system through active interactions with its environment, is an essential property of human development and should be considered in models of cognitive development. I evaluate this claim on the basis of evidence from cortical development, cognitive development, and learning theory.

In an empirical evaluation of this claim, I then present a constructivist neural network model of the acquisition of the English past tense and of impaired inflectional processing in German agrammatic aphasics. The model displays a realistic course of acquisition, closely modelling the U-shaped learning curve and more detailed effects such as frequency and family effects. Further, the model develops double dissociations between regular and irregular verbs. I argue that the ability of the model to account for the human data is based on its constructivist nature, and this claim is backed by an analogous, but non-constructivist model that does not display many aspects of the human behaviour. Based on these results I develop a taxonomy for cognitive models that incorporates architectural and developmental aspects besides the traditional distinction between symbolic and subsymbolic processing.

When the model is trained on the German participle and is then lesioned by removing connections, the breakdown in performance reflects the profiles of German agrammatic aphasics. Irregular inflections are selectively impaired and are often overregularized. Further, the model shows frequency effects and the regularity-continuum effect that are also observed in aphasic subjects. The model predicts that an aphasic profile with selectively impaired regular inflections would be evidence for a locally distinct processing of regular and irregular inflections.

Based on these results, I propose that inflectional processing, often claimed to involve qualitatively distinct mechanisms including a mental rule, is better explained by a model that operates with a single mechanism for both regular and irregular inflections but develops dual representations in a constructivist learning process.

The arguments from biology, development and learning theory together with the empirical results presented in this thesis make a strong case for modelling cognitive development with constructivist neural networks.

Contents

List of Figures

Chapter 1

Introduction

The question of how we learn and acquire knowledge of the world has kept philosophers busy since ancient times, and more recently, psychologists, linguists, biologists and many other researchers have joined in to find answers to this fundamental problem. This thesis is based on one particular theory of knowledge acquisition, constructivism.

1.1 Constructivism

Constructivism is the epistemological notion that knowledge is actively constructed by a learner. As such it stands against two other important theories: empiricism, which claims that knowledge arises from sensory experience alone, and rationalism, where knowledge derives from domain-specific innate principles.

The constructivist view is based on the insight that a subject can have no access to an external reality but can build knowledge only on the basis of stimulation of the sensory neurons, in which the nature of the stimulus is not encoded (von Foerster, 1973). To build knowledge thus amounts to constructing an interpretation of the world that is based on nothing more than different patterns of sensory neural activation in the subject. It is in principle impossible to evaluate what the relation between that interpretation and the (inaccessible) reality is. The role of an external reality in constructivism is to constrain, but not to determine, the construction of a cognitive system in an evolutionary way: cognition is adaptive and serves the organization of experience, and when this organization fails the constructed knowledge becomes useless and is devalued in favour of another interpretation. The structure and order of the external world do not exist in an objective sense but are imposed by the subject to create a viable interpretation that allows him to function in it (von Glasersfeld, 1984).

Constructivist theories have had a great influence in the study of cognitive development, namely through Jean Piaget's Epistemological Constructivism. Piaget claimed that all knowledge derives from active interactions with the environment and that information is never just passively recorded by the child, but integrated into her cognitive schema and thus interpreted in terms of what is already known. Through learning, the child adapts her cognitive schema and becomes able to integrate more unusual information. In this way, child and environment exist in a balanced state where the child adapts the world to herself, and adapts herself to the world.

In this thesis, constructivism is viewed from such a developmental perspective and I focus on the notion that the learner develops through interactions with its environment to build more complex knowledge structures and representations based on simpler ones. The motivation behind this approach is to contribute to a recent renewed interest in development (Karmiloff-Smith, 1992; Elman, Bates, Johnson, Karmiloff-Smith, Parisi, and Plunkett, 1996) and the relationship between brain and cognitive development (Johnson, 1997; Quartz and Sejnowski, 1997), and to develop alternatives to theories that deny the importance of development for the understanding of cognition and instead rely on strong nativist assumptions in their explanations (e.g. Chomsky, 1980; Pinker, 1984; Piattelli-Palmarini, 1994). The contributions made here to these issues are in the form of constructivist neural network models of developmental phenomena.

1.2 Principles of Neural Networks

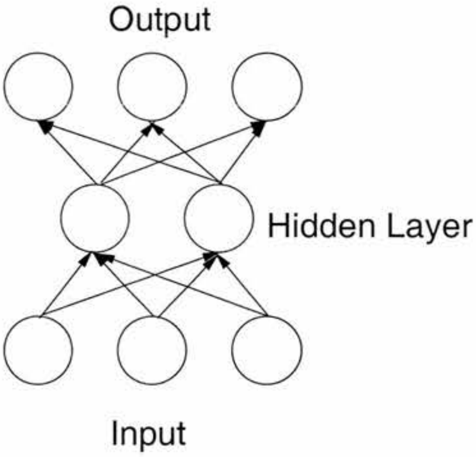

Figure 1.1: A simple neural network with three layers that are fully interconnected by weighted connections.

Neural networks represent a relatively new framework for modelling cognitive development and processing (e.g., Rumelhart, McClelland, and the PDP Research

Group, 1986b; McClelland, Rumelhart, and the PDP Research Group, 1986; Ellis and Humphreys, 1999), and they have been successful in suggesting alternative explanations to more traditional box-and-arrow models and processing theories that rely on symbolic processing (see e.g. Elman *et al.*, 1996). Neural networks come in many different shapes, but they all consist of a number of simple processing elements (called *units* or *nodes*) that are linked by weighted connections (often called *weights*) (figure 1.1). A unit in a neural network can receive external input or input from other units through the weights. In the most common case, a unit adds up the inputs and computes its output as a function of that net input. The activation function can be linear, but of more interest are non-linear functions such as *threshold* functions or *logistic* functions (figure 1.2). In a threshold function, the unit is activated when the input exceeds a threshold value. Such a function is not differentiable which is necessary for some learning algorithms, but a sigmoid function is, while maintaining a close resemblance to a threshold function. Most networks also contain a *bias unit* which is always active and has connections to the other network units. The effect of a bias unit is to adjust the threshold or the "default" value of an activation function (0 in figure 1.2).

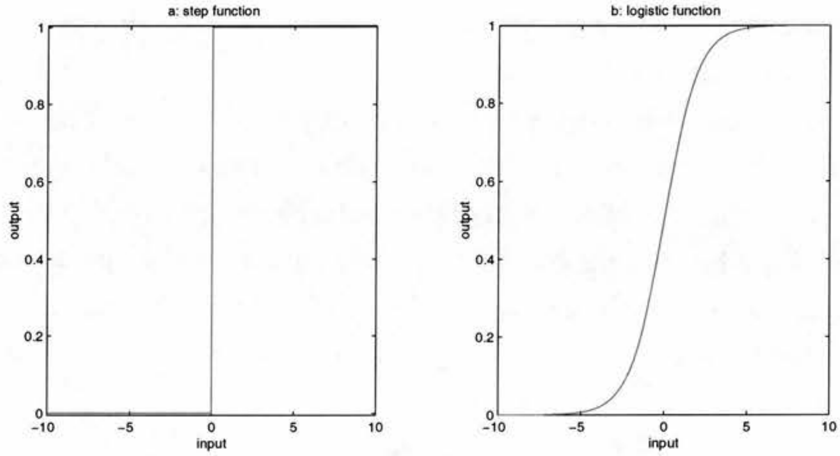

Figure 1.2: Activation functions for units in a neural network. a.: a threshold function with the threshold value 0. b.: a logistic function.

Learning in neural networks proceeds by adjusting the connection weights between the units. There are paradigms for supervised and unsupervised learning, but in this thesis only supervised learning is considered. In supervised learning, a network is presented with an input and a target value. The output produced by the network in response to the input is compared with the target value, and the weights are adjusted so that in a subsequent presentation of the same input/target pair, the network output is more similar to the target. Different algorithms for adjusting the weights exist: for networks without a hidden layer (so-called *perceptrons*), the perceptron algorithm (Rosenblatt, 1958) is often used, whereas the best known method for networks with hidden layers (so-called *multi-layer perceptrons*) is the backpropagation algorithm (Rumelhart, Hinton, and Williams, 1986a).

1.3 Why Modelling?

The neural networks developed in this thesis are fully implemented models, and the importance of modelling as a means of scientific investigation is stressed here by making a distinction between *models* which represent fully specified systems (these can be formalized algorithmic or implemented as a computer program), and *theories*, which represent less specified intuitions about a process.

But why is modelling important?

A model that is based on a theory enforces a full specification of the details of that theory. As such it helps to uncover gaps, contradictions and so-called "magic steps" where the process described by the theory is underspecified. A model can also bring to light additional assumptions that have to be made in putting the theory to work, such as extra mechanisms and parameters, and the format of the data on which the modelled process operates.

A working model can then be used to test the underlying theory by comparing its performance with empirical observations. The weakness of underspecified theories is that they may not be falsifiable because their claims and prediction are too general. Falsifiablity, however, is the defining characteristic of scientific theories (Popper, 1959), and a model is precise enough to allow its falsification by data for which it cannot account. In that case, the model can then be refined or modified, along with its underlying theory.

Apart from testing a theory, a model can also generate predictions. The components of the model can be changed in ways that would be difficult to do in the original system (e.g., lesioning connections in a neural network to model brain lesions), and the resulting behaviour can be observed. By varying different aspects of the model independently from each other it becomes possible to assess their importance for the modelled process.

When several theories aim to explain the same data, the common principle to choose between them is *Occam's Razor*: the idea that the simpler theory be preferred. The simplicity of a theory can be expressed in the strength of the assumptions it makes, and a model can help to evaluate these assumptions and thus contribute to the comparison of theories.

Although a model is often developed as a specification of a theory, neural network models of cognitive processing are sometimes not explicitly based on a theory except the vague notion that the observed data can be generated on the basis of complex, nonlinear associations between stimuli. It is therefore important, when a working model has been developed, to formulate the theory that it expresses. This process makes it necessary to distinguish between implementational details of the model and central aspects of its functioning.

Similarly, it is important to consider whether the obtained results are really the consequence of the processes that are claimed to be modelled, or whether they rely on what are considered the implementational details of the system. For example, much of the criticism of the historically most important language processing neural network, Rumelhart and McClelland's (1986) past tense model, showed that its success hinged on the distribution and representation of the training data (Pinker and Prince, 1988; Lachter and Bever, 1988); aspects that were not considered central to the theory modelled by Rumelhart and McClelland.

Finally, a model always involves an abstraction of the original process. Ideally, all non-essential and uninteresting aspects of the original system are abstracted away in a model, and in this way it becomes possible to identify which are the essential aspects of the original system for the modelled function. These features will differ depending on the level that is modelled. For example, while a model of neural response properties might not work if it does not take the functioning of individual ion channels into account, this might be unnecessary in a neural model of ocular dominance formation. Therefore, in developing a model care has to be taken not to abstract away too much, namely properties of the original system that are essential for its functioning.

1.4 Aim of the Thesis

The central aim of this thesis is to argue that constructivist learning is one such an essential feature of cognitive development and should not be abstracted away in models of development, and to empirically test this claim by modelling the acquisition of the English past tense and impaired adult processing in agrammatic aphasia with constructivist neural network models.

1.5 Outline of the Thesis

The thesis is organized in two parts.

In chapters 2, 3 and 4 I will develop the argument for constructivist learning based on different aspects of cognitive development, and in chapters 5 and 6 I will use a constructivist neural network for the modelling of the acquisition of the English past tense and impaired processing in German agrammatic aphasics, respectively. Based on these results, I will develop a new taxonomy for cognitive models, and a new theory of inflectional processing that is based on constructivist learning.

Chapter 2 reviews the role of activity in the development of the cortex across several levels of organization, and from the earliest stages of development to old age. I will argue that activity, often derived from sensory experience, has profound influences on the development of the cortex which is thus shaped in a constructivist way.

In chapter 3 I then discuss how brain development is related to cognitive development, and I review evidence that initially limited cognitive abilities that are due to immature brain systems allow the gradual building of complex representations and the acquisition of adult competence. Together with chapter 2, this suggests a constructivist view of cognitive development: a changing brain structure gives rise to changes in cognition, which in turn lead to new experiences that change the structure of the brain even further. The chapter closes with a description of the most influential constructivist theory of cognitive development, that of Jean Piaget.

Chapter 4 takes a theoretical standpoint and I discuss how constructivist learning differs from learning in static systems. I will review arguments that several principled limitations of static learning are overcome in constructivist systems, undermining strong claims about human learning that have been made on the basis of static systems. Together with the two previous chapters, this result makes the argument for constructivist models of cognitive development: if cognitive development proceeds in a constructivist way and constructivist learning is fundamentally different from learning in static systems, then this constructivist property should not be abstracted away from in models of cognitive development.

The chapter continues with a review of constructivist neural network algorithms and I develop a taxonomy of such networks. Then, I describe in detail a new constructivist algorithm (CNN) for the simulations in the subsequent chapters. The chapter closes with a brief review of previous constructivist neural network models of cognitive development.

In chapter 5 the CNN is used to model the acquisition of the English past tense and is evaluated against human data and against previous models. I first give an overview of the English past tense and its acquisition by children, and I proceed by discussing the most relevant previous models, both connectionist and symbolic. Then, the experiments with the new model are described. The CNN model closely simulates child development data and performs better than the previous models. I argue that these results are due to the CNN's constructivist nature, and this claim is backed by analogous non-constructivist network models that fail to display many aspects of the human behaviour. Based on this result I propose a new taxonomy for describing cognitive models.

In chapter 6 the CNN model is applied to an aspect of impaired adult language processing, namely, to the simulation of verb inflections in adult German agrammatic aphasics. Here, the constructivist learning process leads to a dissociation between regular and irregular verbs that has traditionally been attributed to two qualitatively distinct mechanisms. On the basis of the model I develop a novel account of inflectional processing that argues for a single mechanism employing dual representations.

Chapter 7 discusses the main results of this thesis:

- Cognitive development proceeds in a constructivist way in which the cortex develops guided by the experience and activity of the learner. This constructivist property is central and should not be abstracted away in models of cognitive development.

- Models of cognitive development can be classified along four dimensions to establish a basis for their comparison: *symbolic* vs. *subsymbolic processing*, *homogeneous* vs. *non-homogeneous architecture*, *single mechanism* vs. *multiple mechanisms*, and *static architecture* vs. *constructivist development*.

- Inflectional processing, which has been argued to involve qualitatively distinct mechanisms including a mental rule, is better explained by a model that operates with a single mechanism but develops dual representations in a constructivist learning process. This model accounts for details of the acquisition of the English past tense better than previous, fixed-architecture models, and, when lesioned it represents a valid and accurate model of impaired inflectional processing in agrammatic aphasia.

- Constructivist neural networks represent a valid formalization of constructivist theories of cognitive development.

Chapter 2

Activity-Dependent Cortical Development

A central aspect of constructivist learning is that learning itself creates and modifies the architecture of the learning system. For learning in humans and animals this means that the external environment leads to neural activity through sensory experience, and this activity will effect "useful" changes in the neural architecture of the brain. In constructivist learning, this modified architecture would then allow different representations of experience, leading to further changes in neural architecture. This chapter reviews how activity, spontaneous or environmentally derived, can effect changes in the neural architecture mainly of the cortex.

The development of the nervous system proceeds in two overlapping stages. In the first stage, which does not involve activity-dependent processes, the basic architecture and coarse connection patterns are laid out. In the second stage this initial architecture is refined in activity-dependent ways. However, these two stages cannot be entirely separated, and recently it has become clear that processes that were thought to be activity-independent do in fact rely on the spontaneous activity of neurons (e.g. Herrmann and Shatz, 1995; Catalano and Shatz, 1998). On the other hand, even detailed patterns of neural connectivity might emerge independent from experience (Crowley and Katz, 1999).

This chapter reviews the processes that lead to the mature state of the nervous system, with an emphasis on the neocortex. The first two sections give a brief overview of the principles of neural structure and function and the basic architecture of the neocortex. Activity-independent developmental mechanisms from the early stages of embryonic development to the establishment of coarse connections between neurons are described in section 2.3. In the subsequent sections, starting with section 2.4, I discuss developmental mechanisms on different levels that depend on spontaneous or environmentally derived neural activity. Section 2.5 reviews activity-dependent plasticity on the subcellular level of ion channels, section 2.6 describes the influence of activity on neurite outgrowth and morphology, and section 2.7 discusses how connections between neurons are established in activity-dependent ways using the example of ocular dominance column formation in the primary visual cortex. Recently, trophic factors, especially the neurotrophins, have emerged as substances to translate short-term neural activity into long-term morphological changes, and in section 2.8 I review the current state of knowledge about their function. Moving on to the level of the cortex, constraints on the formation of specialized cortical areas from an initially equipotential protocortex are discussed in section 2.9. Activity-dependent plasticity does not end with development, and in section 2.10 I review evidence for changes in the adult brain that are due to the exposure to complex environments and the learning of complex tasks. The last section, section 2.11, puts the chapter in the general context of the thesis by discussing whether all activity-dependent neural changes can be viewed as evidence for constructivism or if other theories, such as selectionism, should be favoured.

2.1 Principles of Neural Function

The nervous system is very complex. Billions of neurons from hundreds of cell types develop and interact in myriad ways, and therefore every concise description must make many generalizations. This section is no exception.

2.1.1 Neural Structure

A neuron consists of a cell body (*soma*), several *dendrites* and often just a single *axon* that is covered with a myelin sheath (fig. 2.1). Information processing within a neuron proceeds through electrical impulses in the form of a depolarization of the cell membrane. The flow of information is often viewed as from the dendrites via the soma to the axon (from top to bottom in fig. 2.1). Dendrites receive inputs from other neurons, and the signals so generated travel along the dendrites to the soma. There, if the signals are strong enough, they may initiate an *action potential*, which travels along the axon at high speed and without loss, through the rapid opening and closing of ion channels that are permeable to sodium (Na^+) and potassium (K^+). At the tip of the axon sits a presynaptic bouton that forms part of the synapse by which one neuron can transfer information to another. Dendrites often have small protrusions called *spines* which form the preferred location of axodendritic synapses.

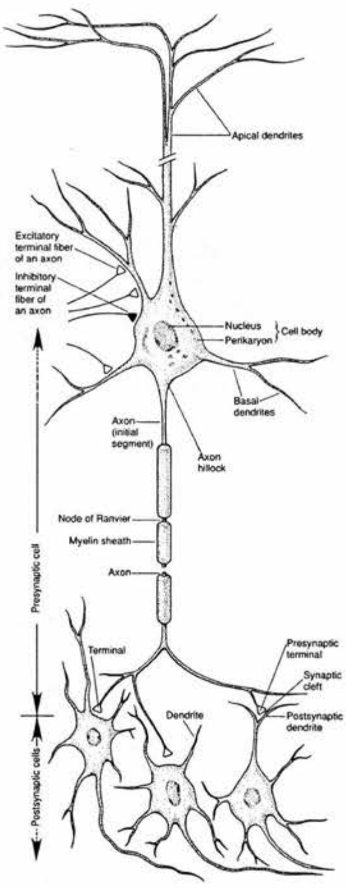

Figure 2.1: A typical pyramidal neuron, showing the cell body, apical and basal dendrites, and the axon (which is foreshortened here) where synapses with several other postsynaptic neurons are formed. (From Kandel *et al.*, 1991)

2.1.2 Synaptic Communication

Neurons communicate via synapses, most of which are chemical synapses (fig. 2.2). When an action potential reaches the presynaptic terminal at the tip of the axon, the depolarization of the cell membrane causes the opening of calcium (Ca^{2+}) channels and the influx of extracellular Ca^{2+}. The increased Ca^{2+} concentration leads synaptic vesicles to fuse with the cell membrane and to release *neurotransmitters* into the synaptic cleft.

The postsynaptic terminals of neurons have receptors to which the neurotransmitters can bind. There is a great variety of neurotransmitters that require specialized receptors and that have different effects on the postsynaptic neuron. The most com-

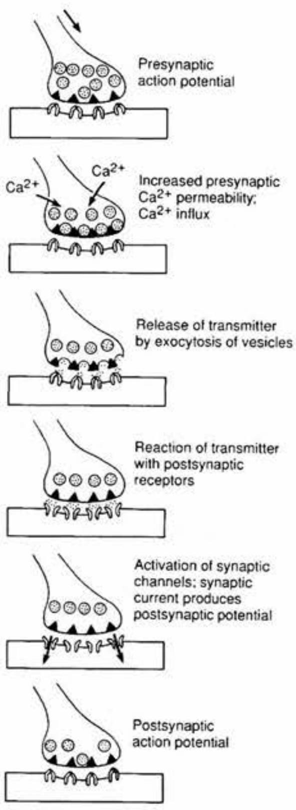

Figure 2.2: The stages of synaptic transmission at chemical synapses. See text for details. (From Kandel *et al.*, 1991)

mon neurotransmitter in the brain is *glutamate*, and it binds to different receptor types, the best known of which in the central nervous system are α-amino 3 hydro 5 methyl 4 isoxazole propionic acid (AMPA) and *N*-methyl-D-aspartate (NMDA). Binding of glutamate to an AMPA receptor results in the opening of Na^+ and K^+ channels, leading to influx of Na^+ and outflux of K^+ and the depolarization of the cell membrane. The function of the NMDA receptor is slightly more complicated and its importance in the activity-dependent development of neurons will become clearer below: the Ca^{2+} channels controlled by NMDA receptors are blocked by a magnesium (Mg^{2+}) ion at resting potential. An initial depolarization of the membrane removes the Mg^{2+} block and allows Ca^{2+} to flow into the cell, leading to a further depolarization of the membrane along with other effects that Ca^{2+} may have in second messenger functions and neural plasticity (see below). In this way, an NMDA receptor is gated by both voltage and the neurotransmitter glutamate (Kandel and Schwartz, 1991).

Because glutamate leads to a depolarization of the neural membrane it is called an *excitatory* neurotransmitter.

There are also *inhibitory* neurotransmitters, the most well known being γ-amino-butyric acid (GABA). GABA mainly causes the opening of chlorine (Cl^-) channels, counteracting the excitatory influx of Na^+ into the cell and thus reducing or preventing depolarization. Inhibitory synapses are most often found on the cell body, allowing them to modulate the excitatory signal effectively, as opposed to excitatory synapses which are usually located at the dendrites.

The effects of synaptic transmission are not limited to the opening of ion channels and the depolarization of the postsynaptic membrane. Far more complex effects on post- and presynaptic neurons are mediated through *second messenger* systems. Receptor families for second messenger systems include *metabotropic* receptors which respond to so-called adrenergic neurotransmitters but also to GABA, glutamate, serotonin, and neuropeptides, and tyrosine-kinase (TrK) receptors responding to hormones, growth factors (e.g. neurotrophins), and neuropeptides. The binding of substances to these receptors can trigger long chains of chemical reactions which lead to much longer lasting changes in the cell. Many of these changes depend on intracellular calcium, $[Ca^{2+}]_i$, which seems to play an essential role in the activity-dependent development and plasticity of neurons.

Highly diffusible gases like nitric oxide (NO) and carbon monoxide (CO) may also effect long lasting changes in a cell. These gases are released by other neurons and can easily permeate the membranes of neighbouring cells, and they can therefore act independently from receptors.

In summary, neurons can interact in varied ways through neurotransmitters, second-messenger substances, and diffusible gases, transmitting action potentials but also effecting longer lasting changes in the cell.

2.2 Structure of the Neocortex

The highest level of information processing in the human brain occurs in the cortex. The cortex is responsible for the high-level processing of sensory inputs that have been gated via the thalamus, for the generation of motor commands, and for practically all high-level cognitive functions.

The human cortex is a highly convoluted sheet folding around the other parts of the brain (fig. 2.3). It is 2–4 mm thick, and stretched out it covers an area of roughly 2400 cm^2 (Shepherd, 1994). Each mm^3 of cortex contains roughly 100,000 neurons

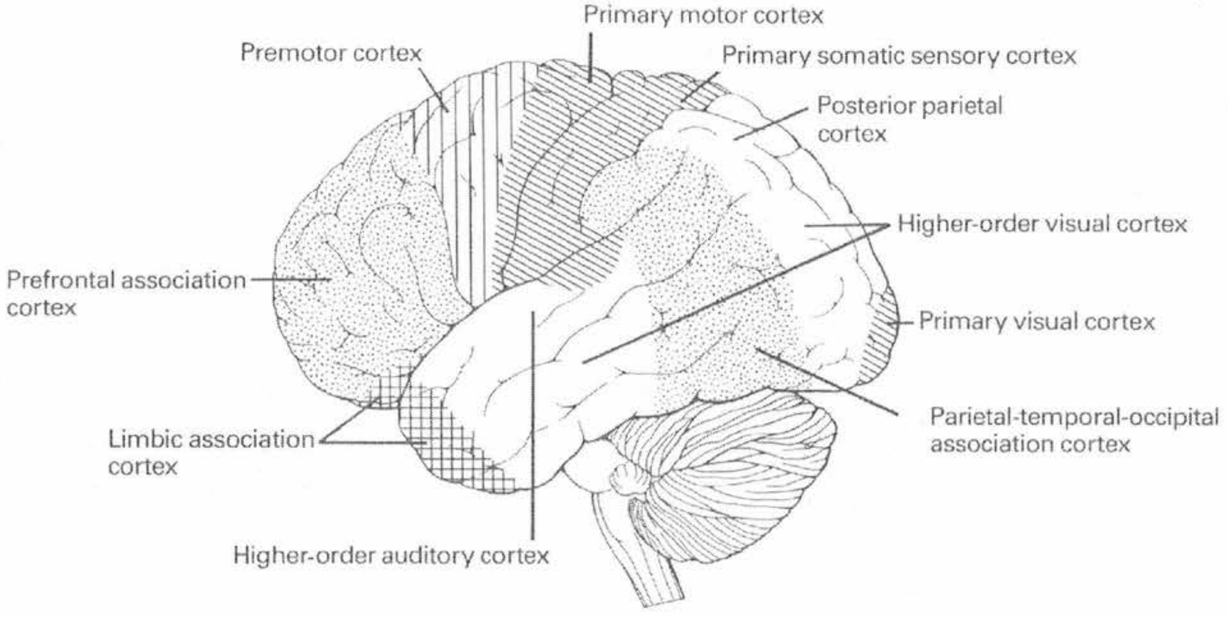

Figure 2.3: The human cortex. (Modified from Kandel *et al.*, 1991)

and 1,000,000,000 synapses (Churchland and Sejnowski, 1992); these numbers are even greater in the primary visual cortex. On the outside the cortex is surrounded by the protective pial surface and on the inside by the white matter which contains myelinated axons.

There are about 25 different types of neurons in the cortex, but 80% of all neurons are *pyramidal cells*, so-called because of their pyramidal shape (see fig. 2.1). These neurons have a dendritic branch pointing towards the surface of the brain, and an axon which is orthogonal to the brain surface, usually stretching below the cortex into the underlying white matter. These axons can form connections with remote cortical neurons and with subcortical structures, indicating the role of pyramidal neurons in the communication between different areas of the nervous system.

Non-pyramidal neurons typically have round cell bodies with axons branching within their own regions. The role of these neurons is in local processing within an area. The overall interconnectivity within the brain is sparse: a cortical neuron is on average connected to only 3% of the neurons underlying that mm^3 of cortex (Churchland and Sejnowski, 1992).

The other major group of cortical cells are *glial* cells which outnumber neurons by a factor of 10 to 50. The traditional view has been that glial cells provide a scaffolding for neurons and a chemically stable extracellular environment, as well as forming myelin sheaths around neural axons and removing debris after neural death, but that they play no role in information processing (Kandel, 1991a). Recent evidence (Araque, Parpura, Sanzgiri, and Haydon, 1999), however, suggests a possible active role for cortical and peripheral glial cells in the modulation of neural synaptic transmission.

Although many different cortical areas can be distinguished on the basis of their cytoarchitecture (as famously undertaken by Brodmann, 1909, see fig. 2.12 on page 38), the basic overall structure of the cortex is rather uniform: one can distinguish six layers throughout the cortex that are characterized by specific cell types and connection patterns (fig. 2.4).

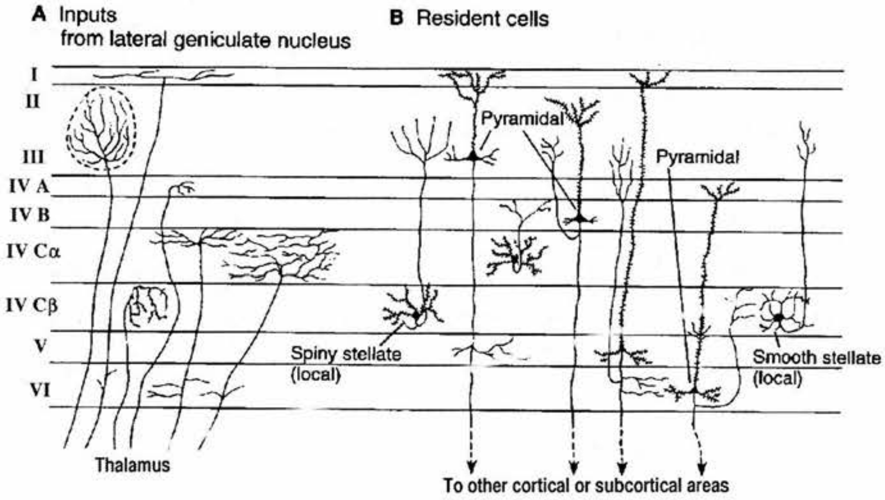

Figure 2.4: The layered structure of the cortex. The left side shows incoming, the right side outgoing connections. This figure shows the primary visual cortex where layer IV can be subdivided into four sub-layers, and where layer V is particularly small. (Modified from Kandel *et al.*, 1991)

The six cortical layers are numbered beginning with the outermost layer I. This layer contains some neuron bodies, as well as axons running laterally to the surface of the brain that synapse with apical dendrites for local processing. Layers II and III contain mainly small and large pyramidal cells, respectively. These layers process the output signals to other areas of the cortex. Layer IV is the terminal for inputs from the thalamus and it contains mainly non-pyramidal cells such as *stellate* cells with small cell bodies and often spiny dendrites. Layer V contains the largest pyramidal cells that send their outputs to areas outside the cortex. The lowest layer, layer VI, contains pyramidal cells that project back to the thalamus.

Although these six layers exist in all areas of the cortex, their thickness may vary considerably. Specifically, layer IV which receives sensory inputs via the thalamus, is expanded in the main sensory areas, and in the primary visual cortex it can be divided into four sub-layers (fig. 2.4). Layer V is thin in sensory areas but thick in the motor areas, containing very large pyramidal cells that project to the whole central nervous system (CNS). By contrast, the size of layer IV in the motor areas is markedly reduced.

2.3 Activity-Independent Developmental Mechanisms

This section gives an overview of the processes of nervous system development that are independent from neural activity. While neural activity is obviously absent in the early stages of development, even at relatively late stages development can proceed independently from activity. On the other hand, some processes that have generally been considered as activity-independent have recently been found to involve activity-dependent components. Hence, the two stages of early activity-independent and later activity-dependent development cannot be clearly separated.

Much of the evidence relating to neural development is conjectural, and in the following only a superficial review of the main results can be given. For a much more detailed treatment of cortical development, see (Price and Willshaw, in press).

2.3.1 Precursor Proliferation

The early embryo differentiates into three distinct cell layers making up the so-called *embryonic disc*: an outer layer called *ectoderm*, a middle layer called *mesoderm*, and an inner layer called *endoderm*. The nervous system has its origin in the region of the ectoderm called *neuroephithelium*. Its development is triggered by signals from the adjacent mesoderm. A section of the ectoderm thickens, forming the *neural plate*. The edges of the neural plate roll up, forming the *neural tube* which is the basis of the spinal cord and brain.

2.3.2 Neurogenesis

New neurons for the CNS are generated in the so-called *proliferation zone* surrounding the central ventricle of the embryonic brain. Here the precursor cells (*neuroblasts*) differentiate through repeated cycles into neurons, glial cells, and new germinative cells (from which further neurons and glial cells are produced). The question of when generated cells acquire their identity (i.e., cell type) has not yet been conclusively answered. It seems, however, that the type of a specific cell is determined both by lineage (i.e., the identity of the ancestor cell) and by cell-cell interactions.

2.3.3 Cell Migration

Once a neuron has been "born" it migrates to its final position. Migration proceeds along radial glial cells that only exist during this stage of embryonic development. These glial cells play a permissive rather than an instructive role for neurite migration, i.e., they allow the neurite to grow along its fibres but do not instruct it to select specific target areas (Gasser and Hatten, 1990).

In the cortex the migration proceeds in an inside-out sequence: earlier neurons migrate to deeper layers of the cortical plate, and later neurons migrate past them into more superficial layers.

Cell migration seems to be controlled at least partly by Ca^{2+} and by neurotransmitters: blockade of Ca^{2+} channels and of NMDA receptors selectively inhibits migration, while it is accelerated by the application of glutamate (Komuro and Rakic, 1992, 1993).

2.3.4 Axonal Outgrowth

Neural differentiation, that is, the outgrowth of axonal and dendritic processes from the neuron body, starts during or shortly after migration. The maturation process is very drawn out and in fact extends far into adulthood.

In the developing nervous system axons often have to travel across long distances along complex pathways, and yet their final innervation patterns are very precise. The mechanisms by which axons find their targets has been the focus of extensive research. In order to find a target, outgrowing neurites develop at their tip an enlargement called a *growth cone* (fig 2.5). From the growth cone project several thin extensions called *filopodia* which are responsible for its forward movement. The filopodia constantly extend and retract in response to signals in the extracellular environment (see below). As the axon extends, new cell membrane is synthesized in the soma, packaged into vesicles and transported to the growth cone. In the growth cone these vesicles are fused into the expanding surface membrane.

Outgrowing axons show a high specificity in finding their appropriate target areas and in forming connections with other neurons. The mechanisms by which this spe-

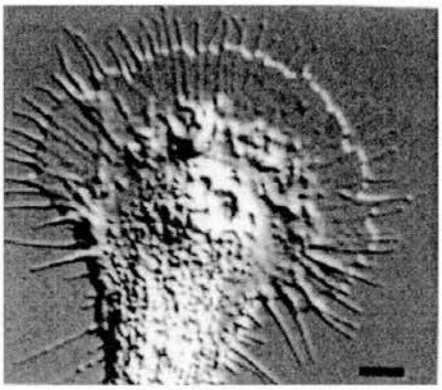

Figure 2.5: A growth cone from a neuron isolated from the marine snail *Aplysia californica*. The filopodia extending from the growth cone are clearly visible. Scale bar = $5\mu m$. (From Forscher and Smith, 1988)

cificity is achieved have been extensively investigated in studies of neural regeneration after axons have been artificially severed, or by studying developing neurons *in vitro* or in the embryo while manipulating the extracellular environment. Whereas many aspects of axonal pathfinding remain unclear, from these studies a varied picture has emerged (Jessell, 1991; Gilbert, 1997; Purves *et al.*, 1997).

The pathfinding of axons and the formation of specific connections is generally believed to involve an early, activity-independent phase followed by a later phase which depends on neural activity and in which connections are refined. These two phases do not occur in two distinctive time periods, but rather, activity-independent and activity-dependent mechanisms seem to overlap and interact during development. Further, different mechanisms are employed to different degrees in various parts of the developing nervous system (Goodman and Shatz, 1993). In the following, the activity-independent mechanisms are described that lead to the outgrowth and pathfinding of axons.

2.3.4.1 Stereotropism

An outgrowing axon can be guided by physical cues in its environment, following the path of least resistance, e.g., along channels between cells. This form of axon guidance is called *contact guidance*, or *stereotropism*. It has also been shown that abrupt changes in the direction of the growth cone trajectory can be triggered by its contact with certain cells, often immature neurons (these are called *guidepost cells*). Stereotropism can only give rough directional cues to the axon and is alone insufficient to explain the highly specified connectivity patterns between neurons.

2.3.4.2 Haptotaxis

An axon can also be guided by gradients of adhesive molecules in the extracellular matrix (*haptotaxis*). The growth cone has receptors for certain molecules that are present on the surface of surrounding glial cells (*cadherins* and *CAMs*) and in the extracellular matrix (especially *laminin*), and it can recognize small differences in the concentration of these molecules across its surface. This mechanism allows the growth cone to move up the concentration gradient (see Goodhill, 1998, for a mathematical analysis of this process). Certain molecules are expressed only at certain stages of axonal outgrowth and in restricted areas of the developing nervous system, providing the axon with multiple guidance cues.

2.3.4.3 Labelled Pathways Hypothesis

Another mechanism for guided axonal growth is by *labelled pathways*: here, the axon grows along another earlier axon. The growth cone can distinguish between different axons and only uses very specific ones as scaffold, while others in its vicinity are ignored even when the guiding axon is artificially destroyed. This highly selective mechanism relies on the time-dependent expression of adhesive cell-surface molecules by the neurons and it leads to the growth of axonal bundles (*fascicles*) where axons grow along each other over large distances and separate only in the target region.

2.3.4.4 Chemotropism

Important guidance cues for an outgrowing axon can also come from diffusible molecules generated by the target cell (*chemotropism*). *In vitro* experiments have shown that target tissue can attract the appropriate growth cone from a distance (*chemoattraction*). Different targets seem to secrete different chemoattractants. More recently it has been shown that growth cones respond to certain factors not only with attraction, but also with repulsion (*chemorepulsion*) (e.g. Goodman, 1996): the growth cone changes its path, and on contact with the repellent it collapses. The role of chemorepulsion in the guidance of axons might be as important as that of chemoattraction, and the path of an axons is likely to be guided by a combination of the two. The same substance can act as an attractor to one axon and a repellent to another, allowing for the establishment of precise connections e.g., in the retinotectal pathway (Goodman and Shatz, 1993). More recent results have shown that the same substance can even act as an attractive or repellent cue for the same growth cone, depending on the internal state of the growth cone (Mueller, 1999).

Investigations of the innervation of the limb muscles by motor neurons in vertebrates, and the development of projections from retinal neurons to the brain indicate that even in the outgrowth of single axons several of the described guidance mechanisms are at work simultaneously.

Once an axon has reached its target area it can form very specific connections with other neurons. Migrating axons encounter many possible target cells and yet the selected targets are very specific. This becomes especially evident in the optic tectum of lower vertebrates where connections are highly ordered and form a point-to-point correspondence between the retinal and the tectal cells. This precise target selection appears to depend on adhesive or repellent gradients that enable the axon to find a small target area. The actual formation of synaptic connections then relies on competition between several neurons (see next section).

2.3.5 Synapse Formation

The main studies of synapse formation come from the neuromuscular junction (NMJ) where neural axons form synapses with a muscle fibre. Forming a synapse involves changes both in the pre- and postsynaptic structures as the result of an initial contact between an axonal growth cone and the target cell. The muscle fibre has receptors for the neurotransmitter acetylcholine (ACh) that are initially distributed evenly over its surface. As the axon approaches and the growth cone makes an initial unspecified contact with the fibre, the ACh receptors relocate to the site of the contact. Additionally, new receptors are generated at that site, resulting in a density about 10,000 times higher than at sites away from the contact. This process does not result from presynaptic activity (i.e., release of ACh) but is due to cues from a diffusible substance released by the axon. At the same time the axon terminal accumulates synaptic vesicles containing neurotransmitter, and the membranes of both axon and fibre thicken at the site of the contact. When a synapse has formed in this way, ACh receptors on the muscle fibre which are not at the synaptic site die. The receptors at the synaptic site change their properties towards higher conductance and shorter opening times, allowing for more precise synaptic transmission.

After the axon makes the initial contact with the muscle fibre, other axons are attracted to the same region and form additional synapses with the fibre. Through a process of competition between these axons all but one are eliminated so that eventually each fibre is innervated only by a single axon (Purves and Lichtman, 1980). At the same time the surviving axon becomes more complex: it increases its endplate area and acquires more release sites.

2.3.6 Cell Death

Neural cell death is an integral part of the development of the nervous system. During embryonic development a large overproduction of neurons occurs, and subsequently up to half of all generated neurons are lost in all areas of the nervous system (reviewed by Oppenheim, 1991). Neural cell death is regulated by a combination of intrinsic and extrinsic factors. Receptors on the cell can respond to extrinsic death signals that trigger a cascade within the cell leading to its degeneration. Other receptors respond to extrinsic trophic factors that suppress an intrinsic automatic suicide program. A common view is that such extrinsic trophic factors, like the neurotrophins (see section 2.8) are released by target neurons in limited supply, thus leading to competition between the innervating neurons. Indeed neural activity or membrane depolarization reduces cell death (e.g., Ghosh, Carnahan, and Greenberg, 1994), indicating that active neurons might have an advantage in the competition for neurotrophins. In this way, active neurons stabilize through the uptake of trophic factors, whereas their unsuccessful competitors die.

The function of programmed cell death remains elusive: possibilities range from the correction of erroneous projections, the creations of pathways for axon outgrowth, and transient functions for certain populations, to the creation of sexually dimorphic structures. A popular hypothesis is that the generated surplus of neurons allows for the above mentioned competitive processes to occur and thus provides a mechanism to achieve the right amount of target innervation (Purves and Lichtman, 1985), although this might be an overly simplistic view (Price and Willshaw, in press).

2.3.7 Summary of Activity-Independent Development

In its early stages, from generation of neural precursor cells to neurite outgrowth, the development of the nervous system proceeds largely independently from neural activity. Even some early aspects of synapse formation are activity-independent. Finally, some of the mechanisms of cell death seem to be mediated by intrinsic, activity-independent signals.

The next sections discuss those aspects of neural development that are dependent on activity, often generated through sensory inputs from the external environment of the organism. This type of development is therefore often also termed *experience-dependent* development.

2.4 Activity-Dependent Developmental Mechanisms

In recent years it has become clear that neural activity affects and often controls the function and morphology of the nervous system on different levels. Since function and morphology in turn influence neural activity, there exists a feedback loop in which the nervous system controls itself in a constructivist way (fig. 2.6).

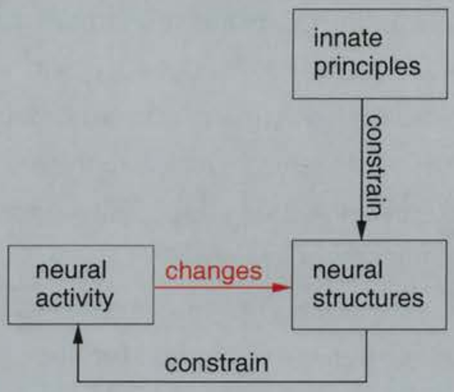

Figure 2.6: The feedback loop between neural activity and structure. Neural structure is determined by innate principles (genes) together with neural activity. Activity can change neural morphology within the boundaries of innate constraints. The neural structures in turn constrain neural activity, thereby changing the mechanisms that change them. The red arrow indicates the subject of the present chapter.

From a constructivist perspective aiming to relate the development of brain and cognition to interactions with the environment, the main interest is in neural activity that derives from sensory inputs. However, spontaneously generated neural activity also plays an important role in the shaping of neural circuits, especially in prenatal development. Although this type of architectural change might be called constructivist if different activity leads to different architectures, it is clearly of less interest in establishing a connection between learning and brain development.

In the following sections the role of activity in brain development is described on the subcellular and cellular levels, on the level of connections between neurons, and on the larger scale level of functional areas in the cortex, both in the developing and adult brain.

2.5 Effects of Activity on the Subcellular Level

Neural activity can influence several subcellular aspects of cell functioning and thereby modulate the cell's response properties. The feedback loop between activity and structural change therefore exists even on the lowest levels of neural networks.

Neurotransmitters, especially those that interact with metabotropic receptors, can induce changes in ion-channels, in neurotransmitter receptor properties, and in the expression of genes. These changes have long-lasting effects on the response properties of a neuron. The sustained opening and closing of ion channels induced by second messenger systems modulates the rapid response properties of cells on a timescale from seconds to minutes (Kandel *et al.*, 1991). Neurotransmitters, via second messengers, can also change the properties of their own receptors: for example, the number of activating receptors (AMPA) is down-regulated after prolonged neural activity whereas the number of inhibitive receptors (GABA) is up-regulated (Shaw and Scarth, 1991). In this way, a neuron can stabilize its activity pattern so that its firing properties depend on the history of its recent activation (Turrigiano, Abbott, and Marder, 1994).

The expression of genes, including those for channels and receptors, can also be influenced by neural activity via second messenger systems (Armstrong and Montminy, 1993). This process can introduce enduring activity-dependent changes in neural functionality.

2.6 Effects of Activity on Neurite Outgrowth and Morphology

Apart from sub-cellular properties of neurons, activity also has a strong influence on neural morphology. Activity can influence the speed of neurite outgrowth from the cell body and its final function (axon or dendrite). Many of these effects are mediated through changes in intracellular calcium ($[\mathrm{Ca}^{2+}]_i$) which can occur through direct influx of Ca^{2+} through voltage-sensitive Ca^{2+} channels or NMDA channels, or through the second messenger-induced release of Ca^{2+} from intracellular stores.

The Ca^{2+} theory of neurite outgrowth (e.g. Kater and Mills, 1991, fig. 2.7) proposes an optimal level of $[\mathrm{Ca}^{2+}]_i$: at very low levels no outgrowth occurs. At slightly higher levels outgrowth is optimal; even higher levels halt it, and at very high levels a retraction of neurites occurs. Different research has indicated that the axon grows out from the site of the cell body with the lowest $[\mathrm{Ca}^{2+}]_i$ concentration (Mattson, Murain, and Guthrie, 1990) or that the longest neurite becomes the axon (Goslin and Banker, 1989), but these results can be reconciled with the Ca^{2+} hypothesis: at the site of lowest $[\mathrm{Ca}^{2+}]_i$ concentration the outgrowth rate will be highest and lead to the longest neurite, which then becomes the axon.

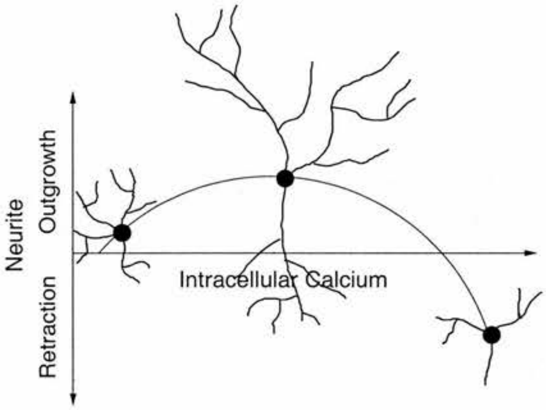

Figure 2.7: The Ca^{2+} theory of neurite outgrowth. There is an optimal level of $[\mathrm{Ca}^{2+}]_i$, below which no outgrowth occurs and above which neurites retract. (Adapted from Kater and Mills, 1991)

Whereas most of the mechanisms for axon guidance are independent of electrical activity (see section 2.3.4), the rate of outgrowth is thus activity-dependent. This result has been further confirmed by Cohan and Kater (1986) who found that neurite outgrowth is reversibly halted and growth cone morphology changed by electrical activity, and that these effects depend on the rate, pattern and duration of the stimulation (Fields, Neale, and Nelson, 1990). However, even in axon guidance there is growing evidence for activity-dependent mechanisms in addition to the activity-independent ones: chemotropism (see section 2.3.4.4) can be effected by gradients of substances such as neurotransmitters and neurotrophins that are released in an activity-dependent way. Growth cones can detect this gradient and turn towards its source (Zheng, Felder, Connor, and Poo, 1994; Ming, Lohof, and Zheng, 1997), and $[\mathrm{Ca}^{2+}]_i$ in the growth cone seems to be important in this process. Furthermore, action potential activity seems to be important for the pathfinding and branching of thalamic axons innervating layer IV in the cortex in fetal cat development (Herrmann and Shatz, 1995).

Dendritic morphology is strongly influenced by neural activity. Neurotrophins, a group of substances that are released and taken up in activity-dependent ways (see section 2.8), exert strong influences on the shape and complexity of dendritic branches (McAllister, Lo, and Katz, 1995; McAllister, Katz, and Lo, 1996, 1997). Dendritic substructures can also be controlled by activity: the dendrites of neurons in the mammalian brain are initially smooth but soon extend thin filopodia. These form into, or are replaced by, spines which are the sites of synapses with axons from other neurons. Maletic-Savatic, Malinow, and Svoboda (1999) investigated the influence of neural activity on the formation of filopodia and spines in rat hippocampal slices and found that the synaptic activation of NMDA receptors induced the localized formation of filopodia and spines. They speculated that this mechanism could lead to the activity-dependent generation of new synapses. Changes of dendritic morphology caused by electrical activity have also been observed in mature neurons (Schilling, Dickinson, Connor, and Morgan, 1991).

2.7 Effects of Activity on Connections Between Cells: Ocular Dominance Columns in the Primary Visual Cortex

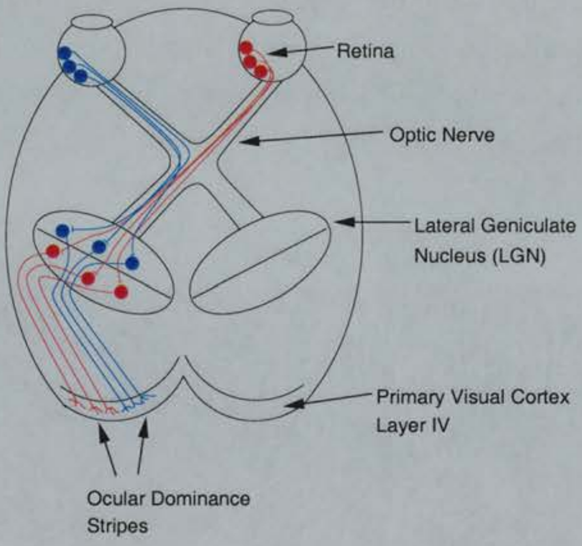

Figure 2.8: The mammalian visual pathway. For clarity, only the pathways of the right visual field are shown. Retinal ganglion cells from both eyes project to the LGN where they innervate separate layers (here the LGN layers have been simplified to two). The geniculate neurons in turn project to separate patches in layer IV of the ipsilateral V1 (ocular dominance stripes). (Adapted from Goodman and Shatz, 1993)

A well-studied example of activity-dependent mechanisms in the formation of precise connections is the development of the primary visual cortex (V1, also called area 17 or striate cortex). V1, like all other cortical areas, has six layers. In contrast to other areas, however, layer IV can be subdivided into four sub-layers that are characterized by different cell types and inputs from different layers of the lateral geniculate nucleus (LGN) (fig. 2.4 page 15).

V1 is the first cortical structure to receive visual input via the thalamus. Fig. 2.8 shows the visual pathway from the eyes to the cortex. The rods and cones of the retina transform light into action potentials that are conducted to the retinal interneurons and further to the retinal ganglion cells. The axons of these cells form the optic nerves which project to the LGN of the thalamus. Neurons from the right visual field of both eyes project to the left LGN and neurons from the left visual field to the right. In the thalamus the axons from both eyes innervate separate layers so that each layer receives input from only one eye. The geniculate neurons project mainly to the spiny stellate neurons in area IV of V1 where axons from different eyes segregate into distinct, regularly alternating patches, or stripes (fig. 2.9). These patches form the anatomical basis for the eye-specific columnar organization of V1, the ocular dominance columns (ODC) (Hubel and Wiesel, 1963). ODC exist in many mammalian species, including humans (Hitchcock and Hickley, 1980), but not in lower vertebrates where the optic tecta in both hemispheres are innervated only by neurons from the contralateral eye. The width and pattern of ODC, however, vary between species (for an overview see e.g., Swindale, 1996).

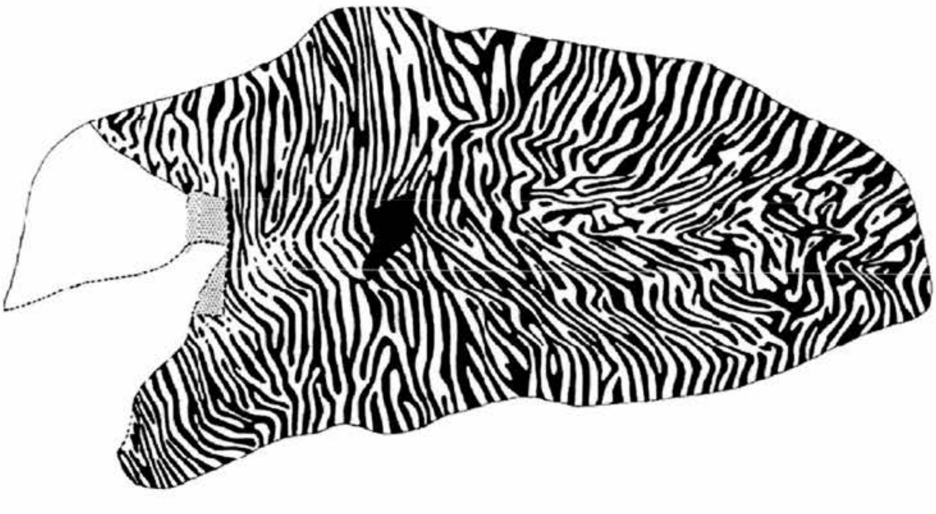

Figure 2.9: A complete reconstruction of the ocular dominance stripes in the primary visual cortex of a macaque monkey. Alternating black and white stripes indicate regions that respond only to one eye. (From LeVay *et al.*, 1985)

How do ODC form in the visual cortex? In newborn cats there are no ODC and geniculate axons representing both eyes completely overlap (fig. 2.10 a). These initial overlapping projections are sparse, and three to four weeks after birth axonal branches selectively retract to form non-overlapping areas accompanied by extensive sprouting and synaptogenesis in the segregated areas (Antonini and Stryker, 1993a, fig. 2.10 b.). This process is completed at around six to eight weeks in the cat (LeVay, Stryker, and Shatz, 1978).

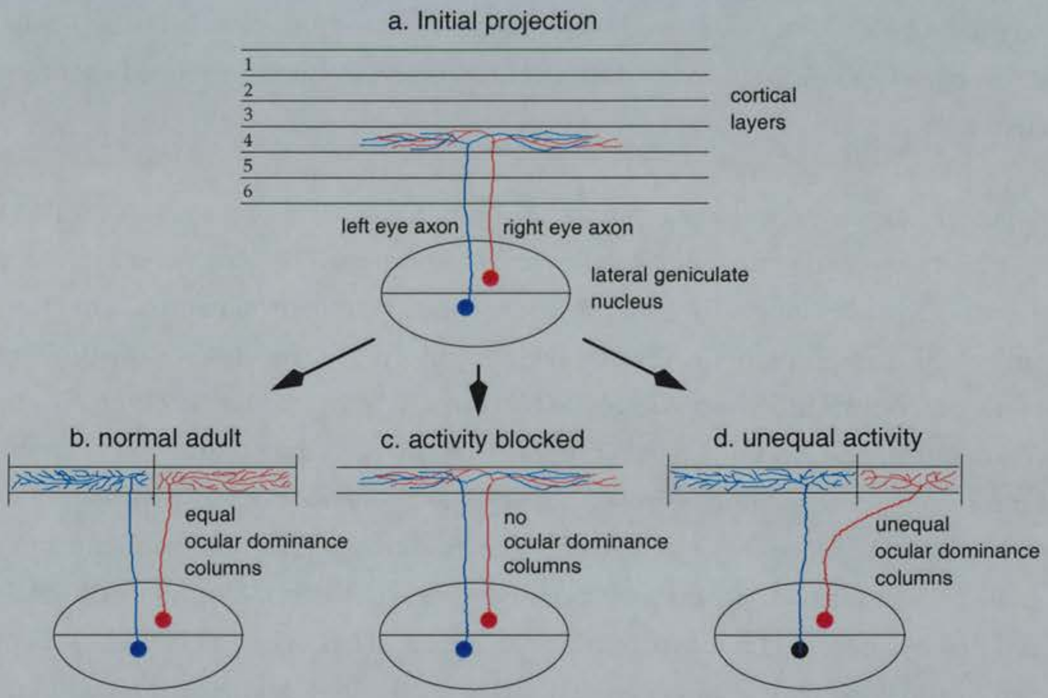

Figure 2.10: Normal and abnormal development of ocular dominance columns. See text for explanation. (Modified from Goodman and Shatz, 1993)

The formation of ODC has been demonstrated to be based on visually driven or spontaneously occurring neural activity. Stryker and Harris (1986) blocked all neural activity in the optic nerve of newborn cats by injecting the antagonist tetrodotoxin (TTX), and as a consequence ODC failed to form (fig. 2.10 c.). Similar results have been obtained by rearing kittens in total darkness and by suturing both eyes (Caplan, Christen, and Duffy, 1985; Swindale, 1981, 1988).

In contrast to cats, in macaque monkeys ODC develop pre-natally and are sometimes fully formed at birth (Horton and Hocking, 1996). While these results question the role of visually-driven neural activity in ODC formation, there is strong evidence that spontaneous neural activity is required. The layered structure of the LGN where each layer is innervated only by axons from one eye develops pre-natally in all species, but it seems to be caused by highly correlated waves of spontaneous activity sweeping over the embryonic retina (Galli and Maffei, 1988; Shatz and Stryker, 1988; Penn, Riquelme, Feller, and Shatz, 1998). Recent results show that this spontaneous correlated firing of retinal ganglion cells does not only drive the eye-specific innervation of the LGN layers, but that it is transmitted to the LGN cells, leading to highly correlated bursts of action potentials in the geniculocortical pathway (Mooney, Penn, Gallego, and Shatz, 1996). Thus, even in the absence of visual experience cortical V1 cells can receive correlated input from the different LGN layers through correlated spontaneous activity.

Further experiments have established competition between geniculate cells as the most likely mechanism of ocular dominance formation. The geniculate axons representing both eyes compete for synaptic connections with cortical neurons, and the outcome of this competition is driven by neural activity. This process was demonstrated, among others, by Hubel and Wiesel (1963); Hubel, Wiesel, and LeVay (1977); Shatz and Stryker (1978) and Antonini and Stryker (1993b) by occluding one eye in neonate cats and monkeys. The result of even a brief period of such monocular deprivation was a marked alteration of normal ODC development: while both retinal ganglion and geniculate cells of the re-opened eye responded normally to visual input, in V1 the axons from that eye occupied a much smaller space than usual, whereas the axons from the open eye had expanded and occupied a larger area than their usual share (fig. 2.10 d). These results cannot be explained merely by postsynaptic atrophy caused by the disuse of the affected neurons, because the closing of both eyes did not equally result in the global shrinkage of axonal arbours, and because in monocular deprivation the ocular dominance stripes for the open eye did not only remain the same but instead expanded. Therefore these results suggest an activity-based competition for cortical area between the geniculate neurons representing both eyes where the region of the closed eye shrinks due to a competitive disadvantage. This theory is further confirmed by experiments in which one eye was occluded and at the same time postsynaptic activity was blocked (Reiter and Stryker, 1988). In this case, the cortical cells responded better to the closed eye, which is in agreement with Hebbian learning (Hebb, 1949) where the synapses between co-active neurons strengthen and those between non co-active neurons might weaken: the activity of neurons from the occluded eye was more strongly correlated with that of the silenced cortical neurons (both were reduced) and as a consequence these synapses were strengthened, while synapses from the non-correlated open eye did not strengthen (Crair, 1999).

