# **Language Acquisition and Processing**

## **Hierarchically Organized Cognitive Processes**

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> von Grancia TI

Begutachtet von

Dr. Dorothea Weniger Prof. Dr. Rüdiger Wehner Prof. Dr. Stanislas Dehaene

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A Lorena e Giulio, aria e luce.

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## 1. ABSTRACTS

#### 1.1 ENGLISH ABSTRACT

Human natural languages are characterized by a highly flexible system that allows concepts to be conveyed by symbols and this process requires the integration of cognitive, emotional and sensorimotor functions. Despite the great complexity, human infants develop the capacity to properly use and understand language in their first few years of life without explicit instruction. Hierarchical organization is the basic computational mechanism through which our nervous system is thought to coordinate a set of elementary units – such as speech sounds, words, but also gestures, numbers, etc. – into a coherent pattern, the complexity of which can be expanded as needed and with creativity. Due to hierarchical organization, complex combinations of lower-level elements can be generated efficiently and, in turn, higher-order assemblies can be decomposed into elementary units, which can be learned, processed and stored.

The aim of this thesis is to provide evidence that the experimental manipulation of hierarchical organizing principles is a powerful method for investigating important aspects of language processing and acquisition, with the potential of sheding light on some challenging hypotheses about the emergence of language from evolutionary older sensorimotor systems. In addition, hypotheses about the neurotransmission and neuronal mechanisms subserving language will be discussed.

Linguistic theory posits that hierarchical structuring principles are an intrinsic property of natural language grammars, and are found at the phonological, morphological, and syntactic level. The first study constituting this thesis investigated in healthy adult subjects, using Positron Emission Tomography, whether the syntactic linguistic component – traditionally defined by linguistic theory as a system of hierarchical structuring rules governing the combination of words – is actually isomorphic to some neurophysiological process, and subserved by distinct neural

correlates. Hierarchical syntactic structures were manipulated, while leaving the other linguistic components intact, thus allowing to selectively isolate the functional neuroanatomical correlates subserving syntactic processing. The neuroanatomical network identified comprised a deep component of Broca's area, the insular cortex and the caudate nucleus in the left brain hemisphere. The results, which are compatible with the localization of brain lesions observed in patients with syntactic deficits, suggest that hierarchical syntactic relations are processed by a specific brain network, in accordance with the hypotheses made by linguistic theory.

In the second study constituting this thesis the acquisition in adulthood of syntactic rules of a non-native language was investigated, using functional Magnetic Resonance Imaging. No other study has thus far attempted to study the acquisition of natural language on-line – the regional brain modulations underlying language acquisition being largely unknown. We contrasted hierarchical syntactic structures that conform to the universal grammatical principles of human natural languages with non-hierarchical, non-linguistic structures, and were able to show that the acquisition of hierarchical syntactic rules selectively modulates a left-hemispheric perisylvian network including in particular Broca's area (as the main brain region correlating with scores of learning performance such as reaction time and accuracy of response). The results, when compared to those of the first study, suggest interesting hypotheses about a neuroanatomical shift from lateral to deep components of Broca's area and adjacent subcortical regions as native-like proficiency in syntactic processing is attained. Furthermore, they are in agreement with the hypothesis of Broca's area having a modality-independent role in the processing of hierarchical structures in different domains, such as language and action execution/observation.

The third study presented here directly tested the hypothesis that language and action execution/observation share a common neural system. Observations of child development suggest that cognitive processes of comparable hierarchical complexity emerge at the same developmental

stages in the domains of language, gesture, and object manipulation, making it likely that common neural maturation processes are involved. Furthermore, studies in non-human primates suggest that language may have evolved from a domain-general capacity of understanding and imitating actions and intentions performed by others, transcoding these into corresponding motor plans. In our functional Magnetic Resonance Imaging study healthy adult subjects were presented with sentences describing actions performed with mouth, hand, and leg. Activations were found in a fronto-parietal network including Broca's area and body-part-specific regions of the left premotor cortex. The activation of this network suggests that language may not be detached from the evolutionary ancient sensorimotor systems, but strictly linked to them.

The general discussion hinges on the different roles played by Broca's area in linguistic as well as in non-linguistic tasks, pointing to a functional parcellation of this neuroanatomical region. The cellular mechanisms in the prefrontal cortex and adjacent subcortical areas that may regulate linguistic syntactic processing will also be discussed. In addition, some problems posed by the comparison of hierarchical structure processing across different domains will be considered with respect to the third study, and a novel methodological approach will be proposed that takes into account variations of hierarchical structural complexity as a possible confound.

#### 1.2 DEUTSCHE ZUSAMMENFASSUNG

Natürliche Sprachen sind äusserst flexible Zeichensysteme, die Konzepte zu vermitteln erlauben. Dabei kommt es auf eine Integration von kognitiven, emotionalen und sensomotorischen Funktionen an. Trotz der grossen Komplexität natürlicher Sprachen entwickeln Kinder in den ersten paar Lebensjahren die Fähigkeit, Sprache zu verstehen und adäquat ohne explizite einzusetzen. und zwar Anweisungen. Aufgrund hierarchischer Organisationsprinzipien, ein grundlegender Verarbeitungsmechanismus, vermag das menschliche Nervensystem elementare Einheiten wie beispielsweise Sprachlaute, Wörter, aber auch gestische Köperbewegungen und Zahlen zu einem kohärenten Gebilde zu verknüpfen. Die Komplexität dieses Gebildes kann je nach Bedarf und Kreativitätsvermögen vergrössert werden. Komplexe Verknüpfungen von Elementen, die einer tieferen Ebene zuzuordnen sind, können auf einfache Weise generiert werden; andererseits können Verbindungen, die sich auf höheren Ebenen finden, in elementare Einheiten zergliedert werden, die sich lernen, verarbeiten und speichern lassen.

Ziel dieser Dissertation ist es aufzuzeigen, dass sich die experimentelle Manipulation hierarchischer Organisationsprinzipien als Methode besonders dazu eignet, bestimmte Aspekte der Sprachverarbeitung und des Spracherwerbs aufzudecken. Die Methode führt auch zur Formulierung einiger provozierender Hypothesen über die Entwicklung der Sprache aus evolutionär älteren sensomotorischen Systemen. Ferner sollen Hypothesen über Mechanismen, welche der Sprachverarbeitung zugrunde liegen, diskutiert werden; dabei geht es um neuronale Mechanismen, welche die Neurotransmission betreffen.

Linguistische Theorien gründen auf der Annahme, dass hierarchische Strukturprinzipien ein inhärentes Merkmal natürlicher Sprachen sind und sich auf der phonologischen, morphologischen und syntaktischen Ebene nachweisen lassen. In der ersten experimentellen Untersuchung - eine

Positron Emissions Tomographie Studie mit gesunden erwachsenen Probanden - wurde der Frage Komponente tatsächlich isomorph nachgegangen, ob die syntaktische einigen neurophysiologischen Prozessen ist und spezifische neuronale Korrelate hat. In linguistischen Theorien wird die syntaktische Komponente der Sprache als ein System von hierarchisch gegliederten Regeln definiert, welche die Kombination von Wörtern bestimmt. Hierarchisch gegliederte syntaktische Strukturen wurden manipuliert, ohne dabei die übrigen linguistischen Komponenten zu verändern. Dieses Vorgehen erlaubte es, die funktionellen neuroanatomischen Korrelate zu isolieren, die der syntaktischen Verarbeitung zugrunde liegen. Das ermittelte neuroanatomische Netzwerk umfasste Strukturen der linken Hirnhemisphäre: kortikal tiefe Anteile der Broca Area, die Insula und den Nucleus Caudatus. Die Ergebnisse sind vereinbar mit dem Läsionsort, der sich bei Patienten mit syntaktischen Verarbeitungsstörungen findet, und legen nahe, dass die Verarbeitung von hierarchisch gegliederten syntaktischen Relationen in einem spezifischen neuronalen Netzwerk erfolgt - im Einklang mit Hypothesen linguistischer Theorien.

Die zweite Untersuchung - eine funktionelle Magnetresonanz Tomographie Studie - befasst sich mit dem Erwerb syntaktischer Regeln in einer Fremdsprache, und zwar im Erwachsenenalter. Bislang ist noch nie untersucht worden, wie eine natürliche Sprache in Echtzeit erworben wird; die regionalen Modulationen, die dem Spracherwerb zugrunde liegen, sind weitgehend unbekannt. In dieser Untersuchung wurde der Erwerb von hierarchisch gegliederten syntaktischen Strukturen, die mit den universellen grammatischen Gesetzmässigkeiten natürlicher Sprachen vereinbar sind, mit dem Erwerb von nicht hierarchisch gegliederten, nichtsprachlichen Strukturen verglichen. Es konnte gezeigt werden, dass der Erwerb von hierarchisch gegliederten syntaktischen Strukturen selektiv ein neuronales Netzwerk in der linken perisylvischen Hirnregion aktiviert, das auch die Broca Area umfasst (die Hirnregion mit der die Lernleistungen, welche verhaltenspsychologisch mit der Messung von Reaktionszeiten und Anzahl richtiger

Lösungen festgehalten wurden, korrelierten). Vergleicht man die Ergebnisse dieser zweiten Untersuchung mit den Ergebnissen der ersten Untersuchung, drängen sich weiterführende Hypothesen auf; sie betreffen die Verlagerung der neuronalen Aktivierung von den lateralen zu den kortikal tieferen Anteilen der Broca Area und den angrenzenden subkortikalen Regionen mit zunehmender Fertigkeit in der syntaktischen Verarbeitung. Die Ergebnisse sind auch vereinbar mit der Hypothese, dass die Broca Area eine modalitätsunabhängige Rolle spielt bei der Verarbeitung hierarchischer Strukturen in den verschiedenen kognitiven Bereichen wie Sprache, Ausführung und Beobachtung von Handlungsabläufen.