The described alterations in the structure of ocular dominance columns can be induced only during a certain *critical period* in early postnatal life (until six to eight months in the cat, four to five years in the human), and monocular deprivation after this period does not lead to a re-organization of the ODC. However, the absence of visual input in early postnatal life can prolong this critical period (Caplan *et al.*, 1985). This result makes it unlikely that the critical period is genetically specified; instead, it seems to rely on the onset of neural activity in the visual pathway.

Is the formation of ocular dominance columns specific to the regions in which it normally occurs, possibly mediated by molecular markers in these regions, or are they an outcome of a more general competitive process between neurons? This question was addressed by Constantine-Paton and Law (1978) by grafting a third eye onto a frog embryo. The retinal ganglion cells of the extra eye innervated one optic tectum along with the axons from the normal eye. The optic tectum in lower vertebrates is normally innervated only by one eye and therefore does not form ODC. However, when in the three-eyed frog one tectum was abnormally innervated by retinal ganglion cells from two eyes, the axons from both eyes segregated and formed eye-specific stripes. Since normally the tectum does not form these stripes, an explanation based on molecular cues seemed less likely than one based on activity-mediated competition between the axons. Further studies clearly established the role of pre- and postsynaptic activity in the formation and stabilization of these eye-specific tectal stripes (Cline, Debski, and Constantine-Paton, 1987; Constantine-Paton, Cline, and Debski, 1990). Additional evidence against a purely molecular marker-based formation of ODC came from studies where an eye in Xenopus was compounded by two half-eyes (Fawcett and Willshaw, 1982) or where parts of a developing eye were removed and the remainder grew into two identical half-eyes (Ide, Fraser, and Meyer, 1983). In each case, the single eye projections to the tectum developed ODC, indicating competition between the two halves.

The question of how neural competition leads to the formation of ocular dominance columns was investigated by Stryker and Strickland (1984): they blocked synaptic transmission to the optic nerves by application of TTX but implanted electrodes to allow for their controlled stimulation. They found that synchronous stimulation of the nerves from both eyes prevented the formation of ODC. By contrast, when both nerves were stimulated asynchronously, ODC formed normally. This result suggested that not neural activity *per se*, but its temporal and spatial pattern was essential for the normal development of ODC. A similar result was obtained by rearing goldfish in stroboscopic light (Schmidt and Eisele, 1985). In goldfish and other lower vertebrates, retinal projections to the optic tectum form a coarse topographic map that is later refined by visual experience. The refinement consists in the retinal axons restricting the area of the optic tectum to which they project their branches by retracting from inappropriate areas. However, in goldfish that were reared in stroboscopic light after crushing the optic nerve, the usually observed refinement of the topographic map did not occur.[1] Stroboscopic light presumably leads to the simultaneous firing of the retinal ganglion cells from both eyes, indicating that asynchronous activation which results from the spatial and temporal light pattern in a normal environment is essential for normal visual development.

Thus, the formation of ocular dominance columns in the primary visual cortex seems to be based on activity-mediated competition between neurons from both eyes. When axons from both eyes are always synchronously active, none of them have a competitive advantage and the columns fail to form. Only through activity that is more correlated between axons from one eye than between axons from different eyes does the competition lead to a segregation of axon terminals into discrete areas.

The functional role of ocular dominance columns remains unclear, and possibly they have no function at all (Swindale, 1996). Stereopsis, which is important for depth viewing, would be an intuitive candidate, but squirrel monkeys have been shown to possess stereopsis even without ODC (Livingstone, Nori, Freeman, and Hubel, 1995). The results for three-eyed frogs described above as well as results from modelling (Goodhill, 1992; von der Malsburg and Willshaw, 1976) indicate that ocular dominance columns might emerge incidentally in the formation of two (or more) topographic maps on a single area of cortex.

The cellular mechanisms responsible for the formation of ODC have been argued to involve Hebbian synapses (see e.g., Goodman and Shatz, 1993). A Hebbian synapse can act as a coincidence detector where the connections from all inputs that simultaneously activate the postsynaptic cell are strengthened. In this way, cells from one eye that show correlated activity due to the correlated visual input develop strong connections with a particular cortical cell. An input to the same cortical cell from the other eye, by contrast, will show decorrelated activation and its connection will therefore be weakened (*cf.* Willshaw and von der Malsburg, 1976).

Such a Hebbian mechanism might involve NMDA receptors on the postsynaptic membranes of cortical neurons (Goodman and Shatz, 1993), because they need an ini-

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[1] The retinotectal systems of fish and frogs do not have a critical developmental period so that synaptic changes can be effected throughout life.

tial depolarization to remove an Mg^{2+} block from their channels before glutamate has a depolarizing effect (see section 2.1.2). In this way, an NMDA channel can be opened by the coinciding activity within a certain time window of two or more presynaptic cells. The changes affecting the synapses could involve long term potentiation (LTP), an increase of synaptic efficacy after stimulation that is also found in hippocampal cells during learning. Evidence for this theory is that NMDA activated channels are permeable to Ca^{2+} which seems to play a role in LTP-like changes to synaptic strength (Kandel, 1991b).

NMDA receptors exist in V1 and they display a functional decline towards the end of the critical period (Fox, Sato, and Daw, 1989). Further, infusion of NMDA receptor antagonists prevents the effects of monocular deprivation (Kleinschmidt, Bear, and Singer, 1987). The most direct evidence for the proposed role of NMDA channels is that visual experience triggers a rapid increase in the number of NMDA receptors in visual cortex (Quinlan, Philpot, Huganir, and Bear, 1999).

2.8 Mechanisms of Neural Plasticity: The Role of Neurotrophins

What are the mechanisms translating correlated and decorrelated neural activity into the observed long term structural changes such as axonal and dendritic remodelling, changes in synaptic efficacy, and the formation of new synapses (*synaptogenesis*)? In answering this question two types of change in neural structure have to be distinguished: one is the strengthening or weakening of existing synapses, and the other, the increased sprouting of axons and dendrites and the establishment of new synapses.

The activity-dependent regulation of NMDA receptors, as well as many other aspects of activity-dependent neural plasticity, have recently been found to involve neurotrophins.

The neurotrophins are a group of four structurally related proteins: Nerve Growth Factor (NGF), Brain-Derived Neurotrophic Factor (BDNF), Neurotrophin-3 (NT-3), and Neurotrophin-4/Neurotrophin-5 (NT-4/5), and they bind to two types of receptors, TrK and p75.

Especially NGF has long been implicated in regulating long-term survival and differentiation of neurons especially in the peripheral nervous system (PNS) (reviewed e.g. in Purves, 1988; Lewin and Barde, 1996), but BDNF also plays a role in the survival of cortical neurons, perhaps through the upregulation of intracellular Ca^{2+} (Ghosh *et al.*, 1994). The role of the neurotrophins in the modulation of synaptic efficacy and the activity-dependent regulation of neural morphology has only recently been established (reviewed by e.g., Black, 1995; Thoenen, 1995; Katz and Shatz, 1996; Lu and Figurov, 1997; McAllister, Katz, and Lo, 1999).

Neurotrophins satisfy four conditions that elucidate their role in the activity-dependent regulation of neural function: they are synthesized in activity-dependent ways, they are secreted in activity-dependent ways, they are taken up in activity-dependent ways, and they effect dramatic yet specific changes in neural function and morphology. In this way, neurotrophins can act as a target-derived, retrograde messenger to effect both pre- and postsynaptic changes in active neurons. These aspects are reviewed in the next subsections.

2.8.1 Activity-Dependent Neurotrophin Synthesis

While in the PNS neurotrophins are expressed by different cells in both activity-independent and activity-dependent ways, in the CNS they are predominantly expressed by neurons in an activity-dependent way. The activity-dependent synthesis of neurotrophins has been demonstrated in various experiments, and it has become clear that different neurotransmitters can selectively regulate expression of different neurotrophins in different areas of the nervous system. The expression of BDNF and NGF mRNA in cultured hippocampal neurons is mediated by non-NMDA glutamergic receptors, but not by NMDA receptors (Zafra *et al.*, 1990), and by depolarization and impulse activity (Lu, Yokoyama, Dreyfus, and Black, 1991). This mechanism relies on Ca^{2+} influx into the cell (Tao *et al.*, 1998). In the CNS, an activity-dependent down-regulation of BDNF and NGF occurs through the inhibitory neurotransmitter GABA (Lindholm *et al.*, 1994). These changes are rapid and pronounced: for example, BDNF mRNA increased ten-fold within three hours after stimulation of hippocampal neurons (Zafra, Castrén, Thoenen, and Lindholm, 1991). Sensory input has also been shown to strongly regulate neurotrophin expression: keeping adult rats in the dark leads to a significant reduction of the mRNA of BDNF and of that of its receptor TrKB in the visual cortex, and normal levels are restored after re-exposure to light (Castrén, Zafra, Thoenen, and Lindholm, 1992). Similarly, the stimulation of rat whiskers increases BDNF mRNA in the barrel cortex (Rocamora, Welker, Pascual, and Soriano, 1996). Neurotrophins can even affect each other's synthesis and the synthesis of their own receptors: for example, NT-3 is up-regulated by BDNF (Lindholm *et al.*, 1994), and NGF regulates the mRNA of NGF receptor (Lindsay *et al.*, 1990).

2.8.2 Activity-Dependent Neurotrophin Release

Not only the synthesis, but also the postsynaptic release of neurotrophins in the CNS is rapidly regulated by neural activity (Blöchl and Thoenen, 1995; Wang and Poo, 1997). For example, BDNF release from depolarized hippocampal postsynaptic neurons increased fivefold within 30 minutes after stimulation (Goodman *et al.*, 1996). Similarly, NGF release from hippocampal neurons is increased by depolarization with potassium and glutamate and can be suppressed by AMPA antagonists. The release depends on intracellular Ca^{2+} and is mediated by sodium influx via sodium channels and non-NMDA glutamate receptors (Thoenen, 1995; Blöchl and Thoenen, 1996). Neurotrophins can also induce their own release, indicating a potential positive feedback loop (Canossa *et al.*, 1997).

The sites of neurotrophin release have been identified to be primarily at dendrites (Thoenen, 1995; Blöchl and Thoenen, 1996). However, anterograde transport and a presynaptic release have recently been reported (reviewed by Altara and DiStefano, 1998), suggesting that the role of neurotrophins might stretch far beyond that of a target-derived retrograde signal.

2.8.3 Activity-Dependent Neurotrophin Uptake

Theoretically, neurotrophins that are released from depolarized postsynaptic dendrites could affect all synapses in their vicinity. One argument against this hypothesis is their highly localized release (Wang, Berninger, and Poo, 1998). However, it has also been shown that the uptake of neurotrophins by presynaptic neurons is dependent on depolarization of the cell membrane (Birren, Verdi, and Anderson, 1992; McAllister *et al.*, 1996; Gottschalk, Pozzo-Miller, Figurov, and Lu, 1998; Boulanger and Poo, 1999). Effects on presynaptic neurons were observed in the presence of neurotrophins after depolarization, but not for neurotrophins or depolarization alone. In this way, only presynaptic neurons that participate in the activation of the postsynaptic cell will be affected by the neurotrophins.

2.8.4 Synaptic Effects of Neurotrophins

Neurotrophins can effectively modulate the efficacy of synapses in different ways and on different timescales. Different neurotrophins, especially BDNF and NT-4/5, have been found to rapidly increase synaptic transmission (Levine, Dreyfus, Black, and Plummer, 1995b, 1996; Wang and Poo, 1997). This effect occurs within minutes after application of the neurotrophins and can persist for hours (Kang and Schuman, 1995).

One mechanism by which synaptic efficacy is regulated by neurotrophins is through an increased release of neurotransmitter, especially glutamate (Knipper *et al.*, 1994; Lessmann, Gottmann, and Heumann, 1994; Wang and Poo, 1997; Sala *et al.*, 1998). Evidence for this mechanism has been gained from showing that both blockade of TrKB, the BDNF receptor, and of glutamergic receptors suppress the observed effects. Alternatively, neurotrophins (NT-3) can suppress GABAergic function, thus increasing postsynaptic action potentials (Kim, Wang, Olafsson, and Lu, 1994). Further evidence for the effect of neurotrophins on neurotransmitter release comes from the finding that neurotrophins rapidly increase $[\mathrm{Ca}^{2+}]_i$ in the presynapse, which is a prerequisite for neurotransmitter release (Berninger *et al.*, 1994; Levine, Dreyfus, Black, and Plummer, 1995a).

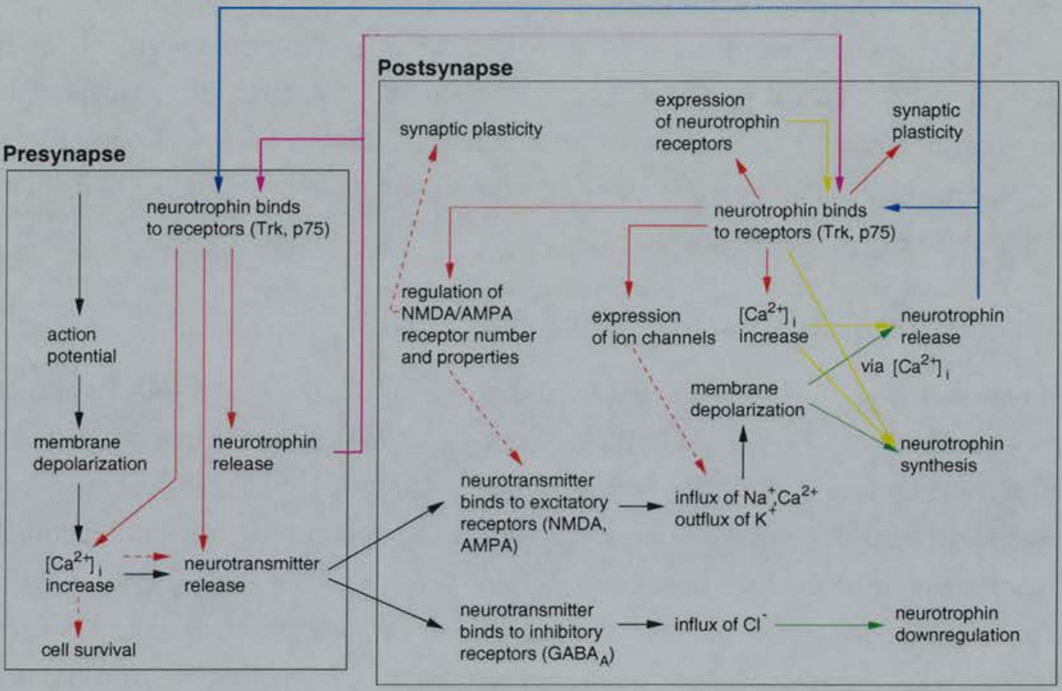

Figure 2.11: Schema of activity-dependent effects of the neurotrophins (esp. BDNF) on synaptic transmission. Black arrows indicate the traditional model of synaptic communication, blue and magenta the pathways of post- and presynaptically released neurotrophin, respectively. Green arrows indicate the effect of normal synaptic transmission on neurotrophins, yellow the effect of neurotrophins on themselves or on other neurotrophins, and red arrows show the effects of neurotrophins on synaptic transmission. Red dotted lines show secondary effects. The figure generalizes over neurotrophins and timescales.

A second, postsynaptic mechanism of synaptic modulation is the increased expression of neurotransmitter receptors through neurotrophins. It has been shown in both developing and adult neocortex that application of BDNF or NGF leads to the increased expression of NMDA receptors and to changes in receptor properties (Muzet and Dupont, 1996; Bai and Kusiak, 1997; Jarvis *et al.*, 1997; Suen *et al.*, 1997; Levine, Crozier, Black, and Plummer, 1998), as well as increased expression of AMPA receptors (Narisawa-Saito *et al.*, 1999). Visual experience also leads to a rapid increase of NMDA receptors in the visual cortex (Quinlan *et al.*, 1999).

Modulation of neural excitability is effected through the neurotrophin-induced expression of ion channels in the postsynaptic membrane (reviewed in McAllister *et al.*, 1999). Different neurotrophins can have different effects on channel expression: whereas e.g., BDNF increases the number of sodium and calcium channels, leading to increased neural excitability, NT-3 mediates the expression of potassium channels, having the opposite effect (Lesser, Sherwood, and Lo, 1997). These subtle and varied effects of different neurotrophins indicate an instructive rather than a permissive role of neurotrophins in synaptic modulation (McAllister *et al.*, 1999).

Finally, BDNF also plays a role in long-term potentiation (LTP) of hippocampal synapses (Akaneya, Tsumoto, Kinoshita, and Hatanaka, 1997; Kang, Bonhoeffer, and Schuman, 1998). LTP is believed to form the basis of learning and memory in the brain.

2.8.5 Morphological Effects of Neurotrophins

Besides modulating the efficacy of existing synapses, the neurotrophins have also strong influences on neural morphology. It is interesting to note that these effects are independent from the actual existence of synapses; all that is needed are receptors for the neurotrophins (Katz and Shatz, 1996). In this way, the morphology of axons and dendrites can be regulated at early stages, and neurotrophins might even be involved in activity-dependent synaptogenesis.

Evidence for the role of neurotrophins in axonal development, which is generally believed to proceed independently from activity (see section 2.3.4), is not very abundant, but two possible mechanisms have been described: first, gradients of target-derived non-NGF neurotrophins seem to play a role in chemotropic axon guidance (Ming *et al.*, 1997), although there is clear evidence for many non activity-dependent mechanisms (*cf.* section 2.3.4.4). Second, neurotrophins regulate the sprouting and complexity of axons: Cohen-Cory and Fraser (1995) showed that injection of BDNF into the optic tectum of *Xenopus* tadpoles led to rapidly and persistently increased axon branching and complexity, whereas the injection of BDNF antibodies reduced arborization and complexity. Similar results have been found in cultured axons (Inoue and Sanes, 1997). Effects of NGF on axon sprouting have also been observed in adult rat brains (Isaacson, Saffran, and Crutcher, 1992).

The effects of the neurotrophins on dendritic branching are far more established and it has become clear that they play indeed a central role in regulating the complexity of developing dendrites (Purves, Snider, and Voyvodic, 1988; Snider, 1988; Ruit and Snider, 1991) and the number of dendritic spines (Shimada, Mason, and Morrison, 1998). Different neurotrophins lead to increased dendritic growth in different parts of the nervous system, and the roles of the individual neurotrophins can be very specific: in neocortical pyramidal neurons, basal and apical dendrites of the same neuron are affected by different neurotrophins (McAllister *et al.*, 1995), and different neurotrophins act on neurons in different cortical layers: while BDNF increases the complexity of basal dendrites in layer IV visual cortex, NT-3 inhibits dendritic growth in this layer. These roles are reversed in layer VI, where NT-3 stimulates dendritic growth which is inhibited by BDNF (McAllister *et al.*, 1997). Growth of basal dendrites in layers V and VI is further enhanced by NT-4 (McAllister *et al.*, 1995). Again, these highly specific effects of different neurotrophins indicate an instructive role for dendritic development. However, conflicting results suggest that the presence of afferents, but not neural activity is required to initiate dendritic branching, while the formation of dendritic spines requires activity (Kossel, Williams, Schweizer, and Kater, 1997).

There is so far only sparse evidence that neurotrophins are involved in synaptogenesis (Snider and Lichtman, 1996). However, in the hippocampus BDNF and NT-3 lead to a dramatic (seven-fold) increase in synaptogenesis with different effects: BDNF regulates the creation of excitatory and inhibitory synapses, whereas NT-3 induces formation of excitatory synapses only (Vicario-Abejon, Collin, McKay, and Segal, 1998).

2.8.6 Neurotrophins and Ocular Dominance Column Formation

Given the strong evidence for the role of neurotrophins in regulating many aspects of neural plasticity, it comes as no surprise that they have a profound influence on the development of ocular dominance columns in the primary visual cortex: application of NGF can prevent the effects of monocular deprivation in the rat visual cortex (Maffei *et al.*, 1992; Berardi *et al.*, 1993), and anti-NGF antibodies disrupt normal development of the visual system (Berardi, Cellerino, Domenici, Fagiolini, Pizzorusso, Fagiolini, Pizzorusso, Cattaneo, and Maffei, 1994). More importantly, infusion of BDNF or NT-4/5 into cat primary visual cortex prevents the formation of ocular dominance columns (Cabelli, Hohn, and Shatz, 1995), and blockade of BDNF and NT-4/5 receptors has the same effect (Cabelli, Shelton, Segal, and Shatz, 1997). Blocking NGF and NT-3, however, does not affect column formation. These results indicate that a specific amount of BDNF and/or NT-4/5 needs to be present in V1 to enable the formation of ocular dominance columns. This claim has been strengthened by recent models that define competition between synapses for limited amounts of neurotrophic factors as the basis for their formation (Elliott and Shadbolt, 1998; van Ooyen and Willshaw, 1999). An oversupply of neurotrophins (Cabelli *et al.*, 1995) as well as the absence of neurotrophins (Cabelli *et al.*, 1997) eliminate this competition.

In summary, depolarized postsynaptic neurons release neurotrophins as retrograde signals that increase the synaptic efficacy of co-active presynaptic neurons and thus implement a Hebbian-type coincidence detector. The increase in synaptic efficacy might be effected through the expression of NMDA receptors and the increase of presynaptic glutamate release, and through the upregulation of $[Ca^{2+}]_i$ in the presynapse. These mechanisms, together with the other evidence discussed in this section, suggest that the neurotrophins play a strong role in modulating different aspects of activity-dependent neural plasticity, in the developing and in the mature nervous system.

2.9 Neural Activity and Regional Specification of the Cortex

The general structure of the cortex is rather homogeneous throughout (see section 2.2): all cortical areas have six layers, and the number of different neural types in a "radial traverse" through the layers is remarkably constant, with the exception of the primary visual cortex, where the number of cells is much higher. The basic scheme of output connections from the individual layers to other cortical and subcortical structures is constant as well, with layer 6 neurons projecting to the thalamus, layer 5 neurons to other subcortical areas, and neurons in layers 2 and 3 projecting intra-cortically.

However, there are also significant differences between cortical regions that have allowed for the distinction of separate regions based on their cytoarchitecture alone (Brodmann, 1909, see fig. 2.12). These differences consist in the thickness of the individual layers which can vary considerably over the regions (see section 2.2). Further differences can be found in the properties of individual cells, such as the distribution of receptors, cell size and density, and also in the connections from the thalamus and to other subcortical regions (O'Leary, 1989). Often these cytoarchitectonally different regions can be related to functional regions.

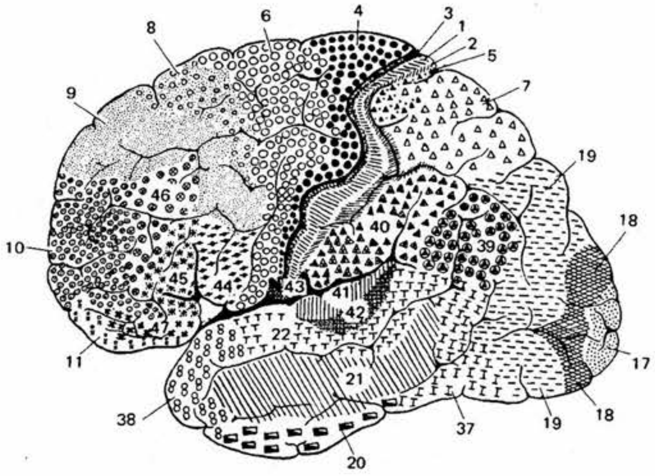

Figure 2.12: Cytoarchitectonally different areas as found by Brodmann (1909)

How do these areas come about? Much of the answer to this question remains unclear, but two main theories have been formulated: the *protomap* theory (Rakic, 1988) maintains that precursor cells in the ventricular zone are already committed to generate neurons that are destined for specific functional regions, which implies that the functional specification of cortical regions is genetically predefined. By contrast, the *protocortex* view (O'Leary, 1989) holds that the developing cortex is less differentiated and that specialized areas emerge due to input from subcortical or from other cortical structures.

There is considerable evidence favouring the protocortex hypothesis: when neurons from late foetal visual cortex are transplanted into the sensorimotor cortex they develop the characteristics of their destination area and not of the area from which they originate (O'Leary and Stanfield, 1989; O'Leary, Schlaggar, and Stanfield, 1992). Similarly, when in ferrets retinogeniculate pathways were re-routed to project to the somatosensory or auditory area of the thalamus which project to the somatosensory and auditory cortex, respectively, the response properties of those cortical neurons resembled those usually found in the visual cortex, developing orientation and direction selective cells (Frost, 1981; Sur, Garraghty, and Roe, 1988). The new area was functional and the ferrets could perform visual discrimination tasks. This result was taken as evidence that cortical neurons process information in a principled way and area specificity is established through the specific inputs from the thalamus.

The question why, given that the cortex is initially little differentiated and can process inputs from different sensory modalities, the overall organization of functional areas is very similar between individuals has been addressed by Johnson (1993b) and Johnson, Oliver, and Shrager (1998). They attributed the inter-individual similarity in brain structure to different *extrinsic* and *intrinsic* constraints.

Constraints that are *extrinsic* to the cortex are derived from the environment, or from subcortical brain structures. Among environmental constraints one can distinguish the species typical environment (STE) and the individual specific environment (ISE) (Johnson and Morton, 1991). The STE is normally shared between all members of a species, e.g., gravity and patterned light for all organisms, and the exposure to language for humans. Alterations to the STE such as dark rearing or monocular deprivation often have drastic effects on cortical development (see section 2.7). On the other hand, the ISE is different for every individual and it includes the specific aspects of the environment of the developing organism, e.g., social interactions and the particular language to which a child is exposed.

Constraints dependent on subcortical areas have been shown in the above-mentioned transplantation and re-routing studies: a cortical area takes on a specific function and representational structure based on the thalamic (or, for higher areas, presumably the cortico-cortical) input it receives. Another type of sub-cortically mediated constraint emerges through the immaturity of developing sensory channels: Turkewitz and Kenny (1982) have argued that initial limitations in the functioning of sensory channels can be beneficial to development. For example, the inability of an infant to focus on most objects significantly reduces the complexity of the world which she has to learn to represent, and more complex representations can be gradually built while the sensory system develops. This *starting small* hypothesis will be discussed in greater detail in the next chapter.

A third sub-cortical constraint has been investigated in chick imprinting: a newborn chick imprints preferentially on a mother hen that is present at hatching, and only in the absence of a hen it imprints on other objects. This mechanism has been shown to be mediated sub-cortically: the chick has an innate predisposition to orient towards conspecifics which then allows it to construct cortically based representations of the mother hen. In this way, a sub-cortical attention bias leads to the development of specific cortical representations (Johnson and Morton, 1991).

Intrinsic constraints on cortical plasticity are present in the uniform six-layered structure of the cortex (see section 2.2), but also in the time course of cortical development: different cortical areas mature at different rates (Chugani, Phelps, and Mazziotta, 1987; Huttenlocher, 1990; Turkewitz and Kenny, 1982), and within a given area the deeper cortical layers develop prior to the more superficial layers. From this developmental schedule it follows that some of the cortico-cortical feedback pathways from higher to lower cortical areas (e.g., higher visual areas to V1) mature before their corresponding feed-forward pathways, which might guide the development of these feed-forward pathways.

The final set of constraints on cortical plasticity are *dynamic* constraints. It has been hypothesized that the cortex is traversed by a *wave of plasticity* mediated by trophic factors that induces high plasticity at its peak and that reaches different cortical areas at different times (Thatcher, 1992). At the peak a high degree of synaptogenesis occurs, and synaptic loss takes place after the wave has passed.

These sets of constraints together with the Hebbian-based competitive and cooperative mechanisms outlined in section 2.7 are assumed to be responsible for the common clustered, topographically and hierarchically organized representations in different areas of the cortex (Johnson, 1993b; Oliver, Johnson, and Shrager, 1996).

Despite these constraints on cortical plasticity, however, there are sometimes considerable differences between individuals in the size of functionally defined brain regions: two- to threefold differences have been reported in human primary visual cortex (Stensaas, Eddington, and Dobelle, 1974; Leuba and Kraftsik, 1994) and the sensorimotor cortex (White *et al.*, 1997) as well as in the rat somatosensory system (Riddle and Purves, 1995).

2.10 Plasticity after Development

Brain plasticity does not end with development. In fact, many researchers now argue that there is no real distinction between development and adult plasticity, since the same mechanisms are at work at all stages of life and new information is learned and stored in the brain even in adults. On the other hand, many activity-dependent adjustments to neural structures can be effected only during a certain *critical period*. Such a critical period exists for example in the formation of ocular dominance columns (see section 2.7) where monocular deprivation prevents column formation only during the first few weeks of life. How can these conflicting results be reconciled?

Black and Greenough (1986) have argued for two complementary types of development and learning processes: *experience-expectant* and *experience-dependent* learning, which are supported by different underlying neural processes. Experience-expectant learning describes adaptation to aspects of the environment that are shared by all members of a species. In their view, learning this type of information involves an initial overproduction of synapses followed by a selective stabilization of useful and a pruning of surplus connections. As a consequence, experience-expectant processes are subject to a critical period, because once the surplus connections have been pruned, further large-scale adjustments can no longer be made. The formation of ocular dominance columns represents such an experience-expectant process, and interference with it through dark rearing or monocular deprivation during the critical period leads to profound and irreversible alterations to the neural system.

Experience-dependent learning describes those aspects of the environment that are unique for each individual and that allow adaptation to the specific circumstances in which an individual exists. This type of learning requires life-long flexibility and therefore cannot be subject to a critical period. Black and Greenough (1986) argued that experience-dependent learning involves mainly constructivist processes, that is, the directed construction of new synapses.

The distinction between experience-expectant and experience-dependent learning resembles the distinction made by Johnson and Morton (1991) between the species-typical environment and the individual specific environment (see section 2.9). However, a significant difference between these categorizations is that Black and Greenough (1986) associate different neural mechanisms with theirs (see Johnson, 1993c)', although a distinction between different neural mechanisms is not always possible: for example, as was described in section 2.7, in the formation of ocular dominance columns as an instance of experience-expectant learning, axons retract from inappropriate areas, but the sprouting of axons within the correct areas is also a significant factor in the establishment of the final pattern. Both selective and constructive mechanisms seem therefore to be at work also in experience-expectant learning. The relationship between selectionist and constructivist learning is further discussed in section 2.11.

In the study of cognitive development, experience-dependent learning is the more interesting case because it reflects individual differences in neural structure that are the outcome of different experiences. Furthermore, experience-expectant learning is confined to early developmental stages and thus plays no role in adult plasticity. This section will therefore focus on the study of experience-dependent learning.

Experience-dependent learning is often studied by comparing rats that are reared in different types of environment or adult rats that are placed in such environments (reviewed in Greenough, Black, and Wallace, 1987; Rosenzweig, 1996). This *environmental complexity paradigm* distinguishes between three conditions: in the Environmental Complexity Condition (EC), groups of up to twelve rats live in big cages with many different toys that are exchanged on a regular basis, and the rats can exercise in running wheels or walk through mazes. The Social Cage Condition (SC) sees small groups of rats, mostly just two, in normal laboratory cages without any objects to play with. In the Individual Cage Condition (IC) rats are kept individually in small cages, again without objects, and sometimes in dim light.

Rats from EC environments show substantial differences in their brain size and anatomy compared with both SC and IC rats: their cortex is thicker in many areas with larger neural cell bodies, and there are more glial cells. Detailed studies have revealed that the structure of neurons is also more complex: in V1, there are about 20% more dendrites per neuron (Greenough and Volkmar, 1973), and there are also more dendritic spines (Globus, Rosenzweig, Bennett, and Diamond, 1973). Synaptic density per neuron in upper visual cortex is 20% to 25% higher than in other rats (Turner and Greenough, 1985), but differences also exist in the auditory and the frontal cortex and in subcortical structures. Synaptic changes in the cerebellum due to motor activity have been shown to persist for at least four weeks after training, even without any further training (Kleim, Vij, Ballard, and Greenough, 1997). An interesting result is that merely observing a complex environment does not lead to these changes, but an active interaction with the EC environment is necessary (Ferchmin and Bennett, 1975).

More recently it has also been shown that an enriched environment influences the rate of neurogenesis in adult mice hippocampus (Kempermann, Kuhn, and Gage, 1997), suggesting the possibility of a novel mechanism of brain plasticity that involves the generation of new neurons in response to interactions with the environment. Most importantly, in contrast to long-established textbook knowledge, neurogenesis in the hippocampus of adult humans has recently been reported (Eriksson *et al.*, 1998). Although it is not clear yet whether the newly generated neurons are functional and whether activity influences neurogenesis in humans as well, this new result suggests the possibility of a role of neurogenesis in constructivist learning (Gould, Tanapat, Hastings, and Shors, 1999).

That the morphological changes of neural structure in adult brains are task specific has been demonstrated by training rats on complex maze tasks requiring visuospatial memory after occluding one eye and surgically disconnecting the two cerebral hemispheres (Chang and Greenough, 1982). After training, the side of visual cortex receiving input from the non-occluded eye showed more growth in dendritic branching than the other side. Similarly, training adult rats on specific motor skills leads to localized growth in the cortical areas that are responsible for the control of the trained limbs (Greenough, Larson, and Withers, 1985).

Further experiments established that the generation of new synapses seems in fact to be due to the learning of novel tasks rather than to the exercising of already existing abilities. Black, Isaacs, Anderson, Alcantara, and Greenough (1990) examined the brains of four different kinds of rats that had lived in different experimental environments: Acrobatic Condition (AC) rats learned different obstacle paths over a period of 30 days involving balancing, see-saws and rope bridges. Forced Exercise Condition (FX) rats walked on a treadmill for long times, Voluntary Exercise Condition (VX) rats had free access to a running wheel, and Inactive Condition (IC) rats were kept in normal laboratory cages. Therefore, AC rats had to learn continually during their exercise, whereas FX and VX rats exercised essentially without learning anything. At the same time, FX and VX rats made more than ten times the number of repetitive locomotor movements than the AC and IC rats. In this way, learning (in AC rats) could be dissociated from exercise (in the FX and VX rats). When Black *et al.* examined the cerebellar region of the different rat populations, they found striking dissociations. Most significantly, whereas there was evidence for the creation of new blood vessels in FX and VX rats, the AC rats showed evidence for synaptogenesis. These results indicated that exercise alone leads to the formation of new blood vessels, presumably to support the increased metabolic activity of the neurons involved in the movements, while only learning seems to lead to the formation of new synapses.

2.11 Does Activity-Dependent Mean Constructivist?

This chapter has reviewed the activity-dependent development of the cortex across different levels, from the sub-cellular level to the functional specialization of cortical areas, both in development and adulthood. The aim of this review has been to make the point for constructivist brain development in which the environment instructs the brain as to what connections to form and how to modulate the properties of neurons. There are, however, other possibilities by which activity could modulate brain structure. Neural activity could perhaps only trigger an intrinsic genetic program for a prespecified brain development, and in the absence of relevant activity some genes would not be expressed. However, there is considerable evidence against this genetic prespecification as a general mechanism: first, the genetic information available (perhaps 100,000 genes in mammals) is not sufficient to specify the full connectivity pattern between all neurons (as many as 10^{14} synapses). Second, in evolution the number of genes has not kept pace with the increasing complexity of the brain: while the total amount of DNA per cell is roughly the same between mouse and human, the human brain is far more complex (Changeux, Heidmann, and Patte, 1984). Third, organisms with identical genes show significant variation in synaptic organization (Macagno, Lopresti, and Levinthal, 1973), which would not be expected if brain organization was strictly prespecified.

However, in investigating the role of neural activity on brain development it is important to consider whether activity is only *permissive* for other mechanisms to shape development, or whether it is *instructive* and directly moulds neural connections. For example, in the formation of synapses, target neurons could have molecular markers that are recognized by certain neurons with complementary markers (the *chemoaffinity* hypothesis), but actual innervation could require activity. While this mechanism might exist at some stages of cortical development, e.g., the early stages of axon guidance, much of the evidence reviewed in this chapter points instead towards an instructive role of neural activity. A distinction between instructive and permissive roles for neural activity can be made by varying the pattern, but not the overall amount of activity, assuming that instructive activity will lead to different neural architectures in response to different activity patterns (Crair, 1999). Such experiments have been conducted in the formation of ocular dominance column by Stryker and Strickland (1984, see section 2.7): when neural activity between the two eyes was artificially correlated, ocular dominance columns failed to form. Decorrelated activity, however, induced ODC formation. Further experiments in ODC formation also support an instructive role for neural activity: when a third eye was grafted onto a frog and made to innervate the optic tectum, ODC suddenly formed (Constantine-Paton and Law, 1978). This result makes the presence of molecular markers for ODC formation unlikely but instead indicates that ODC form based on an instructive, competitive process.

In many cases of neural plasticity, the instructive role of activity seems to be mediated via neurotrophins (McAllister *et al.*, 1999): the complex and very specific roles that different neurotrophins play in different cortical layers and even at different parts of one neuron (see section 2.8.5) make a purely permissive role unlikely.

It is important to note that not only activity from sensory input but also spontaneous neural activity can act in an instructive manner: correlated waves of neural activity in the developing mammals guide the innervation of LGN neurons by retinal cells and, in some species, the early stages of ocular dominance column formation. After eye opening, this spontaneous activity is replaced with sensory input that is more highly correlated within eyes than between eyes. In this way, only a single constructive mechanism is required for pre- and postnatal development.

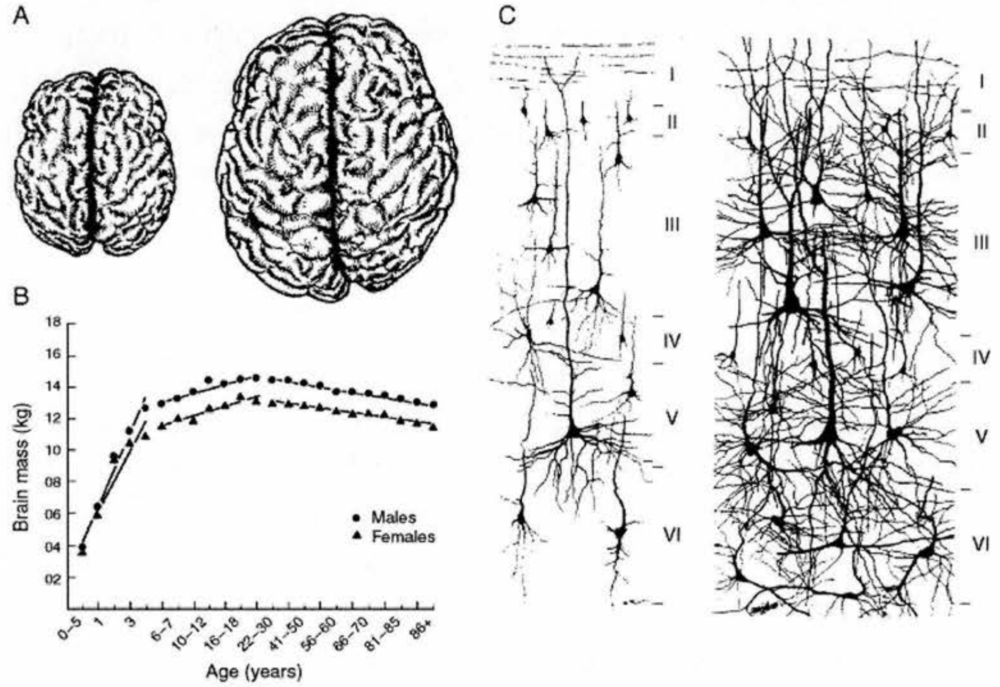

Figure 2.13: Postnatal development of the brain. (A) A normal brain at birth (left) and at six years of age (right). (B) The duration of human brain growth (measured in brain mass), based on 4,000 neurologically normal subjects. (C) A Golgi-stain of neurons in the parietal cortex of a neonate human (left) and in a six-year-old (right). An increased cell body size and markedly increased branching are clearly visible. (From Purves *et al.*, 1996)

An alternative way in which activity could guide brain development in a non-constructivist way is to act in a *selectionist* way where an initial overproduction of synapses (or other neural structures) is followed by the activity-dependent selective stabilization of some and the loss of other synapses (Changeux *et al.*, 1984; Edelman, 1987; Changeux and Dehaene, 1989). The initial neural structures in this paradigm would be generated independently from activity through a process combining both genetic and intrinsically generated signals, thus limiting the range of possible functions that could be computed by the cortex. The selectionist view has received support from studies reporting a significant overproduction of synapses in the cortex followed by a loss of a large percentage (Huttenlocher, 1979, 1990), although these data are hard to interpret conclusively (Huttenlocher, 1990; Quartz and Sejnowski, 1997). Although a significant loss of connections does occur, there is evidence that it might not be the predominant factor in postnatal development. For example, despite the retraction of axon collaterals from inappropriate regions in the formation of ocular dominance columns (see section 2.7) and in other regions of the nervous system, the major factor in brain development is more likely to be the progressive construction and elaboration of neural structure (Purves *et al.*, 1996). The size of the brain quadruples after birth (fig. 2.13 A) and growth extends over more than the first two decades of life (fig. 2.13 B). This growth involves a significant increase in cell body size and the continuous elaboration of neural structures (fig. 2.13 C): the mean total length of dendrites in layer III of the human primary visual cortex at birth is only 30% of the maximum, and in layer V, 60%. Furthermore, only about 10% of all synapses in V1 are present at birth (Huttenlocher, 1990). The maximum number of synapses in V1 is reached at age eight months, and subsequently there is a decline by up to 50% until age 11 years. However, the final number of synapses is still three to four times higher than at birth, indicating that elaboration and loss of connections go hand in hand. Purves *et al.* (1996) argued that a net elimination of synapses occurs only for neurons without dendritic processes, whereas neurons with more complex dendritic geometries show a net gain. Hence, instead of a general process of selective synaptic elimination there seems to be a process of constructive synaptic rearrangements to ensure appropriate levels of convergence in the input to each neuron, and appropriate divergence in the output.

But how can the extensive loss of synapses fit into a constructivist framework of brain development? It is often assumed that constructivism exclusively refers to the addition of structure whereas selectionism refers to its loss. However, constructivist development does naturally involve a regressive element which is needed to correct for stochastic growth (Quartz and Sejnowski, 1997), or for synaptic overproduction in response to salient experiences (Greenough *et al.*, 1987, fig. 2.14). I would like to argue that perhaps surprisingly the distinction between selectionism and constructivism lies not in the loss of connections, but in the way in which structure is created: selectionism involves an initial overproduction of structure that is not goal-directed but that is genetically or even randomly based. By contrast, the formation of connections in the constructivist framework is goal-driven from the onset. More strictly speaking, selectionism attributes all goal-directedness to the loss of connections, whereas constructivism also assumes goal-directedness in their construction.

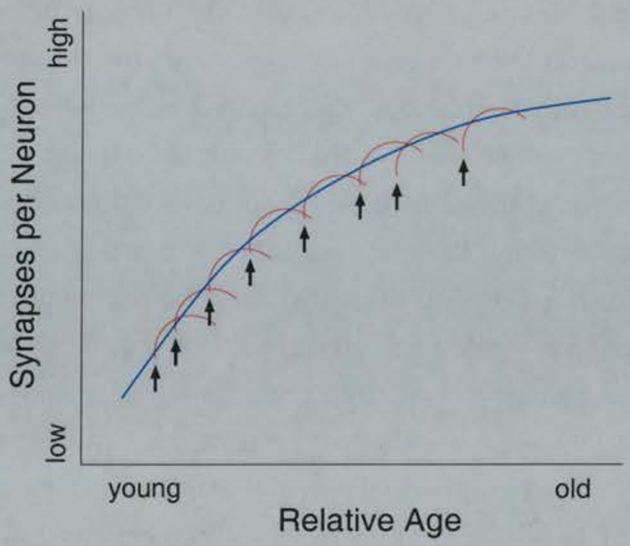

Figure 2.14: Constructivist synaptogenesis involves a regressive element. Arrows indicate salient experiences leading to a burst of localized synaptogenesis followed by the loss of excessive synapses (red curves). The net effect of these repeated growth–pruning cycles is an increase in synaptic numbers per neuron (blue curve). (Adapted from Greenough *et al.*, 1987)

The evidence for constructivist cortical development should not be taken as an argument for *tabula rasa* learning and development. Instead, the development of the brain relies on complex interactions on multiple levels between intrinsic constraints such as genetic predispositions, and extrinsic constraints such as species-typical and species-specific environment (Elman *et al.*, 1996; Johnson, 1997). These interactions have become evident for example in the discovery that neurotrophins that act in activity-dependent ways also lead to expression of genes to alter the structure and functioning of ion channels (section 2.8.4), and in the discussion of constraints on cortical plasticity (section 2.9) where the regional specification of an initially equipotential protocortex is guided by several extrinsic constraints. Constructivist development therefore proceeds through the progressive elaboration of neural structures and the activity-dependent modulation of their functioning, involving constructive and regressive events, always within the framework set by the general intrinsic constraints.

2.12 Chapter Summary

This chapter has reviewed the role of activity in the formation of cortical circuits. Whereas initial phases of neural development are independent of activity, activity does have a strong influence on the subcellular properties of neurons regulating their response properties, on the rate and direction of neurite outgrowth, and especially on axonal and dendritic morphology and synapse formation. In this way, activity is crucial, through interactions with intrinsic constraints, in the shaping of neural circuits and cortical areas of specialization. While some of these effects rely on (prenatal) spontaneous neural activity, alterations of sensory experiences in early development have profound effects on cortical organization. Two complementary developmental mechanisms might be at work: one, referring to learning about the species-typical, or experience-expectant environment that is shared by all members of a species, is subject to a critical period that often stretches over a relatively brief period in early postnatal life. The other, referring to individual specific, or experience-dependent environment is more flexible and allows for life-long modifications of neural structures. Both mechanisms, however, involve constructive and regressive events, leading to a net increase in structure. The effect of activity on neural architecture does not end with development: throughout life, new experiences create new structures, and the learning of complex tasks leads to more complex, yet localized and task-specific modifications of neural morphology.

Many of the activity-dependent effects on development seem to rely on neurotrophins, which in the past few years have become an attractive candidate for retrograde signals exerting pre-synaptic effects in activity-dependent ways. Perhaps the role of neurotrophins in neural plasticity can be integrated with the longer established roles of Ca^{2+} in neurite outgrowth and that of NMDA receptors as coincidence detectors in Hebbian synapses. This possibility arises because neurotrophins have been shown both to rapidly upregulate $[Ca^{2+}]_i$ and NMDA receptors.

In studying whether activity-dependent neural development is constructivist, that is, whether activity is directly guiding the construction of neural circuits, alternative views have to be considered, namely, a genetic pre-specification of connections that is merely enabled by activity, or the selective stabilization of a subset of intrinsically pre-specified connections. While there are clear arguments against a full pre-specification of precise connection patterns, selectionist views have gained much popularity. However, a re-evaluation of the data used to back selectionist views (Purves *et al.*, 1996; Quartz and Sejnowski, 1997), together with new data suggest a progressive elaboration of neural structures rather than synaptic elimination as the main element in the construction of cortical circuits in which synaptic loss might have the role of error-correction or fine-tuning after exuberant growth. It therefore seems that the cortex develops in a constructivist way, in which neural activity, both spontaneous and experience-dependent, interacts with intrinsic constraints on multiple levels to shape the developing and adult brain.

Chapter 3

Constructivist Cognitive Development

The previous chapter reviewed how the developing and adult brain is shaped by activity that is often derived from sensory stimulation. It was shown that experience has a profound impact on the developing neural structures, and in section 2.10 I reviewed evidence that complex experience leads to complex brain structures in the form of more dendrites and spines, in areas specific for the processing of the domain in which the experience is made. However, these results alone do not answer the question of the relationship between brain structures and cognitive abilities. What is needed is evidence of how brain activity relates to cognition, and more specifically, how changes in the brain's architecture correlate with changes in cognitive abilities during development and in adult learning.

The view that it is important to study the brain in order to understand cognition is by no means universally accepted. A belief held by some people is that the neural and cognitive levels are independent of each other, and that the brain is just one possible substrate in which cognitive mechanisms are implemented. According to this view which is called *Functionalism* in philosophy, it is useless and perhaps even to be avoided to study the brain with respect to cognition, because the cognitive level is autonomous and answers about the functioning on this level can be found within itself (e.g. Fodor, 1983; Pylyshyn, 1980).

One of the best arguments against this view is the evidence reviewed in the previous chapter: if the execution of the program modifies the architecture on which it is implemented, and the modified architecture in turn changes the program, then a distinction cannot be made between the two, and both have to be studied with respect to their interactions. The ways in which the program (environmental input as processed by the brain) modifies the architecture (the brain), was described in the previous chapter. The ways in which the architectural changes of the brain correlate with changes in cognitive functioning is the topic of this chapter.

Another argument against the Functionalist view is that it is impossible to tell how far the architecture of the brain can change while the cognitive "algorithm" remains the same (Churchland, 1986). The answer to this question seems to be "very little", and in chapter 4 it will be shown that systems that modify their architecture in response to learning have fundamentally different properties from fixed-architecture systems. Therefore, it seems worthwhile and justified to investigate how brain and cognition, and especially brain development and cognitive development relate to each other, and this new area of research has already led to many valuable insights into the nature of the developing brain and mind (e.g., Elman *et al.*, 1996; Johnson, 1997)

In this chapter, several aspects of cognitive development are discussed that share a recourse to evidence or assumptions about the gradual development of neural architectures and that stress the importance of development in understanding the adult mind. In section 3.1 I will review different ways in which the relationship between brain activity and cognitive functioning can be studied, and I will then discuss a representative theory of linking neural and cognitive development, namely, the idea that face recognition is subserved by two independent neural systems that develop differently. A further important theory how neural development guides cognitive development has been formulated as the "Starting Small" or "Less is More" hypothesis which claims that initially restricted cognitive capacities are essential for the acquisition of adult competence. This hypothesis is discussed in section 3.3. In section 3.4 I then describe the most influential theory of cognitive development, Piaget's Epistemological Constructivism, which has as its central assumption that the child actively builds its cognitive system through interactions with the environment.

3.1 How to Study Brain and Cognition

The study of correlates between brain activity and cognition is based on different methods for visualizing and measuring brain activity. In the following sections, the most important of these methods are described. Measurements of brain activity can be made during the performance of a cognitive task, and changes in the task can be correlated with changes in brain activity. Other methods rely on the analysis of impaired processing where a specific lesion causes specific cognitive deficits. However, these methods are problematic and might not be well suited to help understanding the intact brain.

Studying the developing brain, that is, correlates between structural and behavioural *change*, is more difficult because it requires a diachronic approach. Most straightforwardly, the onset of a certain cognitive ability would be attributed to the development of underlying neural structures, and this approach can also be used for the termination of an ability (e.g., the inability to reach native competence in a language when it is learned after a certain age). Unfortunately, however, such a straightforward relationship does usually not exist.

3.1.1 Measuring and Visualizing Brain Activity

Several methods have been developed to measure and visualize the activity of neurons in response to certain tasks, and this section gives a brief overview of the more popular methods.

3.1.1.1 Single and Multiple Cell Recording

The activity of single neurons or of small groups of neurons can be recorded with microelectrodes that are inserted into the brain to record extracellular or intracellular potentials. This method offers a very high spatial and temporal resolution. In humans, cell recordings are made only in patients undergoing brain surgery, but studies in behaving animals have revealed much about the functional anatomy and plasticity of the brain. Beside its invasive nature, the problem with cell recodings is that neurons are examined individually, and it can be very difficult to find a neuron that is involved in the processing of a certain task. Recently, progress has been made in recording simultaneously from multiple cells, which allows the investigation of the interactions between populations of cells (e.g. Nirenberg and Latham, 1998).

3.1.1.2 Optical Dyeing

In animal experiments, changes in neural activity can be visualized directly with voltage-sensitive optical dyes (e.g. Salzberg, Obaid, Senseman, and Gainer, 1983). The advantage of this method is that it can easily be repeated for different tasks. It also allows for the mapping of relatively large areas of the brain. More recently, more sophisticated reflection measurements have been developed that are independent of dyes (Grinvald *et al.*, 1986).

3.1.1.3 Event-Related Potentials

Changes in the electrical potential of the brain can be recorded in an *electroencephalogram* (EEG). Here, several electrodes are placed on the scalp of a subject and electrical brain potentials are recorded. By itself this method is of limited use because such potentials are very noisy and the spatial resolution is poor, i.e., it is difficult to say in which brain area a recorded change is taking place. More useful are *event-related potentials* (ERP) that can be mathematically extracted from EEG recordings by averaging over several EEG recordings that are time-locked to a certain sensory stimulus or motor event (e.g. Hillyard and Picton, 1987). Then, a specific response (a positive or negative waveform) can be observed at a certain time interval after the stimulus or motor event. These responses are usually characterized by their directionality (positive or negative) and their delay (in *msec*) after the event. Since its introduction, significant progress has been made in identifying specific ERPs for certain aspects of sensory perception. Additionally, High-Density (HD) ERPs have allowed for a better localization of the source of the recorded activity (e.g. Csibra, Tucker, and Johnson, 1998).

ERP is perhaps the most widely used method to study the connection between brain activity and behaviour. This is because it is non-invasive, has a high temporal resolution, does not restrict the movements of the subject as much as e.g., PET and MRI scans (see below), is not noisy, and is relatively inexpensive. Therefore, this method can also be applied to the study of infants (e.g. McIsaac and Polich, 1992; Nelson and Collins, 1992).

3.1.1.4 MEG

Related to EEG recording is the *magnetoencephalogram* (MEG) that measures the magnetic field changes that are due to the electrical activity of neurons (e.g. Williamson, Lü, Karron, and Kaufman, 1991). Similarly to EEG, magnetometers are placed around the skull of a subject and the response to sensory stimuli is measured. While MEG is much less sensitive to noise, localization is worse than with EEG. Recently, methods for combining EEG and MEG recordings have been proposed (Baillet, Garnero, Marin, and Hugonin, 1999) to improve localization of the activity within the brain and to reduce the sensitivity to noise.

3.1.1.5 PET

Positron Emission Tomography (PET) is based on visualizing changes in regional blood flow in the brain that are due to metabolic demands of neural activity. It is based on the idea that a brain region that becomes active will receive an increased blood supply. To visualize this increased blood flow, a slightly radioactive substance is injected into the blood and monitored with external radiation detectors (e.g. Raichle, 1985). The spatial resolution of PET scans is in the range of 5–10 mm and thus very good. The precise location of an event in the brain is achieved by combining PET with anatomical imaging methods such as MRI. The temporal resolution of PET scans is, however, not very high, because increased neural activity is not measured directly and the increase in blood flow lags behind the increase of activity in a specific area.

3.1.1.6 fMRI

Functional magnetic resonance imaging (fMRI) is related to PET in that it visualizes the increased blood flow that results from neural activity in a specific area of the brain. In contrast to PET, however, it does not require injection of a radioactive substance and can therefore be applied more widely. fMRI takes advantage of the differences in the magnetic field between oxygenated and deoxygenated blood which is visualized as differences in the intensity of magnetic resonance images by placing the head of the subject in a huge magnetic coil.

To account for normal background activity of the brain, measurements are usually made by means of a contrastive method: the brain is imaged alternatively under two different conditions (e.g., silent reading and reading aloud). Then, the activity profiles for both conditions are subtracted, and the remaining area of activity is then associated with the difference between the two tasks (e.g., the articulation in the aloud reading task).

Like PET, fMRI provides a very good spatial resolution (down to 1 mm) but a less accurate temporal resolution (several seconds). It can be combined with ERP to yield both good spatial and temporal resolution. Currently, research is under way to develop real-time fMRI (Voyvodic, 1999) that allows an on-line observation of brain activity during a behavioural task.

3.1.2 TMS

A new method to establish a causal link between cortical activation and cognitive function is *transcranial magnetic stimulation* (TMS). This technique consists of applying a short, strong magnetic pulse to the brain by means of a small coil that is held to the head of the subject. The pulse essentially induces a temporary, reversible disturbance in the area under the coil. While TMS relies on the exact timing of the pulse, *repetitive* *transcranial magnetic stimulation* (rTMS) produces a sustained series of pulses and can impair functioning of the underlying brain area over a longer period, stretching to several minutes after the end of stimulation. The precise way in which TMS affects neural functioning, however, remains unknown (Wassermann and Grafman, 1997): it induces activation in a focal area presumably by depolarizing the cell membranes there, but at the same time it impairs the normal functioning of the affected neurons. TMS is especially powerful when combined with other imaging techniques such as PET (Paus *et al.*, 1997), EEG (Ilmoniemi *et al.*, 1997) and fMRI (Terao *et al.*, 1998). This combination allows for the investigation of neural connection patterns by following the path of TMS-induced activation, and of the precise site of the TMS stimulation.

In summary, several methods for recording electrical activity and blood flow in the brain exist to unravel the relationship between behaviour and brain activity. While some of these methods, such as ERP and MEG, offer a very high temporal resolution with a low spatial resolution, others such as PET and fMRI have a high spatial and a lower temporal resolution. Combining two methods from different groups can give a high temporal and spatial accuracy in a single experiment. However, not all methods are suitable for studying young children: methods can be invasive or they are intimidating to an infant (like the noise and vibration of fMRI experiments), and therefore ERP and MEG seem to be the prime candidates for studies with young children.

3.1.3 Animal Studies

While invasive methods such as recording from cells and dyeing of cortical cells are not applied in the study of humans, they are commonly used with animals such as cats, monkeys, and rats (see also chapter 2). The results from these studies are then sometimes transferred to humans, but there are serious problems when they have been derived only from a single non-human species, because evolutionary differences between that species and humans might be ignored (Preuss, 1995). Better results can be achieved by comparing several evolutionary close relatives of humans and extrapolating from these studies to the human case. Such comparative studies have been encouraging. For example, recent research involving nine different mammalian species has shown that the schedule of human brain development can be mapped onto the maturational schedules of other species (Finlay and Darlington, 1995; Clancy, Darlington, and Finlay, in press). This is because the ordering and relative spacing of neural developmental events is very similar across all mammalian species, and the data from other mammals can be mapped onto the human developmental course with a nonlinear function. As a result, events that have not yet been observed in human development can be predicted from the animal data with considerable precision, and can then be correlated with observed changes in cognitive behaviour.

3.1.4 Impaired Processing

Specific lesions in the brain can lead to specific impairments in cognitive processing. It is therefore tempting to assume that the area affected by a lesion is responsible for the aspect of cognitive processing that is impaired. Similarly, some developmental disorders such as Specific Language Impairment (SLI) are claimed to lead to very specific impairment profiles and are therefore sometimes thought to impair an isolated functional module. The inference from impaired processing to the unimpaired brain has been very popular and historically influential. There are, however, serious problems associated with this view: it stems from an assumption that development is largely genetically determined with a unidirectional development from genes via brain structure to brain function. In this view of development, functional modules are predetermined and fixed and they can be selectively impaired even early in development.

However, another view of development that is more in line with constructivism stresses the bidirectional interactions between the levels of genes, brain structures, brain function, and experience (Gottlieb, 1992). In this view, an early lesion or a genetic disorder forms merely an additional constraint on the possible developmental outcome, and the mature system will therefore not correspond to the "normal" mature system minus the lesioned modules, but will be totally different from a system that developed without impairment. As a consequence it is more likely that deficits will never be entirely domain-specific, and, significantly, the seemingly intact functioning of a certain behaviour might be subserved by other cognitive processes than in the normal brain (Karmiloff-Smith, 1998).

Much of the evidence for the plasticity of the developing cortex has been reviewed in the previous chapter, and this evidence has been further backed up by studies of language development after early brain lesions (for a review see Bates, 1999). Children with early (before 6 months age) damage to one side of the brain usually seem to reach a level of language processing in the normal range (Lenneberg, 1967), although they display moderate to severe delays in reaching early language milestones (Bates, Thal, Finlay, and Clancy, in press). Significantly, unlike adults, children do not show a double dissociation between the two hemispheres: whereas adults with left hemisphere damage are usually more language impaired than with right hemisphere damage, in children no such difference in impairment can be observed.

Furthermore, even in normal development major reorganizations of brain areas occur. For example, in infants under 18 months of age, the difference in the brain's response to familiar and unfamiliar spoken words is bilateral with a slightly stronger response on the right. Only after this age a reorganization in the brain occurs and the response difference between familiar and unfamiliar words becomes stronger in the left hemisphere (Mills, Coffey-Corina, and Neville, 1997). This example is just one of several cases where cognitive functions in children seem to be subserved by different neural systems than in the adult.

The impaired-processing approach to understanding brain function is also problematic for the adult brain. Traditionally, double-dissociations have been used to identify brain regions that are responsible for a specific function: when a lesion in one area impairs a specific function A and not another function B, and when a lesion in a different area leads to the opposite profile, the assumption seemed plausible that functions A and B were subserved by two separate "modules" that could be independently impaired. However, more recent research (Shallice, 1988; Plaut, 1995) has shown that this inference cannot be made: double dissociations are possible without modules and can emerge from different lesions to a non-modular system. I will return to this point in the discussion of my simulations of agrammatic aphasia in chapter 6.

3.1.5 Modelling

Modelling, mainly with neural networks, is another possibility for generating hypotheses about the relationship between neural and cognitive development. The modelling approach was already discussed in section 1.3, and a new model of past tense acquisition and aphasic inflectional processing will be introduced in chapters 5 and 6. These models make empirically testable predictions about the types of representations that develop and the structures that support them.

3.1.6 Indirect Methods of Studying Cognitive Development

Because young infants cannot be verbally instructed or made to cooperate in experimental situations, several methods have been developed to analyze their response to stimuli These methods are based on the infants' natural tendency to attend to novel and interesting stimuli. In the *preferential looking* method, infants are presented with two different stimuli and the time they spend looking at each is recorded. A related method is *habituation*, where the same stimulus is presented repeatedly until the infant loses interest, which is marked by a reduction in the time it spends looking at it. Then, a novel stimulus is presented, and if the infant looks at this novel stimulus longer then it can be inferred that it can distinguish between the two stimuli. On the other hand, if looking time does not increase, the infant probably cannot distinguish the new from the old stimulus.

Other methods to establish an infant's response are to measure its sucking rate with sensors on a dummy (e.g. Williams and Golenski, 1979), or its heart rate (e.g. Casey and Richards, 1988). Both sucking rate and heart rate increase for a stimulus that is perceived as novel by the infant.

The *marker task* paradigm (Johnson, 1997) can be applied to link cognitive and brain development: this method is based on specific behavioural tasks that have been related to certain brain regions in adults and non-human primates with one or several of the methods described above. When infants are studied on the same behavioural task at different ages, it can be inferred how changes in performance relate to known aspects of brain development. However, the marker task is associated with similar problems as the inference from impairment to the normal brain: the developing brain undergoes significant reorganization, and different regions of the brain might be responsible for a specific behaviour at different ages.

3.2 Correlates of Brain and Cognitive Development

While the methods described in the previous sections allow for finding correlations between neural and cognitive activity, it is often very hard to establish a clear cause and effect relationship between the two. In some instances, however, the most plausible explanation of improved cognitive behaviour can be the development of the underlying neural substrates. One such area has already been alluded to in section 2.10 and concerns experiments with rats that are kept under varying environmental conditions, and the analysis of the effects these different environments can have on the brain. The most fundamental result of these studies is that rats that are kept in the Enriched Condition (EC) and the Acrobatic Condition (AC) develop bigger brains with more dendrites, spines, and synapses, whereas inactive (IC) or merely exercising (FX and VX) rats show no such effects. At the same time, EC and AC rats develop enhanced learning and problem solving abilities: in general, the more complicated the task, the more likely it is that EC rats perform better than EC or IC rats (reviewed in Rosenzweig, 1996). However, the precise relationship between learning and synaptic development remains unclear (Greenough *et al.*, 1987).

Moreover, in linking brain and cognitive development, it is generally very hard to time lock specific events in cognitive development with events in brain development. For example, nonlinear outcomes can arise from linearly progressing underlying events (Elman *et al.*, 1996), and therefore a sudden burst in cognitive competence that can be observed in many domains need not coincide with a nonlinear change in brain development. In fact, recent research has made it necessary to revise certain assumptions about neural events triggering specific behavioral events such as language development (Bates *et al.*, in press).

Despite these problems, significant progress has been made in relating brain and cognitive development in a new research area termed "Developmental Cognitive Neuroscience" (Johnson, 1993a, 1997).

3.2.1 The Case of Face Recognition

One area of research has been concerned with the neural basis for the development of face recognition in the infant (e.g. Johnson, 1997). This skill is interesting as an example of human perceptual abilities, and in contrast to language development it can also be investigated with other animals.

Research in face recognition has produced two seemingly conflicting types of results: infants as young as 10 minutes preferentially visually track face-like images as opposed to images with scrambled features or blank face outlines (Johnson and Morton, 1991). At the same time, however, investigations using static images and the preferential looking paradigm have failed to establish a difference between face-like and other patterns in the first 2 or 3 months of life, and have therefore suggested a gradual learning of facial features over the first few months of life (Johnson, Dziurawiec, Bartrip, and Morton, 1992).

Much of the neural evidence of face processing has come from studies of chick imprinting. Young chicks imprint the first salient moving stimulus and, after a few hours of exposure, develop a strong and robust preference for this stimulus over others. The brain region involved in imprinting is in the chick forebrain which is thought to correspond to human cortex. Interestingly, however, a lesioning of this area before or after training on an object leads to a severe impairment of imprinting preference only when the object does not resemble a mother hen. By contrast, if the object looks similar to a hen, imprinting is unaffected by the lesion (Davies, Horn, and McCabe, 1985). Further experiments have established that chicks seem to have an innate predisposition to attend to objects resembling a mother hen. These results led to the proposal that there are two independent brain systems that control imprinting in the chick (Horn, 1985; Johnson, Bolhuis, and Horn, 1985). The first system controls a predisposition of the chick to orient towards hen-like objects, and the second system acquires information about the objects to which the chick attends. Current evidence suggests that these two brain systems are independent from one another and that there seems to be no information exchange between them (Johnson, 1997).

The theory of chick imprinting has also been applied to infant face recognition, where evidence for a comparable development comes from studies of cortical development. These studies show that in the first 2 or 3 months of life, visually guided behaviour by the child is mainly controlled by subcortical structures (superior colliculus and pulvinar), and only later on cortical structures start to control sub-cortical processes (Johnson, 1997). At the same time, results from brain damaged patients and imaging studies indicate that in adults, face recognition seems to be largely dependent on cortical structures. The importance of the cortex for face recognition and the very early preference of infants for face-like stimuli can be reconciled by assuming two separate processes for face recognition in human infants as well. Johnson and Morton (1991) argued that the prespecified bias to orient to human-like faces, which is mediated by the sub-cortical visuo-motor pathway, biases the visual input to the developing cortical systems towards human faces and thus allows the gradual build up of cortical representations for facial features. When the cortical areas mature they begin to exert influence on the behaviour of the child, perhaps through inhibition of the earlier, subcortical systems. Evidence for this process is that visual tracking of faces in the infant sharply declines between 4 and 6 weeks after birth (Johnson, Dziurawiec, Ellis, and Morton, 1991), along with other reflex responses assumed to rely on subcortical circuits, which might indicate a developing cortical inhibition of subcortical processes.

Taken together, these results suggest a way in which different neural pathways might guide the development of face recognition, from an initial, subcortical bias to a later, developing construction of cortical representation for faces, and the behaviour displayed by infants is a consequence of the developmental state and the interactions of these pathways.

3.3 Starting Small

Several researchers have argued that the processing limitations of a young learner due to the immature neural systems can be actually beneficial to learning. This so-called

Less is More or *Starting Small* hypothesis is in contrast to the claim that a young learner is qualitatively the same as an adult and learning can be idealized as a jump from the initial to the final state (the *continuitiy hypothesis,* Pinker, 1984). Instead, it emphasizes the role of development for reaching the state of adult competence.

Turkewitz and Kenny (1982) argued that the development of perceptual organization is based on competition within and between different sensory domains, and that limitations of these systems serve to guide this competition. They argued that early competition is mainly within domains to reach a stable organization without interference from other domains. Once other domains have matured enough, this additional information leads to a perturbation in the Piagetean sense, resulting in the re-organization of the system to integrate the information from different domains.

Turkewitz and Kenny (1982) predicted that this process could be disrupted by either delaying the availability of sensory input in a certain domain, or by making information from other domains prematurely available. The normal case, where a certain domain is initially unavailable and then becomes available as development progresses, was claimed to be advantageous over both of these cases. Significantly, Turkewitz and Kenny claimed that the early unavailability of processing capacities constitutes an advantage over a situation in which they are available from the beginning. Turkewitz and Kenny (1982) speculated for example that it is beneficial for children to be able to focus visually only on a narrow range about 10 inches away from the eyes. This limitation might serve to filter out a visually overly complex world and might be needed to learn that the perceived size of objects shrinks with increasing distance. Most significantly, because young children only focus on things close enough to be touched or grasped, this limitation might be a prerequisite for the integration of different sensory modalities.

The first case of disruption of the normal starting-small development, which concerns the unavailability of sensory input from one domain and could therefore be termed "staying small", has been backed by investigations with congenitally deaf people. Neville and Lawson (1987a,b) investigated with ERPs the processes underlying visual attention to central and peripheral stimuli. They found that different pathways and mechanisms are involved in processing these different types of stimuli, and this result was backed empirically by an anatomical study of rhesus monkeys (Baizer, Ungerleider, and Desimone, 1991). When comparing the visual processing of hearing and congenitally deaf adults, Neville and Lawson found no difference for central stimuli. For peripheral stimuli, however, the deaf subjects showed a markedly stronger increase in the respective ERP response. At the same time, the deaf subjects showed a behavioural advantage over hearing subjects in that they were significantly faster to detect the direction of motion of peripheral targets. A control group, hearing subjects born to deaf parents who undergo much of the altered language experience of the deaf, showed responses like other hearing subjects and no elevated response to peripheral stimuli. Similarly, subjects who had become deaf after the age of 4 years did not display the effects of congenitally deaf subjects either (Neville and Lawson, 1987c). Neville and Lawson hypothesized that the changes observed in the congenitally deaf subjects were the results of compensatory hyperactivity of remaining sensory systems together with the functional reallocation of auditory and/or multimodal areas. As a consequence of auditory input not being available, the cortical areas that normally develop to process auditory input were partly taken over to process peripheral visual input, leading to a behavioural modification in deaf subjects.

Comparable results have been obtained by Cohen *et al.* (1997) in experiments with blind subjects. In people that have been blind from an early age, primary visual cortex can be activated by Braille reading and other tactile tasks (Sadato *et al.*, 1996). In order to examine the functional relevance of this activation, Cohen *et al.* transiently disrupted functioning through a TMS stimulation of the visual cortex. They found that this disruption induced errors in the identification of Braille and embossed Roman letters by the blind subjects, but the same stimulation had no effect on the same task in normal-sighted subjects. Instead, TMS stimulation of the visual cortex in sighted subjects disrupts their visual performance (Amassian *et al.*, 1989). The results of this study indicate that in blind people, visual cortex can take on a functional role in somatosensory processing, perhaps partly accounting for the superior abilities of blind people in this domain. This process might be based on the absence of inter-sensory competition at the relevant stage of neural development.

The second way in which the orderly process of inter-sensory competition can be disrupted is the premature availability of a sensory domain (Turkewitz and Kenny, 1982). This scenario, which could be termed "starting big", was investigated by Kenny and Turkewitz (1986) by prematurely opening the eyes of newborn rat pups. These experimental rats displayed a different homing behaviour from control rats when the home could be identified by visual cues: while control rats increased homing until Day 14 and then decreased, the experimental rats increased homing throughout the experimental period. When visual cues were removed and replaced with an odour trace instead, the experimental rats showed the same behaviour as the controls. These results indicate that a normal behavioural pattern can be disrupted by the premature availability of sensory information.

Other evidence for the Stating Small hypothesis has come from studies of language acquisition. Neville (1995) studied early and late learners of American Sign Language (ASL) and found that late learners did not have the same level of mastery as early learners. While this effect is often attributed to a biological, age-related critical period for language learning (e.g., Lenneberg, 1967) after which native competence can no longer be achieved, Neville argued instead for a "Less-is-More" hypothesis, claiming that the processing capacities of late learners were too advanced and that late learners therefore learned and stored signs as a whole. Early learners, by contrast, had limited processing capacities which forced them to break signs down into their components, increasing subsequently the ability to generalize to new situations by re-combining these components in different ways. This claim was backed by an analysis of the errors made by late learners: they used signs as they had been learned in a holistic, "frozen" way without adapting them to new situation. Further evidence for this hypothesis was established by Cochran, McDonald, and Parault (1999) who tried to counteract the "starting big" effect in adult learners by introducing an additional distraction task during the learning of ASL signs, or by alternatively forcing learners to break down the learned signs into their components by focusing on parts of each sign. They found that this procedure did indeed reduce the amount of "holistic" errors in comparison with control subjects, indicating that artificially limiting cognitive resources can have a similarly beneficial effect on learning as limited resources in young learners.

Modelling studies about "starting small" were done by Elman (1993) in a connectionist simulation: Elman trained a recurrent neural network (Elman, 1990) on sentences of a semi-artificial language comprising subject-verb agreement in number, different verb roles, and embedded sentences. When the recurrent network was trained with a full set of complex sentences from the outset it was unable to learn the task of predicting the next letter in the input sequence. The network did learn the task, however, when either the complexity of the sentences was gradually increased through training, or when the processing capabilities of the network were initially restricted (by resetting the recurrent connections at certain intervals) and this restriction was then gradually relaxed. Elman compared the increase of the network's processing power with a maturational increase of a child's memory span, arguing in line with Newport (1990) that an initial restricted memory span of the child was essential for acquiring a system as complex as natural language: the network/child would first learn basic distinctions between nouns, verbs, and relative pronouns, and singular and plural, which would otherwise be obscured by more complex structures, as a necessary basis for more difficult analyses of complex structures with embedded sentences. The processing restrictions were thus essential for focusing learning on the subset of facts that laid the foundations for future learning success. A more recent re-implementation of these experiments (Rohde and Plaut, 1999), however, failed to confirm Elman's results but instead found advantages in starting big. Rohde and Plaut argued that recurrent neural networks extract simple, short-range regularities before more complex ones even in the absence of initial processing limitations, and that Elman's (1993) results were an artifact of his simulation parameters. While Rohde and Plaut claimed that their results were evidence against a Starting Small hypothesis, it is unclear whether these arguments do not merely give evidence that recurrent neural networks are natural "small" learners and are thus not suitable as models of syntactic learning in adults.

Taken together, the results from early and late language learning and from the described animal experiments offer compelling evidence for a theory of learning where initial processing limitations are beneficial to the learner. They suggest that the time course of cortical development is paramount for allowing cognitive development in which a final stage of normal adult functioning is reached.

3.4 Piaget's Constructivism

One of the most important theories of cognitive development is without doubt Jean Piaget´s theory of constructivism (e.g., Piaget, 1937, 1980). Piaget was originally a biologist, and his theory of cognitive development is inspired by biological processes of ontogenetic adaptation to provide a biological explanation of knowledge. Piaget´s writings are known for being often very unclear and not making concessions to the reader, and furthermore, his theories developed and changed throughout his long career. A good overview of a later outline of his theories is (Piaget, 1980). Good secondary sources are (Boden, 1994) and (Glasersfeld, 1995).

Piaget recognized the study of development as essential for understanding the mature cognitive state. According to his theory, the child passes through a succession of certain developmental stages, each of which is built on top of the previous one. The child's knowledge is neither innate (as proposed in nativism) nor just passively recorded from the world (as claimed in empiricism), but is instead constructed through active interactions with the environment. This constructivist process can be described by two central terms: *assimilation* and *accommodation*.

Assimilation describes the integration of new knowledge into the existing cognitive frame. This does not mean, however, that the knowledge is merely recorded and stored; instead, every sensory input is always interpreted in terms of what is already known. It is obvious that at certain stages only certain knowledge can be assimilated: new information is represented as a variation of the old knowledge, and those aspects of the new information that do not fit into the present frame will be ignored.

When the child reacts to something that has been assimilated and expects a certain effect, this expectation might turn out to be wrong because the knowledge was inadequately represented in the current frame. This violation of expectations can take the form of surprise or disappointment, creating a *perturbation* that leads to the process of accommodation.

Accommodation involves the adaptation of the cognitive frame to new information in order to eliminate a perturbation. The original situation that led to the perturbation is re-analyzed and new, previously ignored features might be discovered that require an adjustment of the cognitive frame. Accommodation leads to a higher stage of intelligence where subsequently new, more complex information can be assimilated. It is important to note that accommodation is driven by violated expectations (i.e., perturbations) and not by unusual stimuli *per se*.

Assimilation can be considered as a process of generalization: new information is represented as a variation of what is already known, leading to the same reaction in the child. By contrast, accommodation is a process of specialization: a schema is broken down into sub-schemata, each of which then yields a different reaction. These two processes work in a circular way to reach ever higher cognitive stages, and the driving force behind this development is *equilibration*. Equilibration can be described as the motivation to eliminate perturbations to reach a stable state that yields a consistent idea of the world. In equilibration, the threat to the unity of the whole by splitting schemas into sub-schemas is weighed against the inability to represent distinctions, and schemas are therefore changed as little as possible, but as much as necessary to account for new information.

From his theory of cognitive development, Piaget predicted that every child passes through a certain series of developmental stages, and he and his collaborators designed many experiments to test and describe these stages. These experiments involve the concept of *object permanence* where the child learns that objects that disappear from view do not cease to exist; *conservation*, where the child learns that water poured from one glass into another one of a different size does not change its volume; *seriation*, which involves learning to sort a number of sticks according to length, and the *balance scale task*, where the child learns to predict the movement of a scale which has weights attached on both sides at different distances of the fulcrum.

Piaget maintained that the stages of increasing intelligence and abilities through which the child passes are not the realization of something innate but an authentic construction. What is innate are general learning mechanisms together with equilibration that drives learning. Assimilation and accommodation further require the innate ability to detect regularities and similarities, to remember previous experiences, and to judge the similarities.

Language is, according to Piaget, rooted in prelinguistic sensorimotor intelligence, ranging from birth to about 1.5 or two years of age: the child learns language structure by structuring objects, real or imaginary, in her environment.

Although Piaget's theory has been very influential, it is associated with many problems. Piaget never managed to formalize his proposed developmental mechanisms which led to a rejection of his theory by many (e.g., Piattelli-Palmarini, 1980, 1994). Furthermore, more recent research has shown that Piaget significantly underestimated the abilities of very young children, and that the detailed time scales he associated with each of his proposed stages are more flexible than he believed. For example, an infant recognizes certain linguistic properties such as her native language as opposed to other languages, speech rhythm and intonation very early in life, much before the end of the sensorimotor stage, and therefore this stage cannot be the prerequisite of some basics of language development.

However, the advent of neural network models that learn from experience and build internal representations has re-awakened interest in Piaget´s theories (e.g., Bates and Elman, 1993; Elman *et al.*, 1996), and recently, constructivist neural network models have been proposed as a formalization framework of these theories (Quartz, 1993; Quartz and Sejnowski, 1997; Mareschal and Shultz, 1996). This point will be discussed in more detail in the next chapter.

3.5 Chapter Summary

In this chapter I have reviewed the relationship between brain development and cognitive development. While it is difficult to establish a causal link between the two, several strands of research suggest such a link. One of them is concerned with direct studies of neural and cognitive functioning, and after reviewing methods of investigating this link I presented in more detail one exemplary theory of how neural development leads to cognitive changes, the case of face recognition. The next section presented evidence for the Starting Small hypothesis that emphasizes the importance of progressive neural development to reach adult competence, contradicting theories that see children as partly functional, but essentially equivalent to adults. This evidence comprises studies with congenitally deaf or blind human subjects that display an altered cortical organization, and animal studies in which the eyes of rat pups are prematurely opened, leading to abnormal homing behaviour. The chapter closed with the outline of Piaget's theory of constructivist development that equally stresses the importance of development in constructing an adult mind.

Chapter 4

Constructivist Modelling

The characteristics of a learning algorithm can be viewed from a theoretical basis: what is the time complexity of a specific algorithm? What assumptions have to be made *a priori* to make learning feasible in a certain system? How can learning be characterized in principle? These questions have also been addressed with respect to constructivist neural networks, and one result has been that such algorithms are fundamentally different from fixed-architecture systems and that they can overcome some of the latter's principled limitations. In the rest of this chapter, a general theory of learning, inductive inference, is described (section 4.1). This theory has been applied to explain human learning, which has led to certain strong assumptions about what and how humans can learn in principle (section 4.2). A successful formalization of constructivist learning has provided an alternative theory of human learning that is more powerful and does not rely on these strong assumptions (section 4.3). Empirically, the characteristics of constructivist algorithms can be studied in neural network algorithms in which learning involves structural change, and section 4.5 develops a taxonomy of such algorithms as currently exist. The new constructivist neural network algorithm that I developed for the simulation experiments in this thesis is described in section 4.6. Finally, section 4.7 gives a brief overview of previous models of cognitive development that were developed on the basis of another constructivist neural network algorithm, cascade correlation.

4.1 Inductive Inference

The dominant formal theory of learning is learning by induction, or *inductive inference* (e.g., Shavlik, 1990). In this theory the learner is presented with a set of classified examples, and the goal is to identify the nature of each class and to assign new, unclassified examples to one of the learned classes. Examples are sets of feature attributes together with the class labels, e.g., ("feathers, two legs, beak", "bird") for the class *bird*, or ("bring", "brought") for the class *past tense of bring*. This type of learning is also called *concept learning* because all examples of a certain class can be said to form the concept of that class.

Formally, learning by induction consists of inferring a function f that maps a datum to a class, based on a set of examples x_i that are labelled as belonging to a certain class, i.e., $(x_i, f(x_i))$. The possible functions, or *hypotheses*, are assumed to be from a finite or infinite *hypothesis space*. Inductive inference is seen as a search through this hypothesis space, where hypotheses that are incompatible with the encountered examples are rejected until, in the ideal and non-infinite case, the only remaining hypothesis is the correct one (see e.g. the candidate elimination algorithm, Mitchell, 1982).[1]

4.1.1 The Need for Bias

In its simplest case, the search through the hypothesis space is random. It is clear, however, that this search strategy is infeasible: in an infinite hypothesis space the probability of finding the correct hypothesis tends towards zero. Therefore, some sort of *a priori* restriction has to be put on the hypothesis space or the search algorithm, or both (Blumer, Ehrenfeucht, Haussler, and Warmuth, 1988). Such restrictions are called the *bias* of the learner, and there are two kinds of biases: a *restricted hypothesis space bias* and a *preference bias*.

A restricted hypothesis space bias (RHSB) restricts the size of the hypothesis space by excluding *a priori* certain hypotheses from being considered by the learner. In a hypothesis space defined by logical conjunctions, for example, hypotheses containing a logical *or* could be excluded. In neural network learning, the number of hidden units restricts the possible functions that can in principle be learned: for example, without any hidden units, the network is restricted to the learning of linearly separable functions. The danger in introducing an RHSB into a system is of course that it might exclude the correct hypothesis. In this case, the learner will never succeed, and it will not even necessarily find a best approximation to the correct function. For example, when a single-layer perceptron is trained on a non-linearly separable problem with the standard perceptron learning algorithm, its weights do not converge but oscillate. Therefore, in introducing an RHSB the nature of the target hypothesis has to be anticipated, which is often not possible.

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[1] This algorithm was already formulated by Conan Doyle (1890), where Sherlock Holmes tells Watson: "How often have I said to you that when you have eliminated the impossible, whatever remains, however improbable, must be the truth?"

A preference bias (PB) introduces an ordering over all hypotheses in the hypothesis space, and the learner chooses the most preferred (often, the simplest) hypothesis that is consistent with the data. This is the well-known principle of *Occam's Razor*. The problem here is that a PB does not necessarily give a time benefit in learning. For example, if the PB prefers short hypotheses, whenever the learner chooses a certain hypothesis it has to make sure that there are no shorter hypotheses available that are also consistent with the data. To avoid this prohibitive search for shorter hypotheses, often the preference ordering is achieved with heuristic procedures (Shavlik, 1990), or more complex hypothesis are constructed on the basis of the currently preferred simpler one. In neural network learning there is no *a priori* global preference bias, but a partial ordering is achieved through the learning algorithm, e.g., gradient descent. Here, each new hypothesis is only a slight modification of the previous one, resulting from the gradual adjustment of the weights.

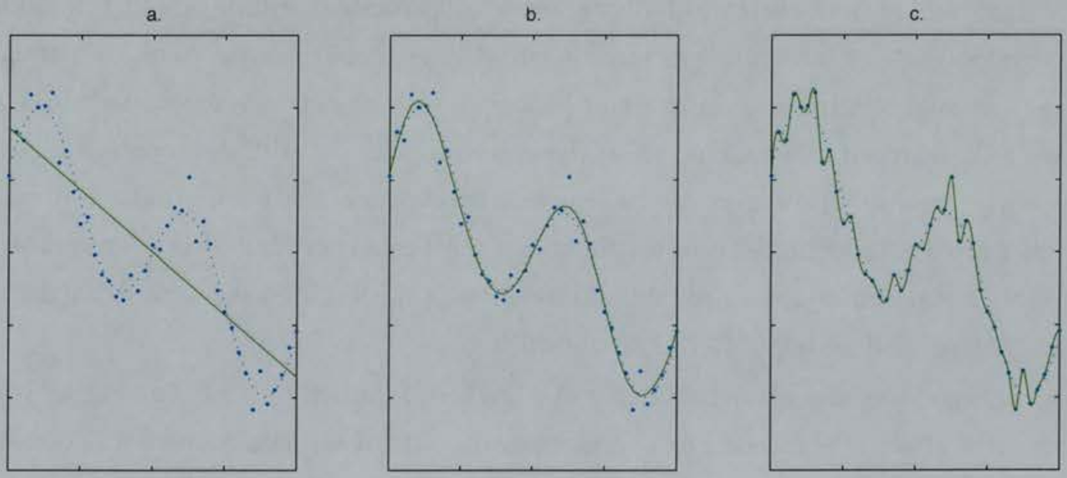

Figure 4.1: Effects of different bias on the modelling of a function sampled from noisy data. The function (dotted lines) is sampled with Gaussian noise (points) and modelled by three different functions (solid lines). a.: the bias is too strong, restricting the class of models to linear functions. The data cannot be faithfully represented. b.: The bias is well-chosen and the model gives a good approximation of the original function. c.: the bias is too weak and the model overfits, leading to poor generalization.

Another reason for introducing bias into a learner is noisy training data. In this case, an assumption (i.e., bias) has to be made about the function from which the data is sampled, to reach a trade-off between modelling the original function and modelling the noisy data. Figure 4.1 shows an example of modelling a function that is sampled with Gaussian noise. In fig. 4.1a., the bias is too strong in that only linear functions can be learned, and therefore the data cannot be represented faithfully. Fig. 4.1b. shows a good choice of bias for the given data set and the modelled function is close to the original. In fig. 4.1c. the model is too unrestricted and *overfits* the data by modelling the noise, which leads to poor generalization abilities.

4.1.1.1 The Bias/Variance Dilemma

Since a bias excludes many hypotheses from needing to be tested, learning in a more biased learner requires less data to succeed than a less biased learner. For example, a learner that is restricted to linear functions needs only two data items to determine the particular function. However, a strong bias comes at the expense of possibly excluding the target hypothesis. In a less biased learner the chance to exclude the target hypothesis becomes smaller, but many more hypotheses will be consistent with a data set and thus more examples are needed to find the correct one. This trade-off is called the *bias/variance dilemma* (Geman, Bienenstock, and Doursat, 1992).

In neural network learning, solving the bias/variance dilemma amounts to finding an appropriate architecture, or more specifically, a suitable number of hidden units for the network. With a low number of hidden units the network has a high bias and can only learn simple functions. In the extreme case of no hidden units at all, only linearly separable functions can be learned. By contrast, with many hidden units the bias decreases and more complex functions can be learned, but at the same time the number of parameters (weights) that have to be adjusted increases, requiring a larger training set and perhaps leading to overfitting.

Bias and variance in neural networks can be quantified in the following way (Geman *et al.*, 1992): the hypothesis space can be thought of as containing all functions that a neural network with a given architecture can in principle learn. Based on different samples from the function to be approximated, different functions will be generated. The network bias is then the average Euclidean distance between the generated functions and the target function in the hypothesis space. The network variance on the other hand is the average Euclidean distance from any learned function to any other. Network bias thus describes how different the learned approximations are from the target function, whereas the variance describes the "variety" of approximations that can be learned. This quantification shows that a bias is always defined in terms of the target function, and therefore a "weak" bias (e.g., 50 hidden units in a neural network) might still be "high" independent of the variance in that it excludes the target function (which might require 60 hidden units to be computed). On the other hand, a "strong" bias (e.g., no hidden units at all) can be "low" if the target function is simple (i.e., linearly separable), and in this case variance will also be low. In the general case, however, there is a trade-off between bias and variance. The network error can then be decomposed into a bias and a variance component (Geman *et al.*, 1992), and the goal is to reduce both components.

4.2 Human Learning as Inductive Inference

Considering human learning as a form of inductive inference has led to a number of strong claims about innate knowledge that have dominated especially the field of language acquisition research for many years. Two main problems have to be addressed in human inductive inference: how does the learner know that the current hypothesis is not overly general? And where do the hypotheses come from?

4.2.1 Overly General Hypotheses

A problem faced by a general inductive learner that learns one class from positive data only (i.e., from data labelled as belonging to this class) is when to know that the correct hypothesis has been found. As discussed before, the learner chooses a new hypothesis and rejects it if data is encountered that is inconsistent with this hypothesis. But what happens if the learner settles on a hypothesis that is too general for the data? With positive data only, a hypothesis like "Every possible data item belongs to this class" will never be disproved. There are only two ways out of this problem: either, *negative* data has to be provided that is labelled as *not* belonging to the class (or as belonging to another class if multiple classes exist), or the learner has to be biased in a way to *a priori* exclude overly general hypotheses.

This insight has had fundamental implications for theories of child language acquisition. Here, the child has to learn only one class, the correct grammar of her language. The data consist of the utterances heard by the child, and all of them are implicitly taken to be grammatically correct, that is, they all constitute positive examples. However, it has been claimed that grammars as complex as those for natural languages cannot be learned based on positive examples alone by a general inductive learner (Gold, 1967). Since empirical data suggest that negative evidence, i.e., corrections of wrong utterances by the parents, are generally not available to the child (Marcus, 1993), the child is claimed to need an innate bias that restricts the class of grammars she can learn. This innate bias is the *Universal Grammar* postulated by Chomsky (1965). Chomsky (1980) formulated the problem of language acquisition in terms of an inductive learner: the child's initial hypothesis space, S_0, is genetically restricted to contain precisely all possible human languages. Language acquisition consists in using some relevant experience E to test a succession of grammars $S_1, S_2, S_3, \ldots$, until a steady state S_s is reached which corresponds to the adult competence. The interest of the linguist lies in determining the nature of the initial state S_0, which can be derived from studying E and S_s: those aspects of the final state S_s that cannot be derived from the experience E must be predetermined in S_0. Chomsky's conclusion was that the initial state S_0 must contain certain very specific linguistic knowledge such as the structure dependence of rules and knowledge about bound anaphora as well as general elements of semantics, phonetics, and phonology.

4.2.2 Fodor's Paradox

Fodor (1975, 1980) used the properties of a general inductive learner to argue directly against Piaget's constructivist position. His argument was that it is theoretically impossible to learn more complex concepts or representations than those initially present in a system's hypothesis space. Therefore even the most complex representations would have to be innate instead of being constructed by the learner, thus undermining Piaget's constructivist theory.

Fodor argued that since the initial hypothesis space must already contain the target hypothesis, nothing new can in principle be learned. Instead of learning, one should therefore speak of a *fixation of belief*, that is, the settling on one of the pre-defined hypotheses. In this way, everything that can be learned in principle must be innate—the learner just "discovers" a more complex hypothesis instead of constructing it on the basis of simpler ones. This view has been taken further to call for the abandonment of the notion of "learning" (Piattelli-Palmarini, 1994). In particular, Piaget's notion of constructing new, more complex hypotheses on the basis of other, simpler ones, was thought to be untenable.

4.3 A Formalization of Constructivist Learning

The problems faced by an inductive learner that have been outlined in the previous section all stem from the basic assumption that the hypothesis space is predetermined, static, and external to the learner. On the other hand, Piaget's constructivist theory, which postulated a stage-wise construction of the hypothesis space, was not formalized and thus under-specified.

More recently, however, constructivist learning has been formalized on the basis of neural network learning (Quartz, 1993). This formalization is made in the framework of the probabilistic *PAC*-learning (Valiant, 1984) which has become the standard model of inductive inference in machine learning (e.g. Dietterich, 1990) and which will be outlined here briefly.

PAC learning is, in contrast to the general inductive learner (Gold, 1967), not concerned with what type of functions are in principle learnable, but which problems are learnable in feasible (i.e., polynomial) time from a restricted class of representations. Further, the definition of learning is fundamentally different in the PAC framework. Instead of finding, after an arbitrary amount of time, a hypothesis that correctly classifies all data, PAC learning sacrifices correctness for feasible learning time: a concept is learned when the algorithm constructs with the probability $1 - \delta$ a hypothesis g from a restricted hypothesis space G so that with probability $1 - \epsilon$, g classifies all examples correctly. δ is called the *confidence parameter* and ϵ the *error parameter*. What the learner does is thus to probably find a hypothesis that classifies the examples approximately correctly. Hence the name: Probably Approximately Correct (PAC) learning.

How can the PAC framework be applied to learning in neural networks? The initial network architecture $\mathcal{G}$ can be identified with the initial restricted hypothesis space G in PAC learning (Baum and Haussler, 1989): the network architecture is defined by its fixed connectivity pattern together with a set of functions F_i that each node i can in principle compute. This initial architecture of the network allows only for a certain set of hypotheses to be computed and corresponds therefore to the restricted initial hypothesis space. Learning in the network corresponds to eliminating hypotheses from this space: through an error-correcting measure (such as the δ-rule for weight adaptation, Widrow and Hoff, 1960; Rumelhart *et al.*, 1986b) the network adjusts its free parameters and settles on a particular architecture with specific weights (computing a particular function) which can then be defined by its connectivity and the specific functions $f_1, f_2, \ldots, f_n$ computed by the nodes $1 \ldots n$. This final architecture (with the associated function that is computed in it) corresponds to a specific hypothesis g from the initial space G. Structure and function in neural networks are therefore closely related, making them attractive for the investigation of general learning properties.

A fixed-architecture network restricts the space of hypotheses that it can compute. Its architecture constitutes a bias in the sense discussed above: in designing the network architecture, the possible solution space for a certain task has to be taken into consideration. This is usually done by choosing different numbers of hidden units through trial-and-error and then using the architecture that yields the best results: with too few hidden units the network has a strong bias that can prevent it from learning the target function, and too many hidden units will lead to overfitting of noisy data and poor generalization.

In order to overcome the limitations introduced by an *a priori* fixed hypothesis space, a neural network (or any learner) can allow for an increase of the initial hypothesis space and thus adjust its bias in a problem-specific way to become able to represent hypotheses that were not part of the initial space. For neural networks, with their equivalence between structure and hypothesis space, this means that they have to allow for modifications of their structure as a function of learning. Such *constructivist neural networks* start with no or very few hidden units and add units as learning progresses.

With no hidden units, a constructivist neural network has a high bias and is therefore limited in the types of functions it can learn. Through the gradual addition of hidden units while more data is encountered, the bias weakens in a way that is appropriate for the target function. It has been shown that a gradual weakening of the bias, where the learner does not pick up the idiosyncrasies of the data, can avoid the bias/variance dilemma and decrease variance simultaneously (White, 1990). In this way, the bias will become designed for the problem at hand and will therefore not exclude the correct hypothesis, at the same time avoiding the search through areas of the solution space that are far removed from the target function. In this way, constructivist neural networks effectively conflate the restricted hypothesis space bias and the preference bias: between node insertions, the network's hypothesis space is fixed and is searched by adapting the connection weights. When a new unit is inserted, the hypothesis space is increased to include more complex hypotheses that require the extra unit to be represented, and the RHSB is relaxed. Because units are inserted one after another, this imposes a preference bias to test simpler hypotheses (that require fewer hidden units) first.

For a constructivist learning theory to be plausible these structural modifications must be based on general principles as a function of learning and not be motivated by the specific task to be learned. Otherwise, an arbitrary process might transform the learner into the target state and trivialize the explanation of learning (Pinker, 1984).

This view of learning shifts the emphasis away from searching through a set of hypotheses to finding the representations on which hypotheses can be constructed. It has been shown that networks that add structure while they learn are *complete representations*, i.e., they are capable of learning in polynomial time any problem that can be learned by any other algorithm in polynomial time (Baum, 1989). By contrast, training a fixed size network is NP-complete[2] (Judd, 1988), even when it has as little as three hidden units (Blum and Rivest, 1988). Therefore, constructivist neural networks are not only attractive from a learning theoretic point of view but should also display good practical properties.

These learning theoretic results also shed a different light on human learning: innate knowledge needs to be presupposed only if a static hypothesis space is assumed. By contrast, when learning is viewed as constructivist, the hypothesis space grows and enables the learner to construct more complex hypotheses on the basis of simpler ones, corresponding to the developmental theory of Piaget (1980). In chapter 2 I reviewed how the human cortex develops in an activity-dependent, constructivist way. Neural measures of representational complexity have been considered by Quartz and Sejnowski (1997) who argued that the degree of dendritic arborization constitutes such a measure. The reasons to choose dendritic development as a measure of representational complexity are that dendritic growth introduces only localized changes into the overall system (*locality*), and that the local changes do not undo previous learning (*stability*). Dendritic growth is significantly more protracted than axonal growth and continues throughout life. The development of dendritic trees in the cortex thus addresses the core problem facing a learner: that of developing representations suitable for learning a task. Constructivist learning thus satisfies both neurobiological and learning theoretic constraints and can offer a powerful model for human learning and development.

4.4 The Argument for Constructivist Models of Cognitive Development

Chapter 2 reviewed evidence that the cortex develops in many parts in a constructivist way and builds structures based on sensory experience. Chapter 3 related brain development to cognitive development, showing how changes in cortical structure correlate with cognitive change and how initial limitations of processing capacities might be an important prerequisite to successful learning in the child. Taken together, these results give evidence for constructivist theories of cognitive development. Finally, in this chapter it was argued that constructivist learning systems are fundamentally different from static systems. Therefore, the constructivist aspect of cognitive development might be central, and by abstracting it away in models of cognitive development they

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[2] An NP-complete problem belongs to the class of the most complex problems that cannot be solved in polynomial time; these problems are therefore considered to be computationally intractable.

might miss an essential aspect of what they aim to model. Models of cognitive development that are based on fixed-architecture neural networks can offer new insights into processes of associative learning based on distributed representations and can inform further research in human development (see e.g. Seidenberg, 1994), but it has been shown (Quartz, 1993) that such models, contrary to common arguments (e.g. Chater and Oaksford, 1990) do not offer an alternative to nativist theories of development. Rather, they serve as an illustration of such theories and of the problems faced by static learners. Constructivist neural network models on the other hand combine associative learning based on distributed representations with a plausible learning process that allows them to develop an architecture appropriate for the learning task, avoiding the necessity to choose an arbitrary architecture corresponding to innate knowledge. It is therefore a promising direction of research to model developmental processes in constructivist neural networks.

The following section gives an overview of constructivist neural network algorithms and develops a taxonomy for them. Section 4.6 then describes the new algorithm that was developed for the cognitive simulations in chapters 5 and 6.

Another group of networks that change their architecture during or after learning and that are often reviewed in connection with constructivist networks (e.g. Ash and Cottrell, 1995; Quinlan, 1998) are *selectionist* networks. These networks delete connections or units from an initially pre-specified architecture, often to improve generalization ability. But since they do not solve the problem of a pre-specified hypothesis space and do not allow for a problem-dependent weakening of the restricted hypothesis space bias which is fundamental here, they will not be discussed further.

4.5 Constructivist Neural Network Algorithms

The motivation for developing constructivist (or constructive, or generative) neural network algorithms has mainly come from practical problems associated with fixed architecture networks. As discussed in the previous sections, the choice of the correct number of hidden units for a multi-layer perceptron is crucial but has to be established on a trial-and-error basis. Further, the time necessary to train fixed-architecture networks is often prohibitive. One reason for this is that in a big network, many parameters (weights) have to be adjusted requiring a lot of training data. Another reason is the "herd effect" (Fahlman and Lebiere, 1990a): due to the error reduction algorithm, all hidden units will often try to correct each error and long training is necessary before different units start to specialize on sub-problems. Finally, for the backpropagation and other related algorithms, convergence cannot be proved and they might get stuck in so-called *local minima*, never finding a good solution to a problem.

Constructivist algorithms come in many flavours, but common to most of them is a repeated two-stage learning process: the network is trained with some error-reduction algorithm in the current architecture. When the network error no longer decreases, an architectural modification, i.e., insertion of one or several units, is made, and training continues with the new architecture.

The following sections develop a taxonomy of constructivist neural network algorithms.

4.5.1 Perceptron-based Algorithms

The most common perceptron-based constructivist algorithms are restricted to one output unit and to binary (0 and 1) or bipolar (-1 and +1) input/output values. They perform a classification of the inputs into two classes. This well-defined task has allowed for theoretical proofs of their convergence which is an advantage over the other types of constructivist algorithms that are described in later sections.

The well-known restriction of perceptrons, i.e., networks without a hidden layer, is that they can only learn linearly separable problems (Minsky and Papert, 1969). A perceptron implements a straight decision boundary in the input space, and training its weights corresponds to adjusting this straight boundary so that the inputs requiring the output 0 (or -1 in the bipolar case) get separated from those requiring the output 1. Convergence of the perceptron training algorithm is guaranteed if the learning problem is linearly separable (Minsky and Papert, 1969), but for non linearly separable problems like the famous XOR, a stable weight-setting cannot be found and the weights oscillate. Several alternative algorithms have been developed to lead to a stabilization of the weights for non linearly separable problems, most notably the Pocket algorithm (Gallant, 1990) and the Thermal Perceptron (Frean, 1992). These algorithms are often used in training perceptron-based constructivist networks.

Constructivist perceptron-based algorithms build one or more hidden layers and thus allow the network to solve even non linearly separable problems. There are in principle two ways of doing this: re-representing the data so that it becomes linearly separable, and constructing non-linear decision boundaries from linear segments.

4.5.1.1 Input Re-Representation

The first class of algorithms re-represents the input in the constructed hidden units in such a way that the problem becomes linearly separable. In this case the hidden layer can be viewed as the new input to a conventional perceptron that is built on top of it. In these types of algorithms, each layer has connections only to the layer directly beneath it. Examples of this type of algorithm are the Tiling (Mézard and Nadal, 1989), Sequential (Marchand, Golea, and Ruán, 1990), and Higher-Order Network (HON) (Redding, Kowalczyk, and Downs, 1993) algorithms, all of which differ in the way in which they re-represent the input data. In the Tiling algorithm, a hierarchy of hidden layers is constructed so that all patterns belonging to the same class have identical hidden representations. From these hidden representations the desired output can then be learned with the perceptron algorithm. The Sequential algorithm builds a single hidden layer by removing all those inputs from the training set that are classified correctly by the network and adding hidden units until all inputs have been accounted for. The HON algorithm adds hidden units that compute linear combinations of the inputs until they become linearly separable, and in a second step converts the resulting HON into a simple feed-forward network, minimizing the fan-in of hidden units.

4.5.1.2 Decision-Boundary Construction

The second way of solving the problem of non-linear separability is to enable the network to learn a non-straight decision boundary, and this approach is taken, for example, in the Tower, Pyramid (Gallant, 1990) and Upstart (Frean, 1990) algorithms. In these algorithms, the output unit always sees the original input, but the construction process inserts additional units that enhance the output in such a way that decision boundaries can be constructed as a combination of straight elements. In the Tower and Pyramid algorithms, a new unit is added on top of the single output unit and connected to the input layer and the immediately preceding (Tower) or all preceding (Pyramid) units. The Upstart algorithm tries to classify as many inputs as possible into two classes, and then adds units that are trained to compensate for the two types of error made by each unit ("wrongly positive" or "wrongly negative"). The trained units are then inserted into the network with weights big enough to override the original mis-classification. The precise nature of the non-linear decision boundaries generated by the Tower, Pyramid, and Upstart algorithms is analyzed in (Chen *et al.*, 1995).

All of these perceptron-based algorithms can be shown to converge in principle. The convergence proofs are based on showing that each unit insertion improves the classification accuracy of the network by at least one data item. More recently, these convergence proofs have been extended to multi-category, real-valued versions of the described algorithms (Parekh, Yang, and Honovar, 1995, 1997a,b; Yang, Parekh, and Honovar, 1996).

4.5.2 Error-Modelling Algorithms

A second class of constructivist neural network algorithms can be called *error-modelling* because they insert hidden units that are trained to minimize an objective error function, independent from the input data. These algorithms are based on multilayer perceptrons that are trained with the backpropagation (Rumelhart *et al.*, 1986a) or quickprop (Fahlman, 1989) algorithms. The network is trained until error reduction stagnates, and a new unit is inserted to reduce the residual error. In the simplest case, like Dynamic Node Creation (Ash, 1989) and Constructive Backpropagation (Hirose, Yamashita, and Hijyta, 1991), a new unit is inserted into the single hidden layer of a backpropagation network and the whole network is retrained to reduce the sum squared error. Despite their simplicity, these networks have been shown to converge faster than fixed-architecture networks, and Hirose *et al.*'s (1991) algorithm includes a pruning stage after the network has converged to find a minimal architecture. However, generalization abilities were not tested in these networks.

4.5.2.1 Cascade Correlation

The other side of the spectrum is taken by the best-known constructivist algorithm, Cascade Correlation (Fahlman and Lebiere, 1990a,b), and this algorithm has been applied to the modelling of cognitive development (see section 4.7). In the Cascade Correlation algorithm, the network starts out with just the input and the output units that are fully interconnected. Training is divided into two phases: in the *output phase*, where only the weights leading to output units are adjusted (with the quickprop algorithm, a faster alternative to backpropagation, Fahlman, 1989), the network is trained on the data until the error reduction stagnates and an improvement is no longer possible within the current architecture. In the following *input phase*, a pool of hidden units that are only connected to the input units and any previously inserted hidden units are trained to maximize the covariance of their activation with the remaining network error. When these correlations no longer increase, the one unit with the highest correlation is inserted into the network as a new hidden layer, and the input weights to this unit are frozen. The unit is then fully connected to the output. With this new architecture, the network enters once more the output phase and training continues. Since each new hidden unit receives input both from the input units and from previously added hidden units, the network can build representations with ever increasing complexity on top of each other. Benchmark tests performed with Cascade Correlation showed a significant improvement in speed and generalization capability over backpropagation in certain classification tasks. Fahlman and Lebiere (1990b) argued that this improvement was due to having a single unit in each hidden layer, avoiding the "herd effect" where all units simultaneously change their weights to solve the same problem, and to the freezing of the input weights which ensured that the newly inserted hidden unit remained a "feature detector" for those aspects of the error that dominated at the time of its insertion.

Straightforward extensions of Cascade Correlation have been developed, e.g., FlexNet (Mohraz and Protzel, 1996), which allow the insertion of multiple units in multiple hidden layers of the network and do not freeze the input weights. These variations improve the benchmark performance, albeit at the expense of running time. Fujita (1992) introduced a correlation function that took the interdependence of hidden unit activations into account and achieved smaller network architectures at the expense of longer running times.

An analysis of the Cascade Correlation algorithm (Hwang, You, Lay, and Jou, 1996) showed, however, that it is not well suited for smooth interpolation in regression problems. This is due to two problems: first, higher order hidden units have a higher fan-in than lower ones (since they receive input from the input layer as well as from all lower hidden units), yet they use the same fixed activation function. Second, the correlation criterion for candidate nodes pushes them into their saturation region, resulting in a zigzag decision boundary.

4.5.3 Data-Modelling Algorithms

The third group of constructivist network algorithms can be called *data-modelling* algorithms, because they build a representation of the data space in the hidden layer and use this representation to produce the output. Algorithms from this class might be the most interesting ones because they use principles that can be argued to be biologically plausible such as *receptive fields* that respond only to a small region of the input space. Furthermore, building the representation of the input space can in principle be done in an unsupervised way and these algorithms show how aspects of supervised and unsupervised learning can be combined.

A general principle underlying many of the data-modelling algorithms is the initial assumption that similar inputs lead to similar outputs, and the constructivist process is used to account for exceptions to this assumption.

Data-modelling networks are often based on *Radial Basis Function* (RBF) networks (Moody and Darken, 1989). In contrast to multi-layer perceptrons with a logistic threshold function, RBF networks have a hidden layer of units with *Gaussian* activation functions that respond to inputs within a certain region as opposed to inputs above a threshold (fig. 4.2). The hidden units cover the whole input space and the output is produced based on the activations of the hidden units. Problems facing RBF networks are (a) the question of how many hidden units to use and (b) where to place them in the input space. When two similar inputs are covered by the same receptive field, they will produce a similar output, but this is not always desired. The constructivist algorithms discussed in this section offer various solutions to the questions of number and placement of the hidden units.

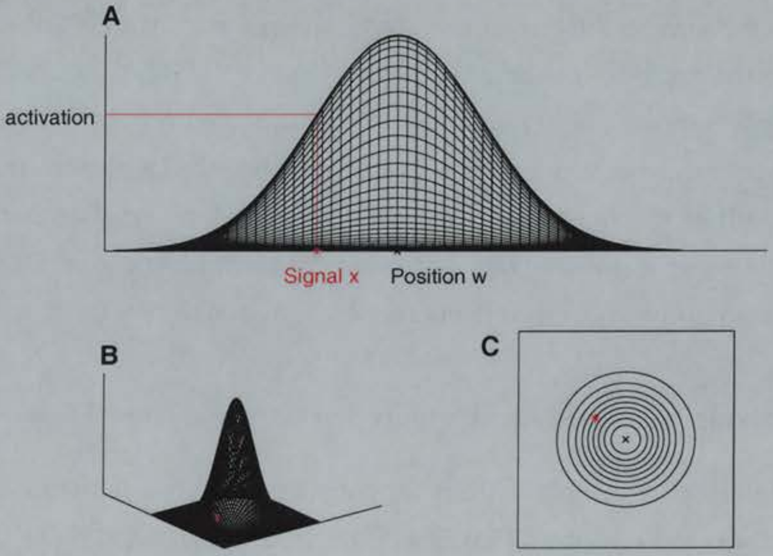

Figure 4.2: A three-dimensional Gaussian activation function that acts as a receptive field to nearby inputs. A. Viewed from the side with a signal activating the receptive field. B. Three-dimensional view, C. Viewed from the top.

The GAL network (Alpaydin, 1991) implements what is basically a nearest-neighbour algorithm for the classification of input patterns: when an input does not belong to the same class as the inputs covered by its nearest hidden unit, a new unit is inserted for this input. Since the construction of the hidden layer depends substantially on the order of presentation, the network also has a dream state: an exemplar unit is activated randomly, and the input pattern is re-created. Then this exemplar unit is disabled, and if the network still responds with the correct class, it is deleted.

A different approach is taken in the Node-Splitting algorithm (Wynne-Jones, 1993): here, the hidden layer is grown by splitting existing nodes, and the criterion for splitting is the degree of oscillation of weight updates. The idea here is that an oscillating unit is used for conflicting purposes and could benefit from splitting. The algorithm works well with Gaussian activation functions.

The Resource-Allocating Network (RAN, Platt, 1991) constructs the hidden layer of an RBF network based on the principle that new units are allocated for unusual patterns. Unusualness is defined by two criteria: the current input has to be dissimilar from other inputs, and it also has to create a high output error. The distance that an input must have from its nearest unit to qualify for insertion of a new unit is shrunk (exponentially) during the course of training, the idea being that the network initially learns the global easy mappings, while local exceptions are learned as the distance limit shrinks. The RAN also adjusts the centres of the Gaussian units in a way so that units that decrease the error for an input are pulled towards this input and units that increase the error are pushed away. Problems of the RAN are that it can produce too many units for noisy data, leading to overfitting. Another problem is the setting of the parameters, especially of the minimal distance that a pattern may have to another while still being treated as an exception. Everything smaller that the minimum distance will be generalized away. The latter problem has been addressed in a probabilistic version of the algorithm (Roberts and Tarassenko, 1994).

4.5.3.1 Growing Neural Gas and Supervised Growing Neural Gas

Two related very effective algorithms for constructing a hidden layer of Gaussian receptive fields are the Growing Cell Structures (GCS) (Fritzke, 1994b) and Supervised Growing Neural Gas (SGNG) (Fritzke, 1994a, 1995). SGNG is based on an unsupervised algorithm, Growing Neural Gas (Fritzke, 1995), a constructivist version of the Neural Gas algorithm (Martinez and Schulten, 1991) that learns the topology of the input space by constructing a layer of prototype units. The GNG network starts with two hidden units. When a data item is presented, the closest prototype unit together with its (topologically defined) neighbours are moved towards the data. This movement ensures that units are actually placed in those regions of the input space where data actually occurs. Then, the distance from the closest (winning) unit to the data item is added onto a local error counter of the winning unit. At regular intervals, new units are inserted between the unit with the highest local error and its highest-error topological neighbour. The idea here is that a unit which is responsible for a large area of the data space will accumulate a high error because it is the nearest unit for far away inputs, and will therefore become the preferential location for the insertion of new units. Similarly, a unit in a very dense area of the data space will accumulate error through a high number of short distances to the data items for which it is the winner, and more units will thus be inserted in such a region as well. With this algorithm, the network architecture comes to faithfully represent the distribution and density of the data items. A problem of the GNG algorithm that it shares with all unsupervised constructivist algorithms is that it potentially grows forever and will eventually allocate one unit for each data item. Possible stopping criteria are a maximum number of units, or a maximum distance from any data item to its nearest unit.

The SGNG algorithm (Fritzke, 1994a) is a straightforward extension to GNG. It works in a supervised way where the constructed GNG layer becomes the hidden layer of a radial basis function network. Each hidden unit is therefore associated with a Gaussian activation function whose width is determined by the average distance to its neighbours. In this way, the receptive fields generated by the Gaussian units partially overlap and cover the whole of the input space.

For the SGNG, the unsupervised GNG algorithm is modified so that the local error of the hidden units is no longer determined by their distance to the input data, but by their contribution to the output error. Therefore, a hidden unit whose activation leads to a high output error will become the preferred location for the insertion of new units. This is the case when similar input data, activating the same hidden unit, require different outputs which therefore cannot be learned by weight adaptation alone. Then, hidden units will be inserted in this region, partitioning the input space to account for the different outputs. A restriction of SGNG is that the input space is effectively considered to be smooth, assuming that similar inputs will lead to similar outputs: nearby units always move towards the input signals, not taking into account that similar input signals might lead to very different outputs if they belong to different classes. A new unit that is placed on an exceptional (i.e., error-creating) input will therefore subsequently be pulled away from this input by other, nearby input signals.

4.6 The CNN Algorithm

For the simulations described in this thesis a new constructivist algorithm, Constructivist Neural Network (CNN), was developed. This algorithm is largely based on the

SGNG algorithm, but includes some aspects of the RAN. Like in SGNG, each hidden unit has a local error counter, and new units are inserted in regions of the input space that create a high error. Hidden units are interconnected with edges to express neighbourhood relations, and the width of each receptive field is calculated as the average distance to its topological neighbours. The neighbourhood relations can change, which is expressed by an aging of the edges, and units without any edges will be deleted. The movement of the hidden units in response to inputs is a combination of the SGNG and the RAN methods: when the activation of the winning unit is below a threshold θ_{act}, the unit is moved towards the input in an SGNG-like way to avoid units that do not respond to any input signal. By contrast, when the unit activation exceeds this threshold, the unit is moved so as to reduce the output error, i.e., when a higher unit activation decreases the output error it is moved towards the input, and otherwise it is moved away.

The CNN algorithm implements lateral inhibition between the Gaussian units in the hidden layer: the maximally activated receptive field suppresses the activation of all other fields. Lateral inhibition is also found in biological neural networks (e.g. Eysel, 1992).

For the weight update in the CNN, the quickprop algorithm (Fahlman, 1989) is used because it leads to faster convergence than the backpropagation algorithm and its variants. Quickprop assumes that the dependency of the network error on a single weight is parabolic, and each weight modification step consists in a direct "jump" to the minimum of that parabola by using the second derivative of the weight-error function.

The most significant difference to both GNG and RAN is that the CNN network is initially fully connected between the input and the output layers. In this way, the network can learn as much of the task as possible without any hidden units, and the hidden layer is constructed to account for those aspects of the problem that cannot be learned in the direct connections alone. Without the hidden layer, the network is effectively a single layer perceptron that can learn only linearly separable problems. Trained on the quickprop algorithm, it will place the decision boundary in a way to minimize the residual error. The hidden units will then be placed in those regions of the data that lie on the "wrong side" of the decision boundary. Therefore, the CNN algorithm combines Input-Re-Representation and Data-Modelling aspects. The hidden layer models the data space, but it merely provides an additional representation to the original input representation.