In der dritten Untersuchung - ebenfalls eine funktionelle Magnetresonanz Tomographie Studie mit gesunden erwachsenen Probanden - wird der Hypothese nachgegangen, dass der Sprache und der Ausführung und Beobachtung von Handlungsabläufen ein gemeinsames neuronales System zugrunde liegen dürfte. Entwicklungspsychologische Beobachtungen legen nahe, dass die kognitiven Prozesse, die sich im Bereich der Sprache, der gestischen Körperbewegungen und der Objektmanipulation ausbilden, einem gegebenen Entwicklungszeitpunkt von vergleichbarer hierarchischer Komplexität sind. Der Reifungsprozess dürfte demnach ein gemeinsames neuronales Korrelat haben. Untersuchungen an höheren Primaten lassen vermuten, dass sich Sprache aus einer allgemeinen Fähigkeit im Erfassen und Nachahmen von gestischen Körperbewegungen entwickelt hat; dabei wurden diese erfassten und nachgeahmten gestischen Körperbewegungen auf eigene motorische Repräsentationen abgebildet. In dieser dritten Untersuchung ging es um die Perzeption von Sätzen, die eine Handlung beschreiben, welche mit dem Mund, der Hand oder dem Bein ausgeführt wird. Es fanden sich Aktivierungen in einem fronto-parietalen Netzwerk, das die Broca Area umfasste als auch spezifische Regionen des linken präfrontalen Kortex, die den jeweiligen Körperteilgebieten entsprechen. Die Aktivierung dieses Netzwerkes legt nahe, dass Sprache nicht eigenständig ist, sondern mit älteren sensomotorischen Systemen verknüpft ist.

Die allgemeine Diskussion befasst sich mit den verschiedenen Funktionen, die der Broca Area bei der Verarbeitung sprachlicher wie nichtsprachlicher Aufgaben zugeschrieben werden. auf Die experimentellen Ergebnisse deuten eine funktionelle Gliederung dieser neuroanatomischen Region. Von besonderem Interesse sind die neuronalen Mechanismen im präfrontalen Kortex und den angrenzenden subkortikalen Arealen, welche die syntaktische Verarbeitung steuern. Anhand der dritten Untersuchung werden auch Probleme erörtert, die sich stellen, wenn hierarchische Strukturen in unterschiedlichen Bereichen miteinander verglichen werden. In diesem Zusammenhang wird auf einen methodisch neuen Zugang verwiesen, der die Variationen in der strukturellen hierarchischen Komplexität zu erklären vermag.

"There are five shelves for each of the hexagon's walls; each shelf contains thirty-five books of uniform format; each book is of four hundred and ten pages; each page, of forty lines, each line, of some eighty letters which are black in color. There are also letters on the spine of each book; these letters do not indicate or prefigure what the pages will say."

#### Jorge Luis Borges, "The Library of Babel"

"Man possesses the capacity of constructing languages, in which every sense can be expressed, without having an idea how and what each word means - just as one speaks without knowing how the single sounds are produced.

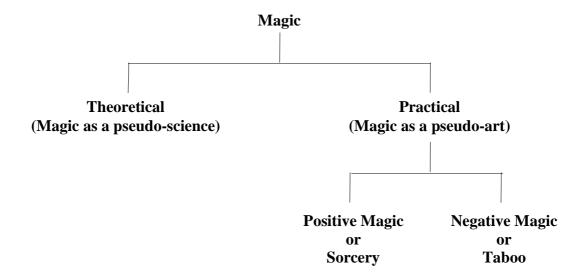
Colloquial language is a part of the human organism and is not less complicated than it.

From it it is humanly impossible to gather immediately the logical of language.

Language disguises the thought; so that from the external form of the clothes one cannot infer the form of the thought they clothe, because the external form of the clothes is constructed with quite another object than to let the form of the body be recognized.

The silent adjustments to understand colloquial language are enormously complicated."

Ludwig Wittgenstein, "Tractatus logico-philosophicus"



James Frazer, "The Golden Bough"

## 2. INTRODUCTION

Human linguistic communication, be it spoken or signed, is characterized by a property that allows infinite possibilities of expression: a finite number of linguistic signs can be combined in an infinite number of rule-governed ways. Signs – such as speech sounds, words, or phrases – can be combined into larger entities by means of recursive computational processes<sup>1</sup>, thus generating hierarchical structures. Likewise, larger entities of hierarchical structure can be decomposed into elementary units that can be learned, processed and stored. Based on such computational mechanisms, human infants autonomously develop the capacity to extract linguistic regularities from fluent speech that allow them to use and understand language.

Hierarchical structuring is not only a property of human language, it also characterizes other higher-order cognitive functions, such as visuospatial and sensorimotor processing. In these domains, too, lower-level units can be hierarchically assembled into higher-level units along specified rules.

The aim of this thesis is to present evidence from own empirical studies showing, at a functional neuroanatomical level, how hierarchical structures are represented in the human brain, with a special focus on language. These functional neuroimaging studies are presented in the context of developmental sudies showing how hierarchical structures are acquired throughout the life span. A further relevant point raised by the three own empirical studies is whether and to what extent sub-specializations in the hierarchical domain are to be found in the human brain.

The nature of linguistic structures will be examined, especially syntax, given that most linguistic theories concerned with syntactic structures have adopted the notion that language is based on recursive hierarchical computation. Special attention will be devoted to sign language, which shows unique properties integrating linguistic, motor and visuospatial functions. These unique properties emphasize the modality-independent, abstract nature of the hierarchical structural principles found in human language. The non-verbal, gestural communicative format used in sign language illustrates the fact that hierarchical structures also subserve motor and

<sup>1</sup> For an account of recursiveness in language, see Hauser et al. (2002).

visuospatial functions: the sign language system exploits hierarchical structures in these non-linguistic domains to increment its structural flexibility. Hierarchical structuring will also be considered in relation to purely non-linguistic functions found in the motor (tool use, gesture), visuospatial, and cognitive domain. From a phylogenetic perspective, hierarchical structuring attains an unparalleled degree of complexity in the human species. The assumption is made that such a degree of complexity is attained during the early stages of development in human infants, with a characteristic time course that is domain-independent, in these early stages. Evidence in favor of such a hypothesis will be presented in this chapter. Later on in life, the language system, less so non-linguistic functions, further expands the typology and complexity of the hierarchical structures used. The analysis of the hierarchical structures found in language is an important step in understanding the extent to which language is a human-specific capacity.

#### 2.1 APPROACHES TO HIERARCHICAL STRUCTURES IN LINGUISTIC THEORIES

Before addressing issues concerning the neuroanatomical mechanisms underlying the processing, representation and acquisition of linguistic and non-linguistic hierarchical structures, it is useful to first consider notions of hierarchical structuring as developed in various linguistic theories. There is general agreement that human language is hierarchically structured. However, a distinction can be made between two different approaches to the study of language. The generative approach is primarily concerned with a formal description of the language structure, i.e. with the tacit linguistic knowledge necessary for speaking and understanding language; the psycholinguistic approach, on the other hand, is largely focused on the flow of linguistic information during the performance of particular linguistic tasks, ranging from word to sentence level.

The term 'hierarchical' in generative linguistic models<sup>2</sup> is broadly taken to indicate that higher-level structures (e.g. sentence-level clauses such as "The yellow fog that rubs its back upon the window panes<sup>3</sup>") consist of a combination of lower-level constituents (e.g phrases such as "The yellow fog" or "upon the window panes"), which in turn can be composed of lower-level entities (e.g. determiners such as "the", adjectives such as "yellow", nouns such as "fog"). Higher-level constituent combinations can be further hierarchically embedded in even more complex structures. Basically, this recursive process can be reiterated infinitively.

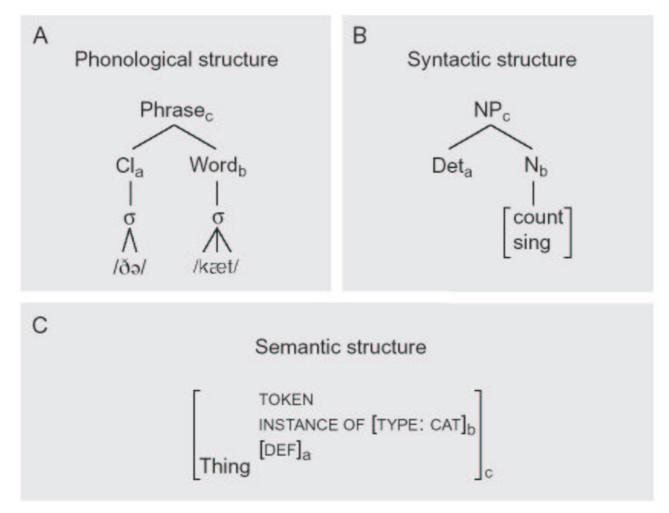
The hierarchical syntactic organization, as reflected in phrase structure, is based on lexical categories such as nouns, verbs, adjectives or adverbs. The words belonging to these lexical categories are represented in a mental lexicon. The mental lexicon specifies, in addition to a

<sup>2</sup> For instance, Principles and Parameters Framework (Chomsky, 1981; 1995), Head driven Phrase Structure Grammar (Pollard and Sag, 1994), X-Bar-Theory (Jackendoff, 1977).

<sup>3</sup> A verse taken from "The love song of J. Alfred Prufrock" by Thomas Stearns Eliot.

word's meaning, information pertaining to its phonological form and its syntactic properties, including inflectional and positional information.

Hierarchical structuring principles are found at all linguistic levels: at the phonological, morphological, syntactic and semantic level (Figure 2.1).