The CNN algorithm is described in detail in the following.

The task to be learned by the network is given by a number of input/target pairs $(\mathbf{x}, \mathbf{t}) \in R^I \times R^T$: for each I-dimensional input signal $\mathbf{x}$, the network has to produce the corresponding T-dimensional target signal $\mathbf{t}$.

The CNN network consists of

- a set of I input units which take the activation of the input signal $\mathbf{x}$, and a bias unit that is always active
- a set of T output units.
- a set H of hidden units, with each unit $c \in H$ obtaining a position $\mathbf{pos}_c \in R^I$ in input space.
- a set W of weighted connections w_{ij} from the input (and bias) and hidden units j to the output units i
- a set N of edges between pairs of hidden units. These edges define neighbourhood relations and are not weighted.

The CNN algorithm works as follows:

1. Start with two hidden units a and b at random positions $\mathbf{pos}_a$ and $\mathbf{pos}_b$ in R^I.
2. Get an input/target pair $(\mathbf{x}, \mathbf{t})$.
3. Determine the nearest unit c_1 and the second nearest unit c_2 to the input signal $\mathbf{x}$ (by measuring the Euclidean distance $\|\mathbf{x} - \mathbf{pos}_{c_i}\|$ between the input signal and the unit positions).
4. If c_1 and c_2 are already connected by an edge, reset the age of this edge to zero. If there is no such edge, create it and thus make c_1 and c_2 topological neighbours.
5. Compute the activation values of the hidden units: each hidden unit has a Gaussian activation function act_c of the form

$$act_c(\mathbf{x}) = e^{(-\frac{\|\mathbf{x}-\mathbf{pos}_c\|}{\sigma_c^2})} \tag{4.1}$$

   where $\mathbf{x}$ is an input signal and σ_c is the standard deviation (width) of the Gaussian. σ_c is the average length of all edges emanating from unit c: If N_c denotes the set of all direct topological neighbours of unit c, then

$$\sigma_c = \frac{1}{|N_c|} \sum_{d \in N_c} \|\mathbf{pos}_c - \mathbf{pos}_d\| \tag{4.2}$$

Due to the lateral inhibition in the hidden layer, the activation of all but the winning unit are suppressed:

$$\forall_{i,i\neq 1} act_i = 0 \tag{4.3}$$

6. Compute the activation values of the output units. An output unit i has a logistic activation function of the form

$$o_i(\mathbf{x}) = \frac{1}{1+e^{-\sum_{j\in H,I} w_{ij} act_j(\mathbf{x})}} \tag{4.4}$$

7. Compute the output error as

$$SE = \frac{1}{2}\sum_{i=1}^{T}(t_i - o_i)^2 \tag{4.5}$$

8. Add the output error to the local error variable of the winning unit c_1:

$$\Delta err_{c_1} = SE \tag{4.6}$$

9. Move the winning unit c_1: if $act_c(\mathbf{x})$ is smaller than an activation threshold θ_{act}, move c_1 towards $\mathbf{x}$ by a fraction ϵ of the total distance:

$$\Delta \mathbf{pos}_{c_1} = \epsilon(\mathbf{x} - \mathbf{pos}_{c_1}) \tag{4.7}$$

If if $act_c(\mathbf{x})$ is greater than θ_{act}, move c_1 according to the following equation:

$$\Delta \mathbf{pos}_{c_1} = \epsilon\frac{2}{\sigma_{c_1}^2}(\mathbf{t} - \mathbf{o})\mathbf{w}_{c_1}(\mathbf{x} - \mathbf{pos}_{c_1}) act_{c_1}(\mathbf{x}) \tag{4.8}$$

10. Increment the age of all edges emanating from the winning unit c_1.

11. Remove all edges with an age larger than a_{max}. If this results in units having no more emanating edges, remove them as well.

After having presented all input-target pairs once (i.e., after each epoch), do the following:

12. Adapt the weights according to the quickprop-algorithm (Fahlman, 1989).

13. Decrease the local errors of all hidden units by multiplying them with a constant d:

$$\forall_i err_{c_i} = d \cdot err_{c_i} \tag{4.9}$$

14. If the average squared error has not changed more than a value e during an interval *patience*, insert a new hidden unit as follows:
    (a) Find the hidden unit q with the highest accumulated error.
    (b) Insert a new hidden unit r halfway between q and its neighbour f with the largest error:

$$\mathbf{pos}_r = 0.5(\mathbf{pos}_q + \mathbf{pos}_f) \tag{4.10}$$

    (c) Insert edges connecting the new unit r with q and f, and remove the original edge between q and f.
    (d) Decrease the local errors of q and f by multiplying them with a constant parameter α.

$$err_q = \alpha err_q \tag{4.11}$$

$$err_f = \alpha err_f \tag{4.12}$$

Initialize the error of the new unit r as

$$err_r = 0.5(err_q + err_f) \tag{4.13}$$

Initialize the weights from the new unit r to the output units i as

$$w_{ir} = 0.5(w_{iq} + w_{if}) \qquad i \in 1, \dots, T \tag{4.14}$$

15. If the sum squared error is smaller than a value err_{min}, stop. Otherwise go back to step 2.

The unit movement in equation (4.8) is derived from the gradient descent rule. The dependency of the output error E on the hidden unit position $\mathbf{pos}_i$ can be rewritten as

$$\frac{\partial E}{\partial \mathbf{pos}_i} = \frac{\partial E}{\partial \mathbf{o}} \frac{\partial \mathbf{o}}{\partial act_i} \frac{\partial act_i}{\partial \mathbf{pos}_i} \tag{4.15}$$

with

$$\frac{\partial E}{\partial \mathbf{o}} = (\mathbf{o} - \mathbf{t}) \tag{4.16}$$

and

$$\frac{\partial \mathbf{o}}{\partial act_i} = \frac{\partial}{\partial act_i} \sum_i act_i \mathbf{w}_i = \mathbf{w}_i \tag{4.17}$$

and

$$\frac{\partial act_i}{\partial \mathbf{pos}_i} = \frac{\partial}{\partial \mathbf{pos}_i} e^{-\frac{(\mathbf{x}-\mathbf{pos}_i)^2}{\sigma_i^2}} = \frac{2}{\sigma_i^2} act_i (\mathbf{x} - \mathbf{pos}_i) \tag{4.18}$$

and therefore

$$\frac{\partial E}{\partial \mathbf{pos}_i} = -\frac{2}{\sigma_i^2} (\mathbf{t} - \mathbf{o}) \mathbf{w}_i (\mathbf{x} - \mathbf{pos}_i) act_i \tag{4.19}$$

Note that due to the definition of σ (equation 4.2) it depends on $\mathbf{pos}_i$ and should be considered in the above derivation (4.18) . However, there was no empirical advantage of that more complex unit movement over the one derived here.

The simulations of English past tense acquisition and agrammatic aphasic inflection processing were performed both with the CNN algorithm (chapters 5 and 6) and the SGNG (Westermann, 1997, 1998; Westermann, Willshaw, and Penke, 1999). The CNN algorithm led to much shorter training times (approximately 25% of SGNG) with fewer units generated in the hidden layer (also about 25% of SGNG). The numerical values for the parameters used in the simulations with the CNN algorithm are given in table 5.4 on page 111.

The next section gives a brief overview of models of development that were based on the cascade correlation algorithm (see section 4.5.2.1), before the simulations with CNN are described in detail in the next two chapters.

4.7 Previous Developmental Models with Constructivist Neural Networks

Cascade correlation networks have been used to model a number of developmental problem solving tasks that had been first described by Piaget. These tasks generally follow a well-defined succession of stages, and the challenge of a model is not only to account for behaviour within a certain stage, but also for the transitions between stages.

Of particular interest is the cascade correlation model of the balance scale task (Shultz and Schmidt, 1991; Shultz, Mareschal, and Schmidt, 1994), because it offers a comparison with previous fixed-architecture neural network as well as rule based models.

In the balance scale task, which was developed by Inhelder and Piaget (1958), the child is shown a balance scale that is supported by blocks so that it stays in a horizontal position. Then, a number of different weights are placed on different evenly spaced pegs on either side of the fulcrum. The child's task is to predict what will happen when the supporting blocks are removed. This task requires the child to integrate weight and distance information: the correct answer can be found by multiplying for each arm of the scale the product of weight and distance from the fulcrum (i.e., the torque), and predicting that the arm with the higher torque will move down, or, for an equal torque, the scale will be balanced.

In children, performance on the balance scale task is characterized by four stages that can be described by increasingly powerful rules (Siegler, 1976, 1981): Stage 1 relies exclusively on weight information: the child predicts that the side with the greater weight will go down. Stage 2 is still based mainly on weight information, but if weights are equal on both sides, distance information is taken into account. Children at stage 3 correctly solve simple problems, but they get confused when one side has greater weight and the other has greater distance. Stage 4 involves near perfect performance. Stage 4 may not be reached by many people at all, and if it is reached it might not indicate the understanding of the underlying principle of torque (Shultz *et al.*, 1994).

McClelland (1989) and McClelland and Jenkins (1991) modelled the balance scale task in a fixed architecture backpropagation network. The network had two hidden units each for processing weight and distance information. The training data was chosen so that it consisted mainly of cases in which the weights on each side of the scale were equidistant from the fulcrum, emphasizing weight as the predictive factor of scale behaviour. This bias was meant to reflect the experience of children lifting up objects, but having limited experience with torque. The network progressed through a sequence of stages where performance on each stage was in line with the above rules. However, the net failed to reach a consistent level of Stage 4 performance. Furthermore, in a detailed analysis of the model, Raijmakers, van Koten, and Molenaar (1996) argued that the changes observed between the stages in the model were not discontinuous and did not correspond to the transitions observed in children.

Shultz and Schmidt (1991) and Shultz *et al.* (1994) applied a constructivist cascade correlation network to the same task. They adopted the same "environmental bias" in that most training patterns had equidistant weights. Additionally, they trained the network incrementally, i.e., they added new training patterns throughout the training process. After each output epoch, the model's performance was evaluated based on the correspondence to one of the four rules. This model progressed through the described stages in an orderly sequence, with soft transitions between them. Skipping of stages and regression to previous stages was also observed . This behaviour was argued to correspond to children's learning (Shultz, Schmidt, Buckingham, and Mareschal, 1995). In contrast to McClelland's (1989) model, the cascade correlation network developed strong stage 4 performance, and it did not rely on a hand-crafted separation of weight and distance information in the hidden units. Shultz *et al.* (1994) concluded that the constructivist network performed more like children than the fixed-architecture backpropagation net (McClelland, 1989), with fewer assumptions about initial architecture and processing differences in the hidden units. They argued that the success of their model was based on the addition of hidden units during the learning process, allowing the network to capture fine-grained distinctions between differences on the weight and distance dimensions. The addition of a new hidden unit triggered the quick progression from one developmental stage to the next.

Other developmental phenomena that were successfully modelled with cascade correlation networks include seriation, i.e., sorting a set of objects along a specified dimension (Shultz *et al.*, 1995), integrating the concepts of distance, time, and velocity (Shultz *et al.*, 1995), and the acquisition of personal pronouns (Shultz and Oshima-Takane, 1994).

4.8 Chapter Summary

This chapter has reviewed the learning theoretic issues relating to constructivist learning. These are built on the insight that every successful learner needs a bias, but that a prespecified bias is problematic if the solution to a learning problem cannot be anticipated. Constructivist learners, in particular constructivist neural networks with their equivalence between architecture and hypothesis space, avoid these problems by relaxing the bias during the learning process through the addition of structure. Constructivist learning is therefore not subject to the strong assumptions that have been made about human learning when viewed from a fixed hypothesis space perspective, namely, the postulation of an innate Universal Grammar and Fodor's paradox that has argued that learning is in principle impossible. The subsequent sections developed a taxonomy for existing constructivist neural network algorithms, and the new CNN algorithm that is used in the simulation experiments (chapters 5 and 6) was described in detail. The chapter closed with a brief review of a previous constructivist network modelling the balance scale task.

Chapter 5

Modelling the Acquisition of the English Past Tense

Models of learning the English past tense have in the past ten years become representative of different theories of language acquisition and cognitive processing in general. While connectionist approaches (e.g., Rumelhart and McClelland, 1986; MacWhinney and Leinbach, 1991; Plunkett and Marchman, 1993) have maintained that both regular and irregular past tense forms can be produced in a homogeneous architecture by a single process, dual mechanism accounts (Pinker and Prince, 1988; Kim, Pinker, Prince, and Prasada, 1991; Pinker, 1991; Marcus *et al.*, 1995; Clahsen, 1999a) argue for two qualitatively distinct mechanisms where regular forms are produced by a rule and irregular forms in an associative memory.

The simulation of past tense acquisition is well suited for evaluating the usefulness of constructivist models of cognitive development. This is because a considerable number of different past tense models already exist, and they have been evaluated and compared against each other in detail. Moreover, the existing models have led to close investigations of children's past tense acquisition, so that detailed human data are now available. Finally, the past tense is a "quasi-regular" systems which consists of a rule together with a set of exceptions to that rule. Such systems exist similarly in other cognitive domains (Seidenberg and McClelland, 1989).

The rest of this chapter is organized as follows: section 5.1 gives an overview of the inflectional system of the English past tense, and section 5.2 describes how children acquire the past tense and the specific errors they make. Section 5.3 describes the best-known previous models of past tense acquisition, both connectionist and rule-based. The simulation experiments with the new constructivist algorithm are outlined in section 5.4, and in section 5.5 the simulation results are reported in detail. To assess the validity of constructivist learning, these results are compared with a non-constructivist version of the algorithm in section 5.6. The overall results are then discussed in section 5.7.

5.1 The English Past Tense

The English Past Tense comprises regular and irregular verbs. The vast majority of all verbs are regular and their past tense is formed by adding the ending `-ed` to the verb stem. Depending on the phonological properties of the verb stem, this ending is realized as /d/ (*use—used*), /t/ (*look—looked*), or /ɪd/ (*want—wanted*). The regular past tense is thus completely predictable from the verb stem, and this fact has made it the prime candidate for a mental rule.

Irregular verbs, which number only about 160, form the past tense in different ways ranging from keeping the present tense form (e.g., *hit – hit*) over a vowel change (e.g., *sing – sang*) to completely idiosyncratic relationships between the stem and the past tense form (suppletion, e.g., *go – went*). Most irregulars have no added suffix though some do (*burn—burnt*, *deal—dealt*, *lose—lost*). Despite their irregularity, within the irregular verbs there are several sub-classes that are characterized by similar transformations from the stem to the past tense form (e.g., *sing—sang*, *ring—rang*, *spring—sprang*, or *blow—blew*, *grow—grew*, *know—knew*, *throw—threw*).

Although English has fewer irregular than regular verbs, irregular past tense forms occur much more frequently: according to a frequency corpus for the English language (Francis and Kucera, 1982), 86% of all past tense *types*[1] are regular and 14% irregular. Counting past tense *tokens*[2], however, regular forms account for only 40% and irregulars for 60% of all verbs. In fact, of the ten most frequent past tense forms in (Francis and Kucera, 1982) (*said*, *came*, *went*, *made*, *took*, *knew*, *thought*, *got*, *saw*, *looked*), nine are irregular.

5.2 Acquisition of the English Past Tense

Research in the acquisition of the English past tense and its characteristic error patterns (e.g., Berko, 1958; Brown, 1973; Kuczaj, 1977; Marcus *et al.*, 1992) has identified three stages of acquisition with smooth transitions between them.

In the first stage, a child uses relatively few past tense forms. These are mainly the ones that are most frequent in adult speech, and they are thus mostly irregular. At this

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[1] Each verb counted just once in a corpus.

[2] Each form counted as often as it occurs in a corpus.

stage, a child might therefore use the past tense forms *said*, *came*, *went*, *took*, *knew*, and *looked*, and not mark any other verbs for past tense.

In the second stage, which starts at around 29 months of age, the number of past tense forms produced by the child increases. At this stage, an interesting phenomenon occurs: irregular past tense forms that had been produced correctly in stage one are now sometimes *overregularized*: for example, the past tense of *come* might now be produced as *comed*, or even as *camed*. Marcus *et al.* (1992) examined in detail the overgeneralization behaviour in children and found rates of 2.5% of all past tense forms. All *come-*, *came-*, and *comed*-type productions occurred simultaneously (but note that at stage one all marked past tense forms are correct), and none of these forms was dominant at any time during this stage.

Marcus *et al.* (1990) argued that the beginning of the overregularization phase coincides with the point at which the past tense is reliably marked by the child, that is, when sentences like *"Yesterday I play."* no longer occur. This phase stretches up to school age, with a consistently low rate of overregularizations. There is no across-the-board overregularization of all verbs simultaneously. Instead, each verb shows a specific course and timing of these errors.

Marcus *et al.* (1992) found a clear frequency effect in the number of overregularizations: irregulars with a high frequency in parental speech were overregularized significantly less often than those with low frequency. A second factor that influenced the overregularization rate is the similarity of an irregular to other irregulars: families of irregulars, i.e., groups of irregulars that rhyme or share a final consonant cluster protect each other from errors. In particular, family size (token frequency) is significantly negatively correlated with overregularization rate (Marcus *et al.*, 1992).

Two factors that have been shown not to influence the error rate are the phonological similarity between the verb stem and the past tense form, and the similarity of irregular stems to regulars (Marcus *et al.*, 1992).

At the third stage of past tense acquisition the child finally produces both irregular and regular forms correctly. However, even for adults overregularizations sometimes occur.

The characteristic developmental profile in which irregular forms are first produced correctly, then overgeneralized until they are finally produced correctly again, is referred to as *U-shaped learning*, and the modelling of this specific profile has been the major challenge to all models of past tense acquisition.

5.3 A Survey of Past Tense Models

The apparent distinction in the processing of regular and irregular English past tense forms has resulted in several models that have claimed a representational distinction between these forms. The dominant view until 1986 was that regular past tense forms are produced by a rule which might be genetically specified or has to be learned by the child, and the representations of irregular verbs were stored in a rote-like list. This view was challenged by connectionist models (Rumelhart and McClelland, 1986) that were based on the claim that both regular and irregular verbs can be learned by a single associative mechanism in a homogeneous architecture. The following sections describe the connectionist and symbolic models and theories of past tense acquisition that have played a major role in this long-raging debate.

5.3.1 Rumelhart and McClelland's Two-Layer Model

The connectionist model by Rumelhart and McClelland (1986) (henceforth R&M) was the first to challenge a rule-based account of regular verb inflection while accounting for psychological data such as the U-shaped learning curve:

> *We have, we believe, provided a distinct alternative to the view that children learn the rules of English past-tense formation in any explicit sense. We have shown that a reasonable account of the acquisition of past tense can be provided without recourse to the notion of a "rule" as anything more than a* description *of the language.* (Rumelhart and McClelland, 1986, p. 267)

Due to its implementation in a two-layer network which has limited power, and the resulting need to encode the input and output data in an implausible way, the R&M model is now mainly of historical interest. However, it initiated an extensive debate on the representation of inflection, and more generally, on the existence of symbolic rules and representations in the brain which continues even after 13 years (see e.g. Elman *et al.*, 1996; Marcus, 1998a,b; Marcus, Vijayan, Rao, and Vishton, 1999; McClelland and Plaut, 1999; Marcus, 1999a; Seidenberg and Elman, 1999a,b; Marcus, 1999b; Christiansen and Curtin, 1999; Marcus, 1999c).

The R&M model elicited detailed criticisms addressing both its implementational details and the general ability of associative models to account for rule-like behaviour (e.g. Pinker and Prince, 1988; Lachter and Bever, 1988; Prasada and Pinker, 1993). These criticisms in turn resulted in a variety of improvements and extensions to the R&M model (Egedi and Sproat, 1991; MacWhinney and Leinbach, 1991; Plunkett and

Marchman, 1991; Daugherty and Seidenberg, 1992; Hare and Elman, 1992; Plunkett and Marchman, 1993; Cottrell and Plunkett, 1994). Modelling the acquisition of past tense has since become a benchmark test for the validity of theories of human language learning in general.

Much of the criticism against the R&M model was directed towards its architecture and data-encoding and will therefore not be discussed here. However, other points were more instructive and played an important role in the design of further models. These points will be discussed here briefly.

Pinker and Prince (1988) closely analysed the architecture, training, and performance of the R&M model. Their most relevant criticism concerned the model's simulation of a U-shaped learning curve: U-shaped learning in the model was, in their view, based on a manipulation of the input data: while initially the network was trained only on the ten most frequent verbs of which eight were irregular, in the second phase of training 410 more verbs were added to the corpus, 80% of which were regular. Therefore the network, which had initially learned to produce the 10 most frequent verbs correctly, was now swamped with regular verbs and started to overregularize the initially correct verbs. Such sharp discontinuities, however, do not exist in the linguistic environment of a child and therefore cannot be used to explain U-shaped learning in children. Longitudinal studies of children show that the proportion of regular verbs in their speech is stable at around 45–60% and does not show a sudden change from 20% to 80% as in R&M's model (Marcus *et al.*, 1992).

Another point raised by Pinker and Prince concerned the generalization capabilities of R&M's network: Of the 72 regular test verbs, 20 were produced incorrectly, corresponding to an error rate with regular test verbs of almost 30%. They argued that this error rate was implausibly high.

Lachter and Bever (1988) added a further criticism which is of relevance beyond the specific model: they argued that rules were implicitly hardwired into the architecture of the network and the data representation; the network did therefore not learn the past tense without any rules as claimed by R&M. They claimed that without these encoded so-called *TRICS* ("The Representations It Crucially Supposes"), the network would have been unable to learn the past tense.

5.3.2 MacWhinney and Leinbach's Backpropagation Model

MacWhinney and Leinbach (1991) (henceforth, M&L) presented an improved version of R&M's past tense model, employing the backpropagation algorithm and inserting layers of hidden units, using a more realistic data encoding and a more realistic training corpus.

The model had two hidden layers with 200 units each and direct one-to-one "copy-connections" from the input to the output layer. It was trained with the backpropagation algorithm (Rumelhart *et al.*, 1986a).

The training corpus for M&L's model corresponded to the actual frequencies of English verbs in a comprehensive corpus of English word frequencies (Francis and Kucera, 1982). The most frequent verbs in this corpus were presented to the network at each epoch, while the least frequent verb was presented only at every 700th epoch. In total, during the training the network was presented with 1.3 million verb tokens, corresponding to 5481 types of all inflectional forms, without any abrupt transitions in the data set like in the model of R&M. The verbs were represented in a template format where each phoneme was encoded by phonological feature vectors. The full verb was presented in a left-aligned template, and the coda of its final syllable additionally in a right-aligned template. The output contained the left-aligned representation of the past tense form. (For further details of the data encoding which is also employed in the simulations reported in this thesis see section 5.4.2).

The M&L model learned to produce the past tense for all of the regular verbs in the training set, but only for 93 of 103 (90.3%) of the irregular verbs. It further failed to account for a U-shaped learning curve: although overgeneralization of irregular verbs occurred, there was no phase of an initial correct usage of those verbs.

After training, M&L tested their network on 13 untrained irregular verbs. However, it is misleading to test a model on irregular verbs which are by definition not predictable. Instead, a model should be tested on pseudo-words that have been tested with humans as well, and the performances of the model and the human subjects should be compared. A corpus of such pseudo-words now exists (Prasada and Pinker, 1993).

Although the M&L model was a clear improvement of the R&M model in terms of network architecture and a more realistic data set, its learning success of only 90.3% of irregular verbs and its failure to account for a U-shaped learning curve do not make it a realistic model of child past tense acquisition.

The M&L model was criticized by Ling and Marinov (1993) for arbitrary design decisions such as direct copy-connections from the input to the output layer, biasing it to preserve the stem. This and other features of the model were argued not to be motivated out of general considerations, but as specifically addressing the problems of the earlier R&M model.

MacWhinney (1993) described a simplified version of the M&L model which used only a single hidden layer, no direct "copy-connections", and a single right-aligned templated input representation. This time the model was trained on 1,200 verbs for 24,000 epochs. Again, the revised model learned all of the regular but only 90.0% of the irregular verbs correctly.

The revised model was tested on the set of 60 pseudo-verbs that had been developed by Prasada and Pinker (1993) to investigate human inflection of novel words. These pseudo-verbs were divided into irregular-like and regular-like groups, each consisting of three sub-classes: *prototypical*, *intermediate*, and *distant*. Pseudo-verbs in different sub-groups were similar to different existing verbs to different degrees, with *prototypical* being the most and *distant* the least similar. The results of testing these pseudo-verbs on human subjects showed one basic result: the tendency to inflect pseudo-irregulars as irregular decreased with decreasing similarity to existing irregulars. By contrast, the tendency to inflect pseudo-regulars as regular is high independently of their similarity to existing regulars.

The test case for associative models in the generalization task is the inflection of the distant regular-like pseudo verbs: here, a regular inflection should be produced which is not based on the similarity to existing verbs, indicating that the regular case has been learned as the default.

MacWhinney (1993) claimed that the revised model performed similar to the human subjects tested by Prasada and Pinker (1993) in that it produced regular forms even for the distant pseudo-regulars. However, these results are inconclusive in that although the network was trained for 24,000 epochs, its generalization ability was assessed at 4,200 epochs. At that point, however, the performance for the irregular verbs was only 80% which indicates a higher tendency of the model to regularize and thus might give an overly optimistic picture of its ability to regularize novel words. The real challenge of a model is to produce all (or most) irregulars in the training set correctly and still produce the regular ending for novel words.

5.3.3 Plunkett and Marchman's Incremental Model

Plunkett and Marchman (1991, 1993) conducted detailed experiments of past tense acquisition, investigating which factors influence learning success and a U-shaped curve. They constructed a set of artificial verbs that consisted of 3 phonemes each with syllable structures permitted in English, and assigned arbitrary past tense forms to these verbs. The four possible past tense transformations were identity mapping (in English e.g., *hit—hit*), vowel change (*draw—drew*), arbitrary (*go—went*), and regular (*look—looked*). Experiments were conducted with three-layer backpropagation networks.

Plunkett and Marchman (1991) systematically varied the number of verbs in their artificial language falling into the four past tense classes as well as their token frequency. They found that the learning success depended on interactions between class size and token frequency, and the type of transformation. Although they claimed to have found U-shaped learning curves in the simulations, it is unclear whether specific verbs were initially produced correctly and subsequently overregularized, or if oscillations between correct and overregularized inflection occurred from the beginning.

Plunkett and Marchman (1993) used the same artificial verbs to investigate the influence of an expanding verb corpus on performance. A new verb with a token frequency of 5 or 3 was added to the corpus every 5 epochs for the first 100 epochs, and every epoch thereafter. This discontinuity in the training set growth was likened to the vocabulary burst in children. Although Plunkett and Marchman observed a decrease in the performance of the network which they explained as U-shaped learning, again it is unclear whether verbs that had initially been produced correctly were subsequently overregularized, or whether the decrease in irregular performance was due to the verbs that had been newly introduced into the training set and were overregularized from their first occurrence onwards. Marcus (1995) analyzed the reported performance of the network in detail and noted that the onset of overregularizations coincided with the increase in frequency with which new verbs were introduced into the training corpus (i.e., epoch 100). This is in contrast to children where the vocabulary burst occurs about a year before the onset of overregularization.

Plunkett and Marchman (1996) replied to this criticism by presenting modified simulations in which the corpus was expanded at a constant (not reported) rate. They showed that the onset of overregularization starts at different points of vocabulary size for different simulations. However, there are three problems with this statement: first, as mentioned before, it is unclear whether the errors concern only new irregulars. Second, Plunkett and Marchman (1996) reported a decrease in the number of correct irregulars, but it was not clear whether all incorrect irregulars were overregularizations. Other possible errors are irregularizations to another verb class, or the failure to produce an output at all. Third, it is unclear if the rate of introduction of new verbs was the same for all reported simulations, or if that rate has an effect on the onset of overregularizations. In any case, Plunkett and Marchman (1996) concluded that a discontinuity in the expansion rate was neither a necessary nor sufficient condition for the onset of overregularization. Instead, the number of regular verbs in the corpus was a better predictor.

5.3.4 Daugherty and Seidenberg's Model

Another three layer backpropagation network for past tense acquisition was presented by Daugherty and Seidenberg (1992) (henceforth D&S). The input and output were in a phonological template format like in the M&L model, and 423 training verbs were presented to the network according to their frequency. This network learned all of the regular and 84.3% of the irregular verbs. D&S did not aim to model the developmental profile of past tense acquisition but instead examined the trained network for its generalization ability and for frequency effects. In this way, the model is one of adult language processing and not of acquisition. D&S identified regular verbs that have no irregular neighbours ("entirely regular verbs", e.g., *like*) and those that rhyme with irregulars ("inconsistent regulars", e.g., *bake* rhyming with *make*). They showed that entirely regular verbs had less errors than inconsistent regulars, which in turn performed better than irregulars. These results corresponded to human response latencies in past tense generation (Seidenberg and Bruck, 1990; Seidenberg, 1992) but were not consistent with rule-based accounts of regular inflection (Pinker, 1991). However, frequency effects that are found in human subjects for irregulars but not for regulars could realistically be modelled only when a modified corpus with fewer irregular verbs was used. With this new corpus consisting of 309 regular and 24 irregular verbs, all of the regular and 92% of the irregular verbs were learned, and there was an interaction between frequency and mean squared error only for irregulars but not for regulars. Furthermore, the second model displayed the same consistency effect as the first model. D&S therefore argued that these phenomena that were taken as evidence for a dual mechanism theory of inflection (Pinker and Prince, 1988; Pinker, 1991) could be modelled in a connectionist network.

The D&S model was the first to account for more detailed aspects of adult language processing, but the modelling of the acquisition of the past tense was not attempted, and it is unclear whether the model would have shown a realistic acquisition profile. Furthermore, the corpus was the smallest of all simulations (333 verbs) with a relatively big hidden layer size of 200 units. It is unclear how the model would have scaled up to a training corpus of the more usual size of 1,000 to 1,600 verbs. Nevertheless, the model was valuable because on the one hand it could account for human data that is not predicted by dual mechanism theories, and on the other hand it modelled data that was generally taken as evidence for such dual mechanism theories in a single, connectionist architecture.

5.3.5 Ling and Marinov's Rule-based Model

MacWhinney and Leinbach (1991) pointed out that is is easier to criticize connectionist models than rule-based theories: whereas models spell out the precise learning mechanisms and data in detail and their performance can be closely investigated, rule-based accounts of past tense acquisition existed only as a theory, leaving many aspects of their implementation underspecified. For a comparison between associative and rule-based theories, a symbolic model of past tense acquisition would be needed.

This challenge was taken up by Ling and Marinov (1993) (henceforth L&M), who presented a symbolic, rule-based model for the acquisition of the English past tense. This model is a general symbolic patterns associator (SPA) based on the ID3 algorithm (Quinlan, 1986). ID3 is a decision tree algorithm to induce classification rules from a set of classified examples. Attributes that are the most discriminating in a subset are chosen as the root of subtrees, and subtrees are built recursively until all elements in a subset belong to a single concept. The SPA is a modification of this N-to-1 classification system to form a general N-to-M pattern associator that builds an individual decision tree for each of the N inputs.

In order to carry out comparisons between the SPA and M&L's connectionist model, L&M used the same training data as M&L. They performed different simulations with different representations of the verbs and with both phoneme-based and feature-based representations of the verbs.

The SPA learned 99.6% of the regular and 96.6% of the irregular training data. It was thus the best of all models in learning irregulars. In order to assess the generalization ability of the SPA, L&M tested their network on the set of 60 pseudo-verbs developed by Prasada and Pinker (1993) that had also been tested with human subjects. In these tests, the SPA matched the psycholinguistic data more closely than R&M's network model and was similar to a re-implementation of the M&L model (MacWhinney, 1993).

Ling and Marinov (1993) claimed to have modelled all three stages of the U-shaped learning curve successfully: frequent irregular verbs were initially produced correctly, then overgeneralized, and finally produced correctly again. This effect, however, was caused by manipulating a parameter (m) that determined how often a verb had to be encountered until it was considered an exceptional rather than a regular word. This parameter was initially set to the value 2, so that the most frequent irregular verbs, occurring more than two times in the initial training phase, would be learned as exceptions and their correct past tense form was produced. In a second stage, m was then set to 6, so that all irregular verbs that occurred less than six times were regularized. For the verbs that had occurred more than two but less than six times, overgeneralization therefore followed on a phase of initial correct production. During the rest of the training, m was left constant at the value 6, so that eventually most irregular verbs, occurring more than six times, were produced correctly. The idea behind adapting this generalization parameter was that

> *Presumably, children initially learn most verbs as exceptions, so in the initial stages of our simulation we set m to be very small, thus even with few examples the SPA builds very large trees accounting for all individual verbs. When more regular and irregular verbs are seen, children start to generalize. This can be modelled by allowing for a larger m.* (Ling and Marinov, 1993, p. 260)

This way of modelling, however, is no more plausible than the abrupt change in the input data in the R&M model. Here, an assumption about the learning of past tense by children is hard-wired into the model through a parameter change, without providing any external motivation for this change. It is precisely the assumption which was hard-wired into the SPA that a successful simulation of a U-shaped learning curve should explain. The transition from the initial storage of verbs as exceptions to the generalization between verbs is what has to be explained; hard-wiring this phenomenon into a model does not give any insights into the underlying mechanisms.

A second point to note about the SPA is that although it was presented as a symbolic alternative to connectionist models, it makes clear that the boundaries between symbolic and subsymbolic systems are blurred. Ling (1994) argued that their model was symbolic because it had localist representations on the phoneme level whereas the M&L model had distributed feature vector representations of phonemes. However, this type of symbolic model is a long way from the symbolic accounts of verb inflection that suggest a rule in the formation of the regular past tense. In the sense of models of inflection, the SPA can therefore not be regarded as a symbolic alternative to associative, single-mechanisms models. Instead, it is a non-connectionist associative single-mechanism model.

Although the SPA had its merits in providing detailed comparisons between a symbolic and a connectionist system, it does not constitute an adequate model of past tense learning.

5.3.6 The Dual Mechanism Theory

The Dual Mechanism Theory (DMT) (Pinker and Prince, 1988; Pinker, 1991; Marcus *et al.*, 1995; Pinker, 1997a,b; Clahsen, 1999a) is an extension of the traditional rule/rote distinction between regular and irregular verbs. This traditional view was based on the insight that the regular inflection is productive and is readily applied to new words, suggesting a mental rule in its production. However, a rote-like representation of irregulars cannot capture sub-regularities such as, in the English past tense, the sub-groups *bleed, feed, breed, lead, read* etc., or *ring, sing, spring*. Such similarity effects between irregulars can best be captured in an associative-memory-like lexicon. The DMT thus postulates two separate, encapsulated mechanisms in the production of regular and irregular forms: regulars are produced "on the fly" by the application of a rule, whereas irregulars have entries in an associative mental lexicon, together with their inflected forms.

To produce a participle, first the lexicon is searched for a corresponding entry, and if no such entry is found, the rule is applied. In the DMT the rule therefore has a default status since it is applied whenever no lexical entry is found. Kiparsky (1982) called this process the *Elsewhere Condition*: specific rules (i.e., irregular inflections) are applied first; the default is the applied "elsewhere". A proposed mechanism for the interaction between lexicon and rule is the *Blocking Principle*: when a lexical entry is found, it blocks the application of the rule. This mechanism implies that the rule is applied whenever a word has no lexical entry, for whatever reason.

The main appeal of the DMT lies in its explanation of several aspects of adult language processing, and it will therefore be discussed in more detail in chapter 6 where impaired adult processing is modelled with a constructivist network model.

Although the dual mechanism theory has become a dominant theory of inflectional processing (see Pinker, 1994, 1999) and seems intuitively attractive to explain a wide range of data, a closer look reveals serious problems that make it seem untenable. In this and the following chapter, simulations with the constructivist model are used to develop an alternative theory of inflectional processing that can account better for empirical data, and that does not rely on two distinct mechanisms to account for the dissociations between regular and irregular verbs.

Here I will only discuss one aspect of the DMT that relates to acquisition. A wider discussion of the DMT will follow in sections 6.3 and 6.9.

Acquisition phenomena such as the U-shaped learning curve have not been explicitly addressed in the DMT, and in fact it is not straightforward to account for them. A recent discussion of the DMT (Clahsen, 1999a) uses acquisition as one point of evidence for the DMT, but it does not go beyond describing the differences between regular and irregular verbs in the acquisition profile. For a more plausible theory, however, it is necessary to discuss precisely how the proposed mechanisms can account for the observed behaviour.

How could U-shaped learning arise in the DMT? The lexical entry for, say, *come – came* would initially have to block the application of the default rule so that the correct *came* would be produced. At the second stage this lexical entry would have to weaken enough not to block the default rule anymore, and *comed* would be applied. Finally, it would again become stronger, and the irregular form *came* would be produced once more. The decrease of the strength of a lexical entry is not plausible, however, since the verb is not heard less often in the second phase of learning. A special problem is posed by forms such as *camed*: how can the output of the associative memory, *came*, be used as input for the rule, where the /d/ is attached? As soon as the entry in the associative memory is found, the rule is blocked! An alternative explanation of U-shaped learning is that the default rule is learned and strengthens over time, indicating a competition rather than a blocking between the rule and the lexicon. In this view, initially only the lexical entries exist and all past tense forms are produced correctly. The default rule, however, would gradually strengthen with linguistic experience, until it overrides the lexical entries and even irregular verbs are produced as regulars. With more linguistic experience the irregular lexical entries would again become stronger than the rule, leading to correct inflections. This explanation raises further questions about the specifics of the interaction between rule and memory: how is the blocking principle dependent on the strength of a rule and a lexical entry? And what happens with regular verbs that are stored in the lexicon at stage 1? According to Pinker (1991), no regular verb has a lexical entry for its inflected forms, and therefore these regulars would have to be eradicated from the associative lexicon once the rule is learned. Given the mechanisms of associative memories, this is an unlikely scenario.

These questions hint at the major flaw of the DMT: it is seriously underspecified, and possible specifications raise problems because they either could not work in principle, or would not account for the data.

In the following sections, a new model of past tense inflection is presented. This model is based on a single, associative mechanism. It develops in a constructivist way, displaying the U-shaped learning curve observed in children and leading to a functional dissociation between regular and irregular inflections. As such, it stands between homogeneous connectionist and hybrid dual mechanism models.

5.4 Experiments

The constructivist model of past tense acquisition described here is based on the CNN algorithm developed in section 4.6. The next section describes how this algorithm can be applied to the modelling of past tense acquisition with its regular and irregular cases. Then, the data and simulation procedure are described.

5.4.1 Constructivist Modelling of Past Tense Acquisition

As detailed in section 4.6 the CNN starts with direct connections from the input to the output layer and just two units in the hidden layer, each therefore covering half of the input space. The CNN tries to learn the task with this architecture by adjusting its weights and the position of the hidden unit receptive fields, and when the error no longer decreases, a new unit is inserted into the hidden layer. The position of insertion is determined by the error that has been caused by treating inputs within one receptive field as similar: the unit that has previously caused the highest error is shrunk and the new unit is inserted next to it. The idea here is that a unit that produces a high output error is inadequate (because it covers inputs with conflicting outputs), and more structural resources are needed in that area of the input space. Since on insertion of a unit the sizes of the receptive fields are shrunk so that they slightly overlap, this in effect leads to a more "fine-grained" resolution in that area. At each epoch, the receptive fields are tuned to respond more to inputs for which they can reduce the error.

Figure 5.1 shows a hypothetical start and end state in a two-dimensional input space for past tense learning. While initially only two receptive fields cover the whole space, later hidden units are inserted to account for the specific learning task. Because in the simulations the verbs are represented phonologically, similar sounding input verbs initially fall into the same receptive field even when they require different outputs (e.g., *fear* and *hear* requiring *feared* and *heard*, respectively). During the training of the network new receptive fields are inserted in the area of such verbs, and eventually similar verbs with dissimilar past tense forms will be discriminated. When similar verbs have the same output class, however, (e.g., *look* and *cook* with *looked* and *cooked*),

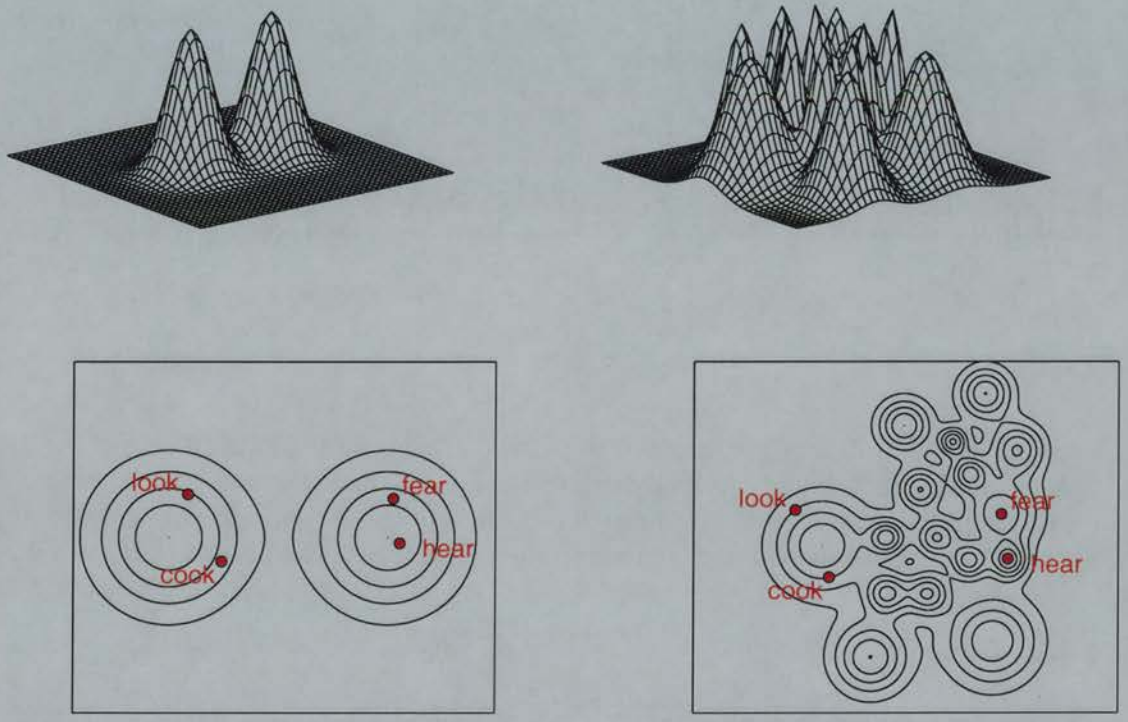

Figure 5.1: Gaussian receptive fields covering the input space at the beginning (left) and the end (right) of learning.

no new receptive field will be inserted there and one such field will cover different verbs without producing output error. Thus, the internal structure of the network will adapt to reflect the learning task. This task-dependent adaptation is in contrast to static systems and to systems that incorporate a pre-programmed development such as an extension of short-term memory span, where the final architecture is independent of the specific problem being learned (see e.g., Elman, 1993).

Figure 5.2 shows the architecture of the CNN. It consists of an input layer taking a phonological representation of the verb stem, and an output layer with one unit for each possible output class (see below). The hidden layer initially consists of only two units but is constructed during the learning process. There are full direct connections from the input to the output layer (IO), and also each hidden unit is fully connected to the output layer (HO).

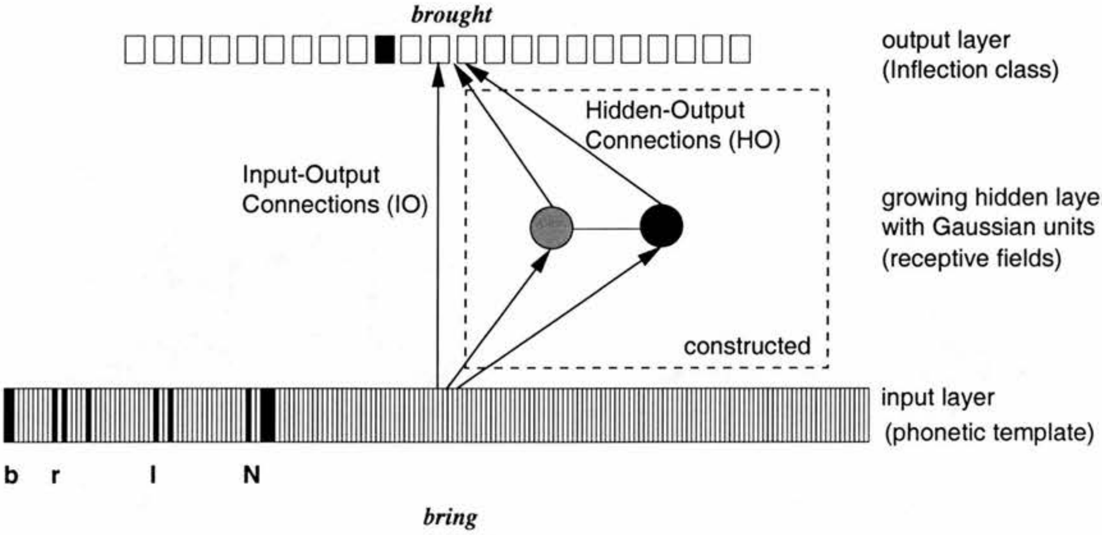

Figure 5.2: The initial architecture of the CNN. The input and output layers and the hidden and output layers are fully interconnected. The weighted connections displayed here from the input layer to each hidden unit can be equivalently viewed as a position of the hidden unit in the input space; this is the view elaborated in the text.

5.4.2 Data

To allow for comparisons between the CNN and previous models, the present experiments employed the same verb corpus and representation format as MacWhinney and Leinbach (1991) in their backpropagation network and Ling and Marinov (1993) in the symbolic SPA model.

This corpus is derived from the Francis and Kucera (1982) corpus of English word frequencies. MacWhinney and Leinbach (1991) retained only one past tense form where many were possible for one verb (e.g., *hang—hanged/hung*) and further eliminated all verbs with more than three syllables as well as all homophones. Hence the corpus does not contain ambiguities that would arise from a purely phonological representation of verbs. From the resulting 6940 most frequent verb forms that included all different inflectional forms, for the experiments described here the 1404 stem/past tense pairs, corresponding to 24802 tokens, were extracted. For the simulations, 8000 tokens were randomly extracted from this corpus according to the frequency of their past tense forms. The structure of the resulting training corpus is summarized in table 5.1. The whole training corpus is given in appendix A.

The verbs were transcribed using UNIBET (MacWhinney, 1991) where each phoneme is encoded by a single ASCII-character. Some examples of phonological transcrip-

	Types		Tokens	
regular	943	(88.4%)	4579	(57.2%)
irregular	123	(11.6%)	3421	(42.8%)
total	1066	(100%)	8000	(100%)

Table 5.1: The structure of the training corpus

tions are shown in table 5.2.

Verb	Transcription
bring	`brIN`
explain	`Iksplen`
point	`p2nt`
recognize	`rEkIgn3z`
shake	`Sek`

Table 5.2: Some examples for the phonological transcription of verb pairs following UNIBET.

The transcribed verbs were then transformed into a left-justified phonological template of the form `CCCVVCCCVVCCCVVCCC`, where `C` stands for a consonant and `V` for a vowel.[3] Table 5.3 shows the template-encoding for the verbs in table 5.2.

Verb	Templated Representation
bring	`br-I-N------------`
Template	`CCCVVCCCVVCCCVVCCC`
explain	`---I-ksp--l--e-n--`
Template	`CCCVVCCCVVCCCVVCCC`
point	`p--2-nt-----------`
Template	`CCCVVCCCVVCCCVVCCC`
recognize	`r--E-k--I-gn-3-z--`
Template	`CCCVVCCCVVCCCVVCCC`
shake	`S--e-k------------`
Template	`CCCVVCCCVVCCCVVCCC`

Table 5.3: Some examples for the template encoding of verbs.

For the input to the model each phoneme was encoded by a subsegmental feature vector. Vowels were described by the eight features *front, centre, back, round, high, middle, low,* and *diphthong*. The ten consonantal features were *voiced, labial, dental, pal-*

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[3] Several experiments were run with left- and right-aligned input data, but the results for all of them were very similar, and here only results for left-aligned inputs are presented.

atal, velar, nasal, liquid, trill, fricative, and *interdental.* The presence of a feature in a phoneme was encoded by 1, absence by 0. In order to have feature vectors of equal width for both vowels and consonants, two zeroes were added to the right of each vowel-feature vector. The feature vectors for each phoneme are given in appendix B. The input to the network consisted thus of 18 10-item-feature vectors, i.e., 180 units.

In contrast to other models of past tense acquisition, in the CNN the formation of the past tense was viewed as a classification task: instead of producing the phonological form of the past tense, the network had to learn a class that determined how the past tense was formed from the verb stem (adapted from Pinker and Prince, 1988). This classification was based on a product-oriented approach (Bybee and Moder, 1983) where similar past tense forms are grouped together even when their stems are different. For example, the class $/x/ \rightarrow /U/$ (where $/x/$ stands for an arbitrary phoneme and $/U/$ is the UNIBET notation of the vowel in e.g., *stood*) contained the verbs *understand, withstand, overtake, stand, shake,* and *take,* and the class $/x/ \rightarrow /6/$ ($/6/$ being the UNIBET notation for the vowel in e.g., *stuck*) comprised *string, strike, swing, stick, fling, cling, spin, hang,* and *dig.* This classification resulted in 23 classes, one for the "stem + *-ed*" (regular) class and 22 for the different irregulars. These classes are listed in appendix C.

Viewing past tense formation as a classification task eliminates several confounding variables. No past tense form is inherently more difficult to learn than any other, and the similarity between stem and past tense is no predictor for acquisition time (Marcus *et al.*, 1992). By contrast, in simulations, complex transformations are harder to learn than simple ones. Viewing past tense learning as a classification task eliminates this disparity between human data and modelling.

In training the CNN, the whole training set of 8000 stem/past-tense-class pairs was presented to the network in random order at each epoch. Weight update took place after every epoch, and hidden units were inserted depending on the learning progress (as described in section 4.6). The network was tested for its performance on the training set prior to each insertion.

The parameters used for the training of all networks are given in table 5.4.

5.5 Results

Apart from using the CNN algorithm, the simulations were also performed with a slightly modified version of Supervised Growing Neural Gas (Westermann, 1998). The results were very similar to those reported here, the main difference being that the

Constructivist Parameters		
ϵ	0.2	fraction by which the winning unit is moved
θ_{act}	0.2	threshold that determines which type of hidden unit movement to use
a_{max}	1000	maximum age of edges before they are removed
d	0.1	factor by which node errors are decreased after each epoch
e	0.1	error decrease considered sufficient during $patience$
$patience$	10	interval (in epochs) during which error decrease is measured to decide whether a new hidden unit is to be inserted
Quickprop Parameters (see Fahlman, 1988)		
μ	1.75	maximal allowed jump-size
α_{io}	0.2	learning rate for input-output weights
α_{ho}	0.5	learning rate for hidden-output weights
$sigprimeoffset$	0.1	value added to sigmoid-prime to avoid flat spots
$slopedecay$	-0.0001	factor added to slope to prevent large weights
err_{min}	0.0005	error at which training is stopped

Table 5.4: The parameters used in the training of the CNN model. For the algorithm itself see page 87 *ff*.

new algorithm learned in about 25% of the time of SGNG and built smaller networks (about 25% of the hidden units of SGNG). This indicates that the main results of the simulations are not an artifact of the specifics of the algorithm (note, however, that the constructivist nature of the algorithms does make a difference, see below).

Six networks were trained with different initial random settings of the weights. The results reported in the following are averaged over these networks which all behaved very similarly. In some cases examples from a selected (typical) individual network are given.

An output class was counted as correct when its unit, but no other output unit, had an activation value over 0.7.

5.5.1 Learning

After an average of 1672 epochs, the CNN had learned to classify 100% of the regular and 100% of the irregular forms correctly. Table 5.5 compares the learning results of the CNN with the R&M, M&L, D&S and SPA models. While all models performed nearly equally well for the regular verbs, the CNN outperformed the other models for the irregular verbs, followed by the symbolic SPA. This success seems to be a direct

	R&M	M&L	D&S	SPA	CNN
Verb types	420	1,650	333	1,038	1,066
Percentage correct					
Regulars	98.0	100.0	100.0	99.6	100.0
Irregulars	95.0	90.7	92.0	96.6	100.0

Table 5.5: The performance on the training data of five past tense models: R&M = Rumelhart and McClelland (1986), M&L = MacWhinney and Leinbach (1991), D&S = Daugherty and Seidenberg (1992), SPA = Ling and Marinov (1993), CNN = the present model.

consequence of the ability of the network to allocate structure (hidden unit receptive fields) where needed and thus specifically for the harder-to-learn irregular verbs.

5.5.2 Developing Network Architecture

The trained networks constructed hidden layers with between 97 and 212 receptive fields (mean: 127.67), i.e., on average each of the receptive fields accounted for 8.35 verbs. However, a closer analysis of the distribution of these receptive fields over the input space showed a large difference between regular and irregular verbs: the 123 irregular verb types were distributed over 70.2 receptive fields, i.e., each irregular verb claimed an average of 57% of a receptive field. By contrast, the 943 regular verb types were distributed on average over just 90.7 receptive fields (some of which covered both regular and irregular verbs), i.e., each regular verb claimed on average just 9.6% of a receptive field, with the number of regular verbs in a single receptive field ranging from 1 to 83. This result clearly shows the advantage of constructivist as opposed to fixed-architecture models in that no *a priori* decision has to be made about the number and location of hidden units. Each hidden unit processes only a small subset of the verbs and can therefore learn the correct output effectively. The final network architecture reflects the properties of the learning problem, in this case, a number of large receptive fields for the regular verbs and small, fine-grained receptive fields for the more difficult irregular verbs.

During the training, an average of 7.5 units were removed from the hidden layer because they had no neighbours left. Furthermore, an average of 21.8 units in the hidden layer were non-functional with all weights to the output layer having the weight 0. This result illustrates that regressive events play a role in constructivist learning, and in a larger system the freed up units could be recruited by a network solving another task.

5.5.3 U-shaped Learning Curve

The most striking feature of past tense acquisition in children is the U-shaped learning curve (see section 5.2). However, most of the existing models have been unable to provide a realistic account of the emergence of U-shaped learning (see section 5.3): whereas R&M relied on the assumption that the learning environment of a child changes from a first stage of mainly irregular verbs to a second stage of mainly regular verbs and chose their training data accordingly, M&L's model could not account for any unlearning of irregular forms. In the SPA, U-shaped learning was achieved by the explicit manipulation of a learning parameter. Plunkett and Marchman (1993) were able to show U-shaped learning in an environment where the training corpus was slowly expanded. However, it might be more plausible to assume that while the learning environment of the child is static, the child himself is undergoing changes that will influence the processing of the environmental input (see also Elman, 1993). Therefore, it was interesting to investigate the behaviour of the CNN in a non-incremental training environment.

The CNN displayed a U-shaped learning curve for many of the irregular verbs in the training corpus, where a period of overregularization (i.e., a classification of the verb as belonging to the regular class) was preceded by a phase of correct classification. Corresponding to psycholinguistic evidence (Marcus *et al.*, 1992) the irregulars generally displayed so-called *micro U-shaped learning*, i.e., a phase of correct production followed by overregularizations at individual times for different verb (as opposed to *across-the-board U-shaped learning* affecting all verbs simultaneously, which does not occur in children).

Figure 5.3 shows six typical overregularization profiles: several frequent verbs were never overregularized (*say*), others displayed phases of alternating overregularization and correct production at different times during learning (*stick*, *feed*, *creep*, *sink*), and some verbs displayed a long phase of overregularization from the beginning (*bleed*).

As Plunkett and Marchman (1996) have pointed out, it is not straightforward how data from a network simulation should quantitatively be compared with data from children: at a given time in training, a non-stochastic network consistently only produces one output for each verb whereas the production of a child might fluctuate. Further, in testing the network at each epoch, all 1,066 verb types will be classified each time, while a child will produce only a fraction of his vocabulary at a given session. However, qualitative comparisons between different kinds of errors can be made

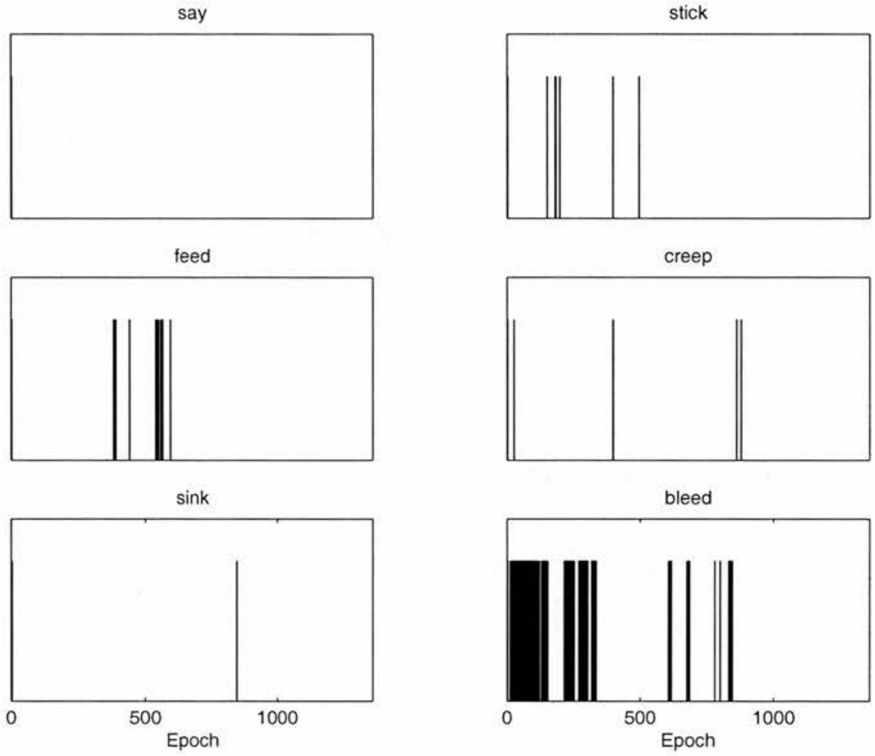

Figure 5.3: Typical overregularization profiles for different verbs during the training of the CNN. A "spike" represents the occurrence of an overregularization. The network was trained for 1358 epochs and constructed 108 hidden units until all forms were learned.

between children and network models.

In children's acquisition of the English past tense, a frequency effect has been found (Marcus *et al.*, 1992): past tense forms that are frequent in the speech of adults talking to the child are significantly less overregularized by the child than infrequent ones. In the simulations this effect can be easily tested because all inputs to the network are known. In line with Marcus *et al.* (1992), the frequencies of all training verbs were converted to logs because a frequency difference from 1 to 10 is expected to have a larger effect than one from 1001 to 1010.

A clear frequency effect was found in the simulations: overregularization rates were correlated negatively with the input frequency: the mean correlation of -0.39 is very similar to that of children where the correlation was -0.37 when parental input to the child was counted (Marcus *et al.*, 1992).

A further effect that has been found in children's overregularizations is a family effect: groups of similar sounding verbs protect each other from overregularization. To investigate this effect, like in (Marcus *et al.*, 1992) the family size of each verb was computed by adding the frequencies (not log frequencies) of all verbs that rhymed with it in both stem and past tense. Also like in (Marcus *et al.*, 1992), to prevent a confounding with the frequency effect, the frequency of the verb itself was not counted.

Like for children, a family effect was found in the simulation: family size was correlated negatively with overregularization rate (mean correlation -0.107). Again, this value is very close to the one established by Marcus *et al.* (1992) which was -0.08.

In summary, the CNN was successful in closely modelling a U-shaped learning curve in past tense acquisition, and its performance corresponded to the details of children's past tense learning, displaying a frequency effect and a family effect on overregularization rate.

How does the U-shaped learning in the CNN occur? Since the verb set was held constant throughout the training, the change in network performance can only be a consequence of the internal reorganization of the network architecture, and specifically, of the construction of the receptive field hidden layer. Initially, the network has only two hidden units which are of little use since they each cover about half of all verbs with their varied past tense forms, and the network therefore has to rely on the direct input-output connections for producing the past tense forms. Given these restrictions, the network initially learns to produce the past tense forms of the frequent irregulars (because of their high token frequency) and of the regular verbs (because of their high type frequency).

During the training process, however, the CNN gradually constructs its hidden layer and adds more receptive fields, which leads to the reorganization of the internal representations mainly of irregular verbs onto the hidden layer. In the hidden layer, localist, identity-based representations are constructed in addition to the original distributed representation in the input layer. These identity-based representations are utilized predominantly by the irregular verbs which form the exceptions from the regular case. The construction process leads to a phase in which the localist representations in the hidden layer are already used, but where the few receptive fields are large and include regular as well as irregular verbs. At this stage, the receptive fields cause errors even for irregular verbs that had initially been produced correctly through the direct input-output connections. This phase, in which the localist representations are still too coarse to be useful for every verb, corresponds to the overregularization stage in children. It is evident that with this mechanism, different verbs would be overregularized at different times, depending on whether they are covered by an individual or conflicting receptive field.

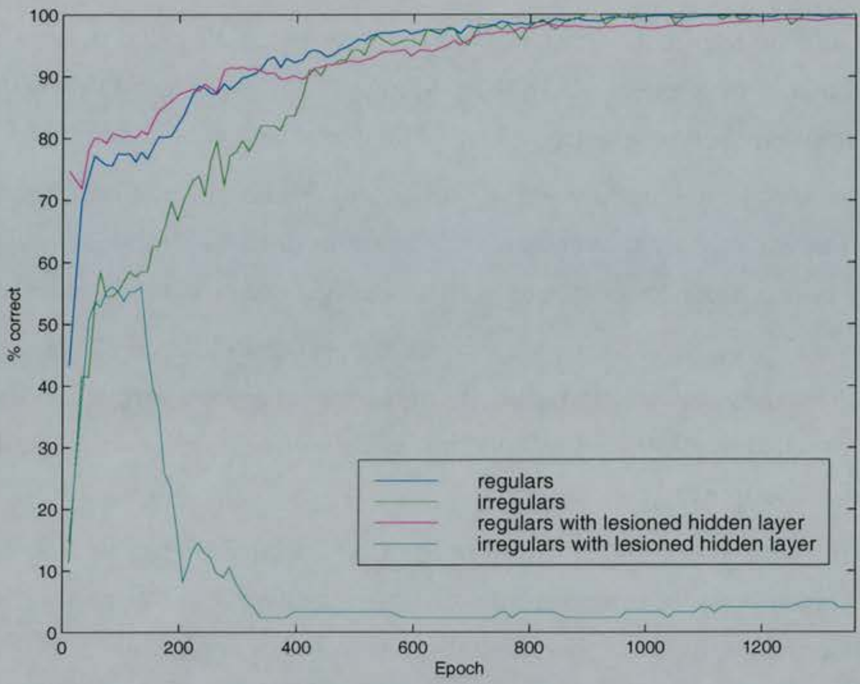

Figure 5.4: The learning curves for the regular and irregular past tense forms in the intact network and with a lesioned hidden layer. The network had learned all verbs after 1358 epochs. For the training parameters see table 5.4.

The process of internal reorganization of the network's representations is illustrated in figure 5.4. This figure plots the learning curve for regular and irregular past tense forms as a function of training epoch. To illuminate the role of the hidden layer in producing the past tense classes of verbs, it was lesioned (the connections from the hidden to the output layer deleted) at different stages during training after the network had been trained with the intact architecture up to that point, and the change in performance was observed. The resulting "lesion-"curves for regular and irregular verbs are also plotted in the figure.

Initially, with only a few hidden units, lesioning the hidden layer has no strong effect on network performance: with or without the hidden layer, performance on the irregular verbs quickly reaches 55%. It then stabilizes at this level until at about epoch 150 a rapid re-organization takes place: while in the intact network irregular performance quickly improves, when the hidden layer is lesioned it drops significantly to under 10%. By contrast, the performance for regular verbs is not affected by the lesioning of the hidden layer: with or without the hidden layer, it increases gradually from 80% to 100%.

This result indicates that even the representations of initially correctly classified irregular verbs are shifted from the direct connections into the growing hidden layer, leading to a breakdown of performance when the hidden layer is lesioned. This reorganization and the further growth of the hidden layer lead in many cases to the temporary wrong production of initially correct irregular past tense forms. The internal reorganization of the network due to a constructivist adaptation of its structure can therefore account for the unlearning of initially correct outputs and for the U-shaped learning curve in the acquisition of the English past tense.

5.5.4 Generalization to Novel Verbs

Generalization to novel verbs is a good test case for the internal representations developed in a model. To evaluate how human subjects inflect novel words, Prasada and Pinker (1993) developed 60 pseudo-verbs and asked subjects to produce the past tense forms of these verbs. The pseudo-verbs were designed to resemble existing regular and irregular verbs to various degrees. *Prototypical pseudo-irregular* verbs rhymed with prototypes of existing irregular clusters; examples are *spling* and *cleed*. *Intermediate pseudo-irregulars* were derived from the prototypical pseudo-irregulars by changing either its initial or its final consonant cluster (e.g., *ning* and *cleef*). *Distant pseudo-irregulars* were derived by changing both the initial and the final consonant cluster of the prototypical pseudo-irregulars (e.g., *nist*, *gleef*). *Prototypical pseudo-regulars* rhymed with many regulars and were designed to have the same vowels as the pseudo-irregular items (e.g., *plip*, *greem*). *Intermediate pseudo-regulars* were very different from existing regular and irregular verbs, beginning with consonant cluster-vowel sequences and ending with vowel-consonant cluster pairs not found in English (e.g., *smeej*, *ploab*). *Distant pseudo-regular* verbs were even more different to existing verbs: they additionally contained final consonant clusters not found in English (e.g., *ploamph*, *smeerg*). The subjects were asked to produce past tense forms for each verb, and they were encouraged to supply multiple forms if they felt them to be appropriate. Then, they had to rate the likelihood of their chosen form to be the "correct" past tense form of the verb.

These experiments had two important results: first, the tendency to inflect pseudo-irregulars as irregular decreased with growing distance from existing irregulars. Second, for pseudo-regulars, regular inflection was high for all groups and did not depend on the similarity to existing regular verbs. Prasada and Pinker interpreted these results as evidence for the dual mechanism theory where irregular forms are stored in an associative memory and regulars are produced by a rule.

The trained CNN was tested on its generalization to these novel verbs. The set of 60 pseudo verbs was transcribed phonologically (appendix D) and presented to the fully trained network. To emulate the situation in the human experiment where the production of multiple past tense forms for each verb was encouraged, all activated outputs that were over the threshold of 0.7 were counted.

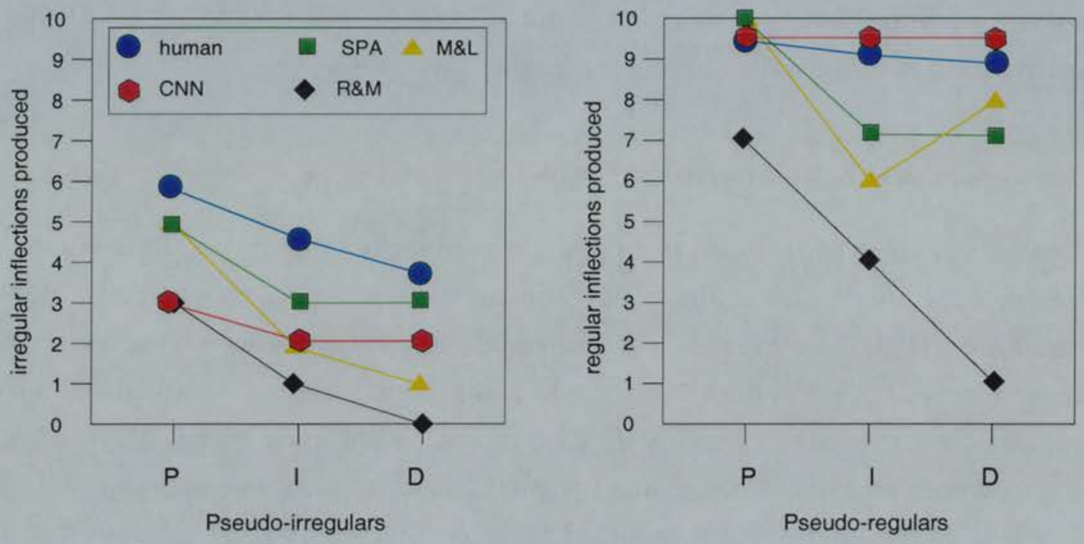

Figure 5.5: Generalization of the CNN to the different classes of pseudo-verbs, in comparison with humans, the SPA, the revised M&L network and the R&M network. P = Prototypical, I = Intermediate, D = Distant. The results are averaged over the six trained networks.

The results of the generalization experiments are shown in figure 5.5 which additionally shows the performance of the human subjects and of the R&M, SPA, and the revised M&L models. The CNN had a stronger tendency to regularize novel irregular-like pseudo-verbs than human subjects but displayed the same tendency as humans in regularizing more verbs with increasing distance from existing irregulars. This tendency is shared by all other models, reflecting the associative-memory nature of their storage of irregulars.

For regular-like pseudo-verbs, the CNN performed more like the human subjects than any of the other models: on average, 28.5 of the 30 pseudo-regulars were regularized, independent of their similarity to existing regular verbs. Even for the most dissimilar group, 9.5 out of the possible 10 regular classifications were produced. This result is in contrast to the other models that show a decline of regular inflection for intermediate and distant pseudo-regulars, and it touches on the main problem of homogeneous architectures: when both regulars and irregulars are stored in associative memory, similarity effects occur as well for regulars. [4] The CNN avoids this problem by exploiting multiple representations for verbs (distributed and localist). It should be noted again, however, that this dissociation between regulars and irregulars in the model is an emergent property of the learning process and is not based on an explicit *a priori* distinction between regular and irregular verbs.

5.5.5 Emergent Dissociations

Functional dissociations between regular and irregular verbs that can be observed in psycholinguistic experiments and also in certain neurological disorders such as agrammatic aphasia and Specific Language Impairment (SLI) have been taken as the main evidence supporting the dual mechanism theory in which these forms are produced by qualitatively distinct mechanisms supported by different neural substrates (e.g., Pinker and Prince, 1988; Pinker, 1991; Marcus *et al.*, 1995; Clahsen, 1999a, see secion 5.3.6).

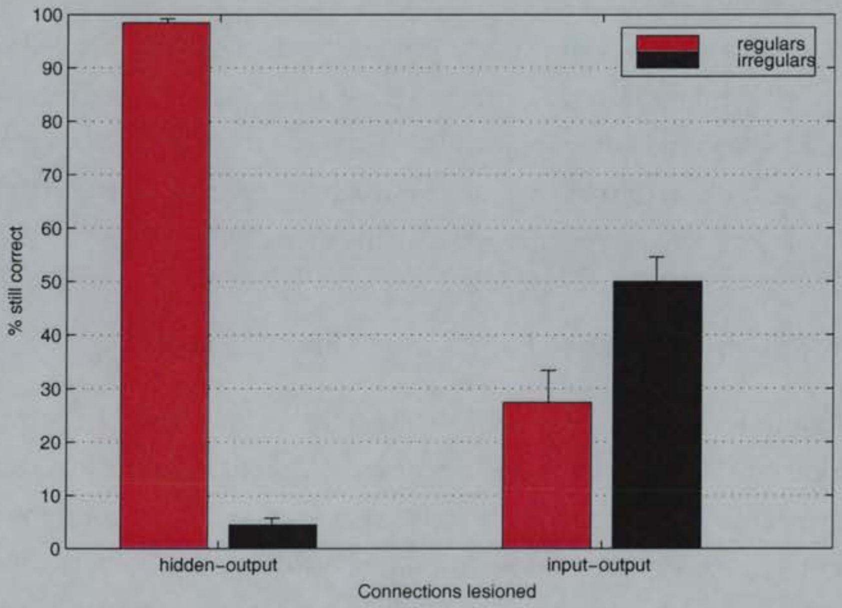

Figure 5.6: The effect of lesioning different pathways on the production of regular and irregular past tense classes.

In the CNN model described here, however, a dissociation between regular and irregular verbs emerged as a direct outcome of the constructivist process, without

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[4] But see (Daugherty and Seidenberg, 1992), where for another set of pseudo-verbs no similarity effects for regulars occured, albeit in a network that had been trained with a very small corpus; see section 5.3.4

having to rely on distinct mechanisms. During learning, the two pathways, the direct input-output connections and the hidden layer, developed to take on specialized functions. While the regular past tense class was produced mainly through the direct Input-Output (IO) connections, most of the irregular classes were produced in the developing hidden layer and the Hidden-Output (HO) connections (see figure 5.4). The double dissociation between regular and irregular verbs in the CNN model is demonstrated by lesioning both the IO and the HO pathways selectively (figure 5.6): lesioning of the HO pathway in the fully trained network left the production of the regular verb class intact (98.5% correct on average) but severely impaired the production of irregular classes (only 4.5% correct on average). 66% of the irregular errors in this case were overregularizations, and in the other cases the network failed to produce any output. By contrast, lesioning the IO connections yielded the opposite profile: here, the production of the irregular classes was less impaired than that of the regular verbs (50.0% vs. 27.4% correct). This functional modularization was not pre-specified but developed solely through the construction of the hidden layer in response to the learning task, and the resulting shift of the internal representations of the irregular verbs to this hidden layer.

The CNN thus suggests an explanation for the dissociations between regular and irregular verbs in human language processing that does not rely on distinct processing mechanisms in separate neural substrates. This aspect of the CNN model will be examined more closely in the next chapter, in which the specific deficits in the inflectional processing of German agrammatic aphasics are modelled.

5.5.6 Producing Past Tense Forms from Class Information

It is not obvious that from the class-information that is learned by the network model, a phonological output form can be easily learned. Without showing that this is possible, one could speculate that a rule is implicitly assumed in constructing the regular past tense form based on the class information, undermining the claim that the constructivist model does not learn in a rule-based way (Marcus, personal communication). Although similar experiments as those described here have also been performed with a phoneme-input-to-phoneme-output mapping and yielded similar results (Westermann, 1997), here an additional experiment was performed in which an extra layer was trained to produce the phonological form of the past tense based on the verb stem together with the learned past tense class. This additional layer can then be integrated with the phoneme-to-class network (fig. 5.7).

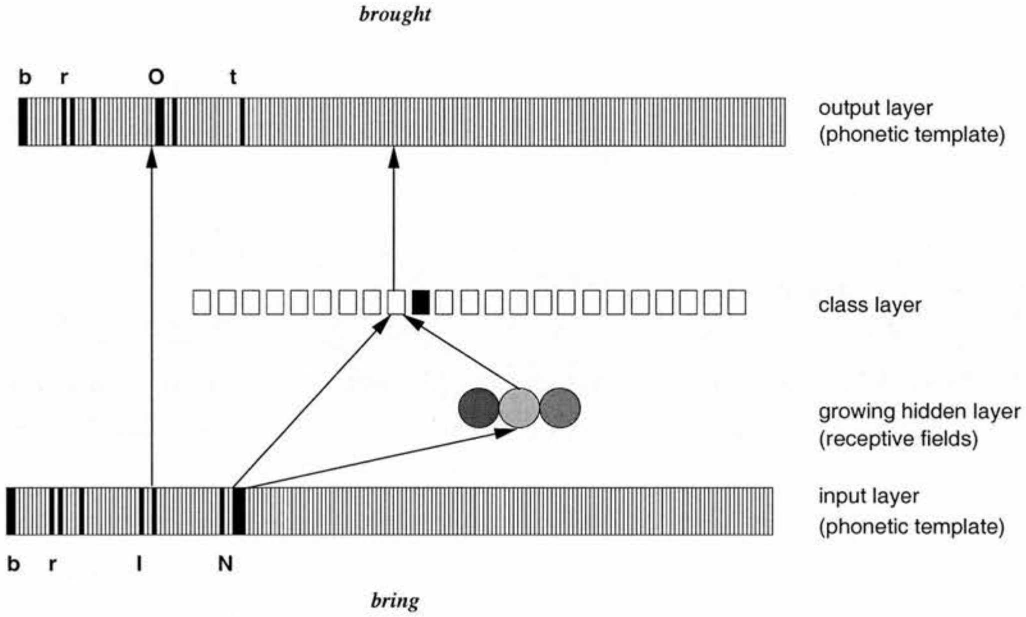

Figure 5.7: The extended network model in which the phonemic past tense form is learned on the basis of the phonemic input and the learned inflectional class.

This network component consisted of two layers: the input layer received the templated phonological representation of the verb stem, and additionally had 23 units for the inflection class information. There was no hidden layer, and the task was to produce in the output layer an equally templated phonological representation of the past tense form of the verb. The weights were adjusted with the quickprop algorithm, with the same parameters as those in table 5.4.

Evaluation proceeded as follows: every output unit with an activation value over a threshold of 0.7 was set to 1.0, and all other units to 0. Then, for each output slot the nearest phoneme was computed by measuring the cosine between the output and phoneme vectors. A closest match was only counted if the cosine was larger than 0.7.

After 210 epochs the network produced all of the 1,066 phonological past tense forms correctly. Since the network had no hidden units, this result shows that the mapping from the stem plus inflection class to the phonological form of the output is a linearly separable problem. The phonological forms of the 60 pseudo verbs were also produced correctly from the input stem and the class output produced in the generalization test, with the exception of a few /th/ that were produced as /z/ - the network had a German accent!

The phonological representation of the past tense can thus be produced either directly in a three layer constructivist network (Westermann, 1997), or in an additional network that is trained on top of the class-learning model presented here. Neither of these processes relies on an explicitly defined rule, and in both models a realistic course of acquisition could be shown.

5.6 Non-constructivist Training

In the previous section it was shown that the CNN outperformed previous models in simulating the acquisition of the English past tense: it displayed a U-shaped learning curve, showed a family effect and a frequency effect in overregularizations, generalized realistically to novel verbs, and developed double dissociations between regular and irregular verbs. In order to establish whether the model's performance was indeed due, as argued, to its constructivist nature, different static, non-constructivist network (NCN) versions of the model were trained on the same data set. For this, the NCN started with a fixed number of hidden units, and no new units were inserted during the training. In order to avoid dead units (i.e., receptive fields not responding to any of the input verbs), the units were randomly placed on the input verbs. The NCNs were based on one of the CNN networks in which the final number of hidden units was 108. To assess the importance of hidden layer size, three non-constructivist simulations were carried out with hidden layer sizes of 78, 108, and 138 units, respectively. The training parameters were the same as in the constructivist case (table 5.4), without those relating to the construction of hidden units. They are repeated in table 5.6 for clarity. The network state was saved every 10 epochs.

	Hidden Unit Parameters	
ϵ	0.2	fraction by which the winning unit is moved
θ_{act}	0.2	threshold that determines which type of hidden unit movement to use
a_{max}	1000	maximum age of edges before they are removed
	Quickprop Parameters (see Fahlman, 1988)	
μ	1.75	maximal allowed jump-size
α_{io}	0.2	learning rate for input-output weights
α_{ho}	0.5	learning rate for hidden-output weights
$sigprimeoffset$	0.1	value added to sigmoid-prime to avoid flat spots
$slopedecay$	-0.0001	factor added to slope to prevent large weights
err_{min}	0.0005	error at which training is stopped

Table 5.6: The parameters used in the training of the NCN models.

Superficially, the results of the NCN resembled those of the constructivist models. The three networks learned all of the regular and irregular inflection classes after 750, 970, and 1000 epochs, respectively. This is faster than the constructivist versions that averaged 1672 epochs, which is due to the fact that receptive fields were initially placed on the verbs, and because the hidden layer was not gradually constructed. Note, however, that since the full network had to be trained from the beginning, the total CPU-time for training was higher for the non-constructivist networks than for the constructivist ones.

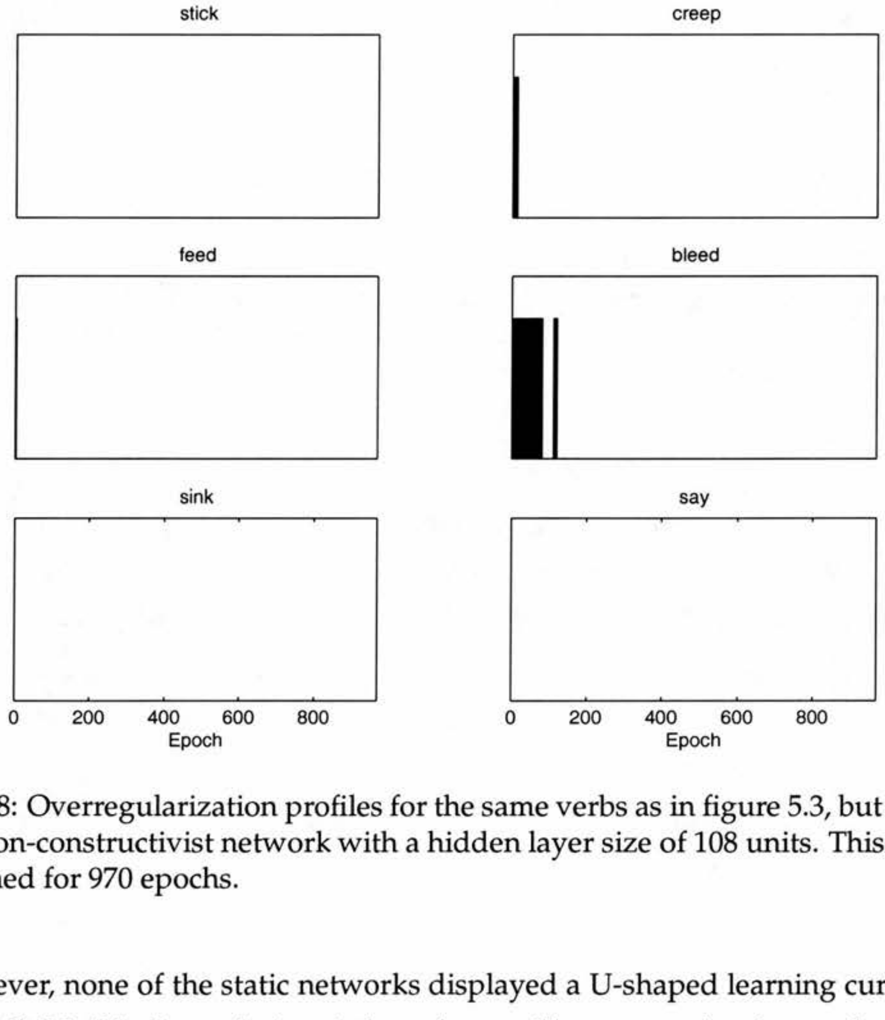

Figure 5.8: Overregularization profiles for the same verbs as in figure 5.3, but this time for the non-constructivist network with a hidden layer size of 108 units. This network was trained for 970 epochs.

However, none of the static networks displayed a U-shaped learning curve in the way the CNN did. Instead, they behaved more like conventional neural networks: with very few exceptions, overregularizations occurred only for a brief period at the beginning of the training, and there was no period of correct production of the irregular verbs before the onset of overregularization. Figure 5.8 shows the overregularization profiles for the six verbs referred to in fig. 5.3 for the constructivist models, this time for the non-constructivist network with a hidden layer size of 108 units, the same

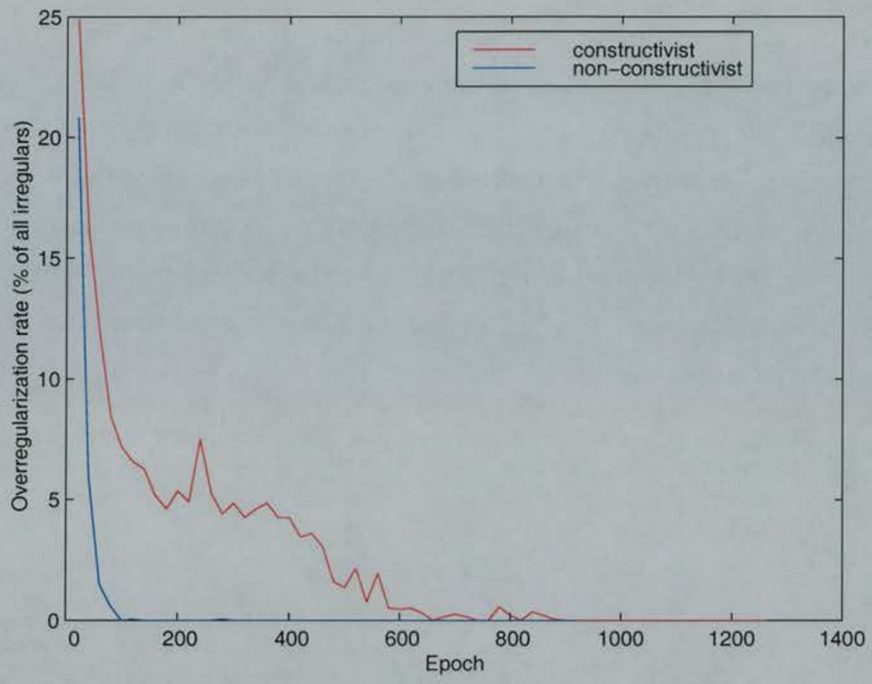

Figure 5.9: The overregularization rate for the constructivist and the non-constructivist networks. The CNN was trained for 1358 epochs and constructed 108 hidden units. The NCN had 108 hidden units and was trained for 970 epochs.

size as the fully trained CNN used for fig. 5.3.

Figure 5.9 displays the overregularization rates for one CNN and the corresponding NCN. While the overregularization rate in the CNN reaches a plateau at 5 to 7% and then gradually decreases to 0%, the NCN overregularizes only very briefly.

In contrast to the CNN, all three static networks failed to display a family effect for overregularizations. The average correlation between family size and overregularization rate was 0.05, compared with -0.11 for the CNN model and -0.08 for children. However, all NCN showed a strong frequency effect (mean correlation between frequency and overregularization rate = -0.46, CNN: -0.37, children: -0.37).

The generalization behaviour of the static networks matched human performance less closely than that of the CNN. Figure 5.10 shows the average generalization of the static networks compared with humans and the CNN, again on the 60 pseudo-words from (Prasada and Pinker, 1993, *cf.* fig. 5.5, p. 118). The static networks failed to model the effect that intermediate pseudo-irregular verbs were less often inflected as irregular than prototypical pseudo-irregulars. Performance for pseudo-regulars was very good, however, and the static network outperformed all previous past tense models except for the CNN, suggesting that a non-homogeneous architecture can be beneficial

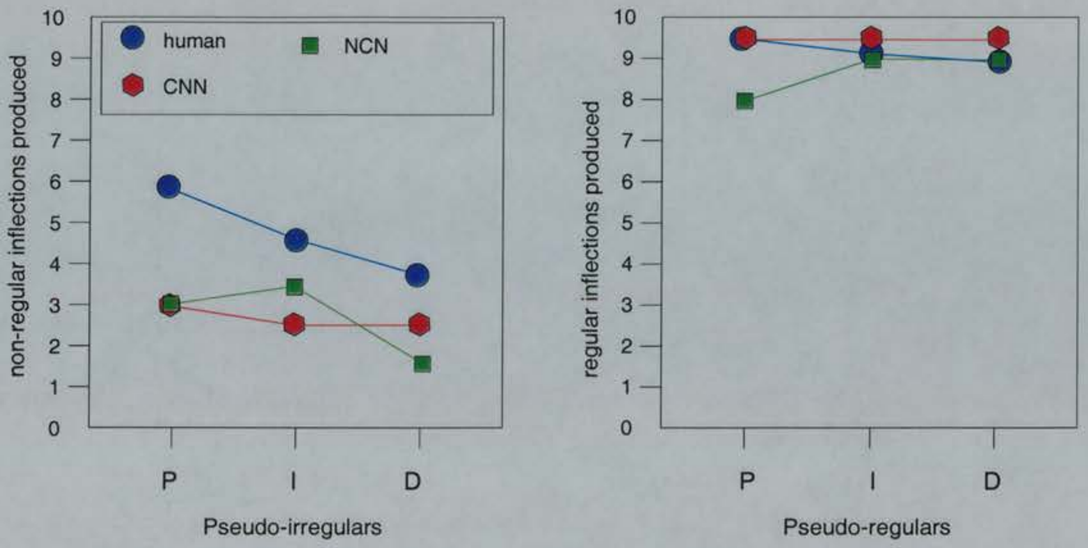

Figure 5.10: The generalization to novel words by the NCN, compared with humans and the CNN. P = Prototypical, I = Intermediate, D = Distant. Results are averaged over the three NCN and six CNN.

even in a non-constructivist system.

In summary, although the static networks learned all regular and irregular inflection classes, they did not display a realistic U-shaped learning curve, they failed to exhibit a family effect in overregularizations, and they modelled generalization to novel irregular verbs less well than their constructivist cousins.

Why do the static networks do worse in accounting for the human data of past tense acquisition? The fact that the NCN do not display the behaviour of the CNN and of children can explained by the absence of an internal reorganization of the verb representations. Whereas in the CNN the representations for the irregular verbs are shifted to the developing hidden layer, in the static version the full hidden layer is available from the start. Figure 5.11 shows the learning curve for regular and irregular past tense classes in the NCN with 108 hidden units. This figure corresponds to fig. 5.4 (p. 116) for the constructivist case where the network developed 108 hidden units during training. In the NCN, lesioning the hidden layer leads to a breakdown in irregular performance from the beginning, while regular performance is only slightly impaired. There is thus no gradual re-location of representations to the hidden layer; instead, the separation between regulars and irregulars occurs already at the beginning of the training.

The early availability of the full hidden layer leads to a less pronounced dissociation between regular and irregular verbs than in the constructivist case: more regular

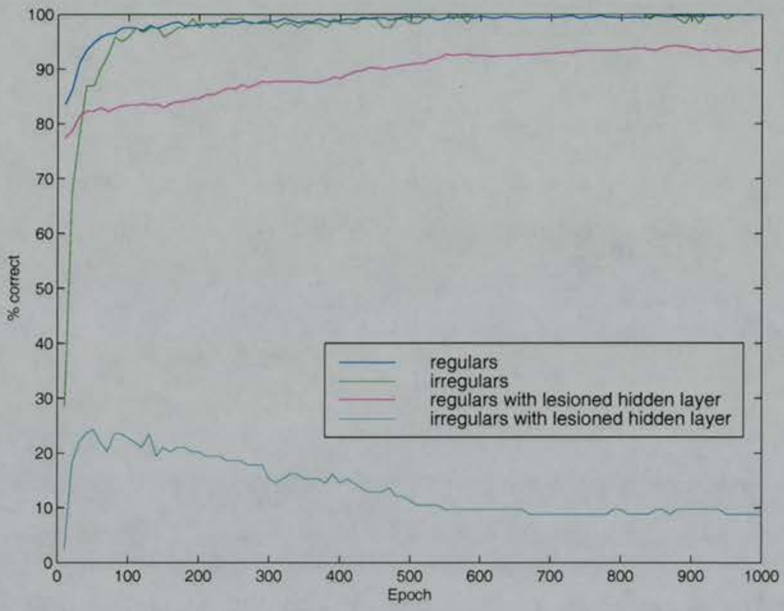

Figure 5.11: The learning curves for the regular and irregular past tense forms in the intact non-constructivist network with a hidden layer size of 108 units, and with a hidden layer that was lesioned at different stages of training, for the non-constructivist network with a hidden layer size of 108 units.

verbs rely also on the hidden layer, and more irregulars on the direct IO connections. Figure 5.12 shows the effect of lesioning the HO connections and the IO connections on the preservation of regular and irregular forms in the constructivist and the static networks. In the static networks, when the HO connections are lesioned, fewer of the regular verbs are preserved than in the CNN, indicating that in those networks more regular verbs rely on the hidden layer for correct production. Similarly, more irregulars are preserved than in the CNN, showing that in the static networks more irregulars are produced in the IO connections alone.

With lesioned IO connections the results are similar: in the static networks, more regular forms are preserved than in the CNN, and fewer irregular forms are preserved. Significantly, the static networks do not display a double dissociation: for both lesioning the HO and the IO connections, regulars are more preserved than irregulars.

This result is also a consequence of the early availability of the full hidden layer: the hidden layer is not employed specifically for the hard, irregular cases, but is used by both regular and irregular verbs early on. This is an example of the "herd effect" (Fahlman and Lebiere, 1990a) where all units in a network try to solve each problem and fail to separate into solving different sub-problems.

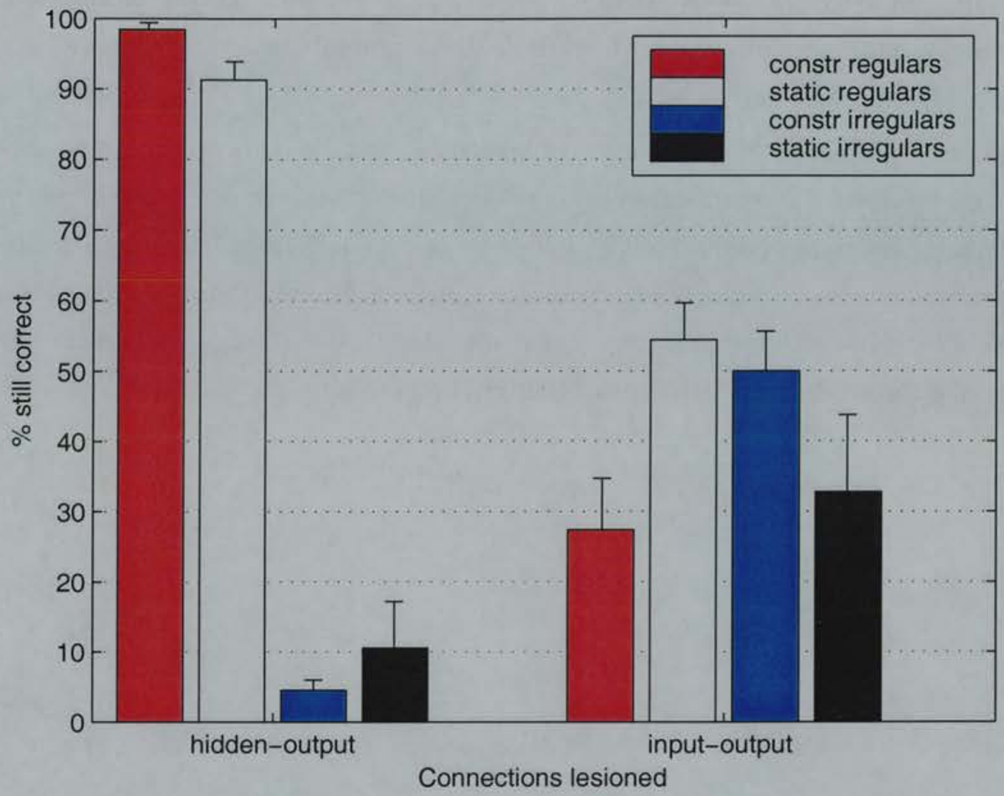

Figure 5.12: Preservation of regular and irregular forms when the hidden-output weights and the input-output weights are lesioned, in the constructivist and the static networks (averaged over six constructivist and three static networks).

5.7 Discussion

The simulations described in this chapter constitute empirical evidence that constructivist neural networks can model the acquisition of the English past tense more closely than other models that rely on fixed architectures. The ability of the CNN to develop its structure in response to the specifics of the learning task not only allowed it to allocate more structure to the difficult-to-learn irregular verbs, but also led to a U-shaped learning curve with realistic frequency and family effects, based on the internal reorganization of representations, and to emergent functional dissociations between regular and irregular verbs. The model thus closely followed the developmental profile observed in children, and reflected in its final architecture properties that are found in adult language processing: it generalized to novel verbs in a way comparable to humans, inflecting pseudo-irregulars depending on their similarity to existing verbs but regularizing pseudo-regulars independently of their similarity to existing regulars. The CNN therefore learned the regular inflection as the default case, applying it to unseen verbs irrespective of how closely they resembled any existing verbs. Lesioning experiments illustrated the double dissociation between regular and irregular verbs that emerged in the CNN.

The only difference between the constructivist and the non-constructivist networks was that in the CNN the hidden layer was gradually built in response to the training data, whereas in the NCN the whole layer was available from the start. The comparison between these two models, in which the CNN modelled the human data more closely than the NCN, therefore suggested that for the modelling of human developmental data a constructivist approach might be necessary.

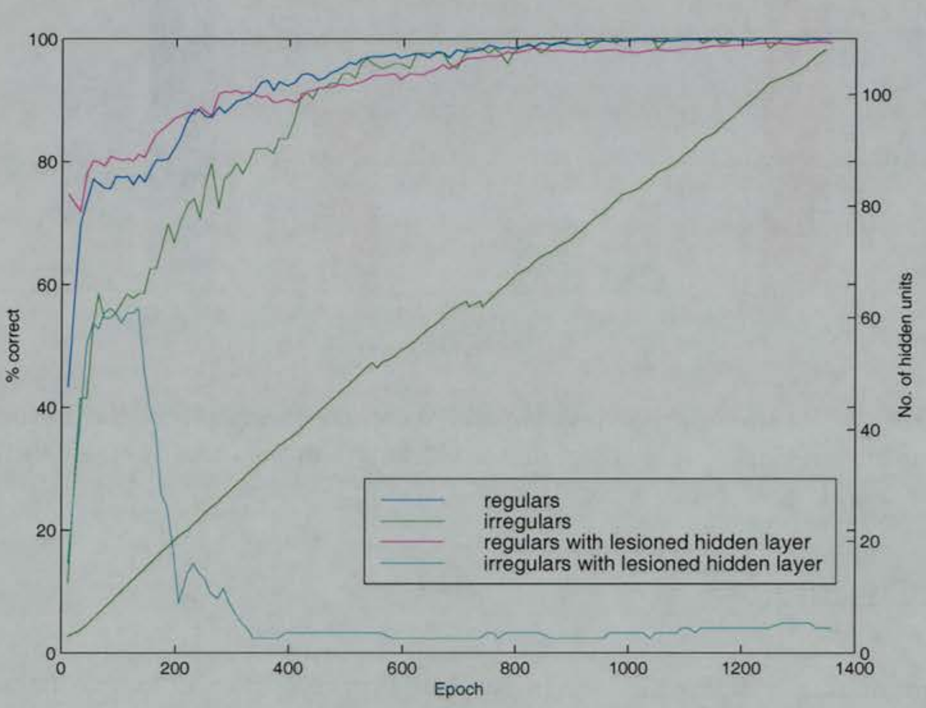

Figure 5.13: The learning curves for the regular and irregular past tense forms in the intact network and with a lesioned hidden layer (*cf.* fig 5.4, p. 116). Additionally, the number of hidden units is plotted. The network was trained for 1358 epochs, developing a hidden layer with 108 units.

The CNN presents further evidence that sudden, nonlinear changes in behaviour need not be based on similar changes in the structure from which the behaviour emerges (e.g. Elman *et al.*, 1996). The rapid re-organization of the network's internal representations that leads to a U-shaped learning curve is not triggered by a nonlinearity in the growth process: figure 5.13 displays again the learning curves for regular and irregular verbs in the intact and lesioned constructivist network (*cf.* fig. 5.4), but this time the number of hidden units is plotted as well. The dramatic and rapid internal reorganisation of the irregular representations onto the hidden layer that starts around epoch 160 and is nearly completed after 40 epochs, takes place during a linear growth of the hidden layer.

While the dissociation in the processing of regular and irregular verbs in children and adults has led to the postulation of a mental rule, the experiments presented here have shown how such a dissociation can emerge from a constructivist learning process in the absence of an explicitly defined rule. Instead, the algorithm allocates structure where and when necessary to solve the problem of past tense inflection, and this process leads to a functional dissociation between verb types. The extraction of a rule from this architecture represents an abstraction of the observed regularities and is a separate process from learning the past tense inflection system. In this way, the rule is a consequence, not the origin, of the learning process.

It is interesting to note that the previous model that was closest in performance to the CNN is the symbolic SPA (Ling and Marinov, 1993; Ling, 1994): it performs well on learning the training data (table 5.5) and on generalizing to novel verbs (fig. 5.5), but it was not tested for frequency and family effects, or for functional dissociations. The SPA was developed as an alternative to neural network models of past tense inflection, contributing to the debate between "symbolic" and "subsymbolic" processing. While Ling (1994) attributed the success of the model to its symbolic nature, in the light of the present results a more convincing explanation might be that its success was due to its constructivist nature: the SPA builds a decision tree based on ID3 (Quinlan, 1986), adding branches in response to the training data as it is encountered. Like in the CNN, the final architecture of the decision tree is thus a direct outcome of the structure of the training data. Based on this view it seems plausible that the dichotomy *constructivist* vs. *non-constructivist* is more fundamental than the traditional *symbolic* vs. *subsymbolic* distinction that previous past tense models have aimed to emphasize. Direct comparisons between symbolic and subsymbolic models can thus only be made either within or without the constructivist framework, with constructivist models conforming better to evidence from neural and cognitive development.

However, the distinction between symbolic and subsymbolic processing is still relevant (see e.g., Smolensky, 1988; Fodor and Pylyshyn, 1988; Seidenberg, 1994; Marcus, 1999a; Seidenberg and Elman, 1999b; Marcus, 1999b; Christiansen and Curtin, 1999; Marcus, 1999c; McClelland and Plaut, 1999; Elman *et al.*, 1996; Marcus, 1998b): in contrast to the SPA, the CNN was able to model realistically a U-shaped learning curve, and this ability was based on its connectionist architecture which allowed for the re-location of representations from one set of weights to another and led to an associative-memory based family effect in overregularizations.

Finally, it is important to note that much of the criticism against connectionist models of cognitive development implicitly assumes that such models have a homogeneous architecture, e.g., a common three-layer backpropagation network (e.g. Clahsen, 1999a). In such models it is indeed difficult to find the detailed functional dissociations that exist in human processing (but see differing opinions such as Plunkett and Marchman, 1991, 1993; Daugherty and Seidenberg, 1992; Elman *et al.*, 1996; Plunkett *et al.*, 1997). However, the CNN is a non-homogeneous neural network: with the growing hidden layer, two pathways develop: the direct connections from the input to the output layer, and the hidden layer. As such, the CNN is a counterexample to the close association of neural network models with a homogeneous architecture.[5]

In contrast to the dual mechanism theory that postulates two qualitatively distinct processing mechanisms in the production of regular and irregular forms, the CNN shows how a distinction between these inflection types can emerge based on a single associative mechanism.

Taken together, these results suggest a classification of models of cognitive development along four dimensions:

1. symbolic vs. subsymbolic processing
2. homogeneous vs. non-homogeneous architecture
3. static architecture vs. constructivist development
4. single mechanism vs. multiple mechanisms

The CNN is, in this classification, a subsymbolic, non-homogeneous, constructivist single-mechanism model. The neural networks of R&M, M&L, D&S and P&M are subsymbolic, homogeneous, static single-mechanism models, the SPA is a symbolic, (presumably) non-homogeneous, constructivist single-mechanism system, and the (not implemented) dual mechanism theory is a hybrid, non-homogeneous, static multiple-mechanism theory. The results described in this chapter suggest that subsymbolic, non-homogeneous, constructivist single-mechanism systems might represent the most realistic models of past tense and, perhaps, cognitive development.

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[5] The question of how to describe the non-homogeneous architecture will be discussed further in chapter 6.

5.8 Chapter Summary

The acquisition of the English past tense has become a benchmark test for different modelling paradigms. In this chapter, a constructivist neural network (CNN) model of past tense acquisition was presented and its performance was compared directly with other, previous models. In contrast to the previous models, the CNN learned all training data and displayed a realistic, U-shaped learning curve, modelling even detailed phenomena of children's overregularization. In comparisons with a non-constructivist version of the same model it was established that this close modelling of the human data was due to the constructivist growth process that allocated resources where and when needed and led to a rapid, non-linear internal reorganization of representations and a functional dissociation between regular and irregular inflections. The CNN also generalized well to novel verbs, indicating that it had learned the regular inflection as the default. Based on these results, a new four-dimensional classification for cognitive models was suggested.

In the next chapter the CNN is extended to model impaired adult inflectional processing, and based on this model an alternative to the dual mechanism theory of verb inflection is developed.

Chapter 6

Modelling Inflectional Processing in Agrammatic Aphasia

6.1 Introduction

In order to understand the mechanisms of language and cognitive processing, investigating the course of acquisition of language and cognitive skills is one useful aspect. Therefore, in the previous chapter a model of English past tense acquisition was developed that could account for the phenomena occurring in child language acquisition such as a U-shaped learning curve and overregularization effects. Based on these results, it was argued that the cognitive architecture underlying verb inflection could be a constructivist learning system that develops two types of representation for each verb and produces the inflected form based on a single associative mechanism.

In this chapter, this model is extended to account for adult language processing, which is the second main aspect in the study of the language system. As in children's acquisition of the English past tense, studies of adult language processing have indicated a dissociation between regular and irregular cases. The model developed here explores the case of participle inflections in agrammatic aphasia to examine whether the developed dissociations correspond to those found in impaired adult processing.

At the same time as turning from child language acquisition to adult processing, empirical research has turned to other languages than English, because English confounds frequency and regularity: the regular English past tense applies to the majority of all verbs, and it is therefore impossible to decide whether the regular case is learned as a rule or because of its majority, making a distinction between rule-based and associative systems difficult. However, frequency and regularity are not necessarily correlated. For example, in the German participle, the regular case applies to less than half of all verb tokens, and in the German plural, only 7% of all noun tokens take the *-s* plural which has been argued to be the regular ending (Marcus *et al.*, 1995). By studying these so-called *minority defaults*, it becomes possible to separate regularity and high frequency.

6.1.1 Dissociations in Adult Inflectional Processing

The evidence for dissociations between regular and irregular inflections in adult processing has been established through a variety of approaches, and in different languages and inflectional systems. These results have mainly been taken as evidence for the dual mechanism theory of inflection (e.g. Marcus *et al.*, 1995; Pinker, 1997a,b; Clahsen, 1999a), albeit without contributing anything to its specification.

Novel words are readily inflected as regular unless they are similar to existing irregulars (e.g., Prasada and Pinker, 1993; Marcus *et al.*, 1995; Clahsen, 1997, see also the previous chapter), and regularly inflected unusual words (e.g., verbs that are derived from nouns, or originally irregular nouns that are presented as proper names, e.g., "John and Julia Child" are the "Childs", not the "Children") are judged as better by subjects than those inflected as irregulars (Kim *et al.*, 1991; Marcus *et al.*, 1995). In visual lexical decision tasks where subjects have to decide as quickly as possible if a string seen on a screen is an existing word, frequency effects are found for irregulars but not for regulars (Prasada, Pinker, and Snyder, 1990; Clahsen, Eisenbeiss, and Sonnenstuhl, 1997b), although other researchers have reported frequency effects for regularly inflected forms as well (Baayen, Dijkstra, and Schreuder, 1997). Moreover, incorrectly inflected regular and irregular forms, respectively, result in different response times in sentence matching experiments (Clahsen *et al.*, 1997b) and they elicit different ERPs (Weyerts *et al.*, 1997; Penke *et al.*, 1997; Say, Kleingers, Clahsen, and Munte, 1998).

Results from priming experiments show a less clear-cut distinction between regulars and irregulars. In these experiments, an inflected form of a word (e.g., *laughed*) is shown to a subject on a screen, followed by the stem of that word (*laugh*). Having seen the first word might reduce the response time for deciding if the second stimulus is in fact an existing word. Such priming effects have been reliably found for regulars (e.g., seeing *looked* reduces the response time for a subsequent *look*), but different researchers have reported different results for irregular cases, from no priming via reduced to full priming (see Clahsen, 1999a, for references). Recent results have also established different ERPs in the priming of regular and irregular English past tense forms (Munte *et al.*, 1999).

Dissociations between inflection types have also been found in children with developmental disorders, namely Specific Language Impairment (SLI) and Williams Syndrome. While it does not seem, as sometimes argued (e.g. Ullman and Gopnik, 1999), that these disorders allow a dissociation of language abilities from other aspects of cognition (Bates *et al.*, in press), they nevertheless show a dissociation within the language system (which might stretch into other cognitive domains as well) between regular and irregular cases (Clahsen and Almazan, 1998). In Williams Syndrome, despite a low IQ, inflection of regular verbs is not impaired, whereas irregular inflection is impaired. The opposite profile can be found in SLI subjects where regular inflection is more impaired than irregular inflection.

Significantly for the simulation in this chapter, dissociations between regular and irregular inflections have also been found in impaired adult processing, namely, in acquired agrammatic aphasia. Here, subjects show difficulties in producing irregular participles (Penke, Janssen, and Krause, 1999, these results will be discussed in more detail below as they form the basis of the simulations presented in this chapter). However, priming experiments with English agrammatic aphasics (Marslen-Wilson and Tyler, 1997, 1998) have established the somewhat confusing result that irregular priming is preserved whereas regular priming is not. The opposite case was found in a subject with more extensive brain damage, particularly in the right hemisphere. These subjects were not assessed for their ability to produce regular and irregular inflections, however, although their comprehension was selectively disturbed for regular cases. The significance of a possible selective impairment of regulars will be discussed below.

The rest of this chapter is organized as follows: in section 6.2, the structure of the German participle is described. Section 6.3 returns to the dual mechanism theory already briefly described in section 5.3.6 and discusses it in the broader context of adult language processing. Section 6.4 gives details about agrammatic aphasia and the dissociations between inflection classes that have been observed in this disorder. Sections 6.5, 6.6, and 6.7, respectively, describe the adaptation of the constructivist model to the participle task, the training data, and the training procedure. The results of the simulations are reported in section 6.8, and section 6.9 discusses how they contribute to the understanding of inflection processing in humans.

6.2 The German Participle

German participles are comparable in usage to the English past tense in describing an event in the past. There are three groups of participles: *Weak* participles are formed by a (prosodically determined) prefix *ge-*, the verb stem, and the ending *-t*, e.g., *sagen* (say) → *gesagt* (said), *lachen* (laugh) → *gelacht* (laughed). *Strong* participles take the ending *-en*, e.g., *geben* (give) → *gegeben* (given) and they may also change the verb stem, e.g., *gehen* (go) → *gegangen* (gone), *nehmen* (take) → *genommen* (taken). A few strong verbs have idiosyncratic participle forms, e.g., *sein* (be) → *gewesen* (been). The third group are *mixed* verbs that take the weak ending *-t* but change their stems like strong verbs: *wissen* (know) → *gewusst* (known), *denken* (think) → *gedacht* (thought). Like in English, the participles are combined with a modal verb (*sein* (be) or *haben* (have)) to form different perfective tenses (present perfect, past perfect, future perfect). It is generally claimed that the weak verbs form the regular class, while strong verbs are irregular, and the terms regular and irregular will here be used in this sense.

The CELEX database (Baayen, Piepenbrock, and van Rijn, 1993) lists 3015 German participles with a frequency of at least one. After cleaning out some obvious errors and homophones and choosing the more frequent of different participle forms of one stem, the remaining corpus of 2992 verb types has the distribution shown in table 6.1.

	type		token	
Regular	1936	(64.7%)	40196	(46.9%)
Irregular	956	(32.0%)	41276	(48.1%)
Mixed	100	(3.3%)	4243	(5.0%)
Sum	2992	(100.0%)	85715	(100.0%)

Table 6.1: Distribution of the participles of the different verb groups in German (analyzed from the CELEX database).

As indicated above, in contrast to English, German does not have a majority of regular tokens, and the majority of types is less pronounced than in English (*cf.* table 5.1, p. 109).

6.3 The Dual Mechanism Theory Revisited

In this section I am returning to the Dual Mechanism Theory (DMT) that was already briefly discussed in the context of past tense acquisition (section 5.3.6).

The DMT was developed to account for the dissociations between regular and irregular inflections (Pinker and Prince, 1988; Pinker, 1991), and in turn these dissociations have been taken as evidence for the DMT (Marcus *et al.*, 1995; Jaeger *et al.*, 1996; Marslen-Wilson and Tyler, 1997, 1998; Clahsen, Bartke, and Gollner, 1997a; Ullman *et al.*, 1997; Clahsen and Almazan, 1998; Clahsen, 1999a; Ullman and Gopnik, 1999).

Regular and irregular inflections are claimed to be processed in locally distinct brain areas, by qualitatively different processing mechanisms. Similar dual-route models have also been described to account for the reading of familiar and non-words (e.g. Coltheart, 1978; Reggia, Marsland, and Berndt, 1988; Coltheart, Curtis, Atkins, and Haller, 1993), arguing for the rule-based production of "regular" pronunciations and a lexical look-up for exceptions and nonwords. In the DMT, these mechanisms are claimed to be a mental rule for the regular case, and an associative memory-type lexicon for irregulars. However, although the DMT has become a dominant theory of inflection processing (Pinker, 1994, 1999) a closer look reveals serious flaws that will be discussed in the following sections.

6.3.1 Why the Dual Mechanism Theory Does Not Work

The DMT was originally formulated in a criticism of Rumelhart and McClelland's (1986) neural network model of English past tense learning (Pinker and Prince, 1988). It was born out of the insight that the regular past tense ending *-ed* is productive and readily applies to novel verbs, whereas irregular verbs show associative effects such as phonologically similar sub-groups (*sing*, *ring*, *spring*). Therefore, an intuitively attractive assumption was to postulate two separate mechanisms in their production. But there are two main problems with the DMT that make it seem untenable as a general theory of inflectional processing: first, although it can intuitively describe the dissociations between regular and irregular inflections, it is too underspecified to explain in detail how inflections are produced. Second, although it could account for the data at the time of its publication, newer evidence contradicts its most fundamental predictions.

6.3.1.1 Underspecification of the Dual Mechanism Theory

The DMT is highly underspecified. In particular, if regular and irregular forms are produced by different mechanisms, it is necessary to explain how these mechanisms interact to produce an inflected form. One such explanation was put forward by Marcus *et al.* (1995): they argued for a *Blocking Principle* in which an entry in the associative lexicon blocks the application of the mental rule. Although this principle can intuitively explain why novel verbs and verbs that are derived from nouns are preferentially inflected as regulars (i.e., because they do not have a lexical entry), its formalization has not been achieved. Nakisa, Plunkett, and Hahn (1997) performed comparisons of implemented single- and dual-mechanism models of inflections and showed that a dual mechanism implementation incorporating the Blocking Principle yields no advantages in the performance of single-mechanism models. This is because in an associative memory, activation of an entry is not binary, but entries can be partially activated depending on their similarity to the input. Therefore, a similarity threshold parameter has to control whether the lexical entry is chosen or the the default rule is activated. However, the setting of this parameter is problematic: if a regular verb is similar to an irregular, this irregular might wrongly be activated and produce an irregular inflection. To avoid this, the threshold must be high enough not to activate e.g., *feel* when the past tense of *peel* is to be produced, or *hear* for *fear*, *fly* for *try*, or *wake* for *ache*. At the same time, the threshold must be low enough to account for the irregularization of novel words that are similar to irregulars (e.g. Prasada and Pinker, 1993), where e,g, *spling* will be inflected as *splang*. The problem of having to find a suitable threshold parameter arises from the fact that in the DMT, irregular inflections can be produced based on the similarity to other existing irregulars, whereas regular inflections of both existing and novel verbs, neither of which have lexical entries, are solely based on the *dissimilarity* to existing *ir*regulars. In their implementations, Nakisa *et al.* (1997) found that no value of the threshold parameter accounted for these cases, given a realistic distribution of regular and irregular verbs. Thus, while it is important to specify the interactions between associative and rule mechanism, the implementation of the Blocking Principle proposed by Marcus *et al.* (1995) did not yield positive results. Indeed, a recent comprehensive exposition of the dual mechanism theory (Clahsen, 1999a) makes no reference at all to possible interactions between the two mechanisms, leaving the theory even less specified than before.

Another aspect where the DMT is underspecified concerns what exactly is stored in the lexicon for the formation of irregular past tenses. Pinker (1991) claimed that irregular forms are stored fully in the lexicon and used this as the explanation why irregular, but not regular forms can occur in compounds (e.g., *mice-infested* vs. **rats-infested*), namely, because they are not assembled by a rule but are retrieved from the lexicon.[1] However, if full irregular forms are stored it is hard to explain the productive use of irregular inflection. For example, a pseudo verb that is similar to an existing irregular should then produce the past tense of that irregular. In the case of *spling*, which is similar to *spring*, the past tense would be produced by retrieving the full

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[1] Whether the "no regulars in compounds" rule holds for German as well is highly controversial: here, the regular genitive ending *-s* occurs in composita (e.g., Landesverräter) as well as the arguably regular plural ending *-en* (e.g., damenhaft) (Penke, personal communication). Clahsen (1999b), however, defends the rule even for German by claiming that the genitive *-s* is really a linking morpheme, and that *-en* is not a regular plural.

stored form associated with *spring*, i.e., *sprang*. In this view there is thus no way in which novel irregular past tense forms can be produced, a prediction that is clearly out of line with the evidence (Prasada and Pinker, 1993).

A different approach to lexical storage is taken in Minimalist Morphology (Wunderlich and Fabri, 1995): here, each irregular stem is connected to a transformation rule (e.g., *spling*—[. . . æ . . .]), whereas regulars are combined with a separate lexical entry of an inflectional ending ([-ed]). While such a system can account for novel irregulars, it now becomes more difficult to distinguish between those items for which the regular rule has been applied and that cannot be used in compounds, and those for which an irregular rule has been applied and that can occur in compounds. While this point might seem pedantic, it is often on these detailed questions that formalizations fail.