**Figure 2.1.** Hierachical structure of 'the cat', at the phonological (A), syntactic (B), and semantic (C) level. At the phonological level, a phonological phrase consists of a combination of two syllables. At the syntactic level, a noun phrase consists of a determiner and a singular count noun. The semantic structure consists of the conceptualization of an instance of the category of feline animals, i.e. a cat, and marked definite (i.e. assumed by the speaker to be known to the hearer from previous discourse or world knowledge). The constituents of the three structures (phonological, syntactic and semantic) are linked by subscripts (a, b, c), pointing to a possible parallel mental representation (adapted from Jackendoff, 1999a).

At the phonological level, phonemes form syllables, which in turn form words. With a finite number of phonemes an infinite number of words can be generated. At the morphological level, word formation is governed by rules specifying how particular morphemes can be combined; for instance in German, compounds display a left-branching structure (e.g. 'Korkenzieher' (English 'cork-screw')), whereas in French they display a right-branching structure (e.g. 'tire-bouchon' (English "screw-cork")). At the syntactic level, as already mentioned, constituents are grouped together into phrases, and at a higher level phrases are grouped into clauses. Furthermore, at the semantic level the components of meaning can also be shown as having a hierarchical organization, e.g. the relationships linking individual words to a particular semantic category, such as musical instruments or fruits (Jackendoff, 1999a).

In order to fully understand the nature of hierarchical organization principles in language, one need only consider that the generation of the set of all the well-formed linguistic expressions, and only these, is strictly constrained by structural relations that can operate non-linearily and non-locally. In other words, the distribution of linguistic elements into composite sequences is not determined by specification rules that map elements to discrete positions along a linear segment or by rules that predict the position of a certain element as a function of the preceeding one<sup>4</sup>. Rather, the position of elements in higher-order units is specified by context-sensitive boundaries that can be extended by inserting an undetermined number of further elements. These boundaries also constrain the number of positions that a particular element can take to a specific subset (for example, depending on whether a sentence has an active or passive form, a particular word will take two different contextually constrained well-defined positions, which are associated with disctinct functional roles (Jackendoff, 1968)).

As already pointed out, psycholinguistic models are primarily concerned with the flow of linguistic information. The assumptions made with respect to the structural organization of language

<sup>4</sup> Such rules were indeed assumed within linguistic models of the Markovian finite state grammars type, or models based on local transition probabilities of words in sentences.

do not differ substantially from the notions of phrase structure grammar, as developed in the generative approach. For instance at the syntactic level, after words have been retrieved from the lexicon and grammatical functions such as subject and object have been assigned to them, a control hierarchy is generated, which specifies the order in which words are produced; it also captures dependencies among grammatical functions. Morphosyntactic inflections are realized by a fine-grained hierarchical expansion of phrases and words such as subdividing a word into the corresponding stem and an affix node (e.g. Bock and Levelt, 1994).

Contrary to generative linguistic models, psycholinguistic models provide an explicit account of the types of errors produced in speech. Errors are interpreted as wrong assignments of one or more constituents to the sentential hierarchical structure. Different types of errors are to be expected, depending on the level in sentence formation in which the wrong assignment is made. Such levels include word retrieval, positional syntactic specification, phonological encoding, etc.

Neurally oriented models of language processing, which are related to psycholinguistic models, are usually not so specific in terms of the hierarchical notions that underlie human language. These models are based either on anatomo-functional observations gathered from neuroimaging studies and from clinical studies, or on simulations of brain functioning. With the more sophisticated neuroimaging techniques and neural network models that have been developed more recently, linguistic hierarchical structures can now be investigated more readily. In the following, a few examples of such models will be described.

A model exploiting knowledge about learning and memory systems to account for language processing has recently been forwarded by Ullman (Ullman et al., 1997; Ullman 2001a). In this neuroanatomically based model, called 'declarative/procedural model', the mental lexicon and mental grammar are associated with two distinct domain-general memory systems. According to this model, the declarative memory system subserves an associative memory that underlies stored knowledge about words, including their sounds and their meanings. The procedural memory system in turn

subserves the non-conscious (implicit) learning and use of aspects of a symbol-manipulating grammar, across grammatical sub-domains, including syntax, morphology, and phonology. This system may be particularly important in the learning and computation of sequential and hierarchical structures (Ullman, 2001b). The model has been shown to predict patterns of language acquisition and the processing of language in healthy subjects and in brain-damaged patients.

Another example of neurally oriented linguistic models, are connectionist models. These are based on artificial neural networks, simulating the behavior of the nervous system in relation to the performance of complex tasks and to language processing, representation and acquisition. One type of connectionist models, mutiple constraint satisfaction models (MacDonald et al., 1994; Tanenhaus and Trueswell, 1995; Taraban and McClelland, 1990), considers the syntactic structure to be governed by sequential, local transition probabilities. Such models do not explicitly account for hierarchical syntactic relations, given that all sequential features are considered to be acquired by detecting probabilistic distributions, with which, for instance, the next word within a sentence can be predicted (Cleeremans et al., 1989; Elman, 1991; Lawrence et al., 2000). Some more recent accounts, however, while considering mechanisms of language acquisition that are probabilistically-driven as the null-hypothesis that needs to be falsified, recognize that some specific learning mechanisms that are sensitive to non-transition, higher-order grammatical structures might be necessary for language learning (cf. Seidenberg et al., 2002).

A second type of connectionist models, modular two-stage models, have generally attempted to explicitly account for hierarchical syntactic representations (Lane and Henderson, 1998; Mayberry and Miikkulainen, 2000). The CAPERS model (Stevenson, 1994), for instance, includes a symbolic module, based on Chomsky's Government and Binding Theory, where hierarchical structures are explicitly represented by activations spreading through the neural network. While simple hierarchical long-distance dependencies between constituents can be established, this is only possible with major simplifications (Palmer-Brown et al., 2002).

Most connectionist models, at least until present, lack the technical capacity to represent or

acquire the full variety of grammatical hierarchical structural relations. But with respect to this issue, connectionist research is particularly well-suited to address a long-standing issue in the domain of language acquisition. This issue hinges on the argument about whether grammatical knowledge in the human brain is innate or extracted from the linguistic input (e.g. Pinker, 1994 vs. Tomasello, 2000). Connectionist models provide an attempt to explicitly determine whether linguistic input is sufficiently rich in information content to support the extraction and representation of regularities. For some linguistic domains, sufficient clues may be inherently present in the linguistic input so that relatively simple neural models are able to acquire the corresponding structures. For other structures that are non-transparently mapped onto the linguistic input, in turn, more constrained neural architectures may be needed. The latter case may be taken to suggest that such constrained neural architectures are at least in part innately determined. In general, it has become clear that some language acquisition researchers have grossly underestimated the structural regularities that can be extracted from the input (Plunkett, 1998). Connectionist models may thus provide a preciser definition of the trade-off between architecturally-based and computationally-based language acquisition, and also a better understanding of the properties that the nevous system must possess to acquire language.

#### 2.1.1 NEUROBIOLOGY OF LANGUAGE ACQUISITION

As discussed above, human natural language is organized according to multiple levels of hierarchical relationships at the phonological, morphological, syntactic, and in a broader sense also at the conceptual/semantic level. However, only a subset of these hierarchical properties is transparent at the surface structure level of language, i.e. at the level of language production and perception. Most hierarchical relations are established at an abstract level and are not obviously mirrored by surface structures. The fact that complex hierarchical principles are not physically manifest at the language surface level poses intriguing questions about the mechanisms underlying language acquisition. Children are not given instructions as to the properties that human language must conform to, yet most of them develop the capacity to properly use and understand language in their first few years of life.

At the surface structural level, a crucial problem that every child is faced with, is to segment fluent speech such that the boundaries that separate adjacent words can be identified. The sensitivity to the phonemic properties of spoken language might be attained very early during development, possibly even before birth (Mehler et al., 1986; Jusczyk et al., 1993). Neonates as young as 4 days are capable of discriminating sentences in their native language from sentences in a foreign language and from native speech played backward (Bertoncini et al., 1989; Dehaene-Lambertz and Houston, 1998; Mehler, 1988). Event Related Potentials (ERP) and functional Magnetic Resonance Imaging (fMRI) studies have shown that 3-to 6-months-old babies dispose of neural structures that respond selectively to the phonemic and prosodic contours of the infants' native language (Cheour et al., 1998; Dehaene-Lambertz et al., 2002; Dehaene-Lambertz and Dehaene, 1994)<sup>5</sup>. This sensitivity to the phonemic and prosodic contours of natural languages is assumed to guide infants in determining the segmental transitions across words. This is a difficult

<sup>5</sup> Phonemic and prosodic discriminations do not seem to be human-specific capabilities, given that they have been demonstrated also in a number of non-human species, and might reflect general-domain auditory processing mechanisms (see Kuhl, 2000 for a review).

learning process, as word boundaries in fluent speech are inconsistently marked by acoustic cues such as pauses<sup>6</sup>. Nevertheless, not later than at 7 months of age, children are able to identify single words (Jusczyk, 1997). One possible mechanism by which children learn which sound combinations are words is by the extraction of statistical (probabilistic and distributional) regularities from linguistic input, i.e. by the detection of consistent sequential patterns of sounds. This is in principle possible, because the probability that a particular syllable follows another one tends to be higher when the two syllables belong to the same word than when they are each part of one of two subsequent words. It has indeed been shown that 8-months-old infants can detect and use syllabic distribution information to segment words they have never encountered before, after no more than 2 minutes of exposure (Aslin et al., 1998; Saffran et al., 1996). Another set of experiments (Marcus et al., 1999) with 7-months-old infants demonstrated that, apart from picking up statistical information, children are also capable of learning abstract rules, analogous to algebraic representations (e.g. non-hierarchical rules of the type ABA, or AAB). In these experiments the words presented during familiarization never occurred in the test phase. Performance in the test phase was interpreted as reflecting a generalization of the learned abstract rules. These results, however, have led to opposing interpretations, as to whether the infants were indeed using abstract rules to make generalizations or whether they were instead relying on statistical information (e.g. McClelland and Plaut, 1999; Seidenberg and Elman, 1999).