6.3.1.2 Blends between Regulars and Irregulars

Both in language acquisition and in adult language processing, forms can be found that combine regular and irregular elements. Such forms should not exist according to the DMT where processes are strictly separated and encapsulated.

One example of such blends are German mixed verbs: these verbs, which represent about 5% of all participle tokens, combine a strong stem change with the weak *-t* ending (e.g., *denken—gedacht*). Therefore, either an interaction between regular and irregular mechanisms must be assumed, or *-t* has to be considered as both a weak and a strong ending because mixed participles are stored as full forms in the lexicon. Neither option agrees well with the DMT, and mixed verbs are usually ignored in discussions of how the DMT can explain verb inflection (e.g. Clahsen, 1999a).

A similar problem of blending between the two mechanisms concerns the acquisition of the English past tense: here, children occasionally make mistakes such as *broked* and *tooked*, where the regular ending is attached to an irregular past tense form (e.g., Marcus *et al.*, 1992). In the DMT, the activation of an irregular entry would have to be strong enough to produce a form like *broke* which would then have to act as input to the rule mechanism which is not blocked by the activated irregular entry. While such a scenario is in theory possible, its formalization poses a difficult challenge when a threshold parameter for the interactions between the mechanisms is assumed.

Further, the DMT cannot account for a grading of regularity: it has been established in different inflectional systems that regular inflections can be graded depending on their similarity to irregulars: in the generation of English past tense forms, regulars that are similar to irregulars show higher response latencies than those that are dissimilar to irregulars (Seidenberg and Bruck, 1990; Seidenberg, 1992). In German agrammatic aphasics, irregular-like regulars are more impaired than other regulars (Penke *et al.*, 1999). Further, regular forms that are claimed to be produced by a rule in all cases have been shown to be instead stored in the lexicon under certain circumstances: in Dutch, regular noun plurals ending in *-en* behave like irregulars in response-time experiments, indicating that they are stored in the lexicon (Baayen *et al.*, 1997). In the English past tense, frequent regular past tense forms are less prone to mispronunciations than infrequent ones; a result that can be best understood by assuming the storage of the inflected form (Stemberger and MacWhinney, 1986). These results directly contradict the predictions of the DMT where the regular inflection is created "on the fly" and not stored, and they seem to be more in line with a view of regularity as a continuum (e.g. Daugherty and Seidenberg, 1992; Westermann, 1995).

6.3.1.3 Impairment Profiles

It is unclear whether an agrammatic aphasia profile exists where regular verbs are selectively impaired and irregulars are preserved. Although such profiles have been reported in the English past tense based on priming (Marslen-Wilson and Tyler, 1997, 1998) and production and reading (Ullman *et al.*, 1997) experiments, in English the issues of regularity and separable ending are confounded because the regular case is the only one that receives an ending. A selective impairment for regulars could therefore be an impairment of suffixation in general. This confound is avoided in e.g., the German participle where both regular and irregular verbs have separable endings (*-t* and *-en*, respectively). For German, in 11 agrammatic aphasic subjects studied by Penke *et al.* (1999) none showed a selective sparing of irregulars. More research will be needed to resolve this question.

6.3.2 Summary for the Dual Mechanism Theory

Taken together, the DMT seems like a good first approximation of the mechanisms of verb processing, explaining dissociations between regular and irregular inflections. However, it does not stand up to formalization and is directly contradicted by more recent data. The postulation of two mechanisms might therefore be a post hoc rationalization of the observed dissociations.

In the rest of this chapter I will develop a theory of inflectional processing that is based on the constructivist CNN model, and I will show how a single mechanism together with a constructivist learning process can lead to a system with emerging double dissociations between regular and irregular verbs. I will show how the empirical data contradicted by the DMT can be modelled with the CNN.

6.4 Agrammatic Aphasia

Agrammatic (Broca's) aphasia is a language disorder that is typically caused by a stroke or injury affecting the posterior portion of the third frontal convolution of the cortex (the peri-Sylvian region, Broca's area), and the surrounding motor and premotor areas as well as underlying white matter and the insula (figure 6.1).

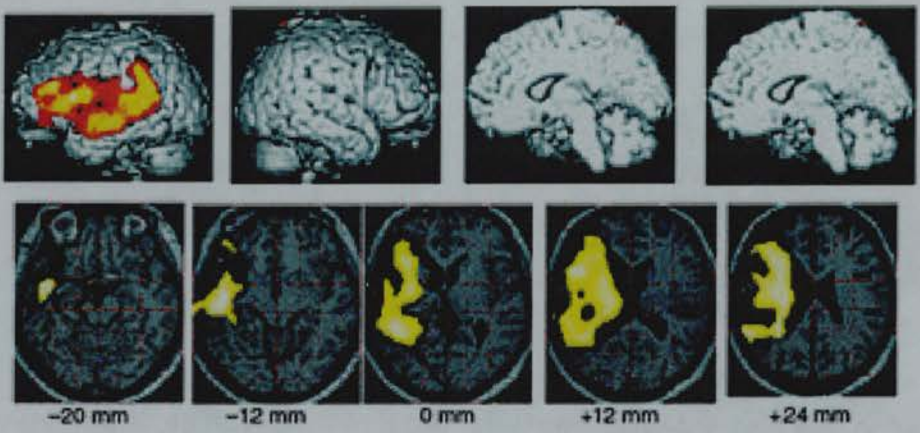

Figure 6.1: Area of brain damage in a subject that displayed agrammatic aphasia. The upper four images are 3D reconstructions based on a structural MRI scan. The bottom five images show transverse sections through the patient's brain, showing the deeper regions of the damage to the left frontal and temporal lobes. There is extensive damage to Broca's area and the surrounding areas, but no damage to the right hemisphere. (Reprinted from Marslen-Wilson and Tyler, 1998).

Patients suffering from a lesion in this area often show the symptoms typical of agrammatic aphasia: slow, halting speech which is telegraphic in that many nonessential words are left out and sentences are formed just with important content-words. Goodglass (1976) gave an example from the speech of a patient who is trying to explain that he has returned to the hospital for work on his gums:

> *Ah … Monday … ah, Dad and Paul Hanney [*referring to himself by his full name*] and Dad … hospital. Two … ah, doctors … , and ah … thirty minutes … and yes … ah … hospital. And, er, Wednesday … nine o'clock. And er Thursday, ten o'clock … doctors. Two doctors … and ah … teeth. Yeah, … fine.* (cited from Ellis and Young, 1988)

Comprehension in agrammatic aphasia is also impaired, especially when it involves more complex syntactic knowledge such as passives and embedded sentences. In a sentence such as "The girl is kissed by the boy", aphasics might therefore have difficulty in deciding who is kissing whom.

One of the characteristic symptoms of Broca's aphasia that is of interest here is the tendency to omit or substitute inflectional morphemes. Where a word without an inflectional morpheme is a real word in itself (e.g., English *walked* → *walk*), the inflectional morpheme is often omitted. In cases where omission of the morpheme would lead to a non-existing word (e.g., Italian *rossa* → *ross*), it is either preserved or substituted with another morpheme (e.g., *rosso*) (Grodzinsky, 1984).

Investigating the precise nature of the inflectional morphology deficits in agrammatic aphasia can therefore lead to insights into the representation of inflections in the brain. For this purpose, Penke *et al.* (1999) analyzed data from eleven German agrammatic aphasics who had been classified with the *Aachen Aphasia test-battery* (Huber, Poeck, Weniger, and Willems, 1993). All subjects were right-handed native speakers (age 22–63, average age 50), without language problems prior to aphasia, and had suffered a left hemispheric insult at least three years prior to the investigations. Their behaviour had therefore stabilized.

The subjects each had to produce 39 regular and 39 irregular participles in a sentence completion task, transforming a given first person singular present verb (e.g., (ich) *gebe*) into the appropriate participle (*gegeben*). Penke *et al.* varied the verbs that were used in the experiments with respect to lemma frequency, participle frequency, and frequency of ablaut patterns, and they analyzed their results for regular and irregular errors, overregularizations and irregularizations, frequency effects, and effects of ablaut-patterns on error rates.

Penke *et al.* (1999) found that six of the subjects produced significantly more errors with irregular than with regular participles. Two subjects made too few errors for statistical evaluation, and three subjects showed no significant difference in error rates between regular and irregular participles. They also found that the subjects with no impairment of regular verbs tended to overregularize irregular participles, while they only rarely irregularized regular participles. Further, when the subjects were tested on the inflection of pseudo-verbs, all but one preferred the regular to the irregular case, a result that is in line with data from unimpaired subjects (e.g. Prasada and Pinker, 1993). Taken together, whereas a selective impairment of irregulars occurred in 6 of the 11 subjects, none of the subjects displayed a selective impairment of regulars. Penke *et al.* interpreted their results as evidence for a theory of verb inflection where regular and irregular participles are produced by two qualitatively distinct mechanisms, affix-based for the regulars, and stored for the irregulars.

The aim of the constructivist network simulations described here was to model the results obtained by Penke *et al.*, while providing an alternative explanation that does not rely on a qualitative distinction between regular and irregular verbs.

The results obtained by Penke *et al.* were slightly re-interpreted for the simulations reported here: whereas Penke *et al.* did not analyze errors that were not overtly marked as participles, these were counted as wrong for comparison with the simulations.

6.5 The Network Model

The simulations described here employed the CNN network model that was also used for the modelling of past tense acquisition in the previous chapter. Additionally, simulations were run with the Supervised Growing Neural Gas algorithm (Fritzke, 1994a), with very similar results (Westermann *et al.*, 1999).

Figure 6.2 shows the network architecture. Like in the past tense model, the input layer takes a phonological representation of the verb infinitive, and the output layer has one unit for each possible output class (see below). The hidden layer initially consists of only two units but is grown during learning. There are full direct connections from the input to the output layer, and each inserted hidden unit is fully connected to the output layer.

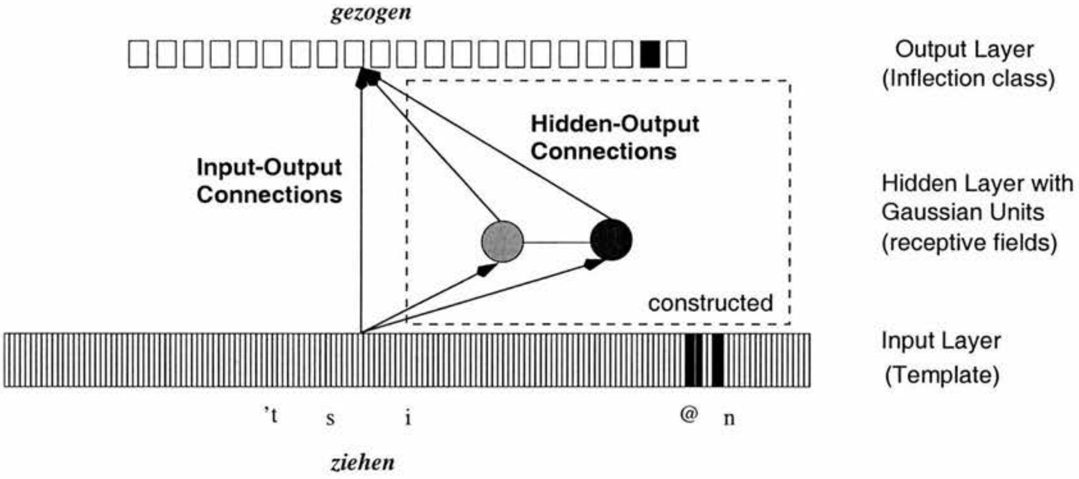

Figure 6.2: The initial architecture of the network. The input and output layers and the hidden and output layers are fully interconnected.

6.6 Data

German verbs are often formed by modifying other existing verbs with a separable prefix or particle, e.g., in the CELEX database the simplex verb *fahren* (drive) occurs in 28 composite forms (*hinausfahren, losfahren, hinfahren, festfahren, vorfahren, radfahren, ausfahren, fortfahren, mitfahren, auffahren, anfahren, abfahren, zurückfahren, heimfahren, hochfahren, umfahren, weiterfahren, totfahren, zusammenfahren, zufahren, durchfahren, heranfahren, einfahren, vorausfahren, vorbeifahren, nachfahren, wegfahren, fahren*). Since a prefix does not alter the way in which the participle of a simplex verb is formed, all composite forms were combined into one simplex form, e.g., the 28 types made from *fahren* were added up into the single type *fahren*. This simplification of the corpus considerably altered its type distribution (table 6.2): the total number of types reduced from 2992 to 1140, showing that 1852 types in the original corpus (table 6.1, p. 136) were composite verbs. The type frequency of regular verbs increased dramatically from 64.7% to 86.7%, indicating that most of the composite verbs that were lost in the simplex version were irregulars.

	type		token	
Regular	988	(86.7%)	40196	(46.9%)
Irregular	139	(12.2%)	38190	(44.6%)
Mixed	13	(1.1%)	7329	(8.5%)
Sum	1140	(100.0%)	85715	(100.0%)

Table 6.2: The distribution of the different verb groups in the simplified corpus.

Many verbs in the corpus had a very low token frequency and hence for the simulations, all verbs with a frequency of less than 5 were removed, except those that had been used by Penke *et al.* (1999) in their experiments with agrammatic aphasics. While the resulting number of verb types of this reduced corpus was just 664, the token distribution was well preserved in comparison with the full corpus (table 6.3).

	type		token	
Regular	518	(78.0%)	39275	(46.5%)
Irregular	134	(20.2%)	41090	(48.5%)
Mixed	12	(1.8%)	4280	(5.0%)
Sum	664	(100.0%)	84645	(100.0%)

Table 6.3: Distribution of the corpus when low frequency verbs were removed.

The 664 participles were classified according to the way in which their participles are formed, resulting in a total of 22 classes, one of which was the "stem + *-t*" (regular) class, six were for mixed verbs, and 15 for irregular verbs (see appendix F).

Each phoneme was represented by a 7-bit feature vector with features such as *fricative, plosive, voiced* etc. for consonants, and *front, high, open* etc. for vowels. Presence of a particular feature was encoded with 1 and absence with 0 (see appendix G).

For the training of the network, the phonological representation of the infinitive of each verb was then inserted into a template consisting of three syllables: XCCCVVCC-XCCCVVCC-XCCCVVCC; C stands for consonant, V for vowel, and X for whether the syllable is stressed or not. Since the endings of verbs are significant for the determination of the participle class, the verbs were right-aligned in this template so that the endings occurred in the same slots. Table 6.4 shows examples of the template representation.

empfinden	0---E-m-1pf-I-n-0d--@-n-
schreiben	0-------1Sr-W---0b--@-n-
fliessen	0-------1fl-i---0s--@-n-
sein	0-------0-------1z--W-n-
Template	XCCCVVCCXCCCVVCCXCCCVVCC

Table 6.4: Template representation of the verb infinitives.

The resulting network had 150 input units (three syllables with seven phonemes each represented by seven features, plus one stress-bit per syllable), and 22 output units for the 22 inflection classes.

6.7 Training

The task to be learned by the network was the mapping from the phonological representation of the verb infinitive to the class of its participle. Like in the English past tense, viewing the learning of the participle as a classification task avoids confounding it with phonological details such as different pronunciation of participle forms depending on the last stem phoneme (*holen* → *geholt* vs. *landen* → *gelandet*), and the phonologically determined prefix *ge-*. It assumes a component that, given the phonological representation of the infinitive and the participle class, can produce the phonological form of the participle (it was shown in the previous chapter for the English past tense that this transformation can be learned in a single layer perceptron).

From the corpus of 664 simplex verbs 20000 verb tokens were randomly extracted according to their frequency. To ensure that each verb occurred at least once, all verb types which had not been randomly selected were added onto the resulting corpus with a token frequency of one (this applied to 18 verbs). The full training corpus is listed in appendix E.

The structure of the resulting training corpus is shown in table 6.5. The regular case in this data set applies to 78.0% of all verb types, but only to 46.5% of tokens. This is in contrast to the English past tense, where the regular case forms the majority of both types and tokens (see table 5.1, p. 109). The German participle thus is an example of a minority default when token frequencies are considered.

	type		token	
Regular	518	(78.0%)	9306	(46.5%)
Irregular	134	(20.2%)	9717	(48.5%)
Mixed	12	(1.8%)	995	(5.0%)
Sum	664	(100.0%)	20018	(100.0%)

Table 6.5: The structure of the training corpus.

Five constructivist networks were trained on this corpus as outlined in section 6.5 with different random initial weight settings. The training parameters of the network are shown in table 6.6. The networks were tested before the insertion of a new hidden unit. An output class was counted as correct when the corresponding unit, but no other unit, had an activation value over 0.7.

Perfect classification of all verbs was reached after an average of 2386 epochs, ranging from 1498 to 3121 epochs.

6.7.1 Developed Network Structure

The final structure of the CNN networks consisted of an average of 179.8 hidden units (receptive fields, *rfs*, ranging from 119 to 211), corresponding to an average of 3.69 verbs per unit. However, as an outcome of the constructivist growth process, in each network there were hidden units (mean: 68.2) with all weights turned to zero that therefore did not contribute to the computation of the output. These units were disregarded in the further analysis of the network structure.

Like in the English past tense simulations, the distribution of regular and irregular verbs revealed a significant difference: on average, each regular verb used only 16.5% of a receptive field, whereas irregulars used 55.8%, and mixed verbs 80.0%. The preferred allocation of resources to the irregular/mixed verbs thus occurred even when the regular case applied to less than 50% of all verb tokens (and could thus in theory

Constructivist Parameters		
ϵ	0.08	fraction by which the winning unit is moved
θ_{act}	0.2	threshold that determines which type of hidden unit movement to use
a_{max}	2000	maximum age of edges before they are removed
d	0.1	factor by which node errors are decreased after each epoch
e	0.1	error decrease considered sufficient during $patience$
$patience$	10	interval (in epochs) during which error decrease is measured to decide whether a new hidden unit is to be inserted
Quickprop Parameters (see Fahlman, 1988)		
μ	1.75	maximal allowed jumpsize
α_{io}	0.2	learning rate for input-output weights
α_{ho}	0.5	learning rate for hidden-output weights
$sigprimeoffset$	0.1	value added to sigmoid-prime to avoid flat spots
$slopedecay$	-0.0001	factor added to slope to prevent large weights
err_{min}	0.0005	error at which training is stopped

Table 6.6: The parameters used in the training of the CNN model for modelling agrammatic aphasia. For the algorithm itself see page 87 *ff*.

be considered as irregular). The determining factor for resource allocation in the networks seems to be the size of verb classes counted in verb tokens: the smaller the class size in tokens, the more hidden units are allocated per verb in that class because they form hard-to-learn exceptions (correlation "class size in tokens" with "hidden units per class" = -0.79).

Numerical evidence for the uneven distribution of the rfs in the input space comes from computing the mean and standard deviation of the average distance from each unit to its nearest neighbour, and comparing the result with a random distribution of the units in the input space. For an example trained network with 109 hidden units the mean distance from a hidden unit to its nearest neighbour was $d = 5.06$ with a standard deviation $\sigma = 4.0987$. This result was compared with averaging over 100 trials with 109 randomly distributed units which yielded $d = 8.9706$ and $\sigma = 4.3581$. d being smaller in the network than in the random distribution indicates that the units populate only a subspace of the input space.

6.8 Lesioning Experiments

In order to model the results obtained with the agrammatic aphasics (Penke *et al.*, 1999), the network models were lesioned in different ways. It was assumed that the removal of connections in the network model corresponds to the destruction of neural tissue in the brain by a stroke or injury.

The output in the network model is produced through two sets of connections: the direct connections between the input and the output layer that existed prior to the training of the network, and the connections from the growing receptive field layer to the output layer. The role of these two pathways was investigated by lesioning them individually, and by randomly lesioning the whole network to different degrees.

6.8.1 Localized Lesioning

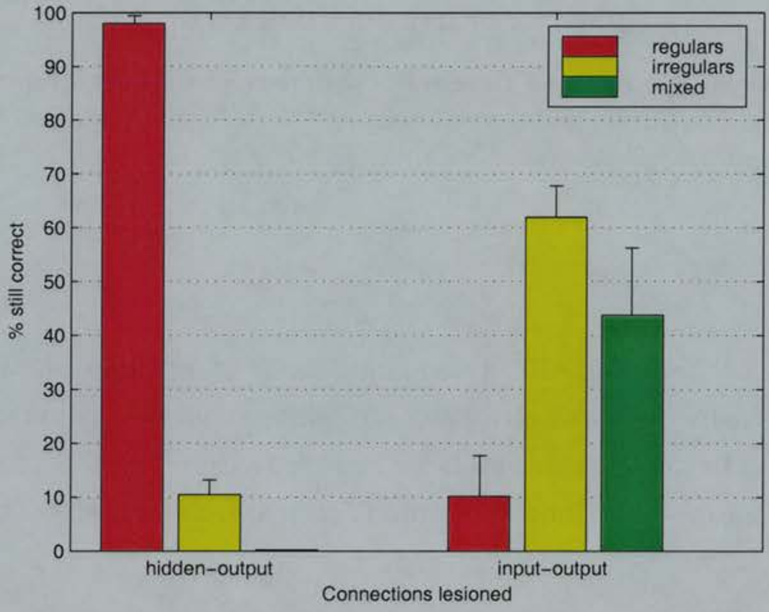

Figure 6.3: Double dissociation between regular and irregular (and mixed) verbs when lesioning the two sets of connections in the network, averaged over four networks. Note that performance for mixed verbs in the HO condition is 0.0.

Like in the English past tense simulations, lesioning the individual sets of connections in the CNN resulted in a double dissociation between regular and irregular verbs, with mixed verbs behaving more like irregulars. Four of the five networks showed a marked difference between regular and irregular performance, and for the remaining one there was no difference between regular, irregular and mixed performance.

Figure 6.3 shows the results of lesioning the IO and HO connections for the four models that displayed a difference between regular and irregular performance. Lesioning the connections from the hidden to the output layer (HO) resulted in a marked decrease of the performance of irregular and mixed verbs, with regular inflections remaining nearly fully intact. Lesioning the direct connections from the input to the output layer (IO) resulted in the opposite profile: performance on regulars was significantly more decreased than on irregular and mixed verbs.

HO-lesioning therefore resulted in a performance of the model that corresponds to the results for agrammatic aphasics reported by Penke *et al.* (1999): six of the eleven tested aphasic subjects made significantly more errors with irregular verbs than with regulars. Lesioning the connections from the receptive fields to the output layer in the network thus modelled the basic deficit in the inflection of agrammatic aphasics.

Based on this result, the performance of the four HO-lesioned CNN models was investigated with respect to the more detailed results found by Penke *et al.*.

The eleven aphasic subjects investigated by Penke *et al.* fall into two groups: six produced significantly more errors with irregular participles than with regulars, and three showed no significant difference between regular and irregular participles (two made too few errors to establish a significant difference, and although they made more mistakes with irregulars they therefore cannot be attributed to any of the groups). These results were reflected in the five runs of the CNN where four of the lesioned networks displayed significantly more irregular than regular errors (mean 89.6% and 2.0%, respectively), while the fifth had a similar error rate for both irregulars and regulars (56.0% and 49.3%, respectively).

6.8.1.1 Overregularization and Irregularization

Penke *et al.* (1999) found that all subjects who made more errors on irregulars than on regulars overgeneralized the regular ending *-t* to irregular verbs, but they only rarely irregularized regular verbs (i.e., their regular errors consisted mainly in using a wrong suffix like *-e* or none at all). Testing the four corresponding CNN models for this behaviour showed a good match with the aphasics (fig. 6.4a): the networks overapplied the regular class to 73.7% of all wrong irregulars (aphasics: 63.3%), but only 6.5% of all regular errors were irregularizations (aphasics: 14.3%).[2]

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[2] The other errors that can be made by the CNN models are no output, or ambiguous output when two (or more) output units are strongly activated.

The networks that corresponded to the investigated aphasic subjects could thus model both overregularization and irregularization behaviour closely, both qualitatively and quantitatively.

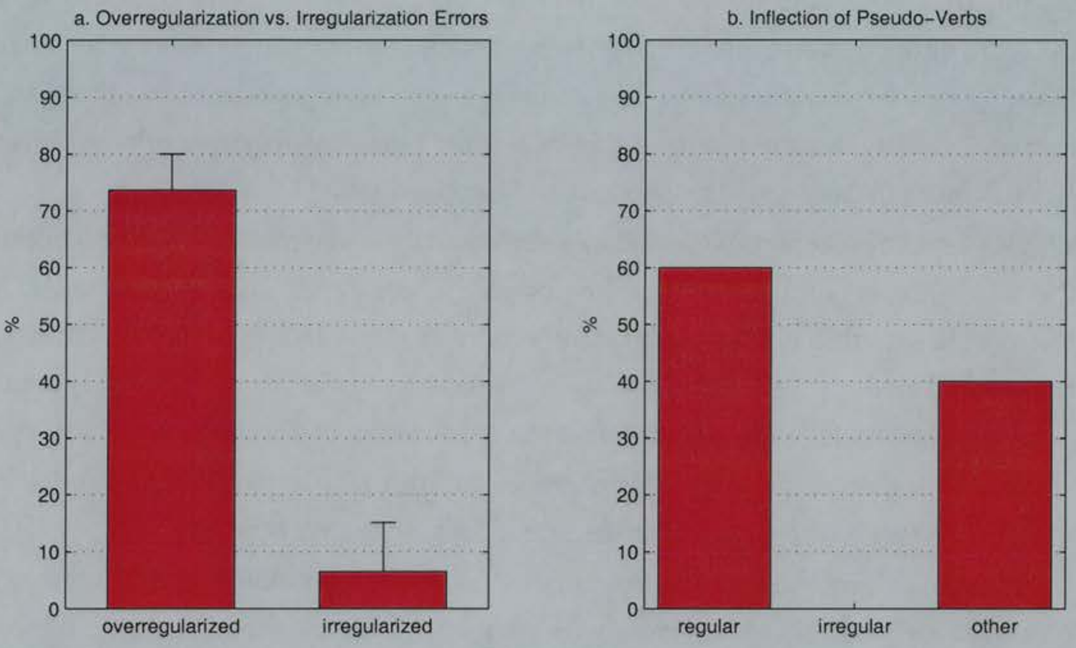

Figure 6.4: a. Overregularization vs. irregularization errors in the HO-lesioned CNN models, averaged over four networks. b. Inflection of pseudo-verbs in the HO lesioned CNN models, averaged over five networks.

6.8.1.2 Inflection of Pseudo-verbs

Penke *et al.* (1999) also tested their aphasic subjects on the inflection of pseudo-verbs that were chosen to be dissimilar to existing verbs (*brewen*, *elmen*, *kersen*, *krelchen*, and *telpen*). According to the results for the English past tense (Prasada and Pinker, 1993), normal subjects should tend to regularize such verbs. Penke *et al.* found that this was also true for the aphasic subjects: each of the eleven subjects was asked twice to inflect each of the five pseudo-verbs. Of the resulting 110 participle forms, 65 (59.1%) were regular, but only 4 (3.6%) irregular. (The rest were either no output or several output units activated simultaneously.) In the five CNN networks, of the 25 produced pseudo-verbs, 15 (60%) were classified as regular and none (0%) as irregular (fig. 6.4b). This result provides an extremely close match to the aphasic data.

6.8.1.3 Frequency Effect for Irregular Participles

Based on the assumption of two qualitatively distinct processing mechanisms, Penke *et al.* (1999) predicted and found a frequency effect in the aphasic inflection of irregulars, but not of regulars: there were significantly more errors for infrequent irregulars than for frequent ones, but no such effect occurred for regulars.

Penke *et al.* constructed groups of low and high frequency verbs by choosing a subset of their test verbs and dividing them into groups with a participle frequency of less than 50 and a lemma frequency of less than 250, and with a participle frequency of over 50 and a lemma frequency of over 250.

The same verbs were used in analyzing the four CNN models that showed selective impairment of irregulars, and here as well a small frequency effect for irregulars but not for regulars was found: the error rate for low frequency irregulars (93.3%) was significantly higher than for high frequency irregulars (89.0%) (Wilcoxon, $p = 0.068$), but error rates for regulars did not differ statistically (1.7% for low frequency and 2.4% for high frequency regulars, $p = 0.273$).

6.8.1.4 Regularity Continuum

Based on a previous neural network model of the acquisition of the German participle (Westermann, 1995), I had argued that regularity and irregularity are two ends of a continuum: a regular verb can be said to be "very regular" if it is similar to other regulars and dissimilar to irregulars. It is "less regular" if it is dissimilar to other regulars but similar to irregulars. The reverse is true for irregulars (see also Daugherty and Seidenberg, 1992)

This assumption is attractive because it integrates mixed verbs which fall between regular and irregular verbs in the way they are formed. Mixed verbs are generally ignored in the DMT because they are hard to consolidate with the qualitative distinction between regulars and irregulars.

In a regularity continuum it would be predicted that "less regular" regulars, being more similar to irregulars, should be more error prone than "very regular" regulars. Penke *et al.* (1999) analyzed the distribution of verbs with respect to stem vowels and found that for the stem vowel <e>, irregulars outnumber regulars, whereas for the stem vowels <au>, <ö>, <ä> and <ü>, regulars outnumber irregulars. Therefore, regular verbs with <e> should have a higher error rate because they are similar to irregulars. For irregular verbs, more overregularizations should occur for verbs with <au>, <ö>, <ä> and <ü> than for <e>, because they are "less irregular".

This prediction was confirmed in the analysis of the aphasic data: all regular suffixation errors occurred with <e>-regulars. To control for the observed frequency effect for irregulars (see section 6.8.1.3), Penke *et al.* considered only low-frequency irregulars. For these irregulars, significantly more errors were made for verbs with <au>, <ö>, <ä> and <ü> than with <e>. While Penke *et al.* interpreted their results within the framework of a qualitative distinction between regulars and irregulars (allowing grading effects for both mechanisms with the qualitatively distinct verb groups influencing each other), a more plausible interpretation is that of a regularity continuum where one mechanism underlies the production of both forms.

Testing the four irregular-impaired CNN models for the regularity-continuum effect yielded the same pattern of results: when tested on the same verbs as the aphasics, 4 out of 5 of the regular errors were for the stem vowel <e>, indicating that these verbs are affected more like irregulars. At the same time, all of the low-frequency irregulars on <au>, <ö>, <ä> and <ü> were overregularized, whereas the 3 only correct irregulars were for the stem vowel <e>.

The effect of an influence of ablaut-clusters on both regular and irregular verbs is a confirmation of the argument for viewing regular and irregular verbs as two ends of a continuum. This continuum, which was found in the aphasic subjects, was thus closely modelled in the constructivist neural network model.

6.8.2 Global Lesioning

As shown in the previous section, the lesioning of the HO pathway in the CNN model can account for a selective impairment in the inflection of irregular verbs and thus model the performance of agrammatic aphasic subjects. This selective and total lesioning of one pathway might suggest that the processing of regular and irregular verbs is subserved by locally different brain structures (though based on a single mechanism) that can be selectively affected by a stroke. Although this position has been argued by some researchers (Jaeger *et al.*, 1996; Ullman *et al.*, 1997; Marslen-Wilson and Tyler, 1997, 1998), there exist considerable difficulties in the interpretation of their results, and in the methodology of some of these studies (Seidenberg and Hoeffner, 1998). The most extensive study (Jaeger *et al.*, 1996) used PET to visualize active brain areas during the production of regular, irregular, and pseudo-verb past tense inflections. While they identified uniquely activated brain areas for each verb type, there were also unique areas for each combination of two of the three verb groups. This result makes it difficult to establish a neural dissociation between the processing mechanisms for the different verb types. The most serious problem with the study of Jaeger *et al.* was, however, that the groups of regular, irregular and pseudo-verbs were presented to subjects in blocks of 46 items each, so that it was very likely that the subjects developed different strategies for producing the different past tense forms that were due to different priming effects for the three verb groups. While this experimental design was a necessary consequence of using the PET imaging technique which has a low temporal resolution and thus requires the repeated processing of similar stimuli, it effectively invalidates the results of the study. Seidenberg and Hoeffner (1998) gave a compelling alternative explanation of the data that does not postulate different neural structures for the processing of regular and irregular verbs: the observed patterns of brain activity could simply result from irregular verbs being more difficult to process and thus generating more brain activity, and from the strongly primed regular verbs employing working memory.

Another study reported a selective deficit of agrammatic aphasics with regular verbs (Ullman *et al.*, 1997). However, their results were based on only a small number of items per condition and a small subject pool, and in their experiments the different verb groups were not matched for frequency which is a strongly confounding factor (see section 6.8.1.3). Further, despite the higher frequency of irregulars, for the studied group of five patients with a phonological deficit for which a selective impairment of regulars was claimed, the difference between regular and irregular impairment was not statistically reliable (Joanisse and Seidenberg, 1999).

The studies by Ullman *et al.* (1997) and Marslen-Wilson and Tyler (1997) have yielded conflicting evidence of which areas might subserve which verb types. Specific impairment for irregulars was attributed to right hemispheric damage by Marslen-Wilson and Tyler, to left temporal-parietal cortex by Ullman *et al.*, and to the left mid-temporal gyrus and various other areas by Jaeger *et al.* (1996). Impairment of regular inflection was said to be caused by damage to the left temporal-parietal lobe (Marslen-Wilson and Tyler) which is the same area responsible for *irregular* deficits in (Ullman *et al.*), by a frontal lobe/basal ganglia system (Ullman *et al.*), and by the left dorsolateral prefrontal cortex (Jaeger *et al.*). Therefore, at best it can be said that the data supporting different neural subsystems for regular and irregular verbs is very inconclusive.

Therefore, in addition to lesioning specific connections in the CNN as described in the previous sections, one model was lesioned globally: over 200 trials, the network was lesioned in 5%-steps by randomly removing weights from both pathways without making a distinction between the IO and the HO connections. The result of this global

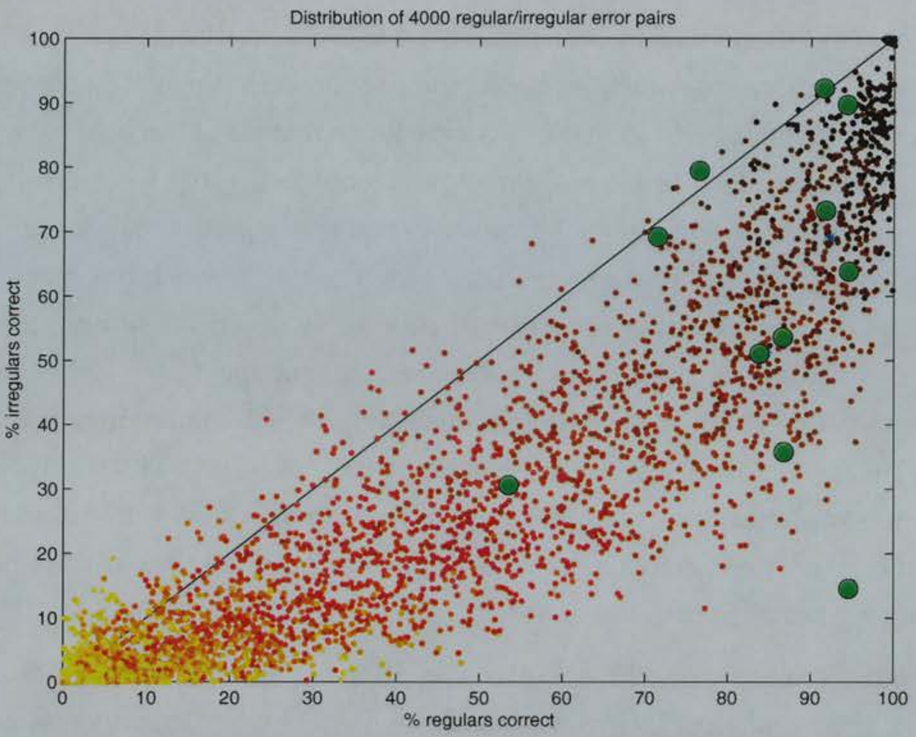

Figure 6.5: Performance on regulars vs. irregulars for 200 lesioning trials at 20 lesioning steps each (in 5%-steps) of one CNN model. The model was fully trained and had constructed a hidden layer with 159 units. Colour indicates degree of lesioning: black is less, yellow is more severe. Data for the aphasic subjects are marked by green circles. To separate overlapping dots, a small noise factor (Gaussian with zero mean and $\sigma = 0.5$) was added on each data point.

lesioning is shown in figure 6.5. The 4000 lesioned networks showed some variety of regular vs. irregular errors, but, like with the aphasic subjects, there was never a selective sparing of irregulars with a breakdown of regular participles (top left of the plot). Instead, in most cases impairment of irregulars was stronger than of regulars (below the diagonal).

The data for the eleven aphasic subjects from (Penke *et al.*, 1999) are also displayed in figure 6.5. All aphasic data are within the range of performance predicted by the simulations, showing that although there is variability in the performance of agrammatic aphasics, different lesioned CNN networks can model the performance of each of them. The model is not over-general, however: like in aphasic subjects, a selective sparing of irregulars with a breakdown of regular inflection did not occur in any of the lesioning trials.

Why does global lesioning in the CNN lead to a profile in which irregular par-

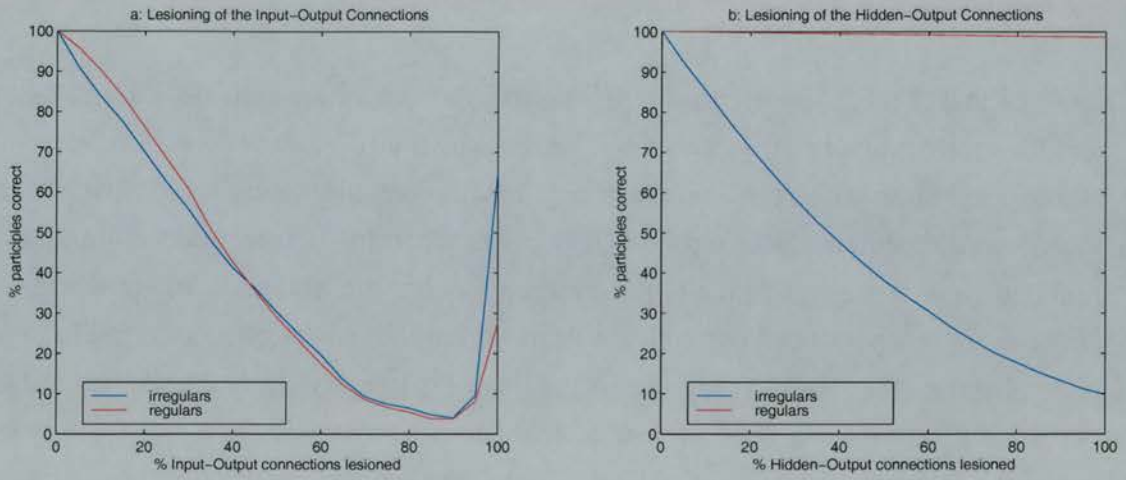

Figure 6.6: Performance on regular and irregular participles when the input-output (a) and hidden-output (b) connections are selectively lesioned at different degrees in one CNN. The results are averaged over 100 trials.

ticiples are more impaired than regulars? An answer to this question can be found in the profiles for lesioning the individual pathways at different degrees. Figure 6.6 shows the breakdown of regular and irregular inflection when the IO and the HO connections are lesioned (averaged over 100 trials in one network). Surprisingly, when the IO connections are lesioned (fig. 6.6a), both regulars and irregulars decline at the same rate, until 90% of the connections have been removed. Between 90% and 100% lesioning there is a sudden recovery of both regulars and irregulars which is stronger for irregulars and leads to the dissociation displayed in figure 6.3. This recovery is due to the distribution of weights in the IO pathway. Many of these connections are inhibitory, suppressing the activation of the wrong inflection class by other IO connections. This profile is due to the distributed representation of the input: overlapping representations between classes make the inhibition of wrongly activated classes necessary, and with increased lesioning this inhibition is lost. This becomes evident at a lesion rate of 90% with the worst performance on both regulars and irregulars: here, the great majority of wrong outputs is ambiguous, i.e., more than one output class are activated above threshold. By contrast, the HO connections from one receptive field usually contain only one that is strongly excitatory, and a few others are strongly inhibitory. Therefore, the HO weights do not tend to activate a wrong output class. This different weight structure can be explained by the localist nature of the receptive fields: due to the constructivist growth process, receptive fields tend to cover only verbs from one class. Therefore, representations for different classes do not overlap and inhibition is not required.

When all of the IO connections are lesioned, they no longer activate wrong classes and the production of all participles is taken over by the HO connections. As discussed before, the hidden layer develops to handle mainly irregular verbs, which leads to an improved performance of irregulars vs. regulars when the IO connections are totally lesioned. Interestingly, when all of the IO connections are lesioned, 28% of the regular vebs are still produced correctly, indicating that they are produced in the hidden layer. On the other hand, when the HO pathway is lesioned, only 2% of the regular verbs are produced wrongly, indicating that 98% of the regular verbs are produced in the IO pathway. This result indicates that some regular participles are produced independently both in the IO pathway and in the hidden layer. This result corresponds to psycholinguistic evidence that some regular past tense forms are also stored in memory (Stemberger and MacWhinney, 1986).

Lesioning of the HO connections leads to a nearly linear decline for irregular verbs without affecting regular verbs at all (fig. 6.6b). The hidden layer produces mainly irregulars, and the HO connections are very specific. The loss of a single HO connection can therefore disrupt the inflection of all verbs covered by the receptive field of a hidden unit.

Given the individual lesioning profiles it becomes clear why global lesioning leads to a stronger impairment of irregulars: while the IO lesioning affects regular and irregular verbs equally, lesioning the HO connections selectively impairs irregular inflections. In sum then, irregular verbs are affected more by a global lesioning, and the selective sparing of regular inflections cannot be taken as evidence for two separate mechanisms, or even two locally distinct processing areas, for regular and irregular inflections.

A lesioning profile in which irregular inflections are selectively spared could only arise from a total lesioning of the IO connections together with no or weak lesioning of the HO connections. Based on the CNN model therefore the prediction is made that a selective impairment of regular inflections would be evidence for a locally separated processing of regular and irregular inflections. The question whether this would also imply two separate mechanisms for regulars and irregulars as proposed by the DMT, will be discussed below.

6.9 Discussion

The results presented in this chapter show that the CNN model not only can account for the course of acquisition of past tense inflection (chapter 5), but lesioning the trained network also yields results that are compatible with impaired adult inflectional processing. Together, these results suggest that the CNN constitutes a valid, implemented model of human inflectional processing.

At the same time, the CNN avoids the problems of the dual mechanism theory (see section 6.3), i.e., underspecification and contradiction of the empirical data.

In contrast to the DMT, the CNN is a fully specified, fully implemented model. The main problem of the DMT, the need to specify the interactions between rule mechanism and associative lexicon, does not arise in the CNN. This is because the CNN employs only a single mechanism, associative learning, and the IO and HO connections organize interactively to produce the correct output. Whereas in the DMT regular verbs have no lexical entries and the regular inflection is only applied when no lexical entry is activated, in the CNN both regular and irregular verbs lead to a weight adaptation during learning, and therefore even those regulars that are very similar to irregulars are inflected correctly.

Further, the CNN can naturally account for combinations between regular and irregular forms such as blends (*camed*) in acquisition, and for German mixed verbs: each verb is produced through an interaction (excitatory and inhibitory) between the IO and HO connections, and the degree of regularity is determined by the activation of the regular class. Blends between classes are possible when several of them are activated concurrently.

Unlike the DMT, the CNN can also account for the similarity effects of regulars that have been observed in aphasics (Penke *et al.*, 1999) and normal subjects (Seidenberg and Bruck, 1990; Seidenberg, 1992). There are no qualitatively distinct mechanisms in the production of regulars and irregulars. Instead, they form two ends of a continuum being produced by a single mechanism, but based on two representations. The regularity of a verb is determined by the degree of activation in both pathways, and therefore not only irregulars but also regular verbs are represented in a graded fashion. Further, the CNN shows that the observed selective impairment of irregulars in aphasics (Penke *et al.*, 1999) cannot be taken as evidence for two different mechanisms or even localized processing areas for the production of irregular and regular inflections.

Finally, while in the DMT, where the two mechanisms would be supported by distinct neural substrates, a selective sparing of irregulars is clearly possible, the CNN makes different predictions: a global lesioning of the network leads to the observed profile of a selective sparing of regulars. Based on the model, the prediction is made that the discovery of a selective sparing of irregulars (in systems where both regulars and irregulars have inflectional endings) would be evidence for a locally distinct processing for regular and irregular verbs. However, as shown in the model, this can be achieved with a single mechanism in which the two processing areas closely interact. The observed range of human aphasic data, however, could be modelled by globally lesioning the CNN without assuming locally distinct processing areas. The model can thus simultaneously account for the considerable variability between aphasic subjects and the absence of certain profiles (selective irregular sparing).

6.9.1 Is the CNN an Implementation of the Dual Mechanism Theory?

Although the CNN was shown to account for data that contradicts the DMT, the model might at first sight be viewed as an implementation of the DMT that provides merely its specification: the direct IO connections and the HO connections via the constructed hidden layer could be viewed as two functionally distinct processing pathways. The hidden layer with its overlapping receptive fields acts as an associative memory and it develops to process mainly the irregular verbs, whereas the IO connections could be said to implement the default regular case.

However, there are significant differences between the CNN and the DMT that make it clear that the CNN represents an alternative to the DMT, not its instantiation:

- The qualitative distinction between the mechanisms for regular and irregular inflections lies at the heart of the DMT. However, in the CNN a single associative mechanism is employed. The difference to previous single-mechanism models is that the CNN is a constructivist model that develops a non-homogeneous architecture.

- The DMT postulates an encapsulation and strict separation of the two pathways, or mechanisms. By contrast, the interaction between the IO and HO connections is the basis of the functioning of the CNN model. Each verb, regular, irregular, and mixed, produces activation in both pathways, and the correct output is generated through these interactions. In addition, the development (weight setting and unit creation) of the IO and HO connections are highly interdependent: a hidden unit is only created when the correct output cannot be learned in the direct connections and the already existing hidden units, and the growth of the hidden layer leads to a rapid re-organization of the representations of some verbs from the IO to the HO connections (section 5.5.5). Many of the weights of the HO connections are negative, indicating that the response generated in the IO connections is often controlled and overridden by the HO connections.

- The DMT postulates two modules in the traditional sense (e.g. Fodor, 1983), and these modules are claimed to be the explanation for the observed double dissociations in inflectional processing. By contrast, the CNN, although it has a non-homogeneous architecture, cannot be said to be modular in this sense. The "pathways" are not encapsulated, not independent from each other, and they do not clearly separate regular from irregular verbs but instead represent two ends of a regularity-continuum. Therefore, the pathways in the CNN should be regarded as *areas of specialization* instead of as modules. Several researchers have called into doubt the assumption that double dissociations imply different processing modules. Shallice (1988); Farah (1994); and Plaut (1995) demonstrated this empirically for a connectionist model of word reading. The CNN is therefore another example of how double dissociations can arise in a non-modular, non-homogeneous system through different types of damage (instead of damage to different modules).

In summary, although the CNN superficially resembles a dual route model, it contradicts the three basic tenets of the DMT: modularity, encapsulation, and a qualitative distinction between the processing mechanisms. The CNN represents therefore a model that is more closely related to traditional connectionist models than to the hybrid (symbolic + associative) DMT.

6.9.2 How Inflections are Learned and Stored

In this section I will formulate, based on the results from the CNN model, a new theory of the processing of verb inflections.

Whereas the DMT proposes two mechanisms operating on a single representation of a verb stem, the CNN develops so that a single mechanism operates on two representations of the verb. The direct phonological input is used in the IO pathway to produce the output. For verbs for which the output cannot be learned through this structural representation alone, the CNN develops through a constructivist process additional representations in the hidden layer. In contrast to the structure-based input representations, these new representations are identity-based and localist: the activation of a hidden unit receptive field only indicates the presence of a certain input, without information about its structure. The CNN is therefore a single mechanism, dual representation model.

This dual representation view sheds a different light on the dissociations between regular and irregular forms. The DMT does not assume that any regular verbs are produced by the irregular mechanism, or vice versa. The common aphasic profile where both regular and irregular cases are partially impaired (albeit to different degrees) is therefore often attributed to performance errors or the unpredictability of aphasic impairment (Penke, personal communication). A more compelling explanation is offered by the CNN: here, the dissociations that become visible in the lesioning trials are not clearly along the lines of regulars vs. irregulars. Instead, all verbs for which the inflection class cannot be learned in the direct IO pathway are shifted to the developing hidden layer and the HO pathway. This shift concerns regular, irregular, and mixed verbs, to different degrees. The dissociation between verbs is thus better described as *easy* vs. *difficult*, with the difficult forms relying on the hidden layer, whereas easy forms are produced in the IO-pathway alone. This distinction can account better for the data such as mixed verbs, a regularity continuum, or the different aphasic profiles.

But what factors determine whether a form is easy or difficult? The fact that the empirical results from past tense acquisition and agrammatic aphasic processing could be modelled in the CNN where inflection is viewed as a classification task indicates that the difficulty is not in the transformation of the stem to the inflected form. Instead, the degree of difficulty is determined by several interacting distributional factors that can be derived from the principles of associative learning:

1. Frequency: a frequent transformation is easier to learn than an infrequent one. Therefore, inflection classes with a high summed token frequency will be easier to learn than those that only apply to rare verbs.

2. Class size: a transformation that applies to many different verbs is easier to learn than one that just applies to one verb. Therefore, inflection classes with many members (counted in types) are easier to learn than those confined to only a small group of verbs.

3. Similarity of class members to members of other classes: the inflection class of a verb is easier to learn if other similar verbs share the same class, and it is harder

if similar verbs belong to different classes.

4. Ambiguity of inflectional morpheme: an inflection is easier to learn if it applies uniquely to members of its class, i.e., if it does not exist in other contexts as well. For example, the *-ed* suffix in English is highly indicative of the past tense/participle: an analysis of the CELEX corpus showed that 99.6% of all word types in English that end in *-ed* are past tense/participle forms, and furthermore, none of the other 0.4% (bed, bobsled, embed, featherbed, hundred, shed, shred, sled, wed) can be separated into an existing word + *-ed*. By contrast, the German irregular participle ending *-en* is much more ambiguous: it also occurs in verb infinitives (*gehen*, to go), noun plurals (*Wiesen*, meadows), and as part of noun singulars (*Drachen*, kite).

These factors influence each other, and further research will be needed to establish in detail how they interact. But they show a fundamental difference to the regular/irregular dichotomy: while for each verb its regularity can be defined in isolation based on that verb alone, a verb's "easiness" can only be established by taking into account the frequency and distributional properties of all other words in the language corpus. Nevertheless, these factors show that the *regular—irregular* distinction is a good first approximation of the *easy—difficult* distinction: the regular inflection, although it does not apply to the most frequent individual verbs, is the single most frequent inflection in both English and German: 57.2% of English past tense tokens and 46.9% of German participle tokens are regular. At the same time, these classes are also the biggest in type size (88.4% and 64.7%, respectively). The third point, similarity of class members to members of other classes, does not separate along the lines of regular and irregular verbs, however: many regular verbs are similar to irregulars which should make them harder to learn in this view. And in fact the regularity continuum that has been shown for aphasics indicates that regulars that are similar to irregulars are more prone to impairment than others, that is, they rely more on storage in the lexicon.

A similar analysis of factors influencing errors in past tense formation has been conducted with human subjects. Marchman (1997) tested school-aged children on an elicited past tense production task and observed the produced errors. She analyzed for each tested verb its frequency, the number of similar sounding stems with a similar mapping pattern to the past tense ("friends"), the number of similar sounding stems with different past tense forms ("enemies"), and phonological characteristics of the stem and past tense forms. Based on these analyses she defined different "vulnerability levels" expressing the predicted susceptibility to production errors. Verbs with a high vulnerability had, among others, a low frequency and many "enemies". Marchman found a significant relationship between item vulnerability and error rate, and this result indicates that item frequency and similarity of class members to members of other classes are predictors for errors in humans as well.

The final factor determining how "difficult" a form is, namely, uniqueness of the inflection, has been investigated by Baayen *et al.* (1997): based on response-time experiments they claimed that in Dutch the plural suffix *-en*, despite its high frequency and productivity, is nevertheless stored in the lexicon. They attributed this storage to the fact that *-en* is mainly used as a verb ending and it is therefore time-costly to disambiguate noun plurals with *-en*.

Taken together, although the dissociations of verbs into easy and difficult corresponds largely to the regular-irregular dissociation, it nevertheless suggests that the regular case is a post-hoc extraction and idealization of the developed structure of the inflectional processing system. In order to make parsing by the listener easier, the speaker can then apply the extracted "regular", which is highly indicative of its function, to novel forms. For example, since *-ed* is highly indicative of past tense, the speaker will apply it to novel words such as *to out-Gorbachev* or *to rhumba* to produce *out-Gorbachev'd* and *rhumba'd*. In this view, the regularization of unusual and noun-derived verbs is motivated out of semantic rather than phonological/lexical principles.

The results presented in this and the previous chapter therefore suggest a novel account of inflection learning and processing: it is a dual representation, single mechanism system that emerges from a constructivist learning process. This mechanism leads to a realistic acquisition profile with its characteristic errors, and the lesioned mature system displays the same deficits as agrammatic aphasics. The system separates verbs along the lines of easy vs. hard to learn/process and can thus better explain empirical results that have been taken to be evidence for the dual mechanism theory.

A way to test the validity of the model empirically is to abandon the regular/irregular distinction in favour of an easy/hard distinction, by identifying "hard" regulars and "easy" irregulars. Such a distinction should then better predict impairment profiles in agrammatic aphasics. Although this has already partly been done by Penke *et al.* (1999) who found grading effects also for regulars (see section 6.8.1.4), more research along these lines will be needed to empirically verify the dual-representation model of verb inflection.

Recently, a similar model to the CNN was suggested (Joanisse and Seidenberg, 1999, henceforth J&S) that accounted for the impairments of inflection in agrammatic aphasia (fig. 6.7). Like in the CNN, the input layer of this neural network model consists of a templated phonological form of the verb and additionally a layer of semantic units where each verb is represented by one individual unit. The input layer components feed into a hidden layer with 100 units which in turn feeds into the output layer where a phonological templated form of the verb is produced. Additionally, the hidden layer feeds back into the semantic input component. Both the semantic component and the output layer are recursively connected to so-called "clean-up units".

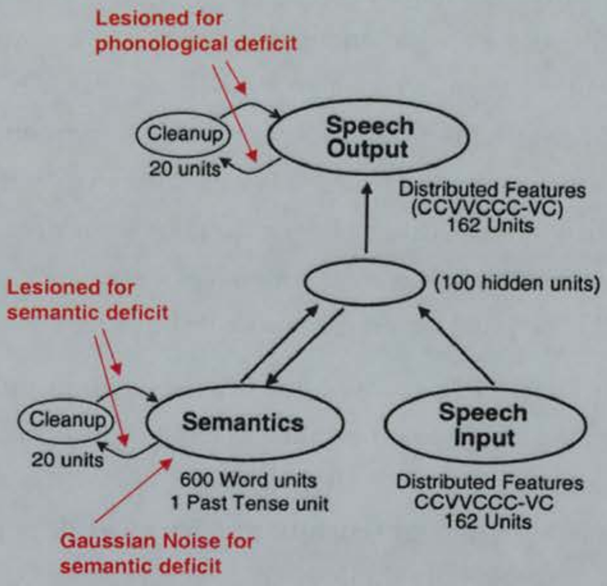

Figure 6.7: The J&S model. Modified from (Joanisse and Seidenberg, 1999)

This model was trained on 600 present tense/past tense verbs, of which 64 were irregular, according to their frequency, and it had to learn four tasks: "speaking" consisted in producing the present or past tense form as output based solely on the semantic input. "Hearing"consisted in learning the semantic representation based on the phonological input. "Repeating" involved taking a phonological code as input and producing the same code at the output. "Transforming" consisted in producing the past tense form based on the phonological and semantic input together. The fully trained model was then lesioned in different subcomponents to simulate semantic and phonological deficits (see fig. 6.7). J&S found that inducing a "phonological deficit" affected regular and irregular forms alike, while a "semantic deficit" lesioning together with Gaussian noise in the semantic component affected mainly irregulars. These results are very similar to those for lesioning the IO and HO connections in the CNN model (fig. 6.6). Why is this?

In both the CNN and the J&S networks, the output is produced on the basis of two representations of the input: one is the distributed phonological representation, the other is a localist representation. In the CNN this essentially localist representation is developed in the growing hidden layer, in the J&S network it consists of the semantic component where each verb is represented by a dedicated single unit. In both networks, lesioning the connections from the distributed representations leads to impairments of both regular and irregular verbs, whereas lesioning the localist component impairs mainly the irregulars. The difference between the two networks is that in the CNN the localist representation is developed constructively and is based on the phonology of the stem, whereas in the J&S network it is arbitrary (one localist unit per verb) and pre-specified. The J&S network therefore corresponds more closely to a non-constructivist version of the CNN (see section 5.6) with one hidden unit per verb. Although such a network develops a double dissociation as well, I showed in section 5.6 that this dissociation is less pronounced than in the constructivist case and that several aspects of the data cannot be modelled in such an architecture.

The J&S network takes into account that often a semantic deficit is correlated with problems in producing irregular inflections (Marslen-Wilson and Tyler, 1998; Clahsen, 1999a) and explains such irregular deficits on the basis of a semantic impairment. However, experiments show that semantic and irregular deficits can be decorrelated in certain priming experiments (Marslen-Wilson and Tyler, 1998). Further backing for this result comes from the CNN model that shows irregular deficits without a semantic component. The explanation for the correlation between semantic and irregular deficits could instead be that both rely on identity-based representations of the verb: neither the meaning nor the past tense form of an irregular verb can be predicted from its structure. The semantic component in the J&S model thus takes the place of any identity-based representation. However, the fact that this semantic component contains a unit for each regular and irregular verb would most likely prevent it from modelling more detailed aspects of agrammatic aphasia such as frequency effects and a regularity continuum (see sections 6.8.1.3 and 6.8.1.4). These effects emerge in the CNN as a result of the constructivist growth process and the allocation of receptive fields mainly to irregular verbs.

Nevertheless the J&S model presents further evidence in addition to that provided by the CNN, that double dissociations can emerge without a modular system, and in the absence of qualitatively different mechanisms for the inflection of different verb types. Additionally, the J&S model illustrates that a full model of speech production needs to incorporate a semantic component.

6.10 Chapter Summary

In this chapter the CNN model developed for modelling the acquisition of the English past tense was extended to account for impaired processing in German agrammatic aphasia. Lesioning the network at specific locations resulted in dissociations between regular and irregular verbs that are also found in aphasic subjects, and even detailed effects such as a frequency effect for irregular preservation and a regularity continuum effect could be modelled. Even a global, unspecific lesioning lead to dissociations that match the profiles of eleven investigated aphasic subjects.