Transition probabilities between subsequent syllables are based on non-hierarchical properties of surface structures. To understand and produce well-formed sentences in their native language, children must also learn to assign words to grammatical categories – such as nouns, determiners or verbs – and to combine words into phrases and phrases into clauses. This requires knowledge of the underlying abstract hierarchical principles of the grammar. The mechanisms by which they learn to do so are still largely unknown. Several observations are concordant in

<sup>6</sup> Pauses and other prosodic cues tend to systematically mark clause boundaries. 6-months-old infants exploit this information to detect clause boundaries in a language specific manner (Jusczyk PW, 1997; Hirsh-Pasek K et al, 1987).

suggesting that grammatical categories may be assigned to words by the detection of their cooccurrence regularities (e.g. Cartwright and Brent, 1997), and perhaps also by detecting
phonological cues that systematically occur with some categories and not with others (Shi et al.,
1999). Once grammatical categories have been acquired, the distributional behavior of grammatical
categories may in principle be used to determine how words form phrases by learning predictive
dependencies, for example by learning that the appearance of a determiner (such as 'the' in English)
in a sentence predicts that, with high probability, a noun will appear later on (whereas the reverse
prediction is less probable) or by learning that words that make up phrases move together within
and across sentences. Saffran (2001), however, showed that children between 6 and 9 years of age
possess limited abilities to detect such predictive dependencies and use these only to acquire
relatively simple syntactic rules. This suggests that in children the acquisition of syntactic
properties, in particular those of higher hierarchical complexity cannot be reduced to statistical
learning (Saffran et al., 2001). Children may possess other types of learning abilities that enable
them to detect and incorporate linguistic information without explicit guidance, thus developing
full language competence.

With respect to second language learning in adults, the situation may be somewhat different. Saffran (2001) administered the same artificial grammar system to a group of adults. The authors noticed that, compared to the group of children, adults showed significantly better performances in acquiring the same set of simple syntactic rules. They concluded that adult learners can detect phrasal units by just relying on predictive dependencies, i.e. by making inferences on the regularities governing the grouping of word classes into phrases. Indeed, covariance analyses showed that the hierarchical syntactic structure of natural language cannot be acquired by solely extracting distributional properties of surface cues, such as syllabic or graphemic transitions, and generalizing these properties into rules<sup>7</sup>.

<sup>7</sup> In the second study constituting this thesis (section 3.2) – an fMRI study on the acquisition of novel syntactic rules in adulthood – the surface properties of the sentences used (such as phonology and morphology) were all kept invariant

In a different set of related experiments (Peña et al., 2002), it was shown that, at least in adults, language acquisition may be driven by two different computational processes, i.e. statistical computations and non-statistical grammatical rule generalizations. Subjects were presented with streams of continuous synthesized speech composed of syllables (Figure 2.2).

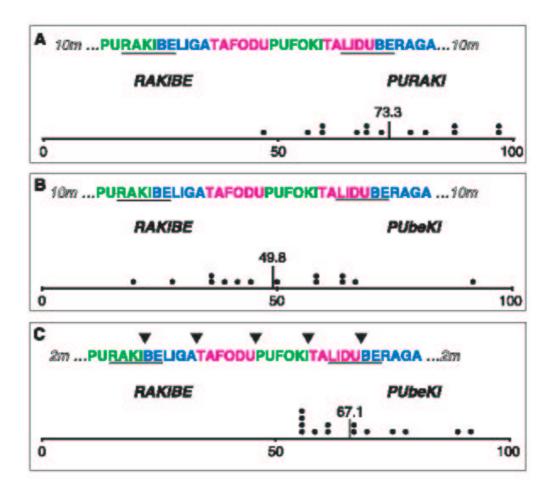


Figure 2.2. The first line of each frame (A, B, C) shows a sample of the familiarization speech stream, and the numbers indicate its duration. Different colors highlight words. Non-target words, i.e. words characterized by weaker transition probabilities, are underlined. The second line of each frame shows an example of a test word pair. Test pairs always compare a non-target word to either a word or a rule word. Each dot represents the percentage of choices for either words (A) or rule words (B and C) of individual subjects averaged across items; the number above the vertical

from the participants' mother tongue, and lexical-semantics was selectively eliminated. As a consequence, subjects could readily identify the syntactic categories of the words by relying on their mother tongue, and the sole piece of information that had to be acquired was the particular novel positional syntactic rule introduced, there being no need to acquire a new phonological or morphological system, nor a new vocabulary. While this experimental approach may be considered simplistic, Saffran's results suggest that the acquisition of novel syntactic rules is indeed not tied to the detection of word form cues, but solely based on the distributional properties of syntactic categories. It can therefore be concluded that the functional neuroanatomical effects observed in our second study are not merely laboratory artefacts, but rather represent biologically relevant correlates of grammatical acquisition.

mark indicates the general mean. (A) After 10-minutes familiarization participants preferred words to non-target words (P < 0.0005), indicating that they can segment the stream on the basis of nonadjacent syllable transition probabilities. (B) After 10-minutes familiarization participants did not show a preference for rule words over non-target words. (C) With a stream that contains, at the edge of each word, 25-ms subliminal gaps (indicated by triangles above the first line), participants showed a preference for rule words over non-target words (P < 0.0005), even if the duration of familiarization was reduced to 2 minutes (adapted from Peña et al., 2002).

The succession of syllables was governed by nonadjacent transition probabilities, according to which syllables could be grouped into discrete trisyllabic segments (i.e. "words"), as transition probabilities were stronger within segments than across segments. Nonadjacent relations of the type used here8, although of a simple nature, are compatible with the hierarchical structure of human language (in contrast to adjacent transition probabilities of the type used in similar studies discussed above). Furthermore, the "words" delimited by such probabilistic constraints all conformed to an underlying abstract rule (of the type A<sub>i</sub>XC<sub>i</sub>, see also footnote 8). After listening to the speech stream, subjects were required to choose from a test word pair the word that resembled more closely words present in the speech stream. The results showed that chunking of fluent speech into single words could indeed be carried out by statistical computation on the basis of nonadjacent transition probabilities (Figure 2.2A). However, when subjects were confronted with word pairs, in which the item congruent with generalization had not appeared in the familiarization set (a rule word), they responded at chance, suggesting that they had failed to infer the underlying grammatical rule (A<sub>i</sub>XC<sub>i</sub>) (Figure 2.2B). In the presence of subliminal pauses of 25 ms duration between words, however, subjects did show generalization to novel items according to the rule, indicating a computational switch from a statistical to a non-statistical mode. Under these conditions, more closely reflecting natural languages, rule acquisition was found after only 2 minutes of exposure (Figure 2.2C). These data suggest that to discover grammatical regularities, the representations of words, possibly acquired through statistical information, serve as the basis 8 A<sub>i</sub>XC<sub>i</sub>, where A<sub>i</sub>, X, C<sub>i</sub> are different syllables, and A<sub>i</sub> predicts the appearance of C<sub>i</sub> with a probability of 1.

for projecting, non-statistically, structural, abstract generalizations. The extent to which such representations could also be gained by sophisticated statistical computations, presently not understood, is currently debated (Seidenberg et al., 2002).

The neuroanatomical correlates subserving the acquisition of the hierarchical grammatical structures of natural language are still largely unknown. A recent study has investigated acquisition of phonetic aspects in adults. Golestani and colleagues (2002) studied volumetrically the neuroanatomical correlates underlying the acquisition of novel non-native speech sounds in healthy adult individuals. They found that fast learners compared to slow learners presented with a larger volume of white matter in the parietal lobes, more pronouncedly in the left hemisphere. The same effect was found in relation to non-linguistic sounds with rapidly changing frequencies. Volumetrically more white matter, possibly reflecting greater myelination, may thus reflect a domain-general psychoacoustic ability to learn rapidly changing sounds.

The second empirical study constituting this thesis (3.2) is to my knowledge the first attempt to investigate on-line the acquisition of syntactic rules of a non-native language (and, in general, of natural languages). Using minimal manipulations of word order, hierarchical syntactic structures conforming to the universal grammatical principles of human natural languages were contrasted with non-hierarchical, non-linguistic structures. As could be shown, the acquisition of hierarchical syntactic rules selectively modulates a left-hemisphere perisylvian network including Broca's area.

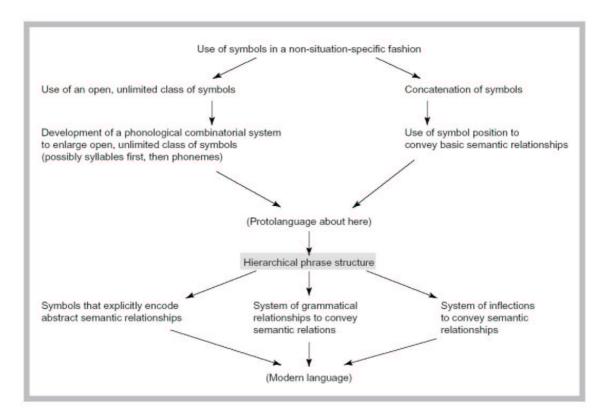
Such types of studies present new conceptual and methodological approaches that may allow, in the near future, to attain an integrated understanding of language acquisition, taking into account phonological, morphological, syntactic, and semantic components. In this context, it will be of particular importance to take hierarchical structural principles into consideration, as this may lead to a better appreciation of properties which are specifically linked to language as opposed to other cognitive functions or, conversely, this may lead to the identification of domain-general learning mechanisms.

#### **2.1.2 SUMMARY**

Language is a hierarchical system that maps multi-dimensional conceptual relationships onto sequences of physical vectors (e.g. phons). Hierarchical organization principles are found at all levels of language grammar, namely at the phonological, morphological and at the syntactic level. As to be seen in the next section, they also represent a fundamental organisation principle in other higher-order brain functions.