While the observed double dissociations between regular and irregular verbs are often taken as evidence for the dual mechanism theory that postulates separate mechanisms for the production of both verb types, I argued that this theory fails on the grounds of underspecification and contradictions to the established data. Based on the modelling results I proposed as an alternative a dual representation theory where the inflection processing system develops in a constructivist process to provide two representations for verbs, based on which a single mechanism produces the inflections of both regulars and irregulars. This system separates verbs not along the lines regular/irregular, but along easy/difficult, and I discussed what makes a verb easy or difficult to process. I predicted that a separation along these lines will account better for the impairment profiles found in agrammatic aphasia.

Chapter 7

Discussion

The aim of this thesis has been two-fold. One aim was to discuss the viability of constructivist models of cognitive development. The reasoning behind this point was that the cortex develops its architecture in many parts in an activity-dependent way, and that this activity can arise from sensory experience (chapter 2). Furthermore, changes in cortical architecture go hand in hand with cognitive development (chapter 3). From a theoretical perspective it can be shown that static and constructivist learning systems differ in fundamental ways, a point that can be illustrated by means of neural networks (chapter 4). Therefore, the ability of a learning system (e.g., the cortex) to change its architecture as a function of learning is a fundamental property of that system, and abstracting away from it in models might prevent the successful modelling of cognitive development.

The second aim was to empirically investigate the idea that constructivist neural networks can be successfully applied to the modelling of cognitive development. For this purpose, constructivist neural network (CNN) models of inflectional processing were developed. The first model simulated the acquisition of the English past tense (chapter 5). This small aspect of cognitive development was chosen because it has acquired a high significance in evaluating different cognitive theories against each other, and because it has been extensively studied empirically. By viewing the production of past tense forms as a classification task, a connection was made to broader aspects of cognitive development that are often based on the ability to categorize and classify (e.g. Lakoff, 1986). The past tense models displayed the same developmental profile that is also observed in children in that many irregular verbs were overregularized after a period of correct production (the U-shaped learning curve), and detailed aspects of this profile such as family effects for similar sounding irregulars and frequency effects on the overregularization rate could also be modelled. The fully trained model was tested on its performance with pseudo-verbs that had also been tested on human subjects, and again a good match to the human data was obtained. Most significantly, the model tended to regularize novel verbs that were dissimilar to any existing verbs, indicating that it had learned the regular case as the default "rule". I suggested that the realistic performance of the model was due to its constructivist nature, and this claim was backed by a set of analogous, but static networks that performed worse than the constructivist version and did not display a realistic acquisition profile. Comparisons with previous models gave further evidence for the suitability of constructivist models of cognitive development: although the CNN performed better than all of the previous models, the model that came closest to it was the equally constructivist symbolic SPA. Based on these results I suggested a new taxonomy for models of cognitive development that allows a better comparison between them: such models should be distinguished along the dimensions *symbolic* vs. *subsymbolic processing*, *homogeneous* vs. *non-homogeneous architecture*, *static architecture* vs. *constructivist development*, and *single mechanism* vs. *multiple mechanisms*. I argued that subsymbolic, non-homogeneous, constructivist single-mechanism systems like the CNN might be the most suitable models of cognitive development.

A second set of experiments addressed impaired adult processing. For this purpose, the CNN was fully trained on German participles, and then connections were lesioned in different ways and the resulting breakdowns in performance were investigated. The network developed specialized processing areas in two pathways, and the selective lesioning of the connections from the constructed hidden to the output layer resulted in an impairment profile that corresponded closely to that observed in a study with German agrammatic aphasics: performance on irregular verbs was selectively impaired, and the model displayed detailed aspects of the human impairment such as frequency effects and a stem-vowel effect for regulars ("regularity continuum"). When the model was lesioned globally by randomly removing connections in either pathway, it reflected the spectrum observed in the human aphasic subjects (selective irregular impairment or equal impairment of regulars and irregulars), and like in human subjects, a selective sparing of irregulars was never observed. Such a selective irregular sparing could, however, be obtained by lesioning only the connections from the input to the output layer. This result led to the prediction that a human profile in which irregulars are selectively spared would be evidence for a locally distinct processing of regular and irregular verbs because processing areas could then be selectively affected by a stroke, whereas the selective sparing of regulars did not allow this prediction because such a profile could be obtained even by a global, non-selective lesioning of the network.

Based on the results of this second group of experiments I proposed a new model of inflectional processing that differs both from homogeneous associative models and from a dual mechanism theory. This model is based on the constructivist development of a dual-representation processing system, where a distributed structural representation of each verb is supplemented by a localist, identity-based representation for those verbs whose inflection cannot be learned based on the former representation alone. The inflected form of a verb is then produced by a single mechanism operating on these two representations. Instead of a dichotomy *regular* vs. *irregular* that lies at the basis of the dual mechanism theory, I proposed a split that develops along the lines of *easy to learn/process* vs. *hard to learn/process*. Whereas regularity and irregularity are binary grammatical descriptions and the regularity of each verb is determined in isolation based on how its participle is formed, the "processing difficulty" of a verb is determined by all other verbs (and other words) in a corpus based on their distributional properties. Although this distinction roughly corresponds to the regular–irregular dichotomy, the match is not perfect. I suggested that the notion of "regular" is a post-hoc extraction and generalization of the "easy" group of verbs, and I predicted that a re-analysis of aphasic data along the "easy"–"hard" distinction would yield a clearer selective impairment profile.

Perhaps like other abstract linguistic categories, the notion of "regularity" is a projection of formal linguistic analysis onto the human data. Because according to formal linguistics, human language data does not correspond to the abstract "competence" but is instead corrupted as "performance", data that does not correspond to the predictions of the formal theory can therefore be attributed to performance. In the DMT which predicts a clear split between regular and irregular forms, "performance" would be drawn in to explain cases in which this split is less clear, i.e., where some regulars behave like irregulars and vice versa. However, this approach makes the DMT hard to falsify on the basis of such data. Falsifiability is, however, a prerequisite for scientific theories (Popper, 1959).

In contrast to the DMT, the CNN model shows how the actual human data can be modelled without recourse to a competence-performance distinction and it therefore represents a better model of inflectional processing than theories based on formal linguistics. Whereas the abstract category of "regularity" remains a good formal description of language structure, the fallacy is in drafting it into service as a *processing* category, as done in the DMT.

In a recent paper, Mayall (1998) discussed aspects that increase the validity of connectionist models of cognitive neuropsychological disorders. Like the CNN model of aphasic processing discussed here, such models simulate the effects of strokes or brain injury by lesioning connections and units. According to Mayall, a model should behave normally prior to the lesioning, it should account for the sometimes considerable variability between patients suffering from the deficit that is modelled, it should include multiple symptoms that are displayed by patients, and it should try to incorporate different syndromes within a model following different lesions and display double dissociations in performance.

These requirements are met in the CNN model: its normal functioning before simulating impairment was demonstrated in the acquisition of the English past tense, and in its generalization behaviour to novel words. In the model of aphasic processing, different degrees of random lesioning led to a variability in performance that matched the spectrum displayed by the human subjects but that was not overly general in producing every possible profile. Different symptoms of aphasic processing such as frequency effects for irregulars, overregularizations, and a regularity-continuum effect were modelled. While no selective impairment of regular inflection in German aphasics has been reported, the model predicted that such a profile would be evidence for a locally distinct processing of regular and irregular inflection. By selectively lesioning the developed pathways (or, areas of specialization), double dissociations emerged in the model. In this way, the CNN meets the criteria for a valid model of a cognitive disorder.

A final aspect discussed by Mayall (1998) is the ability of a model to account for rehabilitation and recovery after a stroke. This point was not extensively studied in the CNN and it will be an interesting area of further research. Preliminary experiments have elucidated several important constraints on the modelling of rehabilitation: should the network be allowed to grow new units in the hidden layer, or should re-training proceed in the lesioned architecture? If the insertion of units continues after the lesion, the network will eventually reach perfect performance again, a result that is inconsistent with the human data. By contrast, re-training in the lesioned architecture led to a decrease in the performance of regulars because the remaining connections re-organized themselves to handle both regulars and irregulars. To my knowledge, no studies of the recovery of inflection processing in aphasics exist, and such a study would be valuable in understanding the mechanisms underlying rehabilitation. Another question raised by the model is what effects different degrees of lesioning of the two pathways have on the re-learning of irregular and regular inflections. This question is closely linked to the previous one, because even severe lesioning can be compensated by allowing the model to grow new units during re-learning. In this case, a severe lesioning of the hidden-output connections leads to a breakdown of irregulars, and re-training would temporarily decrease performance on regulars while all verbs are produced in the input-output connections, until enough hidden units have been created to process the irregulars again. A specific lesioning of the input-output connections leads to a breakdown for the regulars, and these would be re-learned by inserting hidden units for them. Although a re-trained network in such a scenario would reach perfect performance on both regulars and irregulars, even regulars would then be treated as exceptions (with the "rule processing area" being destroyed), which should result in no—or only weak—dissociations between regulars and irregulars. This prediction of the model could also be tested empirically.

7.1 Connectionism and Constructivism

"Can Connectionism Save Constructivism?" This was the title of a recent paper by Marcus (1998a). In it, Marcus discussed claims made in (Elman *et al.*, 1996) that connectionist models presented there represent a formalized framework of constructivist learning, avoiding pre-specifications both of representations and of functional modules. Marcus rightly pointed out that the homogeneous, fixed-architecture networks to which these claims referred had instead a pre-specified architecture that could be viewed as a functional module in the nativist sense, and that they were unable to learn qualitatively new representations in a constructivist sense. This point had already been discussed by Quartz (1993) and is also the topic of chapter 4 of this thesis. Although Marcus conceded that his criticism was addressed only towards models of the type presented in (Elman *et al.*, 1996), namely fixed-architecture, homogeneous backpropagation or recurrent backpropagation networks, he briefly discussed arguments by Mareschal and Shultz (1996) for cascade-correlation networks as constructivist models of cognitive development (see also section 4.7). Marcus rejected these models for two reasons: his first point was that, even when the models can account for the human course of development, there is "absolutely no guarantee that the solution that the model finds will be the same as the one human finds [sic], that the model can find a solution given a realistic training regime, or that this model has anything to do with human developmental psychology." (Marcus, 1998a, p. 174). This criticism is puzzling as it addresses the basic understanding of what models are. Mareschal and Shultz (1996) reported various cascade-correlation models that simulated the developmental stages of children in different Piagetean tasks. Naturally this can be no proof that humans develop in the same way, but this needs to be shown by data for which the model cannot account and that thus falsifies the model. Then, a new model would have to be developed that accounts for both the previous and the new data. Until then, however, it is legitimate to assume that the current model is a valid model of the developmental process. When there are two models that account for the same data, then the one which has fewer initial assumptions (about architecture, representations, learning mechanisms etc.) is to be preferred according to the principle of Occam´s Razor. In the case of the constructivist models presented by Mareschal and Shultz (1996), they are at present the only models accounting for the developmental data, and Mareschal and Shultz argued convincingly why their models display the stages also observed in children while other models do not. Marcus´ rejection of them must therefore itself be rejected.

Marcus's (1998a) second criticism of cascade-correlation models was that, like fixed-architecture systems, they were not able to learn new representations and thus did not avoid Fodor´s paradox (see section 4.2.2). He argued that instead the networks merely order the hypotheses that they test so that they try linearly separable ones first, then the ones that can be computed with one hidden unit, then the ones with two hidden units, and so on. In learning theoretic terms, what Marcus argued is that cascade-correlation networks have a constant restricted hypothesis space bias, but the growth of hidden units implements a preference bias to try simpler hypotheses first. However, as I have argued in chapter 4, constructivist learning systems effectively conflate these two biases. Every constant architecture (between node insertions) corresponds to a fixed hypothesis space which is searched by the network by weight adaptation. Insertion of a new hidden unit then enlarges this hypothesis space to include functions that could not be computed in the previous architecture. This node insertion therefore relaxes the bias on the hypothesis space, but simultaneously imposes an ordering on the hypotheses in that none of the more complex ones could be tested before the unit was inserted. However, nothing prevents the network from converging on a hypothesis that is less than maximally complex (given a certain architecture), for example when new units are inserted too quickly—this point amounts to the problem of setting the unit insertion interval against the weight adaptation rate which needs further investigation. Therefore, although Marcus is correct in stating that constructivist networks realize a preference bias, contrary to his claims these networks become able to represent more complex hypotheses as learning progresses.

In addressing the suitability of connectionist models for constructivist theories it is useful to make a distinction between *learned* and *emerging* concepts, and Marcus' rejection of constructivist models results from a failure to make this distinction. A concept that is learned consists generally of a mapping from the input to the output representations in a network, and for the learning to be successful, the information that separates members of a concept from non-members must be somehow present in the input data. For example, in the CNN, where the mapping from a phonological input representation to inflection classes is learned, verbs belonging to different classes must have different phonological representations to be distinguishable. Both input and output representation are pre-specified, and Marcus is right in arguing that the concept of "inflection class" is not newly learned. However, he takes this as an argument against connectionist networks for constructivist learning:

> *It is here that the grand dreams of empiricist learning – starting from raw sensation and bootstrapping all the way up to a full adult conceptual system – fall hardest. A real system of representational emergence would develop new concepts where there were none; the models of [Elman* et al. *(1996)], however, do not deliver. [. . .] Rather the problem here is that [(Elman* et al.*, 1996)] never give an account of how a single output representation might 'emerge'; instead, every single output representation in every single model is prespecified.* (Marcus, 1998a, p. 161)

Although this point is directed against the fixed-architecture networks described in (Elman *et al.*, 1996), it applies equally to supervised constructivist networks such as cascade-correlation or the CNN. However, the place to look for new representations is not the pre-specified output layer, but in what lies between the input and the output layers. In the CNN, regularity is nowhere specified in the input and output representations, but it emerges as a concept based on the distribution of the verbs together with the model's constructivist learning process. The concept of regularity, which in the CNN manifests itself both in processing (regularization of pseudo-verbs) and architecture (the IO connections as an emerging area of specialization for regulars that can be selectively impaired by lesioning this pathway), is therefore genuinely new in the constructivist sense.

Although the CNN relies on pre-specified input and output representations, this does not mean that these representations are necessarily innate. Their prespecification in the model is a simplification because only a very small aspect of language (let alone, cognitive) processing is modelled. This simplification does not invalidate the claim made here that the CNN is a constructivist learning system: "regularity" emerges as a higher, more complex concept that is built on top of the input and output representations. Constructivism does not mean that nothing is innate (as Marcus (1998a) claims of the (Elman *et al.*, 1996) version of constructivism). Rather, constructivist learning systems are based on an innate core (e.g., Piaget, 1980) that consists at least of the learning mechanisms and perhaps basic representations.

Similarly, Clahsen (1999a) claimed that the CNN is not constructivist because it has two pathways of which one processes the regular and the other the irregular verbs. However, Clahsen failed to acknowledge that the pathways developed by the network are not pre-specified to process these verb types, but their functional specification emerges from the structure of the training data combined with the learning algorithm (see above). Furthermore, not only the functional specialization but also the physical existence of two pathways can be the direct outcome of the complexity of the learning task: in a network that starts with no hidden units at all, only the direct input-output connections exist and the network can learn only linearly separable problems. If the task is linearly separable, no second pathway will ever develop. In a non-linearly separable problem hidden units will develop, but again their number will depend on the complexity of the problem. To describe the CNN as consisting of "two qualitatively distinct representational devices, a set of direct input-output connections (essentially made for handling regular inflection) and a set of hidden layer units (which act as a memory for irregulars") (Clahsen, 1999b) is therefore misleading. More appropriately, one could describe them as "a direct pathway for that subset of the data that is linearly separable, and another one that develops to account for the remaining non-linearly separable subset".

Taking these arguments together, Marcus's (1998a) question, "Can Connectionism Save Constructivism", can be answered with "Yes, when the connectionist networks themselves are constructivist." The modelling of different aspects of cognitive development with such networks will be a fruitful area of future research.

Appendix A

Corpus for the Past Tense Acquisition Simulations

Nr. of types: 1066
Nr. of tokens: 8000

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
act	acted	&kt	&ktId	3	1
add	added	&d	&dId	23	1
aid	aided	ed	edId	2	1
aim	aimed	em	emd	3	1
ask	asked	&sk	&skt	94	1
bay	bayed	be	bed	1	1
beg	begged	bEg	bEgd	6	1
bow	bowed	b1	b1d	1	1
cry	cried	kr3	kr3d	11	1
die	died	d3	d3d	26	1
don	donned	dan	dand	1	1
dry	dried	dr3	dr3d	1	1
end	ended	End	EndId	15	1
eye	eyed	3	3d	1	1
fit	fitted	fIt	fItId	1	1
fix	fixed	fIks	fIkst	2	1
hop	hopped	hap	hapt	2	1
hug	hugged	h6g	h6gd	1	1
lie	lied	l3	l3d	1	1
lug	lugged	l6g	l6gd	2	1
mop	mopped	map	mapt	1	1
nod	nodded	nad	nadId	18	1
opt	opted	apt	aptId	1	1
owe	owed	o	od	7	1
own	owned	on	ond	6	1
pat	patted	p&t	p&tId	5	1
pay	paid	pe	ped	17	1

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
ply	plied	pl3	pl3d	1	1
pop	popped	pap	papt	3	1
rap	rapped	r&p	r&pt	1	1
rip	ripped	rIp	rIpt	3	1
rob	robbed	rab	rabd	1	1
rub	rubbed	r6b	r6bd	5	1
shy	shied	S3	S3d	1	1
sip	sipped	sIp	sIpt	1	1
sum	summed	s6m	s6md	1	1
tie	tied	t3	t3d	5	1
tip	tipped	tIp	tIpt	1	1
top	topped	tap	tapt	1	1
try	tried	tr3	tr3d	39	1
tug	tugged	t6g	t6gd	1	1
use	used	juz	juzd	48	1
vow	vowed	v1	v1d	1	1
wad	wadded	wad	wadId	1	1
wax	waxed	w&ks	w&kst	1	1
abet	abetted	6bEt	6bEtId	1	1
ache	ached	ek	ekt	1	1
arch	arched	artS	artSt	1	1
back	backed	b&k	b&kt	6	1
balk	balked	bOk	bOkt	1	1
bang	banged	b&N	b&Nd	1	1
base	based	bes	best	2	1
bolt	bolted	bolt	boltId	1	1
bore	bored	bor	bord	2	1
bump	bumped	b6mp	b6mpt	2	1
burn	burned	b6rn	b6rnd	4	1
buzz	buzzed	b6z	b6zd	2	1
call	called	kOl	kOld	53	1
calm	calmed	kam	kamd	1	1
care	cared	kEr	kErd	4	1
chew	chewed	tSu	tSud	1	1
cite	cited	s3t	s3tId	4	1
clip	clipped	klIp	klIpt	2	1
cock	cocked	kak	kakt	1	1
comb	combed	kom	komd	2	1
cook	cooked	kUk	kUkt	1	1
curl	curled	k6rl	k6rld	5	1
dare	dared	dEr	dErd	4	1
dart	darted	dart	dartId	2	1
dash	dashed	d&S	d&St	1	1
deem	deemed	dim	dimd	1	1
deny	denied	dIn3	dIn3d	3	1

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
dine	dined	d3n	d3nd	1	1
dive	dived	d3v	d3vd	2	1
doom	doomed	dum	dumd	1	1
down	downed	d1n	d1nd	2	1
doze	dozed	doz	dozd	2	1
drag	dragged	dr&g	dr&gd	3	1
drip	dripped	drIp	drIpt	1	1
drop	dropped	drap	drapt	19	1
duck	ducked	d6k	d6kt	3	1
dump	dumped	d6mp	d6mpt	1	1
earn	earned	6rn	6rnd	2	1
echo	echoed	Eko	Ekod	2	1
edge	edged	EdZ	EdZd	2	1
envy	envied	Envi	Envid	1	1
face	faced	fes	fest	7	1
fade	faded	fed	fedId	5	1
fail	failed	fel	feld	12	1
fear	feared	fIr	fIrd	4	1
file	filed	f3l	f3ld	2	1
fill	filled	fIl	fIld	14	1
fire	fired	f3r	f3rd	6	1
flip	flipped	flIp	flIpt	1	1
flog	flogged	flag	flagd	2	1
flop	flopped	flap	flapt	3	1
flow	flowed	flo	flod	2	1
fold	folded	fold	foldId	2	1
form	formed	fOrm	fOrmd	5	1
fuse	fused	fjuz	fjuzd	2	1
gain	gained	gen	gend	9	1
gape	gaped	gep	gept	2	1
gasp	gasped	g&sp	g&spt	1	1
gaze	gazed	gez	gezd	4	1
glow	glowed	glo	glod	2	1
grab	grabbed	gr&b	gr&bd	5	1
grin	grinned	grIn	grInd	9	1
grip	gripped	grIp	grIpt	2	1
grok	grokked	grak	grakt	1	1
halt	halted	hOlt	hOltId	1	1
hand	handed	h&nd	h&ndId	6	1
hate	hated	het	hetId	6	1
haul	hauled	hOl	hOld	1	1
head	headed	hEd	hEdId	9	1
heal	healed	hil	hild	2	1
help	helped	hElp	hElpt	11	1
hire	hired	h3r	h3rd	1	1

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
hiss	hissed	hIs	hIst	1	1
hook	hooked	hUk	hUkt	1	1
hope	hoped	hop	hopt	11	1
hunt	hunted	h6nt	h6ntId	1	1
hurl	hurled	h6rl	h6rld	1	1
jerk	jerked	dZ6rk	dZ6rkt	4	1
join	joined	dZ2n	dZ2nd	11	1
jump	jumped	dZ6mp	dZ6mpt	9	1
kick	kicked	kIk	kIkt	4	1
kill	killed	kIl	kIld	17	1
kiss	kissed	kIs	kIst	7	1
lack	lacked	l&k	l&kt	4	1
land	landed	l&nd	l&ndId	3	1
lash	lashed	l&S	l&St	2	1
last	lasted	l&st	l&stId	1	1
leak	leaked	lik	likt	1	1
lean	leaned	lin	lind	13	1
leap	leaped	lip	lipt	6	1
lick	licked	lIk	lIkt	3	1
lift	lifted	lIft	lIftId	9	1
like	liked	l3k	l3kt	11	1
line	lined	l3n	l3nd	5	1
list	listed	lIst	lIstId	3	1
live	lived	lIv	lIvd	18	1
lock	locked	lak	lakt	1	1
long	longed	lON	lONd	1	1
look	looked	lUk	lUkt	98	1
loom	loomed	lum	lumd	1	1
love	loved	l6v	l6vd	14	1
lure	lured	lur	lurd	1	1
lurk	lurked	l6rk	l6rkt	1	1
mail	mailed	mel	meld	2	1
mark	marked	mark	markt	1	1
miss	missed	mIs	mIst	3	1
move	moved	muv	muvd	48	1
muse	mused	mjuz	mjuzd	1	1
nail	nailed	nel	neld	2	1
name	named	nem	nemd	4	1
near	neared	nIr	nIrd	1	1
need	needed	nid	nidId	21	1
note	noted	not	notId	8	1
obey	obeyed	obe	obed	2	1
ooze	oozed	uz	uzd	1	1
open	opened	op6n	op6nd	34	1
pace	paced	pes	pest	4	1

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
pack	packed	p&k	p&kt	1	1
park	parked	park	parkt	5	1
part	parted	part	partId	1	1
pass	passed	p&s	p&st	21	1
peck	pecked	pEk	pEkt	1	1
peel	peeled	pil	pild	1	1
peer	peered	pIr	pIrd	2	1
pick	picked	pIk	pIkt	17	1
pile	piled	p3l	p3ld	1	1
plan	planned	pl&n	pl&nd	8	1
play	played	ple	pled	19	1
poke	poked	pok	pokt	2	1
pose	posed	poz	pozd	1	1
post	posted	post	postId	1	1
pour	poured	por	pord	9	1
pray	prayed	pre	pred	2	1
pull	pulled	pUl	pUld	24	1
pump	pumped	p6mp	p6mpt	1	1
push	pushed	pUS	pUSt	9	1
race	raced	res	rest	2	1
rage	raged	redZ	redZd	1	1
rain	rained	ren	rend	1	1
rake	raked	rek	rekt	1	1
rear	reared	rIr	rIrd	3	1
reel	reeled	ril	rild	1	1
rely	relied	rIl3	rIl3d	1	1
rest	rested	rEst	rEstId	5	1
risk	risked	rIsk	rIskt	1	1
roar	roared	ror	rord	11	1
rock	rocked	rak	rakt	2	1
roll	rolled	rol	rold	18	1
rule	ruled	rul	ruld	5	1
rush	rushed	r6S	r6St	3	1
sail	sailed	sel	seld	3	1
save	saved	sev	sevd	2	1
scan	scanned	sk&n	sk&nd	5	1
seat	seated	sit	sitId	2	1
seem	seemed	sim	simd	106	1
show	showed	So	Sod	39	1
sigh	sighed	s3	s3d	8	1
sign	signed	s3n	s3nd	4	1
size	sized	s3z	s3zd	1	1
skim	skimmed	skIm	skImd	1	1
skip	skipped	skIp	skIpt	1	1
slam	slammed	sl&m	sl&md	5	1

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
slap	slapped	sl&p	sl&pt	4	1
slip	slipped	slIp	slIpt	8	1
snap	snapped	sn&p	sn&pt	4	1
snow	snowed	sno	snod	1	1
soar	soared	sor	sord	1	1
spot	spotted	spat	spatId	2	1
spur	spurred	sp6r	sp6rd	2	1
stay	stayed	ste	sted	19	1
stem	stemmed	stEm	stEmd	2	1
step	stepped	stEp	stEpt	12	1
stir	stirred	st6r	st6rd	4	1
stop	stopped	stap	stapt	39	1
suck	sucked	s6k	s6kt	1	1
suit	suited	sut	sutId	2	1
sway	swayed	swe	swed	3	1
talk	talked	tOk	tOkt	16	1
team	teamed	tim	timd	1	1
tend	tended	tEnd	tEndId	2	1
term	termed	t6rm	t6rmd	1	1
test	tested	tEst	tEstId	3	1
tick	ticked	tIk	tIkt	1	1
time	timed	t3m	t3md	1	1
tire	tired	t3r	t3rd	2	1
toss	tossed	tOs	tOst	9	1
trip	tripped	trIp	trIpt	1	1
trot	trotted	trat	tratId	2	1
tuck	tucked	t6k	t6kt	2	1
turn	turned	t6rn	t6rnd	89	1
urge	urged	6rdZ	6rdZd	6	1
vary	varied	vEri	vErid	4	1
veer	veered	vIr	vIrd	1	1
view	viewed	vju	vjud	1	1
vote	voted	vot	votId	5	1
wail	wailed	wel	weld	1	1
wait	waited	wet	wetId	21	1
walk	walked	wOk	wOkt	46	1
want	wanted	wOnt	wOntId	62	1
warm	warmed	wOrm	wOrmd	3	1
warn	warned	wOrn	wOrnd	5	1
wash	washed	wOS	wOSt	2	1
wave	waved	wev	wevd	5	1
whip	whipped	wIp	wIpt	3	1
whiz	whizzed	wIz	wIzd	2	1
wing	winged	wIN	wINd	2	1
wink	winked	wINk	wINkt	1	1

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
wipe	wiped	w3p	w3pt	3	1
wire	wired	w3r	w3rd	1	1
wish	wished	wIS	wISt	18	1
work	worked	w6rk	w6rkt	21	1
yank	yanked	j&Nk	j&Nkt	2	1
yell	yelled	jEl	jEld	4	1
admit	admitted	6dmIt	6dmItId	9	1
adopt	adopted	6dapt	6daptId	7	1
agree	agreed	6gri	6grid	17	1
allow	allowed	6l1	6l1d	4	1
amend	amended	6mEnd	6mEndId	1	1
amuse	amused	6mjuz	6mjuzd	2	1
apply	applied	6pl3	6pl3d	7	1
argue	argued	argju	argjud	8	1
avoid	avoided	6v2d	6v2dId	3	1
await	awaited	6wet	6wetId	1	1
award	awarded	6wOrd	6wOrdId	1	1
belch	belched	bEltS	bEltSt	2	1
belie	belied	bIl3	bIl3d	1	1
blaze	blazed	blez	blezd	1	1
blink	blinked	blINk	blINkt	1	1
block	blocked	blak	blakt	1	1
bloom	bloomed	blum	blumd	2	1
blurt	blurted	bl6rt	bl6rtId	1	1
blush	blushed	bl6S	bl6St	1	1
bogey	bogeyed	bogi	bogid	2	1
brush	brushed	br6S	br6St	4	1
carry	carried	k&ri	k&rid	15	1
cause	caused	kOz	kOzd	17	1
cease	ceased	sis	sist	3	1
chant	chanted	tS&nt	tS&ntId	1	1
check	checked	tSEk	tSEkt	5	1
chill	chilled	tSIl	tSIld	1	1
choke	choked	tSok	tSokt	2	1
claim	claimed	klem	klemd	10	1
clamp	clamped	kl&mp	kl&mpt	1	1
clasp	clasped	kl&sp	kl&spt	1	1
clean	cleaned	klin	klind	3	1
clear	cleared	klIr	klIrd	5	1
click	clicked	klIk	klIkt	1	1
climb	climbed	kl3m	kl3md	9	1
close	closed	kloz	klozd	17	1
coast	coasted	kost	kostId	1	1
count	counted	k1nt	k1ntId	4	1
cover	covered	k6v6r	k6v6rd	3	1

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
crack	cracked	kr&k	kr&kt	4	1
crash	crashed	kr&S	kr&St	1	1
crawl	crawled	krOl	krOld	4	1
creak	creaked	krik	krikt	1	1
cross	crossed	krOs	krOst	9	1
crowd	crowded	kr1d	kr1dId	1	1
curse	cursed	k6rs	k6rst	4	1
dance	danced	d&ns	d&nst	3	1
decry	decried	dIkr3	dIkr3d	1	1
delay	delayed	dIle	dIled	1	1
dodge	dodged	dadZ	dadZd	1	1
doubt	doubted	d1t	d1tId	3	1
draft	drafted	dr&ft	dr&ftId	1	1
drape	draped	drep	drept	1	1
dream	dreamed	drim	drimd	3	1
dress	dressed	drEs	drEst	4	1
drift	drifted	drIft	drIftId	1	1
drown	drowned	dr1n	dr1nd	1	1
elect	elected	IlEkt	IlEktId	1	1
empty	emptied	Empti	Emptid	2	1
enjoy	enjoyed	IndZ2	IndZ2d	13	1
ensue	ensued	Insu	Insud	1	1
enter	entered	Ent6r	Ent6rd	23	1
erect	erected	IrEkt	IrEktId	1	1
evoke	evoked	Ivok	Ivokt	1	1
exist	existed	IgzIst	IgzIstId	9	1
exude	exuded	Igzud	IgzudId	2	1
fancy	fancied	f&nsi	f&nsid	1	1
favor	favored	fev6r	fev6rd	4	1
flare	flared	flEr	flErd	1	1
flash	flashed	fl&S	fl&St	3	1
flick	flicked	flIk	flIkt	1	1
float	floated	flot	flotId	2	1
flood	flooded	fl6d	fl6dId	2	1
focus	focused	fok6s	fok6st	5	1
force	forced	fors	forst	4	1
frown	frowned	fr1n	fr1nd	1	1
glare	glared	glEr	glErd	3	1
gleam	gleamed	glim	glimd	1	1
glint	glinted	glInt	glIntId	1	1
gloat	gloated	glot	glotId	1	1
gouge	gouged	g1dZ	g1dZd	1	1
grant	granted	gr&nt	gr&ntId	3	1
grasp	grasped	gr&sp	gr&spt	2	1
greet	greeted	grit	gritId	3	1

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
groan	groaned	gron	grond	2	1
grope	groped	grop	gropt	4	1
growl	growled	gr1l	gr1ld	1	1
grunt	grunted	gr6nt	gr6ntId	2	1
guess	guessed	gEs	gEst	4	1
guide	guided	g3d	g3dId	1	1
heave	heaved	hiv	hivd	2	1
honor	honored	an6r	an6rd	1	1
hurry	hurried	h6ri	h6rid	4	1
imply	implied	Impl3	Impl3d	1	1
infer	inferred	Inf6r	Inf6rd	2	1
issue	issued	ISu	ISud	4	1
judge	judged	dZ6dZ	dZ6dZd	2	1
knock	knocked	nak	nakt	5	1
labor	labored	leb6r	leb6rd	1	1
laugh	laughed	l&f	l&ft	17	1
learn	learned	l6rn	l6rnd	11	1
level	leveled	lEv6l	lEv6ld	1	1
limit	limited	lIm6t	lIm6tId	2	1
lower	lowered	lor	lord	2	1
lurch	lurched	l6rtS	l6rtSt	1	1
march	marched	martS	martSt	1	1
marry	married	m&ri	m&rid	6	1
merit	merited	mEr6t	mEr6tId	2	1
mount	mounted	m1nt	m1ntId	5	1
nudge	nudged	n6dZ	n6dZd	1	1
occur	occurred	6k6r	6k6rd	17	1
offer	offered	Of6r	Of6rd	15	1
order	ordered	Ord6r	Ord6rd	11	1
paint	painted	pent	pentId	4	1
pause	paused	pOz	pOzd	10	1
phone	phoned	fon	fond	1	1
pinch	pinched	pIntS	pIntSt	2	1
pitch	pitched	pItS	pItSt	3	1
place	placed	ples	plest	11	1
plant	planted	pl&nt	pl&ntId	3	1
plead	pleaded	plid	plidId	4	1
pluck	plucked	pl6k	pl6kt	2	1
plump	plumped	pl6mp	pl6mpt	1	1
point	pointed	p2nt	p2ntId	15	1
poise	poised	p2z	p2zd	1	1
pound	pounded	p1nd	p1ndId	2	1
press	pressed	prEs	prEst	3	1
print	printed	prInt	prIntId	2	1
prove	proved	pruv	pruvd	13	1

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
quiet	quieted	kw36t	kw36tId	1	1
quote	quoted	kwot	kwotId	3	1
raise	raised	rez	rezd	20	1
range	ranged	rendZ	rendZd	7	1
reach	reached	ritS	ritSt	36	1
react	reacted	ri&kt	ri&ktId	3	1
refer	referred	rIf6r	rIf6rd	4	1
relax	relaxed	rIl&ks	rIl&kst	3	1
reply	replied	rIpl3	rIpl3d	17	1
rouse	roused	r1z	r1zd	1	1
savor	savored	sev6r	sev6rd	1	1
scare	scared	skEr	skErd	2	1
scoop	scooped	skup	skupt	1	1
score	scored	skor	skord	4	1
scowl	scowled	sk1l	sk1ld	1	1
seize	seized	siz	sizd	3	1
sense	sensed	sEns	sEnst	5	1
serve	served	s6rv	s6rvd	21	1
shape	shaped	Sep	Sept	2	1
share	shared	SEr	SErd	3	1
shave	shaved	Sev	Sevd	1	1
shift	shifted	SIft	SIftId	5	1
shout	shouted	S1t	S1tId	9	1
shove	shoved	S6v	S6vd	3	1
shrug	shrugged	Sr6g	Sr6gd	4	1
sidle	sidled	s3d6l	s3d6ld	2	1
slash	slashed	sl&S	sl&St	2	1
slice	sliced	sl3s	sl3st	2	1
slump	slumped	sl6mp	sl6mpt	2	1
smash	smashed	sm&S	sm&St	8	1
smell	smelled	smEl	smEld	2	1
smile	smiled	sm3l	sm3ld	20	1
smoke	smoked	smok	smokt	2	1
snake	snaked	snek	snekt	1	1
snarl	snarled	snarl	snarld	3	1
sniff	sniffed	snIf	snIft	3	1
snort	snorted	snOrt	snOrtId	4	1
sound	sounded	s1nd	s1ndId	12	1
spare	spared	spEr	spErd	2	1
stain	stained	sten	stend	2	1
stalk	stalked	stOk	stOkt	3	1
stall	stalled	stOl	stOld	2	1
stare	stared	stEr	stErd	19	1
start	started	start	startId	49	1
state	stated	stet	stetId	10	1

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
steer	steered	stIr	stIrd	3	1
stoop	stooped	stup	stupt	1	1
storm	stormed	stOrm	stOrmd	1	1
strut	strutted	str6t	str6tId	1	1
study	studied	st6di	st6did	11	1
surge	surged	s6rdZ	s6rdZd	4	1
swarm	swarmed	swOrm	swOrmd	2	1
swirl	swirled	sw6rl	sw6rld	1	1
swish	swished	swIS	swISt	1	1
taste	tasted	test	testId	3	1
thank	thanked	T&Nk	T&Nkt	3	1
total	totaled	tot6l	tot6ld	4	1
touch	touched	t6tS	t6tSt	10	1
track	tracked	tr&k	tr&kt	1	1
trade	traded	tred	tredId	1	1
trail	trailed	trel	treld	1	1
train	trained	tren	trend	1	1
treat	treated	trit	tritId	7	1
trust	trusted	tr6st	tr6stId	1	1
twine	twined	tw3n	tw3nd	1	1
twist	twisted	twIst	twIstId	3	1
utter	uttered	6t6r	6t6rd	1	1
visit	visited	vIz6t	vIz6tId	10	1
waste	wasted	west	westId	2	1
watch	watched	watS	watSt	25	1
water	watered	wOt6r	wOt6rd	1	1
weigh	weighed	we	wed	4	1
whack	whacked	w&k	w&kt	2	1
wheel	wheeled	wil	wild	1	1
whirl	whirled	w6rl	w6rld	1	1
widen	widened	w3d6n	w3d6nd	1	1
wield	wielded	wild	wildId	1	1
wince	winced	wIns	wInst	2	1
worry	worried	w6ri	w6rid	1	1
wreck	wrecked	rEk	rEkt	1	1
yield	yielded	jild	jildId	3	1
abound	abounded	6b1nd	6b1ndId	1	1
absorb	absorbed	6bsOrb	6bsOrbd	1	1
accept	accepted	IksEpt	IksEptId	12	1
accuse	accused	6kjuz	6kjuzd	2	1
adjoin	adjoined	6dZ2n	6dZ2nd	1	1
advise	advised	6dv3z	6dv3zd	7	1
afford	afforded	6ford	6fordId	2	1
allege	alleged	6lEdZ	6lEdZd	1	1
amount	amounted	6m1nt	6m1ntId	1	1

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
answer	answered	&ns6r	&ns6rd	20	1
appeal	appealed	6pil	6pild	1	1
appear	appeared	6pIr	6pIrd	45	1
arouse	aroused	6r1z	6r1zd	2	1
arrest	arrested	6rEst	6rEstId	1	1
arrive	arrived	6r3v	6r3vd	12	1
assert	asserted	6s6rt	6s6rtId	3	1
assign	assigned	6s3n	6s3nd	1	1
assist	assisted	6sIst	6sIstId	1	1
assume	assumed	6sum	6sumd	7	1
assure	assured	6Sur	6Surd	5	1
attach	attached	6t&tS	6t&tSt	1	1
attack	attacked	6t&k	6t&kt	5	1
attend	attended	6tEnd	6tEndId	10	1
attest	attested	6tEst	6tEstId	1	1
babble	babbled	b&b6l	b&b6ld	1	1
beckon	beckoned	bEk6n	bEk6nd	3	1
behave	behaved	bIhev	bIhevd	2	1
bellow	bellowed	bElo	bElod	2	1
belong	belonged	bIlON	bIlONd	4	1
bestow	bestowed	bIsto	bIstod	2	1
borrow	borrowed	baro	barod	2	1
bother	bothered	baD6r	baD6rd	4	1
bounce	bounced	b1ns	b1nst	4	1
cackle	cackled	k&k6l	k&k6ld	2	1
caress	caressed	k6r6s	k6r6st	1	1
center	centered	sEnt6r	sEnt6rd	2	1
change	changed	tSendZ	tSendZd	9	1
charge	charged	tSardZ	tSardZd	4	1
circle	circled	s6rk6l	s6rk6ld	3	1
clutch	clutched	kl6tS	kl6tSt	3	1
commit	committed	k6mIt	k6mItId	3	1
comply	complied	k6mpl3	k6mpl3d	1	1
concur	concurred	k6nk6r	k6nk6rd	1	1
convey	conveyed	k6nve	k6nved	1	1
couple	coupled	k6p6l	k6p6ld	2	1
create	created	kriet	krietId	5	1
crouch	crouched	kr1tS	kr1tSt	5	1
damage	damaged	d&mIdZ	d&mIdZd	1	1
dangle	dangled	d&Ng6l	d&Ng6ld	1	1
darken	darkened	dark6n	dark6nd	5	1
decide	decided	dIs3d	dIs3dId	31	1
deduce	deduced	dIdus	dIdust	1	1
defeat	defeated	dIfit	dIfitId	1	1
defend	defended	dIfEnd	dIfEndId	4	1

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
demand	demanded	dIm&nd	dIm&ndId	12	1
depart	departed	dIpart	dIpartId	2	1
depend	depended	dIpEnd	dIpEndId	6	1
depict	depicted	dIpIkt	dIpIktId	2	1
design	designed	dIz3n	dIz3nd	3	1
desire	desired	dIz3r	dIz3rd	3	1
detest	detested	dItEst	dItEstId	1	1
devise	devised	dIv3z	dIv3zd	1	1
devote	devoted	dIvot	dIvotId	6	1
differ	differed	dIf6r	dIf6rd	4	1
direct	directed	d6rEkt	d6rEktId	2	1
divide	divided	d6v3d	d6v3dId	2	1
double	doubled	d6b6l	d6b6ld	1	1
emerge	emerged	Im6rdZ	Im6rdZd	7	1
employ	employed	Impl2	Impl2d	1	1
enable	enabled	Ineb6l	Ineb6ld	3	1
endear	endeared	IndIr	IndIrd	2	1
engage	engaged	IngedZ	IngedZd	1	1
engulf	engulfed	Ing6lf	Ing6lft	2	1
enlist	enlisted	InlIst	InlIstId	1	1
escape	escaped	Iskep	Iskept	2	1
escort	escorted	IskOrt	IskOrtId	3	1
esteem	esteemed	Istim	Istimd	1	1
evolve	evolved	Ivalv	Ivalvd	1	1
excite	excited	Iks3t	Iks3tId	1	1
excuse	excused	Ikskjuz	Ikskjuzd	2	1
expand	expanded	Iksp&nd	Iksp&ndId	2	1
expect	expected	IkspEkt	IkspEktId	10	1
expose	exposed	Ikspoz	Ikspozd	1	1
extend	extended	IkstEnd	IkstEndId	3	1
falter	faltered	fOlt6r	fOlt6rd	1	1
figure	figured	fIgj6r	fIgj6rd	8	1
finger	fingered	fINg6r	fINg6rd	1	1
finish	finished	fInIS	fInISt	7	1
follow	followed	falo	falod	26	1
fumble	fumbled	f6mb6l	f6mb6ld	2	1
gather	gathered	g&D6r	g&D6rd	9	1
giggle	giggled	gIg6l	gIg6ld	1	1
glance	glanced	gl&ns	gl&nst	11	1
gobble	gobbled	gab6l	gab6ld	2	1
ground	grounded	gr1nd	gr1ndId	1	1
handle	handled	h&nd6l	h&nd6ld	1	1
happen	happened	h&p6n	h&p6nd	28	1
harass	harassed	h6r&s	h6r&st	1	1
hasten	hastened	hes6n	hes6nd	4	1

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
hinder	hindered	hInd6r	hInd6rd	1	1
huddle	huddled	h6d6l	h6d6ld	3	1
ignore	ignored	Ignor	Ignord	9	1
import	imported	Import	ImportId	1	1
impose	imposed	Impoz	Impozd	2	1
inform	informed	InfOrm	InfOrmd	11	1
injure	injured	IndZ6r	IndZ6rd	1	1
insist	insisted	InsIst	InsIstId	12	1
intend	intended	IntEnd	IntEndId	2	1
intone	intoned	Inton	Intond	1	1
invite	invited	Inv3t	Inv3tId	6	1
jingle	jingled	dZINg6l	dZINg6ld	1	1
lessen	lessened	lEs6n	lEs6nd	3	1
linger	lingered	lINg6r	lINg6rd	2	1
listen	listened	lIs6n	lIs6nd	6	1
loathe	loathed	loD	loDd	2	1
locate	located	loket	loketId	3	1
lounge	lounged	l1ndZ	l1ndZd	1	1
manage	managed	m&nIdZ	m&nIdZd	5	1
matter	mattered	m&t6r	m&t6rd	2	1
mumble	mumbled	m6mb6l	m6mb6ld	1	1
murmur	murmured	m6rm6r	m6rm6rd	6	1
mutter	muttered	m6t6r	m6t6rd	8	1
notice	noticed	not6s	not6st	4	1
object	objected	6bdZEkt	6bdZEktId	4	1
oblige	obliged	6bl3dZ	6bl3dZd	1	1
obtain	obtained	6bten	6btend	3	1
occupy	occupied	akj6p3	akj6p3d	2	1
oppose	opposed	6poz	6pozd	2	1
permit	permitted	p6rmIt	p6rmItId	5	1
plague	plagued	pleg	plegd	1	1
please	pleased	pliz	plizd	4	1
pledge	pledged	plEdZ	plEdZd	1	1
plunge	plunged	pl6ndZ	pl6ndZd	4	1
ponder	pondered	pand6r	pand6rd	1	1
praise	praised	prez	prezd	4	1
preach	preached	pritS	pritSt	1	1
prefer	preferred	prIf6r	prIf6rd	8	1
prompt	prompted	prampt	pramptId	1	1
pursue	pursued	p6rsu	p6rsud	1	1
rattle	rattled	r&t6l	r&t6ld	1	1
reason	reasoned	riz6n	riz6nd	1	1
recall	recalled	rIkOl	rIkOld	5	1
reduce	reduced	rIdus	rIdust	3	1
refuse	refused	rIfjuz	rIfjuzd	19	1

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
regain	regained	rigen	rigend	1	1
regard	regarded	rIgard	rIgardId	4	1
reject	rejected	rIdZEkt	rIdZEktId	3	1
relate	related	rIlet	rIletId	4	1
remain	remained	rImen	rImend	27	1
remark	remarked	rImark	rImarkt	13	1
remind	reminded	rIm3nd	rIm3ndId	12	1
remove	removed	rImuv	rImuvd	2	1
render	rendered	rEnd6r	rEnd6rd	1	1
repair	repaired	rIpEr	rIpErd	1	1
repeat	repeated	rIpit	rIpitId	3	1
report	reported	rIport	rIportId	9	1
resent	resented	rIzEnt	rIzEntId	3	1
reside	resided	rIz3d	rIz3dId	1	1
resign	resigned	rIz3n	rIz3nd	3	1
resist	resisted	rIzIst	rIzIstId	3	1
result	resulted	rIz6lt	rIz6ltId	14	1
resume	resumed	rIzum	rIzumd	3	1
retain	retained	rIten	rItend	3	1
retire	retired	rIt3r	rIt3rd	1	1
retort	retorted	rItOrt	rItOrtId	1	1
return	returned	rIt6rn	rIt6rnd	32	1
reveal	revealed	rIvil	rIvild	7	1
review	reviewed	rIvju	rIvjud	3	1
revise	revised	rIv3z	rIv3zd	1	1
scream	screamed	skrim	skrimd	5	1
search	searched	s6rtS	s6rtSt	3	1
select	selected	s6lEkt	s6lEktId	3	1
settle	settled	sEt6l	sEt6ld	15	1
shower	showered	S1r	S1rd	1	1
shriek	shrieked	Srik	Srikt	1	1
shrill	shrilled	SrIl	SrIld	1	1
signal	signaled	sIgn6l	sIgn6ld	1	1
single	singled	sINg6l	sINg6ld	2	1
sizzle	sizzled	sIz6l	sIz6ld	1	1
sketch	sketched	skEtS	skEtSt	1	1
smooth	smoothed	smuD	smuDd	1	1
snatch	snatched	sn&tS	sn&tSt	2	1
soothe	soothed	suD	suDd	1	1
sprint	sprinted	sprInt	sprIntId	1	1
square	squatted	skwEr	skwErd	2	1
squeak	squeaked	skwik	skwikt	1	1
strain	strained	stren	strend	3	1
streak	streaked	strik	strikt	1	1
stress	stressed	strEs	strEst	7	1

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
stroke	stroked	strok	strokt	1	1
submit	submitted	s6bmIt	s6bmItId	3	1
suffer	suffered	s6f6r	s6f6rd	8	1
supply	supplied	s6pl3	s6pl3d	3	1
swerve	swerved	sw6rv	sw6rvd	2	1
switch	switched	swItS	swItSt	4	1
thrash	thrashed	Tr&S	Tr&St	1	1
thrive	thrived	Tr3v	Tr3vd	3	1
travel	traveled	tr&v6l	tr&v6ld	5	1
tumble	tumbled	t6mb6l	t6mb6ld	3	1
twitch	twitched	twItS	twItSt	2	1
unfold	unfolded	6nfold	6nfoldId	2	1
unlock	unlocked	6nlak	6nlakt	1	1
vanish	vanished	v&nIS	v&nISt	4	1
wander	wandered	wand6r	wand6rd	2	1
wiggle	wiggled	wIg6l	wIg6ld	2	1
wobble	wobbled	wab6l	wab6ld	1	1
wonder	wondered	w6nd6r	w6nd6rd	14	1
wrench	wrenched	rEntS	rEntSt	1	1
abandon	abandoned	6b&nd6n	6b&nd6nd	2	1
account	accounted	6k1nt	6k1ntId	2	1
achieve	achieved	6tSiv	6tSivd	5	1
acquire	acquired	6kw3r	6kw3rd	5	1
address	addressed	6drEs	6drEst	2	1
adjourn	adjourned	6dZ6rn	6dZ6rnd	1	1
advance	advanced	6dv&ns	6dv&nst	2	1
appoint	appointed	6p2nt	6p2ntId	1	1
approve	approved	6pruv	6pruvd	5	1
arraign	arraigned	6ren	6rend	2	1
arrange	arranged	6rendZ	6rendZd	1	1
assault	assaulted	6sOlt	6sOltId	1	1
attempt	attempted	6tEmpt	6tEmptId	4	1
attract	attracted	6tr&kt	6tr&ktId	3	1
average	averaged	&vrIdZ	&vrIdZd	6	1
believe	believed	b6liv	b6livd	15	1
breathe	breathed	briD	briDd	3	1
broaden	broadened	brOd6n	brOd6nd	2	1
capture	captured	k&ptS6r	k&ptS6rd	2	1
caution	cautioned	kOS6n	kOS6nd	1	1
cherish	cherished	tSErIS	tSErISt	3	1
chuckle	chuckled	tS6k6l	tS6k6ld	2	1
clamber	clambered	kl&mb6r	kl&mb6rd	1	1
clatter	clattered	kl&t6r	kl&t6rd	3	1
collect	collected	k6lEkt	k6lEktId	2	1
combine	combined	k6mb3n	k6mb3nd	3	1

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
command	commanded	k6m&nd	k6m&ndId	3	1
comment	commented	kamEnt	kamEntId	3	1
compare	compared	k6mpEr	k6mpErd	3	1
compile	compiled	k6mp3l	k6mp3ld	1	1
compose	composed	k6mpoz	k6mpozd	1	1
concede	conceded	k6nsid	k6nsidId	2	1
concern	concerned	k6ns6rn	k6ns6rnd	1	1
condemn	condemned	k6ndEm	k6ndEmd	2	1
conduct	conducted	k6nd6kt	k6nd6ktId	3	1
confess	confessed	k6nfEs	k6nfEst	1	1
confide	confided	k6nf3d	k6nf3dId	3	1
confuse	confused	k6nfjuz	k6nfjuzd	1	1
connect	connected	k6nEkt	k6nEktId	1	1
consist	consisted	k6nsIst	k6nsIstId	7	1
contact	contacted	kant&kt	kant&ktId	2	1
contain	contained	k6nten	k6ntend	18	1
contend	contended	k6ntEnd	k6ntEndId	3	1
control	controlled	k6ntrol	k6ntrold	3	1
convene	convened	k6nvin	k6nvind	1	1
correct	corrected	k6rEkt	k6rEktId	1	1
counsel	counseled	k1ns6l	k1ns6ld	1	1
declaim	declaimed	dIklem	dIklemd	1	1
declare	declared	dIklEr	dIklErd	12	1
decline	declined	dIkl3n	dIkl3nd	6	1
deliver	delivered	dIlIv6r	dIlIv6rd	5	1
deplore	deplored	dIplor	dIplord	1	1
deserve	deserved	dIz6rv	dIz6rvd	2	1
despise	despised	dIsp3z	dIsp3zd	2	1
develop	developed	dIvEl6p	dIvEl6pt	15	1
discuss	discussed	dIsk6s	dIsk6st	3	1
dislike	disliked	dIsl3k	dIsl3kt	4	1
dismiss	dismissed	dIsmIs	dIsmIst	2	1
display	displayed	dIsple	dIspled	4	1
dispose	disposed	dIspoz	dIspozd	1	1
disrupt	disrupted	dIsr6pt	dIsr6ptId	1	1
disturb	disturbed	dIst6rb	dIst6rbd	1	1
divorce	divorced	d6vors	d6vorst	1	1
embrace	embraced	Imbres	Imbrest	2	1
enclose	enclosed	Inkloz	Inklozd	1	1
entitle	entitled	Int3t6l	Int3t6ld	1	1
entreat	entreated	Intrit	IntritId	1	1
examine	examined	Igz&m6n	Igz&m6nd	2	1
exclaim	exclaimed	Iksklem	Iksklemd	2	1
exhaust	exhausted	IgzOst	IgzOstId	1	1
explain	explained	Iksplen	Iksplend	18	1

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
express	expressed	IksprEs	IksprEst	7	1
fashion	fashioned	f&S6n	f&S6nd	1	1
flatten	flattened	fl&t6n	fl&t6nd	1	1
flatter	flattered	fl&t6r	fl&t6rd	2	1
flicker	flickered	flIk6r	flIk6rd	1	1
furnish	furnished	f6rnIS	f6rnISt	1	1
gesture	gestured	dZEstS6r	dZEstS6rd	1	1
glimpse	glimpsed	glImps	glImpst	1	1
imagine	imagined	Im&dZ6n	Im&dZ6nd	6	1
impress	impressed	ImprEs	ImprEst	2	1
improve	improved	Impruv	Impruvd	3	1
include	included	Inklud	InkludId	16	1
indulge	indulged	Ind6ldZ	Ind6ldZd	1	1
inflict	inflicted	InflIkt	InflIktId	2	1
inquire	inquired	Inkw3r	Inkw3rd	8	1
install	installed	InstOl	InstOld	1	1
involve	involved	Invalv	Invalvd	10	1
journey	journeyed	dZ6rni	dZ6rnid	1	1
measure	measured	mEZ6r	mEZ6rd	1	1
mention	mentioned	mEntS6n	mEntS6nd	5	1
obscure	obscured	abskjur	abskjurd	1	1
observe	observed	6bz6rv	6bz6rvd	6	1
perform	performed	p6rfOrm	p6rfOrmd	5	1
persist	persisted	p6rsIst	p6rsIstId	3	1
possess	possessed	p6zEs	p6zEst	8	1
precede	preceded	prIsid	prIsidId	1	1
predict	predicted	prIdIkt	prIdIktId	1	1
prepare	prepared	prIpEr	prIpErd	5	1
present	presented	prIzEnt	prIzEntId	9	1
pretend	pretended	prItEnd	prItEndId	2	1
prevail	prevailed	prIvel	prIveld	2	1
prevent	prevented	prIvEnt	prIvEntId	3	1
proceed	proceeded	prosid	prosidId	8	1
produce	produced	pr6dus	pr6dust	6	1
profess	professed	pr6fEs	pr6fEst	2	1
proffer	proffered	praf6r	praf6rd	1	1
promise	promised	pram6s	pram6st	7	1
propose	proposed	pr6poz	pr6pozd	8	1
protect	protected	pr6tEkt	pr6tEktId	1	1
protest	protested	pr6tEst	pr6tEstId	7	1
provide	provided	pr6v3d	pr6v3dId	11	1
provoke	provoked	pr6vok	pr6vokt	1	1
publish	published	p6blIS	p6blISt	2	1
purport	purported	p6rport	p6rportId	1	1
quarrel	quarreled	kwOr6l	kwOr6ld	1	1

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
radiate	radiated	rediet	redietId	1	1
realize	realized	ri6l3z	ri6l3zd	17	1
receive	received	rIsiv	rIsivd	18	1
recount	recounted	rIk1nt	rIk1ntId	1	1
recover	recovered	rIk6v6r	rIk6v6rd	1	1
reflect	reflected	rIflEkt	rIflEktId	8	1
release	released	rIlis	rIlist	1	1
relieve	relieved	rIliv	rIlivd	1	1
replace	replaced	rIples	rIplest	5	1
request	requested	rIkwEst	rIkwEstId	2	1
require	required	rIkw3r	rIkw3rd	8	1
reserve	reserved	rIz6rv	rIz6rvd	2	1
resolve	resolved	rIzalv	rIzalvd	2	1
respect	respected	rIspEkt	rIspEktId	1	1
respond	responded	rIspand	rIspandId	6	1
restore	restored	rIstor	rIstord	1	1
retreat	retreated	rItrit	rItritId	3	1
revolve	revolved	rIvalv	rIvalvd	1	1
satisfy	satisfied	s&t6sf3	s&t6sf3d	2	1
scatter	scattered	sk&t6r	sk&t6rd	1	1
screech	screeched	skritS	skritSt	2	1
shatter	shattered	S&t6r	S&t6rd	2	1
smolder	smoldered	smold6r	smold6rd	2	1
snicker	snickered	snIk6r	snIk6rd	2	1
snuggle	snuggled	sn6g6l	sn6g6ld	2	1
sponsor	sponsored	spans6r	spans6rd	1	1
squeeze	squeezed	skwiz	skwizd	2	1
stagger	staggered	st&g6r	st&g6rd	1	1
stiffen	stiffened	stIf6n	stIf6nd	2	1
stretch	stretched	strEtS	strEtSt	10	1
stumble	stumbled	st6mb6l	st6mb6ld	6	1
subside	subsided	s6bs3d	s6bs3dId	2	1
succeed	succeeded	s6ksid	s6ksidId	7	1
suffuse	suffused	s6fuz	s6fuzd	3	1
suggest	suggested	s6dZEst	s6dZEstId	12	1
support	supported	s6port	s6portId	6	1
suppose	supposed	s6poz	s6pozd	3	1
survive	survived	s6rv3v	s6rv3vd	3	1
suspect	suspected	s6spEkt	s6spEktId	8	1
swagger	swaggered	sw&g6r	sw&g6rd	1	1
swallow	swallowed	swalo	swalod	1	1
testify	testified	tEst6f3	tEst6f3d	4	1
tighten	tightened	t3t6n	t3t6nd	2	1
tremble	trembled	trEmb6l	trEmb6ld	2	1
trouble	troubled	tr6b6l	tr6b6ld	2	1