An interesting hypothesis that has been recently proposed by linguists is that the mapping of linguistic abstract structures unto linear physical strings of sounds requires that linguistic symbols be linked by hierarchical syntactic relations, in order to adequately (univocally and error-free) convey a vast number of concepts (Jackendoff, 1999b). Some mathematical models of evolutionary dynamics have been developed, showing that in the course of cultural evolution an increase in the number of relevant concepts that humans adopted may have guided the transition from non-syntactic to hierarchical syntactic forms of expression (Figure 2.3) (Nowak et al., 2000; Nowak et al., 2001; Pinker, 2000).

<sup>9</sup> And the increase in evolutionary fitness that this modification may have determined.



**Figure 2.3.** Hypothetical steps in the evolution of language, and the emergence of hierarchical phrase structure, which guided the transition from 'protolanguages' to modern languages (adapted from Jackendoff, 1999b).

Hierarchy in language helps to solve the problem of reconstructing the intended conceptual meaning from the phonemic linear sequence, a problem that, lacking hierarchical organization, would not have unequivocal solutions. As the above mentioned mathematical models (Nowak et al., 2000) maintain, hierarchical syntactic structuring is of no benefit if the lexicon does not exceed a threshold value; this value is defined as a function of the number of meaningful word combinations allowed by the lexicon and of the relative difficulty encountered in memorizing a syntactic signal compared to a non-syntactic one. The use of non-syntactic communication (i.e. the use of elementary signals, such as single words, to refer to entire events, i.e. combinations of objects, places, times and actions) with a large lexicon inevitably leads to a high number of errors in message production and comprehension. Given that signals cannot vary unboundedly (i.e. they must be small in size, in order to be memorable), a large lexicon with many different signals makes

the signals physically indiscriminable, such that they are easily confused (Pinker, 2000). On a more complex level of non-syntactic communication, on which different elementary signals are combined to form complex signals, the lack of hierarchical phrase structure – a stage that has been termed as "protolanguage" (Bickerton, 1990; see Figure 2.3) – allows for unambiguous message communication, however only in cases in which interpretation is driven by the pragmatics of the words involved (e.g. "eat apple Fred", in which only "Fred" can be the agent of the action "to eat"). In the absence of pragmatic cues (e.g. in "kiss John Mary", agent and patient are not univocally defined) ambiguities arise (Jackendoff, 1999b).

Univocity in conceptual interpretation is further given by another characteristic of linguistic hierarchical structures, namely their asymmetrical format (Kayne, 1994; Moro, 2000). If hierarchical syntactic structures were symmetrical, a particular positioning of words in a sentence can be associated with several (not just one) different syntactic structures. In other words, the same word can be assigned to more than just one syntactic role, leading to an ambiguity in language structure that affects both production and comprehension. An hypothesis that will be explored in section 4.2 is that hierarchical structuring has a computational cost for the nervous system. This cost is higher the more complex the underlying hierarchical structures.

The three empirical studies to be presented here all focus on issues of hierarchical structuring. The first study (3.1), exploits the hierarchical notions that have thus far been discussed, manipulating linguistic structures at the syntactic and morphosyntactic level (i.e. manipulating the corresponding hierarchical structures), in order to identify the neural correlates specifically devoted to the processing of each of these grammatical components in the mother tongue.

In the second study (3.2) minimal manipulations are made at the syntactic level, transforming hierarchical linguistic structures into non-hierarchical, non-linguistic structures. As will be shown, the comparison of the hierarchical structures naturally found in language with non-hierarchical, artificially created structures is a valid tool to selectively investigate the specific

neural correlates that mediate language acquisition. As the findings of the second study suggest, such a methodology can also be useful when investigating learning processes in other, non-linguistic domains.

The third study (3.3) addresses the hypothesis of there being common or shared neural substrates underlying the processing of action-related percepts in the linguistic and sensorimotor domains. The hypothesis tested is based on the prediction that language may have evolved from a domain-general capacity of understanding and imitating actions and intentions of others, i.e. by transcoding these onto one's own corresponding internal motor plan (Rizzolatti and Arbib, 1998; Théoret and Pascual-Leone, 2002). Furthermore, a large body of evidence from independent research fields convincingly suggests that during the early stages of the development of human infants the acquisition of abilities in the linguistic domain and in the non-linguistic sensorimotor domain are correlated. This correlation has been captured by analyzing the emergence of hierarchical structuring abilities of an increasing complexity within each domain. In the following sections this point will be addressed specifically.

#### 2.2 SIGN LANGUAGE

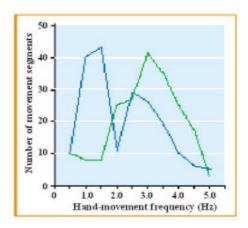
An important question arises, namely whether the hierarchical principles that characterize human natural languages are modality-specific and restricted to the particular mode of linguistic communication treated so far — namely the auditory-oral input-output modality of spoken languages — or whether they reflect abstract structural linguistic principles that are modality-independent. Sign languages — the languages used by deaf persons — offer a unique possibility to investigate this type of question. There is general agreement that, compared to spoken language, sign language presents the same distinctive characteristics that are universally recognized to be essential to the human language faculty. However, in contrast to spoken language, sign language is produced by means of manual and facial gestures and is perceived visually. Spoken and signed language thus provide the opportunity to investigate abstract linguistic structures irrespective of the input-output modality.

Sign language, just like spoken language, is characterized by a set of grammatical features that regulate the relationships between concepts (as specified by lexical entries), at the phonological, the morphological and the syntactic level (Klima and Bellugi, 1979; Petitto et al., 2000). At the phonological level, signs are formed by combining a finite set of meaningless, sub-lexical elements, that can vary along four different dimensions: handshape, movement, location in space and palm orientation. These sublexical elements are assembled into units of higher structural complexity, namely syllables, which constitute the basic perceptual unit of sign language (Hildebrandt and Corina, 2002); syllables, in turn, are assembled into signs (Corina and Sandler, 1993; Perlmutter, 1992). Signs have comparable linguistic properties to words in spoken language. At the morphological level, regular changes in form across classes of signs mark both inflectional and derivational changes in meaning; inflections mark such grammatical categories as person, number, distributional and temporal aspect. In sign language, a sign and its inflectional marker may co-occur in time, as for instance in American Sign Language (Klima and Bellugi, 1979; Poizner,

1983). The possibility to express different linguistic symbols simultaneously, rather than just one at a time as in spoken language, is due to the hand-motor and spatial properties exploited by sign language, which offer more degrees of freedom than the oral-auditory modality of speech (Studdert-Kennedy and Lane, 1980). Finally, at the syntactic level, the relations among lexical items are determined by a combination of sign order and manipulation of sign forms in space, modifying the argumental structure of signs, and a small set of facial expressions that indicate particular syntactic forms, as for example questions or topicalized sentences (Liddell, 1980; Lillo-Martin and Klima, 1990; Lillo-Martin, 1991).

Studies in both profoundly deaf and hearing infants acquiring, respectively, signed language only and both signed and spoken language, have shown remarkable parallels in the mechanisms underlying the acquisition of signed language and spoken language. These parallels are equally consistent if compared to hearing babies who acquire spoken language only. There is abundant evidence that deaf babies acquire signed language along the same maturational time schedule as spoken language (Petitto, 1987; Petitto et al., 2001a). Deaf babies spontaneously start producing babbles<sup>10</sup> in the manual modality between 6 and 8 months of age – at the same age when hearing babies produce their first vocal babbles. Manual babbling is characterized by a specific low-frequency rhythmic hand activity, differing from other types of non-linguistic gestures observed in both signing and speaking children (Figure 2.4) (Petitto et al., 2001b).

<sup>10</sup> i.e. the sequences of reduplicated sublexical (vocal or manual) units, the onset of which occurs at a typical age. The production of such sequences follows characteristic maturational stages (Ledewag et al., 1984).



**Figure 2.4.** Hand movement frequencies calculated for the rhythmic hand activity of sign-exposed (blue line) and speech-exposed (green line) babies across 6 and 12 months of age. Only sign-exposed babies show a bimodal distribution of movement frequencies. The first mode (left peak) falls at around 1 Hz (range 0.5-1.5 Hz); it is unique for sign-exposed babies, and reflects manual babbling. The second mode (right peaks) falls at around 2.5 Hz (range 2.0-3.0 Hz) for sign-exposed babies and at around 3 Hz (range 2.5-3.5 Hz) for speech exposed babies, and reflects non-linguistic hand activity (adapted from Petitto et al., 2001b).

In deaf and hearing children, the first sign, respectively the first word, appears at 10-12 months of age. Typically, this first word or sign is produced from the pool of "phonetic" sublexical unit types rehearsed during the babbling phase. By 12-14 months of age deaf infants produce babbling sequences which resemble whole sentences, in that they display characteristic patterns of rhythm and duration, but are devoid of meaning. Similar sentence-like vocal babbling is produced by hearing infants at this age (Petitto and Marentette, 1991). These observations suggest, above and beyond the linguistic modality used, that there is a predisposition for infants exposed to language to discover on their own the temporal and abstract hierarchical structure of natural language phonology.

The fact that hierarchical principles are intrinsic to human language grammar, independently of modality, becomes even more evident when considering the results of another set of studies. As

Goldin-Meadow and Mylander (1998) report, congenitally deaf children exposed only to spoken language and thus being deprived not only from vocal linguistic input but also of signed linguistic input, nevertheless spontaneously produce syntactically organized sequences of gestures. The syntactic structures of the sequences of gestures are of a different type than those found in the (vocal) languages spoken by their parents (English rsp. Mandarin). Furthermore, the mothers produced complex sequences of gestures to a significantly lesser proportion than their deaf children, and with different syntactic characteristics. It is therefore unlikely that these children learned to produce syntactically organized gestures by mere exposure to their parents' speech and gestures.

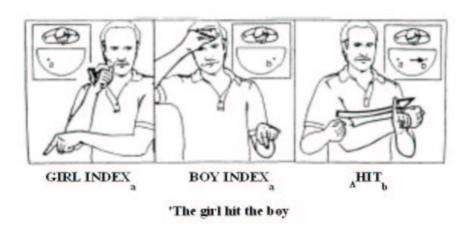
Similarly, before special schools were introduced and Nicaraguan Sign Language (NSL) emerged, deaf children in Nicaragua until the 1980's faced an analogous linguistically deprived environment. The analysis of the signs produced by Nicaraguan children revealed that their utterances were governed by grammatical regularities not to be found in their input (Senghas and Coppola, 2001). In the last two decades, with the spread of NSL, the grammar of NSL has been subject to constant enrichment. The syntactic constructions of today's adults are based solely on sign ordering, whereas those of adolescents, being a generation younger, exploit both sign ordering and spatial relations<sup>11</sup> (Saffran et al., 2001).

These data support the hypothesis that human infants spontaneously develop learning abilities that guide them in the acquisition of the complex hierarchical grammatical relations displayed by human natural languages, and that these mechanisms are independent of the linguistic modalities adopted.

It can be thus concluded that, as in spoken language, the mapping of conceptual meaning onto well-formed sentences in signed language is not performed by subsequent, discrete additions of signs along a linear dimension, but is instead governed by hierarchical rules, at the phonological,

<sup>11</sup> See below and Figure 2.5 for a description of the use of syntactic spatial relations in signed language – a system referred to as "spatialized syntax".

morphological as well as the syntactic level. In contrast to spoken language, however, where speech is physically conveyed by streams of sounds with rapid changes of frequency in time, in sign language manual signs are characterized by unique low-frequency rhythmic gestural patterns (different from other types of non-linguistic gestures) that are realized in space (Petitto et al., 2001b). This characteristic provides an additional parameter along which hierarchical relations can be established, namely a three dimensional space – so-called signing space – that lies in front of the signing person and extends approximately from waist to forehead and where signs can be articulated. Grammatical syntactic relations in signed language are established by using the signing space (Figure 2.5).

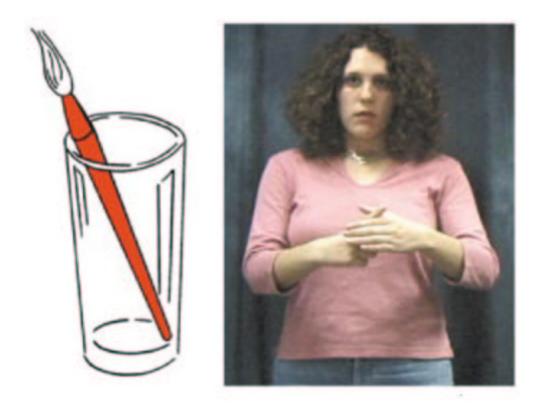


**Figure 2.5.** Example of spatialized syntax in American signed language. As shown by the example sentence 'The girl hit the boy', in sign language noun phrases are assigned arbitrary reference points in a horizontal plane of the signing space, while verb phrases (and more in general, grammatical relations) are realized by hand movements between such reference points (adapted from Bavelier et al., 1998). Notably, an equivalent use of the signing space is made to convey wholly abstract concepts, such as 'Experiences can influence beliefs' (Atkinson et al. 2002).

This visuospatial grammatical organization is hierarchical: signs can be linked together by syntactic and morphosyntactic markings, thus forming sign combinations (phrases) that can be embedded incrementally one into another and give rise to clauses with several levels of hierarchical

complexity. This system is often referred to as "spatialized syntax" (Lillo-Martin, 1991; Poizner et al., 1987).

This hierarchical use of space and motor units in sign language, however, must not be confused with a different use, also found in sign language, which is configurational and non-hierarchical. This second type of spatial reference is of an iconic nature and used to represent the spatial relations holding among real-world objects<sup>12</sup> (Figure 2.6).



**Figure 2.6.** Example of a non-hierarchical classifier construction for the relation 'The paintbrush is in the glass'. This relation is expressed by the two hands signing, respectively, 'paintbrush' and 'glass', located one into the other (adapted from Emmorey et al., 2002).

Notably, a recent neuroimaging study that investigated the functional neuroanatomy underlying the production of such iconic constructions (Emmorey et al., 2002) found specific activations in the inferior parietal cortex of both hemispheres, in a more dorsal and mesial portion than that usually activated in language tasks (i.e. the supramarginal gyrus proper). The same brain

<sup>12</sup> This is referred to as the "classifier system" (Newport and Supalla, 1980)

region, but only in the left hemisphere, was found active in a different study during the comprehension of signed sentences containing iconic constructions (MacSweeney et al., 2002). Such activations may be tied to the processing of the kind of non-hierarchical spatial information implied by iconic constructions.

Given the hierarchical linguistic use of space specific to sign language, one would expect specific brain regions – typically not recruited by spoken language – to be activated during the processing of sign language. Isolated cases of deficits affecting spatialized syntax in native signers following right hemisphere lesions have been reported (Corina, 1998). However, these patients were generally also impaired in their visuo-constructive and visuo-perceptual abilities and their deficits may thus not have been of a linguistic nature proper.

Another interesting piece of evidence comes from a different neuroimaging study (Newman et al., 2001) that investigated differences in brain activation during sign language comprehension between a group of native sign users and a group of signers who had learned sign language in early adulthood<sup>13</sup>. Only native signers showed activations in the right angular gyrus (and to a lesser extent also the right precentral gyrus). This region, which is not typically activated by spoken language, might thus be related to the processing of the hierarchical spatial relations specific to sign language grammar. Nevertheless, the non-native signers included in the study were highly proficient in signed language, and had presumably also mastered hierarchical aspects of spatialized syntax. It is therefore likely that — not having been exposed to signed language until early adulthood — these non-native signers recruited other brain regions than the right angular gyrus in processing such representations<sup>14</sup>.

Interestingly, in the second study constituting this thesis (3.2), it will be shown that a circuit including the angular and the precentral gyri, albeit in the left hemisphere, is specifically involved in the acquisition of hierarchical linguistic syntactic rules. The fact that contralateral hemispheric

<sup>13</sup> Both groups consisted of hearing subjects, who were speakers of English and were highly proficient in American Sign Language.

<sup>14</sup> Still another possibility – but specific data to this point are not provided by the authors – is that non-native signers may only have had limited access, or none at all, to this type of hierarchical representations.

regions appear to be involved in the processing of space-related hierarchical structures in sign language (right hemisphere) and hierarchical linguistic syntactic rules (left hemisphere)<sup>15</sup> is an interesting hypothesis to be further explored. An alternative possibility though, is that – given that abstract hierarchical spatial relations in sign language are mapped onto gestures involving both sides of the body – bilateral hemispheric regions subserve this particular aspect of sign language.

In conclusion, sign language, just as spoken language, is a hierarchically organized system. Compared to spoken language, however, sign language possesses at least an additional domain in which hierarchical linguistic relations can be expressed, namely the signing space. This does not imply per se that sign language is more intricately structured than spoken language. On the contrary, the fact that linguistic relations can be mapped onto hand and arm movements in space and time – as opposed to the essentially linearly concatenated vocalizations produced in spoken language – may to some extent pose fewer constraints on the sign language system. While in sign language real-world space-time relations can be represented in a stylized version in a quasi-isomorphic linguistic space-time domain, in spoken language, elaborate structural solutions, such as word ordering and affixing have to be adopted (Summerfield et al., 1980).

<sup>15</sup> Newman and colleagues (2001) also report activations in both native and non-native signers, in a left-hemispheric circuit including the angular gyrus, Broca's area and the precentral sulcus. This is in agreement with the existence of syntactic hierarchical structures of a non-spatial type in both signed and spoken language.

### 2.3 NON-LINGUISTIC HIERARCHICAL DOMAINS

Hierarchical organization can be identified across many behaviors and cognitive functions in humans, as well as in a number of non-human species. According to Lashley (1951), complex serial behavior cannot be explained in terms of local associations between contiguous acts; order must be generated by some internal higher-level organization of the sequencing of distinct elements and the coordination of simple sequences of elements into complex series of actions cannot be achieved in the absence of a detailed representation/plan of the global structure. The positioning of the different elements within the global structure has to be determined with sufficient accuracy. The inability to achieve such a structuring would inevitably lead to a disorganized behavior. As in the domain of language, also in non-linguistic functional domains, hierarchical organization provides a means of structuring complex combinations of lower-level elements in an efficient way, or reversely, for decomposing higher-order assemblies into meaningful simpler units that can be learned, processed and stored.

A number of non-linguistic cognitive and behavioral domains in which the notion of hierarchical structure is more widely recognized will be discussed in this section, in particular visuospatial processes, object manipulation, manual gestures, tool use, mathematical operations and music will be considered.

## 2.3.1 OBJECT MANIPULATION

Object manipulation can be regarded as a particular instance of symbol manipulation, where 'symbols' are physically located in time and space. Symbol manipulation is generally taken to

<sup>16</sup> As Lashley (1951) beautifully points out, "the coordination of leg movements in insects, the song of birds (...) and the carpenter sawing a board present a problem of sequences of action which cannot be explained in terms of successions of external stimuli."

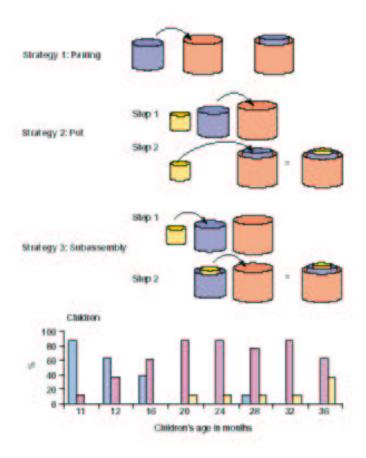
indicate processing of abstract representations that refer to concrete or to other abstract entities (language is an example of symbol combination). We should therefore expect that object manipulation, although physically constrained, is also governed by hierarchical relations. Of interest in this context are the neural mechanisms subserving hierarchical processing; when speaking of object manipulation, it must therefore be kept in mind, that the focus is on the sensorimotor and cognitive functions that are responsible for the particular behavior.