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
undress	undressed	6ndrEs	6ndrEst	1	1
unscrew	unscrewed	6nskru	6nskrud	1	1
venture	ventured	vEntS6r	vEntS6rd	1	1
violate	violated	v36let	v36letId	1	1
welcome	welcomed	wElk6m	wElk6md	5	1
whisper	whispered	wIsp6r	wIsp6rd	7	1
whistle	whistled	wIs6l	wIs6ld	1	1
witness	witnessed	wItn6s	wItn6st	1	1
wrangle	wrangled	r&Ng6l	r&Ng6ld	1	1
wrinkle	wrinkled	rINk6l	rINk6ld	1	1
announce	announced	6n1ns	6n1nst	21	1
approach	approached	6protS	6protSt	10	1
assemble	assembled	6sEmb6l	6sEmb6ld	3	1
brighten	brightened	br3t6n	br3t6nd	1	1
campaign	campaigned	k&mpen	k&mpend	1	1
collapse	collapsed	k6l&ps	k6l&pst	3	1
commence	commenced	k6mEns	k6mEnst	2	1
complain	complained	k6mplen	k6mplend	9	1
complete	completed	k6mplit	k6mplitId	2	1
comprise	comprised	k6mpr3z	k6mpr3zd	1	1
conceive	conceived	k6nsiv	k6nsivd	3	1
conclude	concluded	k6nklud	k6nkludId	7	1
consider	considered	k6nsId6r	k6nsId6rd	9	1
conspire	conspired	k6nsp3r	k6nsp3rd	1	1
continue	continued	k6ntInju	k6ntInjud	26	1
contract	contracted	k6ntr&kt	k6ntr&ktId	1	1
convince	convinced	k6nvIns	k6nvInst	4	1
denounce	denounced	dIn1ns	dIn1nst	1	1
describe	described	dIskr3b	dIskr3bd	9	1
disclose	disclosed	dIskloz	dIsklozd	3	1
discount	discounted	dIsk1nt	dIsk1ntId	1	1
discover	discovered	dIsk6v6r	dIsk6v6rd	11	1
disguise	disguised	dIsg3z	dIsg3zd	1	1
dismount	dismounted	dIsm1nt	dIsm1ntId	1	1
dispatch	dispatched	dIsp&tS	dIsp&tSt	2	1
exercise	exercised	Eks6rs3z	Eks6rs3zd	2	1
flourish	flourished	fl6rIS	fl6rISt	1	1
function	functioned	f6NkS6n	f6NkS6nd	1	1
illumine	illumined	Ilum6n	Ilum6nd	1	1
increase	increased	Inkris	Inkrist	15	1
interest	interested	Intr6st	Intr6stId	1	1
maintain	maintained	menten	mentend	3	1
maneuver	maneuvered	m6nuv6r	m6nuv6rd	2	1
minimize	minimized	mIn6m3z	mIn6m3zd	1	1
minister	ministered	mIn6st6r	mIn6st6rd	1	1

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
mistrust	mistrusted	mIstr6st	mIstr6stId	1	1
multiply	multiplied	m6lt6pl3	m6lt6pl3d	1	1
organize	organized	Org6n3z	Org6n3zd	1	1
outweigh	outweighed	1twe	1twed	1	1
overflow	overflowed	ov6rflo	ov6rflod	1	1
overlook	overlooked	ov6rlUk	ov6rlUkt	2	1
persuade	persuaded	p6rswed	p6rswedId	3	1
petition	petitioned	p6tIS6n	p6tIS6nd	2	1
practice	practiced	pr&kt6s	pr&kt6st	1	1
progress	progressed	pr6grEs	pr6grEst	3	1
purchase	purchased	p6rtS6s	p6rtS6st	3	1
question	questioned	kwEstS6n	kwEstS6nd	5	1
register	registered	rEdZ6st6r	rEdZ6st6rd	1	1
remember	remembered	rImEmb6r	rImEmb6rd	14	1
resemble	resembled	rIzEmb6l	rIzEmb6ld	4	1
schedule	scheduled	skEdZul	skEdZuld	1	1
scramble	scrambled	skr&mb6l	skr&mb6ld	3	1
shoulder	shouldered	Sold6r	Sold6rd	1	1
sprinkle	sprinkled	sprINk6l	sprINk6ld	1	1
struggle	struggled	str6g6l	str6g6ld	1	1
surprise	surprised	s6pr3z	s6pr3zd	2	1
surround	surrounded	s6r1nd	s6r1ndId	1	1
threaten	threatened	TrEt6n	TrEt6nd	4	1
transfer	transferred	tr&nsf6r	tr&nsf6rd	1	1
accompany	accompanied	6k6mpni	6k6mpnid	3	1
advertise	advertised	&dv6rt3z	&dv6rt3zd	1	1
authorize	authorized	OT6r3z	OT6r3zd	2	1
challenge	challenged	tS&l6ndZ	tS&l6ndZd	1	1
criticize	criticized	krIt6s3z	krIt6s3zd	1	1
determine	determined	dIt6rm6n	dIt6rm6nd	2	1
disappear	disappeared	dIs6pIr	dIs6pIrd	6	1
disfigure	disfigured	dIsfIgj6r	dIsfIgj6rd	1	1
dismember	dismembered	dIsmEmb6r	dIsmEmb6rd	1	1
emphasize	emphasized	Emf6s3z	Emf6s3zd	1	1
encounter	encountered	Ink1nt6r	Ink1nt6rd	3	1
encourage	encouraged	Ink6rIdZ	Ink6rIdZd	1	1
entertain	entertained	Ent6rten	Ent6rtend	1	1
establish	established	Ist&blIS	Ist&blISt	6	1
guarantee	guaranteed	g&r6nti	g&r6ntid	2	1
improvise	improvised	Impr6v3z	Impr6v3zd	1	1
interfere	interfered	Int6fIr	Int6fIrd	1	1
intervene	intervened	Int6rvin	Int6rvind	2	1
interview	interviewed	Int6rvju	Int6rvjud	1	1
introduce	introduced	Intr6dus	Intr6dust	4	1
overreach	overreached	ov6ritS	ov6ritSt	1	1

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
prescribe	prescribed	prIskr3b	prIskr3bd	1	1
recognize	recognized	rEkIgn3z	rEkIgn3zd	9	1
replenish	replenished	rIplEnIS	rIplEnISt	1	1
supervise	supervised	sup6rv3z	sup6rv3zd	1	1
surrender	surrendered	s6rEnd6r	s6rEnd6rd	3	1
symbolize	symbolized	sImb6l3z	sImb6l3zd	1	1
telephone	telephoned	tEl6fon	tEl6fond	6	1
accomplish	accomplished	6kamplIS	6kamplISt	2	1
disapprove	disapproved	dIs6pruv	dIs6pruvd	1	1
discipline	disciplined	dIs6pl6n	dIs6pl6nd	1	1
experience	experienced	IkspIri6ns	IkspIri6nst	4	1
relinquish	relinquished	rIlINkwIS	rIlINkwISt	2	1
scandalize	scandalized	sk&nd6l3z	sk&nd6l3zd	2	1
scrutinize	scrutinized	skrut6n3z	skrut6n3zd	1	1
specialize	specialized	spES6l3z	spES6l3zd	1	1
straighten	straightened	stret6n	stret6nd	5	1
lay	laid	le	led	8	1
go	went	go	wEnt	168	3
undergo	underwent	6nd6rgo	6nd6rwEnt	1	3
bid	bid	bId	bId	1	3
cut	cut	k6t	k6t	6	3
hit	hit	hIt	hIt	16	3
let	let	lEt	lEt	10	3
put	put	pUt	pUt	48	3
set	set	sEt	sEt	27	3
wet	wet	wEt	wEt	1	3
beat	beat	bit	bit	6	3
cast	cast	k&st	k&st	2	3
cost	cost	kOst	kOst	2	3
shut	shut	S6t	S6t	1	3
burst	burst	b6rst	b6rst	5	3
split	split	splIt	splIt	4	3
upset	upset	6psEt	6psEt	6	3
spread	spread	sprEd	sprEd	6	3
thrust	thrust	Tr6st	Tr6st	2	3
fall	fell	fOl	fEl	30	4
feed	fed	fid	fEd	4	4
hold	held	hold	hEld	38	4
lead	led	lid	lEd	25	4
meet	met	mit	mEt	29	4
read	read	rid	rEd	10	4
bleed	bled	blid	blEd	1	4
speed	sped	spid	spEd	3	4
befall	befell	bIfOl	bIfEl	1	4
uphold	upheld	6phold	6phEld	1	4

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
hide	hid	h3d	hId	3	5
light	lit	l3t	lIt	3	5
slide	slid	sl3d	slId	7	5
eat	ate	it	et	9	6
give	gave	gIv	gev	101	6
forgive	forgave	f6rgIv	f6rgev	1	6
bend	bent	bEnd	bEnt	5	7
lend	lent	lEnd	lEnt	1	7
send	sent	sEnd	sEnt	21	7
build	built	bIld	bIlt	7	7
spend	spent	spEnd	spEnt	15	7
deal	dealt	dil	dElt	4	8
feel	felt	fil	fElt	88	8
keep	kept	kip	kEpt	41	8
mean	meant	min	mEnt	18	8
weep	wept	wip	wEpt	3	8
creep	crept	krip	krEpt	5	8
kneel	knelt	nil	nElt	4	8
leave	left	liv	lEft	48	8
sleep	slept	slip	slEpt	6	8
sweep	swept	swip	swEpt	3	8
get	got	gEt	gat	117	9
lose	lost	luz	lOst	22	9
shoot	shot	Sut	Sat	9	9
forget	forgot	f6rgEt	f6rgat	10	9
buy	bought	b3	bOt	6	10
seek	sought	sik	sOt	11	10
bring	brought	brIN	brOt	41	10
catch	caught	k&tS	kOt	19	10
fight	fought	f3t	fOt	7	10
teach	taught	titS	tOt	7	10
think	thought	TINk	TOt	102	10
run	ran	r6n	r&n	43	11
sit	sat	sIt	s&t	46	11
ring	rang	rIN	r&N	7	11
sing	sang	sIN	s&N	11	11
sink	sank	sINk	s&Nk	4	11
spit	spat	spIt	sp&t	3	11
swim	swam	swIm	sw&m	3	11
drink	drank	drINk	dr&Nk	9	11
spring	sprang	sprIN	spr&N	5	11
dig	dug	dIg	d6g	2	12
hang	hung	h&N	h6N	11	12
spin	spun	spIn	sp6n	4	12
cling	clung	klIN	kl6N	5	12

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
fling	flung	flIN	fl6N	5	12
stick	stuck	stIk	st6k	2	12
swing	swung	swIN	sw6N	12	12
strike	struck	str3k	str6k	16	12
string	strung	strIN	str6N	1	12
fly	flew	fl3	flu	10	13
blow	blew	blo	blu	6	13
draw	drew	drO	dru	22	13
grow	grew	gro	gru	20	13
know	knew	no	nu	138	13
throw	threw	Tro	Tru	21	13
withdraw	withdrew	wIDdrO	wIDdru	2	13
bind	bound	b3nd	b1nd	1	14
find	found	f3nd	f1nd	85	14
wind	wound	w3nd	w1nd	4	14
bear	bore	bEr	bor	5	15
ride	rode	r3d	rod	20	15
rise	rose	r3z	roz	15	15
tear	tore	tEr	tor	3	15
wake	woke	wek	wok	4	15
wear	wore	wEr	wor	14	15
arise	arose	6r3z	6roz	5	15
awake	awoke	6wek	6wok	3	15
break	broke	brek	brok	23	15
drive	drove	dr3v	drov	18	15
shine	shone	S3n	Son	2	15
speak	spoke	spik	spok	24	15
steal	stole	stil	stol	4	15
swear	swore	swEr	swor	4	15
write	wrote	r3t	rot	59	15
choose	chose	tSuz	tSoz	15	15
stride	strode	str3d	strod	4	15
strive	strove	str3v	strov	1	15
take	took	tek	tUk	133	16
shake	shook	Sek	SUk	17	16
stand	stood	st&nd	stUd	59	16
overtake	overtook	ov6rtek	ov6rtUk	1	16
withstand	withstood	wITst&nd	wITstUd	1	16
understand	understood	6nd6rst&nd	6nd6rstUd	1	16
hear	heard	hIr	h6rd	44	17
say	said	se	sEd	575	18
flee	fled	fli	flEd	4	18
make	made	mek	med	140	19
sell	sold	sEl	sold	2	20
tell	told	tEl	told	96	20

Stem	Past Tense	Stem Phon. Trans.	Past Phon Trans.	Freq.	Infl. Class
come	came	k6m	kem	212	21
become	became	bIk6m	bIkem	81	21
see	saw	si	sO	122	22
undo	undid	6ndu	6ndId	1	23

Appendix B

Phoneme Transcription for the English Past Tense Simulations

Consonants		
p	0100000000	pack
t	0010000000	tick
k	0000100000	come
b	1100000000	be
d	1010000000	dig
g	1000100000	go
m	1100010000	make
n	1010010000	know
N	1001110000	sing
l	1011001000	laugh
r	1010000100	rush
f	0110000010	free
v	1110000010	vote
s	0010000010	see
z	1010000010	use
S	0001000010	show
Z	1001000010	age
j	1001001010	use
h	0000100010	help
w	1100001010	wish
T	0010000011	throw
D	1010000011	bathe

Vowels		
i	1000000000	heat
I	0100100000	hit
e	1000010000	ate
E	1000011000	bet
&	1000001000	add
u	0011100000	choose
U	0111100000	cook
o	0011010000	cope
O	0011001000	cost
a	0100001000	box
6	0100010000	clung (schwa)
1	1011101100	found
2	1011110100	moisten
3	1000101100	hide
$	0000000000	"empty"

Consonantal features are: voiced, labial, dental, palatal, velar, nasal, liquid, trill, fricative, interdental.

Vowel features are: front, center, back, round, high, middle, low, diphthong, not used, not used.

Appendix C

Classification of English Past Tense Forms

Regular verbs				
1	regular	look	→	looked
Irregular verbs				
2	go → went			
3	no-change	hit	→	hit
4	O → E	fall	→	fell
5	3 → I	light	→	lit
6	I → e	give	→	gave
7	End → Ent	bend	→	bent
8	i_ → E_t	keep	→	kept
9	_ → a_t	lose	→	lost
10	_ → Ot	bring	→	brought
11	_ → &	sit	→	sat
12	I → 6	hang	→	hung
13	_ → U	draw	→	drew
14	3 → 1	find	→	found
15	_ → o	wear	→	wore
16	_ → U	take	→	took
17	hear → heard			
18	_ → E	say	→	said
19	make → made			
20	E → o	tell	→	told
21	6 → e	come	→	came
22	see → saw			
23	do → did			

The 23 English past tense classes. Note that some classes have only one member; for these classes only the verb is given. _ stands for any vowel.

Appendix D

The Past Tense Simulation Pseudo-Verbs

Prototypical-Irregular		Intermediate-Irregular		Distant-Irregular	
spling	splIN	fring	frIN	trisp	trIsp
skring	skrIN	ning	nIN	nist	nIst
sprink	sprINk	frink	frINk	blip	blIp
cleed	klid	cleef	klif	gleef	glif
preed	prid	preek	prik	keeb	kib
queed	kwid	queef	kwif	meep	mip
cloe	klo	foa	fo	goav	gov
froe	fro	voa	vo	joam	dZom
plare	plEr	jare	dZEr	flape	flep
quare	kwEr	grare	grEr	blafe	blef
Prototypical-Regular		**Intermediate-Regular**		**Distant-Regular**	
plip	plIp	brilth	brIlD	frilg	frIlg
glip	glIp	glinth	glInD	krilg	krIlg
brip	brIp	plimph	plImf	trilb	trIlb
gloke	glok	ploab	plob	ploamph	plomf
proke	prok	ploag	plog	ploanth	plonD
greem	grim	smeeb	smib	smeelth	smilD
pleem	plim	smeeg	smig	smeenth	sminD
treem	trim	smeej	smidZ	smeerg	smirg
slace	sles	smaib	smeb	smairg	smerg
nace	nes	smaig	smeg	smairph	smerf

The 60 pseudo-verbs developed by Prasada and Pinker (1993) and their UNIBET transcriptions.

Appendix E

Corpus for the German Aphasia Simulations

Nr. of types: 664
Nr. of tokens: 20018

Stem	Participle	Stem Phon. Trans.	Freq.	Infl. Class
abgrenzen	abgegrenzt	'&p-grEn-ts@n	1	1
abriegeln	abgeriegelt	'&p-ri-g@ln	2	1
abschirmen	abgeschirmt	'&p-SIr-m@n	5	1
abstatten	abgestattet	'&p-St&-t@n	2	1
achten	geachtet	'&x-t@n	7	1
ahnden	geahndet	'an-d@n	3	1
ahnen	geahnt	'a-n@n	4	1
anekeln	angeekelt	'&n-e-k@ln	3	1
anprangern	angeprangert	'&n-pr&-N@rn	4	1
anreichern	angereichert	'&n-rW-(@rn	1	1
anspornen	angespornt	'&n-SpOr-n@n	2	1
anstrengen	angestrengt	'&n-StrE-N@n	4	1
antasten	angetastet	'&n-t&s-t@n	4	1
antworten	geantwortet	'&nt-vOr-t@n	11	1
anwidern	angewidert	'&n-vi-d@rn	2	1
anwurzeln	angewurzelt	'&n-vUr-ts@ln	2	1
anzetteln	angezettelt	'&n-tsE-t@ln	1	1
arbeiten	gearbeitet	'&r-bW-t@n	99	1
atmen	geatmet	'at-m@n	1	1
aufbahren	aufgebahrt	'Bf-ba-r@n	1	1
aufbürden	aufgebürdet	'Bf-bYr-d@n	4	1
auffrischen	aufgefrischt	'Bf-frI-S@n	2	1
aufschlüsseln	aufgeschlüsselt	'Bf-SlY-s@ln	2	1
aufstocken	aufgestockt	'Bf-StO-k@n	1	1
aufwühlen	aufgewühlt	'Bf-vy-l@n	2	1
ausbeuten	ausgebeutet	'Bs-bX-t@n	2	1
ausbrüten	ausgebrütet	'Bs-bry-t@n	1	1

Stem	Participle	Stem Phon. Trans.	Freq.	Infl. Class
ausdörren	ausgedörrt	'Bs-d/-r@n	1	1
aushecken	ausgeheckt	'Bs-hE-k@n	1	1
aushöhlen	ausgehöhlt	'Bs-h—-l@n	2	1
auslosen	ausgelost	'Bs-lo-z@n	6	1
auslöschen	ausgelöscht	'Bs-l—-S@n	7	1
ausmerzen	ausgemerzt	'Bs-mEr-ts@n	3	1
ausrotten	ausgerottet	'Bs-rO-t@n	7	1
ausschmücken	ausgeschmückt	'Bs-Smy-k@n	1	1
ausstatten	ausgestattet	'Bs-St&-t@n	21	1
baden	gebadet	'ba-d@n	2	1
bahnen	gebahnt	'ba-n@n	1	1
bannen	gebannt	'b&-n@n	9	1
bauen	gebaut	'bB-@n	170	1
bellen	gebellt	'bE-l@n	1	1
bessern	gebessert	'bE-s@rn	8	1
beten	gebetet	'be-t@n	3	1
betten	gebettet	'bE-t@n	9	1
beugen	gebeugt	'bX-g@n	10	1
bilden	gebildet	'bIl-d@n	59	1
billigen	gebilligt	'bI-lI-g@n	21	1
blenden	geblendet	'blEn-d@n	3	1
blicken	geblickt	'blI-k@n	2	1
blättern	geblättert	'blE-t@rn	3	1
bohren	gebohrt	'bo-r@n	3	1
brauchen	gebraucht	'brB-x@n	16	1
breiten	gebreitet	'brW-t@n	7	1
bremsen	gebremst	'brEm-z@n	6	1
buchen	gebucht	'bu-x@n	6	1
bändigen	gebändigt	'bEn-dI-g@n	4	1
bücken	gebückt	'bY-k@n	3	1
bündeln	gebündelt	'bYn-d@ln	2	1
büßen	gebüßt	'by-s@n	6	1
danken	gedankt	'd&N-k@	5	1
dauern	gedauert	'dB-@rn	6	1
decken	gedeckt	'dE-k@n	38	1
dehnen	gedehnt	'de-n@n	15	1
deuten	gedeutet	'dX-t@n	24	1
dichten	gedichtet	'dI(-t@n	2	1
dienen	gedient	'di-n@n	9	1
drehen	gedreht	'dre-@n	14	1
drillen	gedrillt	'drI-l@n	2	1
drohen	gedroht	'dro-@n	6	1
drosseln	gedrosselt	'drO-s@ln	2	1
drucken	gedruckt	'drU-k@n	17	1
drängen	gedrängt	'drE-N@n	19	1

Stem	Participle	Stem Phon. Trans.	Freq.	Infl. Class
drücken	gedrückt	'drY-k@n	31	1
ducken	geduckt	'dU-k@n	3	1
dulden	geduldet	'dUl-d@n	4	1
dämmen	gedämmt	'dE-m@n	3	1
dämpfen	gedämpft	'dEm-pf@n	3	1
düngen	gedüngt	'dY-N@n	1	1
ebnen	geebnet	'ep-n@n	2	1
ehren	geehrt	'e-r@n	15	1
eignen	geeignet	'W-gn@n	39	1
einbürgern	eingebürgert	'Wn-bYr-g@rn	1	1
eindecken	eingedeckt	'Wn-dEN-k@n	4	1
einen	geeint	'W-n@n	2	1
einengen	eingeengt	'Wn-E-N@n	6	1
einflößen	eingeflößt	'Wn-fl—-s@n	1	1
einigen	geeinigt	'W-nI-g@n	13	1
einkerkern	eingekerkert	'Wn-kEr-k@rn	5	1
einschränken	eingeschränkt	'Wn-SrEN-k@n	20	1
einschüchtern	eingeschüchtert	'Wn-SY(-t@rn	3	1
einwurzeln	eingewurzelt	'Wn-vUr-ts@ln	2	1
einäschern	eingeäschert	'Wn-E-S@rn	1	1
enden	geendet	'En-d@n	1	1
erben	geerbt	'Er-b@n	4	1
erden	geerdet	'er-d@n	2	1
ernten	geerntet	'Ern-t@n	6	1
fahnden	gefahndet	'fan-d@n	2	1
falten	gefaltet	'f&l-t@n	2	1
fassen	gefaßt	'f&-s@n	93	1
fegen	gefegt	'fe-g@n	1	1
fehlen	gefehlt	'fe-l@n	14	1
feiern	gefeiert	'fW-@rn	22	1
feilen	gefeilt	'fW-l@n	1	1
fertigen	gefertigt	'fEr-tI-g@n	32	1
fesseln	gefesselt	'fE-s@ln	10	1
festigen	gefestigt	'fEs-tI-g@n	9	1
feuern	gefeuert	'fX-@rn	7	1
filmen	gefilmt	'fIl-m@n	2	1
filtern	gefiltert	'fIl-t@rn	1	1
flaggen	geflaggt	'fl&-g@n	2	1
flicken	geflickt	'flI-k@n	2	1
flüchten	geflüchtet	'flY(-t@n	12	1
flüstern	geflüstert	'flYs-t@rn	3	1
folgen	gefolgt	'fOl-g@n	28	1
foltern	gefoltert	'fOl-t@rn	2	1
fordern	gefordert	'fOr-d@rn	145	1
formen	geformt	'fOr-m@n	8	1

Stem	Participle	Stem Phon. Trans.	Freq.	Infl. Class
forschen	geforscht	'fOr-S@n	2	1
fragen	gefragt	'fra-g@n	68	1
freuen	gefreut	'frX-@n	6	1
frühstücken	gefrühstückt	'fry-stY-k@n	2	1
funken	gefunkt	'fUN-k@n	2	1
fällen	gefällt	'fE-l@n	15	1
fälschen	gefälscht	'fEl-S@n	3	1
färben	gefärbt	'fEr-b@n	5	1
fördern	gefördert	'f/r-d@rn	25	1
fügen	gefügt	'fy-g@n	27	1
fühlen	gefühlt	'fy-l@n	7	1
führen	geführt	'fy-r@n	463	1
füllen	gefüllt	'fY-l@n	21	1
fürchten	gefürchtet	'fYr(-t@n	6	1
füttern	gefüttert	'fY-t@rn	2	1
glauben	geglaubt	'glB-b@n	26	1
gliedern	gegliedert	'gli-d@rn	14	1
glücken	geglückt	'glY-k@n	9	1
glühen	geglüht	'gly-@n	1	1
gründen	gegründet	'grYn-d@n	38	1
grüßen	gegrüßt	'gry-s@n	3	1
gucken	geguckt	'gU-k@n	2	1
haben	gehabt	'ha-b@n	166	1
hacken	gehackt	'h&-k@n	1	1
handeln	gehandelt	'h&n-d@ln	44	1
hassen	gehasst	'h&-s@n	1	1
heften	geheftet	'hEf-t@n	1	1
hegen	gehegt	'he-g@n	1	1
heilen	geheilt	'hW-l@n	5	1
heiraten	geheiratet	'hW-ra-t@n	24	1
heizen	geheizt	'hW-ts@n	5	1
hemmen	gehemmt	'hE-m@n	7	1
herrschen	geherrscht	'hEr-S@n	2	1
hetzen	gehetzt	'hE-ts@n	6	1
hindern	gehindert	'hIn-d@rn	19	1
hissen	gehisst	'hI-s@n	1	1
hoffen	gehofft	'hO-f@n	7	1
holen	geholt	'ho-l@n	49	1
horchen	gehorcht	'hOr-(@n	3	1
hungern	gehungert	'hU-N@rn	1	1
hämmern	gehämmert	'hE-m@rn	2	1
hängen	gehängt	'hE-N@n	19	1
härten	gehärtet	'hEr-t@n	3	1
häufen	gehäuft	'hX-f@n	3	1
hören	gehört	'h—r@n	174	1

Stem	Participle	Stem Phon. Trans.	Freq.	Infl. Class
hüllen	gehüllt	'hY-l@n	7	1
hüten	gehütet	'hy-t@n	4	1
impfen	geimpft	'Im-pf@n	3	1
irren	geirrt	'I-r@n	7	1
jagen	gejagt	'ja-g@n	8	1
kaufen	gekauft	'kB-f@n	32	1
kehren	gekehrt	'ke-r@n	59	1
ketten	gekettet	'kE-t@n	1	1
kippen	gekippt	'kI-p@n	2	1
klagen	geklagt	'kla-g@n	15	1
klammern	geklammert	'kl&-m@rn	7	1
klappen	geklappt	'kl&-p@n	9	1
klatschen	geklatscht	'kl&-tS@n	3	1
klauen	geklaut	'klB-@n	2	1
kleben	geklebt	'kle-b@n	1	1
kleiden	gekleidet	'klW-d@n	9	1
klemmen	geklemmt	'klE-m@n	5	1
klettern	geklettert	'klE-t@rn	3	1
klingeln	geklingelt	'klI-N@ln	2	1
klopfen	geklopft	'klO-pf@n	2	1
klären	geklärt	'kl)-r@n	32	1
knallen	geknallt	'kn&-l@n	1	1
kneten	geknetet	'kne-t@n	2	1
knicken	geknickt	'knI-k@n	4	1
knipsen	geknipst	'knIp-s@n	1	1
knüpfen	geknüpft	'knY-pf@n	9	1
kochen	gekocht	'kO-x@n	8	1
koppeln	gekoppelt	'kO-p@ln	6	1
kosten	gekostet	'kOs-t@n	19	1
kreuzen	gekreuzt	'krX-ts@n	1	1
kriegen	gekriegt	'kri-g@n	6	1
kränken	gekränkt	'krEN-k@n	4	1
krönen	gekrönt	'kr—n@n	6	1
krümmen	gekrümmt	'krY-m@n	4	1
kämmen	gekämmt	'kE-m@n	3	1
kämpfen	gekämpft	'kEm-pf@n	16	1
kühlen	gekühlt	'ky-l@n	1	1
kümmern	gekümmert	'kY-m@rn	6	1
kündigen	gekündigt	'kYn-dI-g@n	52	1
kürzen	gekürzt	'kYr-ts@n	15	1
küssen	geküsst	'kY-s@n	4	1
lachen	gelacht	'l&-x@n	7	1
lagern	gelagert	'la-g@rn	10	1
landen	gelandet	'l&n-d@n	13	1
langen	gelangt	'l&-N@n	22	1

Stem	Participle	Stem Phon. Trans.	Freq.	Infl. Class
lasten	gelastet	'l&s-t@n	14	1
lauern	gelauert	'lB-@rn	1	1
launen	gelaunt	'lB-n@n	2	1
leben	gelebt	'le-b@n	30	1
legen	gelegt	'le-g@n	301	1
lehnen	gelehnt	'le-n@n	73	1
lehren	gelehrt	'le-r@n	4	1
leisten	geleistet	'lWs-t@n	42	1
leiten	geleitet	'lW-t@n	71	1
lenken	gelenkt	'lEN-k@n	21	1
lernen	gelernt	'lEr-n@n	66	1
leuchten	geleuchtet	'lX(-t@n	1	1
leugnen	geleugnet	'lX-gn@n	4	1
lieben	geliebt	'li-b@n	10	1
liefern	geliefert	'li-f@rn	56	1
loben	gelobt	'lo-b@n	2	1
locken	gelockt	'lO-k@n	2	1
lohnen	gelohnt	'lo-n@n	4	1
lächeln	gelächelt	'lE-(@ln	2	1
lähmen	gelähmt	'l)-m@n	6	1
löschen	gelöscht	'l/-S@n	4	1
lösen	gelöst	'l—z@n	137	1
lüften	gelüftet	'lYf-t@n	2	1
machen	gemacht	'm&-x@n	440	1
magern	gemagert	'ma-g@rn	3	1
mahnen	gemahnt	'ma-n@n	1	1
malen	gemalt	'ma-l@n	13	1
mauern	gemauert	'mB-@rn	3	1
meinen	gemeint	'mW-n@n	58	1
meistern	gemeistert	'mWs-t@rn	2	1
melden	gemeldet	'mEl-d@n	58	1
merken	gemerkt	'mEr-k@n	20	1
mieten	gemietet	'mi-t@n	5	1
mildern	gemildert	'mIl-d@rn	3	1
mimen	gemimt	'mi-m@n	1	1
mindern	gemindert	'mIn-d@rn	4	1
mischen	gemischt	'mI-S@n	3	1
morden	gemordet	'mOr-d@n	2	1
mustern	gemustert	'mUs-t@rn	4	1
mähen	gemäht	'm)-@n	2	1
mästen	gemästet	'mEs-t@n	1	1
mäßigen	gemäßigt	'm)-sI-g@n	1	1
münzen	gemünzt	'mYn-ts@n	2	1
nachahmen	nachgeahmt	'nax-a-m@n	2	1
nageln	genagelt	'na-g@ln	2	1

Stem	Participle	Stem Phon. Trans.	Freq.	Infl. Class
neigen	geneigt	’nW-g@n	13	1
nutzen	genutzt	’nU-ts@n	39	1
nähen	genäht	’n)-@n	5	1
nähern	genähert	’n)-@rn	3	1
nähren	genährt	’n)-r@n	7	1
nötigen	genötigt	’n—tI-g@n	11	1
nützen	genützt	’nY-ts@n	4	1
opfern	geopfert	’O-pf@rn	7	1
ordnen	geordnet	’Or-dn@n	41	1
paaren	gepaart	’pa-r@n	3	1
pachten	gepachtet	’p&x-t@n	1	1
packen	gepackt	’p&-k@n	17	1
parken	geparkt	’p&r-k@n	2	1
passen	gepaßt	’p&-s@n	23	1
peilen	gepeilt	’pW-l@n	2	1
peinigen	gepeinigt	’pW-nI-g@n	2	1
pellen	gepellt	’pE-l@n	1	1
pflanzen	gepflanzt	’pfl&n-ts@n	4	1
pflastern	gepflastert	’pfl&s-t@rn	1	1
pflegen	gepflegt	’pfle-g@n	18	1
pflügen	gepflügt	’pfly-g@n	2	1
pilgern	gepilgert	’pIl-g@rn	1	1
plagen	geplagt	’pla-g@n	3	1
planen	geplant	’pla-n@n	57	1
platzen	geplatzt	’pl&-ts@n	4	1
plaudern	geplaudert	’plB-d@rn	1	1
plündern	geplündert	’plYn-d@rn	2	1
polstern	gepolstert	’pOl-st@rn	1	1
prallen	geprallt	’pr&-l@n	2	1
predigen	gepredigt	’pre-dI-g@n	2	1
prellen	geprellt	’prE-l@n	2	1
pressen	gepreßt	’prE-s@n	10	1
proben	geprobt	’pro-b@n	1	1
prägen	geprägt	’pr)-g@n	20	1
prüfen	geprüft	’pry-f@n	37	1
pumpen	gepumpt	’pUm-p@n	3	1
putzen	geputzt	’pU-ts@n	4	1
quälen	gequält	’kv)-l@n	6	1
raffen	gerafft	’r&-f@n	1	1
rahmen	gerahmt	’ra-m@n	3	1
rammen	gerammt	’r&-m@n	3	1
rasen	gerast	’ra-z@n	2	1
rauben	geraubt	’rB-b@n	8	1
rauchen	geraucht	’rB-x@n	2	1
rechen	gerecht	’rE-(@n	24	1

Stem	Participle	Stem Phon. Trans.	Freq.	Infl. Class
rechnen	gerechnet	′rE(-n@n	89	1
reden	geredet	′re-d@n	21	1
regeln	geregelt	′re-g@ln	12	1
regen	geregt	′re-g@n	21	1
reichen	gereicht	′rW-(@n	25	1
reifen	gereift	′rW-f@n	6	1
reihen	gereiht	′rW-@n	6	1
reinigen	gereinigt	′rW-nI-g@n	4	1
reisen	gereist	′rW-z@n	21	1
reizen	gereizt	′rW-ts@n	13	1
retten	gerettet	′rE-t@n	30	1
richten	gerichtet	′rI(-t@n	151	1
roden	gerodet	′ro-d@n	1	1
rollen	gerollt	′rO-l@n	7	1
ruhen	geruht	′ru-@n	4	1
runden	gerundet	′rUn-d@n	2	1
rutschen	gerutscht	′rU-tS@n	3	1
rätseln	gerätselt	′r)-ts@ln	1	1
räumen	geräumt	′rX-m@n	40	1
röten	gerötet	′r—t@n	1	1
rücken	gerückt	′rY-k@n	20	1
rühmen	gerühmt	′ry-m@n	4	1
rühren	gerührt	′ry-r@n	8	1
rüsten	gerüstet	′rYs-t@n	29	1
rütteln	gerüttelt	′rY-t@ln	3	1
sacken	gesackt	′z&-k@n	2	1
sagen	gesagt	′za-g@n	440	1
sammeln	gesammelt	′z&-m@ln	23	1
schaden	geschadet	′Sa-d@n	3	1
schalten	geschaltet	′S&l-t@n	27	1
scharen	geschart	′Sa-r@n	3	1
schauen	geschaut	′SB-@n	2	1
schaufeln	geschaufelt	′SB-f@ln	2	1
scheitern	gescheitert	′SW-t@rn	26	1
schellen	geschellt	′SE-l@n	1	1
schenken	geschenkt	′SEN-k@n	27	1
scheuen	gescheut	′SX-@n	6	1
schicken	geschickt	′SI-k@n	39	1
schildern	geschildert	′SIl-d@rn	16	1
schimpfen	geschimpft	′SIm-pf@n	3	1
schlachten	geschlachtet	′Sl&x-t@n	6	1
schleppen	geschleppt	′SlE-p@n	6	1
schleudern	geschleudert	′SlX-d@rn	9	1
schleusen	geschleust	′SlX-z@n	4	1
schlucken	geschluckt	′SlU-k@n	3	1

Stem	Participle	Stem Phon. Trans.	Freq.	Infl. Class
schmecken	geschmeckt	'SmE-k@n	2	1
schmeicheln	geschmeichelt	'SmW-(@ln	3	1
schmieden	geschmiedet	'Smi-d@n	5	1
schmieren	geschmiert	'Smi-r@n	2	1
schminken	geschminkt	'SmIN-k@n	3	1
schmuggeln	geschmuggelt	'SmU-g@ln	4	1
schmälern	geschmälert	'Sm)-l@rn	1	1
schmücken	geschmückt	'SmY-k@n	6	1
schnallen	geschnallt	'Sn&-l@n	4	1
schnappen	geschnappt	'Sn&-p@n	2	1
schnitzen	geschnitzt	'SnI-ts@n	3	1
schnüren	geschnürt	'Sny-r@n	3	1
schonen	geschont	'So-n@n	3	1
schrauben	geschraubt	'SrB-b@n	3	1
schrecken	geschreckt	'SrE-k@n	2	1
schrumpfen	geschrumpft	'SrUm-pf@n	5	1
schulen	geschult	'Su-l@n	4	1
schwanken	geschwankt	'Sv&N-k@n	2	1
schwemmen	geschwemmt	'SvE-m@n	1	1
schwenken	geschwenkt	'SvEN-k@n	3	1
schwitzen	geschwitzt	'SvI-ts@n	2	1
schwächen	geschwächt	'Sv)-(@n	7	1
schädigen	geschädigt	'S)-dI-g@n	5	1
schämen	geschämt	'S)-m@n	1	1
schänden	geschändet	'SEn-d@n	2	1
schärfen	geschärft	'SEr-f@n	3	1
schätzen	geschätzt	'SE-ts@n	32	1
schöpfen	geschöpft	'S/-pf@n	8	1
schüren	geschürt	'Sy-r@n	2	1
schütteln	geschüttelt	'SY-t@ln	4	1
schütten	geschüttet	'SY-t@n	3	1
schützen	geschützt	'SY-ts@n	30	1
segnen	gesegnet	'ze-gn@n	3	1
sehnen	gesehnt	'ze-n@n	2	1
senken	gesenkt	'zEN-k@n	18	1
setzen	gesetzt	'zE-ts@n	335	1
sichern	gesichert	'zI-(@rn	70	1
sichten	gesichtet	'zI(-t@n	1	1
siedeln	gesiedelt	'zi-d@ln	5	1
siegen	gesiegt	'zi-g@n	8	1
sondern	gesondert	'zOn-d@rn	4	1
sorgen	gesorgt	'zOr-g@n	18	1
spannen	gespannt	'Sp&-n@n	32	1
sparen	gespart	'Spa-r@n	21	1
speichern	gespeichert	'SpW-(@rn	1	1

Stem	Participle	Stem Phon. Trans.	Freq.	Infl. Class
speisen	gespeist	’SpW-z@n	4	1
spenden	gespendet	’SpEn-d@n	6	1
sperren	gesperrt	’SpE-r@n	25	1
spicken	gespickt	’SpI-k@n	2	1
spiegeln	gespiegelt	’Spi-g@ln	2	1
spielen	gespielt	’Spi-l@n	88	1
sprengen	gesprengt	’SprE-N@n	5	1
spritzen	gespritzt	’SprI-ts@n	3	1
spucken	gespuckt	’SpU-k@n	2	1
spüren	gespürt	’Spy-r@n	9	1
staffeln	gestaffelt	’St&-f@ln	3	1
stapeln	gestapelt	’Sta-p@ln	3	1
starten	gestartet	’St&r-t@n	20	1
stauen	gestaut	’StB-@n	1	1
stecken	gesteckt	’StE-k@n	25	1
steigern	gesteigert	’StW-g@rn	22	1
stellen	gestellt	’StE-l@n	667	1
stemmen	gestemmt	’StE-m@n	1	1
stempeln	gestempelt	’StEm-p@ln	4	1
steuern	gesteuert	’StX-@rn	11	1
stiften	gestiftet	’StIf-t@n	4	1
stillen	gestillt	’StI-l@n	3	1
stimmen	gestimmt	’StI-m@n	49	1
stolpern	gestolpert	’StOl-p@rn	1	1
stopfen	gestopft	’StO-pf@n	5	1
stoppen	gestoppt	’StO-p@n	8	1
strafen	gestraft	’Stra-f@n	1	1
straffen	gestrafft	’Str&-f@n	1	1
strahlen	gestrahlt	’Stra-l@n	8	1
streben	gestrebt	’Stre-b@n	10	1
strecken	gestreckt	’StrE-k@n	9	1
streifen	gestreift	’StrW-f@n	1	1
streiken	gestreikt	’StrW-k@n	5	1
streuen	gestreut	’StrX-@n	5	1
sträuben	gesträubt	’StrX-b@n	2	1
strömen	geströmt	’Str—m@n	1	1
stufen	gestuft	’Stu-f@n	4	1
stutzen	gestutzt	’StU-ts@n	1	1
stärken	gestärkt	’StEr-k@n	9	1
stören	gestört	’St—r@n	20	1
stülpen	gestülpt	’StYl-p@n	1	1
stürmen	gestürmt	’StYr-m@n	1	1
stürzen	gestürzt	’StYr-ts@n	34	1
stützen	gestützt	’StY-ts@n	21	1
suchen	gesucht	’zu-x@n	155	1

Stem	Participle	Stem Phon. Trans.	Freq.	Infl. Class
säen	gesät	′z)-@n	4	1
sägen	gesägt	′z)-g@n	1	1
säubern	gesäubert	′zX-b@rn	2	1
säumen	gesäumt	′zX-m@n	1	1
sühnen	gesühnt	′zy-n@n	3	1
sündigen	gesündigt	′zYn-dI-g@n	1	1
tadeln	getadelt	′ta-d@ln	1	1
tanken	getankt	′t&N-k@n	1	1
tanzen	getanzt	′t&n-ts@n	4	1
tarnen	getarnt	′t&r-n@n	2	1
tauchen	getaucht	′tB-x@n	12	1
taufen	getauft	′tB-f@n	4	1
tauschen	getauscht	′tB-S@n	22	1
teilen	geteilt	′tW-l@n	102	1
testen	getestet	′tEs-t@n	4	1
tilgen	getilgt	′tIl-g@n	8	1
tippen	getippt	′tI-p@n	1	1
trauen	getraut	′trB-@n	6	1
trennen	getrennt	′trE-n@n	39	1
trocknen	getrocknet	′trOk-n@n	6	1
trommeln	getrommelt	′trO-m@ln	3	1
träumen	geträumt	′trX-m@n	6	1
trösten	getröstet	′tr—s-t@n	1	1
trüben	getrübt	′try-b@n	1	1
tätigen	getätigt	′t)-tI-g@n	5	1
täuschen	getäuscht	′tX-S@n	12	1
töten	getötet	′t—-t@n	46	1
türmen	getürmt	′tYr-m@n	2	1
wachen	gewacht	′v&-x@n	3	1
wagen	gewagt	′va-g@n	16	1
wahren	gewahrt	′va-r@n	5	1
wandeln	gewandelt	′v&n-d@ln	20	1
wandern	gewandert	′v&n-d@rn	7	1
wappnen	gewappnet	′v&p-n@n	2	1
warnen	gewarnt	′v&r-n@	15	1
warten	gewartet	′v&r-t@	18	1
wechseln	gewechselt	′vEk-s@ln	15	1
wecken	geweckt	′vE-k@n	14	1
wehren	gewehrt	′ve-r@n	5	1
weigern	geweigert	′vW-g@rn	8	1
weihen	geweiht	′vW-@n	20	1
weilen	geweilt	′vW-l@n	7	1
weinen	geweint	′vW-n@n	8	1
weiten	geweitet	′vW-t@n	5	1
werten	gewertet	′ver-t@n	33	1

Stem	Participle	Stem Phon. Trans.	Freq.	Infl. Class
wetten	gewettet	'vE-t@n	1	1
widmen	gewidmet	'vIt-m@n	33	1
winken	gewinkt	'vIN-k@n	2	1
wirbeln	gewirbelt	'vIr-b@ln	1	1
wirken	gewirkt	'vIr-k@n	23	1
wirtschaften	gewirtschaftet	'vIrt-S&f-t@n	1	1
wischen	gewischt	'vI-S@n	3	1
wohnen	gewohnt	'vo-n@n	17	1
wollen	gewollt	'vO-l@n	15	1
wundern	gewundert	'vUn-d@rn	3	1
wählen	gewählt	'v)-l@n	107	1
währen	gewährt	'v)-r@n	23	1
wälzen	gewälzt	'vEl-ts@n	6	1
wärmen	gewärmt	'vEr-m@n	3	1
wünschen	gewünscht	'vYn-S@n	27	1
würdigen	gewürdigt	'vYr-dI-g@n	14	1
würgen	gewürgt	'vYr-g@n	2	1
würzen	gewürzt	'vYr-ts@n	1	1
zahlen	gezahlt	'tsa-l@n	51	1
zaubern	gezaubert	'tsB-b@rn	3	1
zehren	gezehrt	'tse-r@n	1	1
zeichnen	gezeichnet	'tsW(-n@n	77	1
zeigen	gezeigt	'tsW-g@n	135	1
zerren	gezerrt	'tsE-r@n	2	1
zeugen	gezeugt	'tsX-g@n	4	1
zielen	gezielt	'tsi-l@n	4	1
zieren	geziert	'tsi-r@n	4	1
zollen	gezollt	'tsO-l@n	1	1
zumuten	zugemutet	'tsu-mu-t@n	4	1
zuspitzen	zugespitzt	'tsu-SpI-ts@n	4	1
zweifeln	gezweifelt	'tsvW-f@ln	3	1
zählen	gezählt	'ts)-l@n	20	1
zögern	gezögert	'ts—g@rn	3	1
züchten	gezüchtet	'tsY(-t@n	1	1
zügeln	gezügelt	'tsy-g@ln	2	1
zünden	gezündet	'tsYn-d@n	5	1
ändern	geändert	'En-d@rn	60	1
ärgern	geärgert	'Er-g@rn	7	1
äußern	geäußert	'X-s@rn	33	1
öffnen	geöffnet	'/f-n@n	41	1
üben	geübt	'y-b@n	29	1
blasen	geblasen	'bla-z@n	8	2
braten	gebraten	'bra-t@n	1	2
essen	gegessen	'E-s@n	14	2
fahren	gefahren	'fa-r@n	85	2

Stem	Participle	Stem Phon. Trans.	Freq.	Infl. Class
fallen	gefallen	'f&-l@n	93	2
fangen	gefangen	'f&-N@n	51	2
fressen	gefressen	'frE-s@n	9	2
geben	gegeben	'ge-b@n	494	2
graben	gegraben	'gra-b@n	8	2
halten	gehalten	'h&l-t@n	216	2
hauen	gehauen	'hB-@n	2	2
heißen	geheißen	'hW-s@n	7	2
kommen	gekommen	'kO-m@n	348	2
laden	geladen	'la-d@n	80	2
lassen	gelassen	'l&-s@n	96	2
laufen	gelaufen	'lB-f@n	47	2
lesen	gelesen	'le-z@n	52	2
messen	gemessen	'mE-s@n	40	2
raten	geraten	'ra-t@n	38	2
rufen	gerufen	'ru-f@n	99	2
schaffen	geschaffen	'S&-f@n	120	2
schlafen	geschlafen	'Sla-f@n	19	2
schlagen	geschlagen	'Sla-g@n	164	2
sehen	gesehen	'ze-@n	393	2
spalten	gespalten	'Sp&l-t@n	9	2
stoßen	gestoßen	'Sto-s@n	45	2
tragen	getragen	'tra-g@n	159	2
treten	getreten	'tre-t@n	128	2
wachsen	gewachsen	'v&k-s@	65	2
waschen	gewaschen	'v&-S@n	9	2
befehlen	befohlen	b@-'fe-l@n	11	3
bergen	geborgen	'bEr-g@n	19	3
bersten	geborsten	'bEr-st@n	1	3
brechen	gebrochen	'brE-(@n	93	3
dreschen	gedroschen	'drE-S@n	1	3
empfehlen	empfohlen	Em-'pfe-l@n	30	3
fechten	gefochten	'fE(-t@n	3	3
flechten	geflochten	'flE(-t@n	2	3
gelten	gegolten	'gEl-t@n	4	3
heben	gehoben	'he-b@n	90	3
helfen	geholfen	'hEl-f@n	35	3
melken	gemolken	'mEl-k@n	1	3
nehmen	genommen	'ne-m@n	703	3
schelten	gescholten	'SEl-t@n	1	3
scheren	geschoren	'Se-r@n	1	3
schmelzen	geschmolzen	'SmEl-ts@n	2	3
schwellen	geschwollen	'SvE-l@n	1	3
sprechen	gesprochen	'SprE-(@n	286	3
stechen	gestochen	'StE-(@n	8	3

Stem	Participle	Stem Phon. Trans.	Freq.	Infl. Class
stehlen	gestohlen	'Ste-l@n	21	3
sterben	gestorben	'StEr-b@n	75	3
treffen	getroffen	'trE-f@n	135	3
verderben	verdorben	fEr-'dEr-b@n	4	3
werben	geworben	'vEr-b@n	29	3
werden	geworden	'ver-d@n	1546	3
werfen	geworfen	'vEr-f@n	100	3
beißen	gebissen	'bW-s@n	6	4
bleiben	geblieben	'blW-b@n	123	4
gleichen	geglichen	'glW-(@n	9	4
greifen	gegriffen	'grW-f@n	33	4
leiden	gelitten	'lW-d@n	8	4
leihen	geliehen	'lW-@n	5	4
meiden	gemieden	'mW-d@n	1	4
pfeifen	gepfiffen	'pfW-f@n	4	4
preisen	gepriesen	'prW-z@n	3	4
reiben	gerieben	'rW-b@n	3	4
reiten	geritten	'rW-t@n	3	4
reißen	gerissen	'rW-s@n	36	4
scheiden	geschieden	'SW-d@n	29	4
schleichen	geschlichen	'SlW-(@n	1	4
schleifen	geschliffen	'SlW-f@n	3	4
schmeißen	geschmissen	'SmW-s@n	3	4
schneiden	geschnitten	'SnW-d@n	32	4
schreiben	geschrieben	'SrW-b@n	139	4
schreien	geschrien	'SrW-@n	5	4
schreiten	geschritten	'SrW-t@n	6	4
schweigen	geschwiegen	'SvW-g@n	2	4
steigen	gestiegen	'StW-g@n	80	4
streichen	gestrichen	'StrW-(@n	16	4
streiten	gestritten	'StrW-t@n	3	4
treiben	getrieben	'trW-b@n	22	4
weichen	gewichen	'vW-(@n	10	4
weisen	gewiesen	'vW-z@n	151	4
schwören	geschworen	'Sv—r@n	4	5
binden	gebunden	'bIn-d@n	173	6
dringen	gedrungen	'drI-N@n	23	6
empfinden	empfunden	Em-'pfIn-d@n	26	6
finden	gefunden	'fIn-d@n	290	6
gelingen	gelungen	g@-'lI-N@n	62	6
klingen	geklungen	'klI-N@n	6	6
mißlingen	mißlungen	mIs-'lI-N@n	3	6
ringen	gerungen	'rI-N@n	24	6
schlingen	geschlungen	'SlI-N@n	9	6
schwinden	geschwunden	'SvIn-d@n	38	6

Stem	Participle	Stem Phon. Trans.	Freq.	Infl. Class
schwingen	geschwungen	'SvI-N@n	2	6
singen	gesungen	'zI-N@n	9	6
sinken	gesunken	'zIN-k@n	23	6
springen	gesprungen	'SprI-N@n	15	6
trinken	getrunken	'trIN-k@n	31	6
winden	gewunden	'vIn-d@n	38	6
zwingen	gezwungen	'tsvI-N@n	84	6
wissen	gewußt	'vI-s@n	37	7
gehen	gegangen	'ge-@n	324	8
brennen	gebrannt	'brE-n@n	19	9
kennen	gekannt	'kE-n@n	232	9
nennen	genannt	'nE-n@n	155	9
rennen	gerannt	'rE-n@n	5	9
senden	gesandt	'zEn-d@n	22	9
wenden	gewandt	'vEn-d@n	40	9
beginnen	begonnen	b@-'gI-n@n	109	10
biegen	gebogen	'bi-g@n	4	10
bieten	geboten	'bi-t@n	86	10
entrinnen	entronnen	Ent-'rI-n@n	1	10
fliegen	geflogen	'fli-g@n	24	10
fliehen	geflohen	'fli-@n	4	10
fließen	geflossen	'fli-s@n	8	10
frieren	gefroren	'fri-r@n	4	10
gewinnen	gewonnen	g@-'vI-n@n	94	10
gießen	gegossen	'gi-s@n	3	10
riechen	gerochen	'ri-(@n	1	10
schieben	geschoben	'Si-b@n	22	10
schießen	geschossen	'Si-s@n	37	10
schließen	geschlossen	'Sli-s@n	206	10
schwimmen	geschwommen	'SvI-m@n	7	10
sinnen	gesonnen	'zI-n@n	6	10
spinnen	gesponnen	'SpI-n@n	2	10
wiegen	gewogen	'vi-g@n	2	10
stehen	gestanden	'Ste-@n	40	11
denken	gedacht	'dEN-k@n	126	12
bringen	gebracht	'brI-N@n	351	13
sein	gewesen	'zWn	500	14
gebären	geboren	g@-'b)-r@n	36	15
gären	gegoren	'g)-r@n	1	15
wägen	gewogen	'v)-g@n	2	15
bitten	gebeten	'bI-t@n	108	16
liegen	gelegen	'li-g@n	40	16
sitzen	gesessen	'zI-ts@n	24	16
können	gekonnt	'k/-n@n	3	17
mögen	gemocht	'm—-g@n	3	17

Stem	Participle	Stem Phon. Trans.	Freq.	Infl. Class
ziehen	gezogen	'tsi-@n	157	18
lügen	gelogen	'ly-g@n	6	19
trügen	getrogen	'try-g@n	1	19
tun	getan	'tun	158	20
dürfen	gedurft	'dYr-f@n	2	21
saufen	gesoffen	'zB-f@n	1	22
saugen	gesogen	'zB-g@n	2	22

Appendix F

Classification of German Participles

Regular verbs				
1	regular	sagen	→	gesagt
Mixed verbs				
2	E → A + t	kennen	→	gekannt
3	ö → O + t	mögen	→	gemocht
4	wissen → gewußt			
5	denken → gedacht			
6	bringen → gebracht			
7	dürfen → gedurft			
Irregular verbs				
8	no-change	lesen	→	gelesen
9	E → O|o	werden	→	geworden
		befehlen	→	befohlen
10	ai → I|i	greifen	→	gegriffen
		schreiben	→	geschrieben
11	I → U	binden	→	gebunden
12	i|I → O|o	schliessen	→	geschlossen
		fliegen	→	geflogen
		beginnen	→	begonnen
13	au → O|o	saufen	→	gesoffen
		saugen	→	gesogen
14	ü → o	lügen	→	gelogen
15	ä → o	gebären	→	geboren
16	gehen → gegangen			
17	stehen → gestanden			
18	sein → gewesen			
19	sitzen → gesessen			
20	bitten → gebeten			
21	ziehen → gezogen			
22	tun → getan			

The 22 German participle classes. Note that some classes have only one member; for these classes only the verb is given. Length of the stem-vowel was not distinguished in this classification.

Appendix G

Phoneme Transcription for the German Aphasia Simulations

Consonants		
b	1 1 0 1 0 0 1	binden
d	1 1 1 1 0 0 1	denken
f	1 1 0 1 1 0 0	freuen
g	1 0 0 0 0 0 1	gucken
h	0 0 0 1 1 0 0	helfen
j	1 0 0 1 1 0 1	jagen
k	1 0 0 0 0 0 0	kleben
l	0 1 1 1 1 0 1	lachen
m	0 1 0 1 0 1 1	machen
n	0 1 1 1 0 1 1	nicken
p	1 1 0 1 0 0 0	prüfen
r	0 0 0 0 1 0 1	rasen
s	1 1 1 1 1 0 0	sagen
t	1 1 1 1 0 0 0	trauen
v	1 1 0 1 1 0 1	wachsen
z	1 1 1 1 1 0 1	lösen
N	0 0 0 0 0 1 1	fa**ng**en
S	1 0 1 1 1 0 0	forschen
(	1 0 0 1 1 0 0	fe**ch**ten
x	1 0 0 0 1 0 0	kochen
_	0 0 0 0 0 0 0	-

Vowels		
&	0101000	fallen
a	0101001	sagen
)	0101101	schämen
/	0100110	können
—	0100111	hören
@	0100000	sagen
B	0000010	glauben
E	0100100	essen
I	0110100	filmen
O	0100010	formen
U	0110010	gucken
W	0000100	feiern
X	0000110	feuern
Y	0110110	glücken
e	0100101	gehen
i	0110101	frieren
o	0100011	holen
u	0110011	rufen
y	0110111	führen

List of Acronyms

AC	Acrobatic Condition *Page 43*
ACh	acetylcholine *Page 20*
AMPA	α-amino 3 hydro 5 methyl 4 isoxazole propionic acid *Page 12*
BDNF	Brain-Derived Neurotrophic Factor *Page 31*
CNN	Constructivist Neural Network *Page 85*
CNS	central nervous system *Page 16*
DMT	Dual Mechanism Theory *Page 104*
EC	Environmental Complexity Condition *Page 42*
FX	Forced Exercise Condition *Page 43*
GABA	γ-aminobutyric acid *Page 13*
HO	Hidden-Output *Page 120*
IC	Individual Cage Condition *Page 42*
IC	Inactive Condition *Page 43*
IO	Input-Output *Page 120*
ISE	individual specific environment *Page 39*
LGN	lateral geniculate nucleus *Page 25*
LTP	long term potentiation *Page 31*
NCN	non-constructivist network *Page 122*
NGF	Nerve Growth Factor *Page 31*
NMDA	*N*-methyl-D-aspartate *Page 12*
NMJ	neuromuscular junction *Page 20*
NT-3	Neurotrophin-3 *Page 31*
NT-4/5	Neurotrophin-4/Neurotrophin-5 *Page 31*

ODC	ocular dominance columns	*Page 26*
PAC	Probably Approximately Correct	*Page 75*
PB	preference bias	*Page 71*
PNS	peripheral nervous system	*Page 31*
RHSB	restricted hypothesis space bias	*Page 70*
SC	Social Cage Condition	*Page 42*
SLI	Specific Language Impairment	*Page 135*
STE	species typical environment	*Page 39*
TRK	tyrosine-kinase	*Page 13*
TTX	tetrodotoxin	*Page 27*
VX	Voluntary Exercise Condition	*Page 43*

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