Behaviors based on hierarchical object manipulation are part of our daily experiences. An example could be refilling one's fountain-pen with a new ink-cartridge and then putting the 'pen with ink' assembly back into its case and the 'pen-ink-case' assembly back in the drawer. This requires selecting a cartridge that is compatible with the fountain-pen, unscrewing the pen components and finally putting all elements back again in the correct order. A more complex example could be an architect designing a house, where many different parts have to be put together in constructing walls, rooms, installing heating systems, etc. Some of these compositions will be conceived based on physical laws, others based on cultural habits and still others based on creativity and esthetics. To accomplish such tasks a sufficiently detailed mental representation of the pertinent objects' structure is necessary. Furthermore, the individual components, subassemblies, and the structural or functional relations holding between them must be identified.

Of great relevance is the developmental time course in acquiring object manipulation skills, as it shows that human infants progressively pass to stages in which object manipulation is characterized by increasing hierarchical complexity. For example, object manipulation strategies have been investigated with a 'nesting cup' task. Children were presented with cups of three different sizes, small, medium and large (Greenfield et al., 1972). At 11 months of age, children first adopt a simple strategy – the so-called 'pairing' strategy – in which one cup is placed in or above another one. At a later developmental stage a second strategy – the so-called 'pot' strategy – is observed: two cups are placed, one after the other (at different times), in or above a third one. <sup>17</sup> By 36 months,

<sup>17</sup> An hypothesis to be explored in relation to the pot strategy is whether in the case that the child "accidentally" puts together the three cups, such that the medium cup is inserted into the large cup and the small one into the medium one

children have attained a third level of combinatory complexity, in adopting a so-called 'subassembly' strategy: two cups are put together to form a higher-order unit (i.e. one cup in the other), and this higher-order unit is in turn combined with the third cup to form the final assembly. In the pairing and pot strategies only one hierarchical level of combination is implied, whereas for the subassembly strategy two hierarchical levels are required <sup>18</sup> (Figure 2.7).



**Figure 2.7.** The upper part of the figure schematically shows the 'pairing', 'pot' and 'subassembly' combinatorial strategies used by human infants, between 11 and 36 months of age. The graph below shows the percentage of human infants in the experimental group that used a particular strategy. Children initially used the pairing strategy (blue bars), then the pot strategy (magenta), and

<sup>(</sup>thus having generated a hierarchically ordered combination), the child may be led to "discover" hierarchical regularities. Of course, the child must be at such a developmental stage that allows him to infer such a generalization, and the result must be for him a rewarding experience.

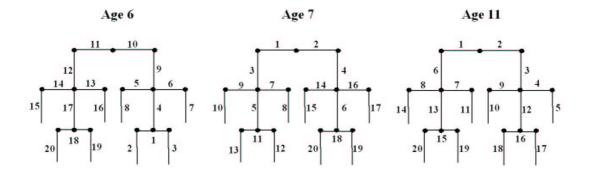
<sup>18</sup> Greenfield (1991) draws qualitative parallels between the increasing hierarchical complexity observed in object manipulation strategies and that observed in linguistic production during the first two to three years of development. While this is an interesting hypothesis, no details are provided here, as this hypothesis was not supported by formal testing, and also because Greenfield's treatment of hierarchical linguistic structures has not found unanimous approval (see Bickerton, 1991; Greenfield, BBS 1998; Swann, BBS 1998). However parallels between manual and linguistic development will be examined in section 2.3.3.

eventually incorporated the subassembly strategy into their routines (adapted from Conway and Christiansen, 2001).

Similar observations were made in observing infants in their second year of life, while they freely manipulated and combined objects of different shapes (Langer, 1986; Langer et al., 1998). By 18 months of age, children display elementary routines in serial and parallel object manipulations – analogous to the 'pairing' and 'pot' strategies outlined above – in which a target object is prepared, for example by setting a container in upright position, and one or more objects are then put in the container. By 24 months of age, infants progressively develop more complex manipulations, consisting of subroutines integrated in higher-order routines, according to hierarchical organization principles.

Later in the course of ontogenetic development, children become familiar with more complex hierarchical structures. Between 2 and 4 years of age, complex grammars of object combination emerge (Beagles-Ross and Greenfield, 1979; Goodson and Greenfield, 1975; Greenfield, 1978; Greenfield and Schneider, 1977). In an experiment concerned with the drawing skills of children, Greenfield and Schneider (1977) demonstrated that, when children were shown a schematic tree structure and subsequently asked to reproduce it from memory, 6-year-old children adopted a non-hierarchical, chain-like strategy (i.e. an element – or tree 'branch' – would be placed adjacent to the one just drawn, with no reference to hierarchical principles). 7-year-old children used a hierarchical surface-structure strategy, switching back and forth between hierarchical levels; 11-year-old children adopted a fully hierarchical strategy (i.e. completing a higher hierarchical level first, before switching to the immediately lower one), indicating that they had internalized the hierarchical organisation of the model (Figure 2.8).

<sup>19</sup> Interestingly, using the same tree structure drawing task, Grossman (1980) showed that adult aphasic patients with left-hemisphere anterior lesions (who typically have linguistic expressive deficits, with telegraphic, syntactically and inflectionally poor, but semantically rich speech (Mohr et al., 1978)) failed to correctly reproduce tree structures from memory and were mostly chain-like in their placement strategy. This suggests that Broca's area may be a supramodal hierarchical processor; but see studies 3.1 and 3.2 constituting this thesis for a more detailed treatment.



**Figure 2.8.** Typical construction strategies at different ages. Numerals indicate the serial order in which the pieces were added (Greenfield and Schneider, 1977).

Gathering from such data it appears that humans have the capacity to form representations of object manipulations of great complexity, involving a large number of hierarchical levels. As has been proposed, the acquisition of object manipulation skills is an indispensible prerequisite for the development of hierarchical symbolization (Langer, 1986; 1993; 1994). However, the kind of hierarchical relations that characterize object manipulations are physically constrained. Thus, while it is possible to construct hierarchically complex object structures<sup>20</sup>, clear parallels with hierarchies in language are difficult to draw.

Just like language, complex hierarchical object manipulation seems to be a human-specific ability (Conway and Christiansen, 2001). Evidence in favor of this hypothesis was provided by a nesting cup experiment – similar to the one developed by Greenfield and colleagues (1972) – that was administered to populations of capuchin monkeys, chimpanzees and bonobos (Johnson-Pynn et al., 1999). None of the three non-human primate species ever used the subassembly strategy as the dominant one, relying instead on the pairing and pot strategies. In a different set of experiments (Langer et al., 1998; Spinozzi and Langer, 1999; Spinozzi et al., 1998), in which the occurrence of

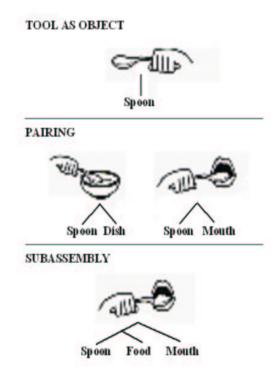
<sup>20</sup> One could for instance think of a hierarchical physical structure that is in equilibrium only to the extent that two distant elements, not in direct physical contact, are at balance; if one of the two elements is too heavy or displaced, the structure falls apart.

hierarchical object combinations in a naturalistic setting (subjects were left free to play with the objects) was observed, cross-species comparisons between chimpanzees and human infants were made. Only 8% of the primates' total manipulative actions manifested hierarchical organization – i.e. the integration of two separate elementary object combinations into a complex whole. This was far less than observed in human infants. In addition, this type of behavior was observed in primates at a much later developmental stage than in human infants.

## 2.3.2 **TOOL USE**

Tool use is an object and goal oriented action, in which a single object, or an assembly of objects, serves as an instrument to act on a second object, in order to achieve a specific goal. In humans, quite complex hierarchical relations can be achieved both at the level of tool construction, and at the level of the elements upon which the action is exerted.

An increase in hierarchical complexity in tool use is evidenced during the development of human infants. An interesting example is the use of a spoon. Children 11-12 months of age adopt a 'pairing' strategy – in analogy to the studies on object manipulation – when given a spoon to eat with: the spoon is repeatedly put in and out of the food dish, or in and out of the mouth, with no food on the spoon (Connolly and Dagleish, 1989; Greenfield, 1991). At an intermediate ontogenetic stage (16 months of age), children may adopt a 'pot' strategy: food is brought to the mouth with the hand, instead of with the spoon, and the spoon is then put in the mouth with no food on it; in other words, spoon and food are never combined into a single subassembly. Children older than 19-20 months of age learn the culturally-encouraged 'subassembly' strategy, where the spoon is first filled with food, and the two are then put in the mouth together (Figure 2.9).



**Figure 2.9.** Developmental stages in the hierarchical organization of spoon use. The first stage (top) is not referred to in the text because it is precombinatorial, i.e. the child is limited to grasping the spoon, like any other object (adapted from Greenfield, 1991).

Hierarchical complexity in tool use appears to be higher in humans, as compared to non-human primates (Gibson, 1993; Greenfield, 1991). In the wild, chimpanzees and macaques seem to be restricted in their tool use to two-level hierarchical structures: two-level hierarchical relations of the 'subassembly'-type are observed for instance when chimpanzees "fish" for ants with a stick, which is used as a kind of spoon. And actual spoon use has been learned in captivity by different chimpanzee species. In the wild, however, non-human primates appear to be unable to establish more complex hierarchical relations such as combining two or more objects to make an initial tool, then combining the first tool with one ore more objects to create a secondary tool, which could then be used to act on a target object (McGrew, 1993). There is however a paucity of observations made in the wild:

instances of three-level hierarchical tool combinations (combining two stones, one representing an anvil and a second one having a stabilizing function; a third stone is used as a hammer for nut cracking) have been reported at least in one case (Matsuzawa, 1991). Further observations on the frequency of hierarchically organized tool use in non-human species are desirable.

## 2.3.3 GESTURES

Gestures are particularly relevant to the study of hierarchical structures in language as they consist of a wide range of motor acts that are hierarchically organized and often convey communicative intentions. Gestures often accompany linguistic communication, and they may have a facilitatory impact and also contribute specific semiotic or symbolic intentions. At least five different gestural classes with a semiotic value can be distinguished (Ekman and Friesen, 1969): 1) emblems, which are gestures that can be used instead of speech (such as shaking the head for negation); 2) illustrators, which can help the receiver to decode messages more easily (such as pointing when giving directions); 3) regulators, which support the interaction and communication between sender and recipient (such as gaze of the eyes); 4) affect displays, such as facial expressions reflecting the intensity of an emotion; 5) adaptors, which are gestures that were at one point used for personal convenience but have turned into a habit (such as adjusting glasses in a tense situation).

Parallels between early language development and manual communicative gestures have been recognized, reinforcing the view that linguistic and non-linguistic symbolic communication may be somewhat correlated (see Bates and Dick, 2002 for a review). Two different empirical frameworks have guided more recent research in this domain: on the one hand, the work of Piaget (e.g. 1954) suggesting that linguistic and non-linguistic symbol use may have a common sensorimotor origin, on the other hand a tradition derived from Vygotsky's ideas about social influences on child language acquisition (Vygotsky, 1987), showing how children learn to attend to objects and events that adults

are watching or indicating (Tomasello and Akhtar, 1995).

In the development of gestures, children also progress from a stage in which gestures display rudimental hierarchical structuring to stages in which gestural sequences of a higher hierarchical complexity are produced. This is illustrated by the fact that, for example, the onset of babbling coincides with the onset of rhythmic hand banging or clapping (Ejiri and Masataka, 2001; Locke et al., 1995). In 12-18 months old infants the first instances of naming and gesturing are positively correlated (Shore et al., 1990; Volterra et al., 1979). The produced gestures, just as names, symbolize a particular concept (e.g. mimicking the action of putting a phone to the ear with a clear communicative intent). Somewhat later, two-item combinations are produced: the first two-word combinations are accompanied or slightly preceded by gesture-word (e.g. pointing to an object while uttering its name) and gesture-gesture combinations (e.g. mimicking the action of stirring with a spoon and then drinking from a cup) (Capirci et al., 1996; Iverson and Goldin-Meadow, 1998; Shore et al., 1984). At 24 to 30 months of age, children produce syntactically complex utterances rich in function words and inflections, and are able to remember and imitate arbitrary sequences of manual actions, the two developments again being positively correlated (Bauer et al., 1998a; 1998b; Bauer and Thal, 1990).

The use of gestures in non-human primates seems to be quite limited. However, gestural sequences in which two motor acts are combined have been observed in wild-roaming chimpanzees (Plooij, 1978). An example of such a gestural sequence is observed in the context of mother-child interaction, when chimp mothers teach their young how to use a tool (Boesch and Boesch, 1993; Plooij, 1978). This use of gestures with a communicative intention seems to be restricted to one-level hierarchical structures in chimpanzees.

While a detailed comparison between the types of hierarchical structures governing such complex behaviors as action and gesture on the one hand, and language on the other, has to our knowledge not been attempted, these data, taken together, suggest that both language and gesture possess a hierarchical structure. Such structures are almost exclusively human-specific, they develop

together in ontogenesis and might be subserved by partially shared neural structures. As it will be discussed in more detail in the third study constituting this thesis (3.3), mirror neurons<sup>21</sup> are thought to be the common neural basis that links both behaviors together. The third empirical study provides some functional neuroanatomical evidence which shows that listening to sentences describing actions performed with different body parts (mouth, hand and leg) activates a body-part specific visuomotor circuit that is also active during observation, imitation and execution of the action.

## 2.3.4 VISUOSPATIAL HIERARCHICAL PROCESSING

Visuospatial processing allows one to represent and remember the location of objects or other entities in space, with respect to a visual frame of reference. Visuospatial processing also underlies object manipulation; hierarchical organization in the visuospatial domain is therefore related to the properties discussed for object manipulation (see section 2.3.1). Visuospatial skills can also be used for the processing of arrays of more abstract elements such as symbols, and possibly also for language (see empirical study 3.2 for a discussion). Furthermore, they are crucial in the acquisition of the sequential order of elements, with and without hierarchical structure.

While both humans and non-human primates are capable of categorizing fixed, non-hierarchical sequences of elements (geometrical shapes), the strategies adopted to accomplish the task differ. This suggests that sequential information is represented differently in the brain of humans compared to that of primates (Oshiba, 1997). Primates proceed in a sequential manner, identifying an item and then responding (serial search strategy), whereas humans use a collective search strategy, identifying the position of all elements in a sequence before responding (Figure 2.10).

<sup>21</sup> Mirror neurons are a family of visuomotor neurons that respond in a highly specific manner both when a particular action is performed, and when the subject observes another individual performing that action. They are therefore believed to allow the understanding of others' actions through a transformation of visual input onto a corresponding motor schema (see Rizzolatti et al., 2001 for a review).

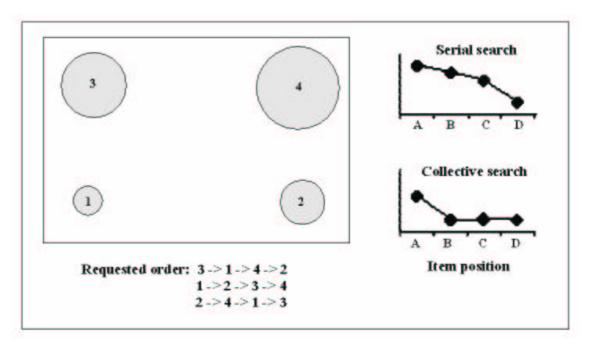


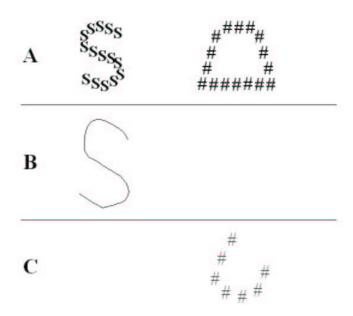
Figure 2.10. Serial ordering of visual stimuli in non-human primates and human adults. On the left, a display with the experimental stimuli is shown. Circles appeared in the four corners of the screen simultaneously. Subjects were trained to touch each item in a given order. The existence of two different reaction time (RT) patterns indicates two different search strategies. Primates used a serial search strategy: in this strategy, RTs decrease incrementally for each item in the list. Humans used a collective search strategy: accordingly, the RT for the first item is slow but for the remaining items, RTs are faster and roughly equal (adapted from Conway and Christiansen, 2001).

Visual processing of hierarchical arrays of non-linguistic symbols (such as geometrical shapes or alphabetic letter sequences) has been only studied in humans. A set of ERP experiments has demonstrated that the visual processing of non-linguistic surface structure (i.e. with no reference to hierarchical structure) and that of the underlying hierarchical structure rely, at least in part, on dissociable neurophysiological processes<sup>22</sup> (Dominey and Georgieff, 1997; Dominey et al., 1997; 1998).

In a more recent ERP experiment (Lelekov-Boissard and Dominey, 2002), the detection of violations in hierarchical sequences of non-linguistic symbols was compared with the detection of

<sup>22</sup> More specifically, a late positive P500 electrophysiological component with centro-parietal distribution was elicited only in the processing of hierarchical structures.

violations in linguistic syntactic structures<sup>23</sup>. Violations in both types of stimulus materials elicited a late positive electrophysiological component (P600). However, the topographical cortical distribution in the two conditions overlapped only partially, the linguistic structures producing effects more lateralized to the left-hemisphere, and non-linguistic structures producing effects more lateralized to the right-hemisphere. As a different set of experiments suggest, the state of affairs may be more complex, and the processing of non-linguistic hierarchical structures may be subserved by the left hemisphere as well. Delis and colleagues (Delis et al., 1988) investigated hierarchical visuospatial processing in two groups of patients, with left- and right-hemisphere damage, respectively. They asked subjects to reproduce drawings with a lower and a higher level of hierarchical organization, such as the shape of a star constructed from numerous smaller stars (Figure 2.11A).



**Figure 2.11.** (A) Examples of drawings with a hierarchical organization. (B) Drawing by a left-hemisphere damaged patient, illustrating correct construction of higher level form. (C) Drawing by a right-hemisphere damaged patient showing correct construction of lower-level forms (adapted from Delis et al., 1988).

<sup>23</sup> In this study, no attempt was made to disentangle the syntactic from the semantic linguistic component (see empirical study 3.1 for a related methodological discussion).

Left-hemisphere lesions were associated with a selective impairment in reproducing the lower hierarchical level (Figure 2.11B), whereas right-hemisphere lesions selectively compromised the reproduction of the higher hierarchical level (Figure 2.11C). Precise neuroanatomical localization of the substrates for high and low level hierarchical processing was forwarded by Fink and colleagues (1996): high-level (global) visual processing was associated with a blood-flow increase in the right lingual gyrus, whereas low-level (local) visual processing was associated with a blood-flow increase in the left inferior occipital cortex. More recently, an ERP study showed that, in addition to occipital regions, frontal regions may also be engaged: frontal regions may be crucial for the selection of local (low-level) elements from hierarchically organized patterns (Han et al., 1999). The use of compound letters (see Figure 2.11A) in the study of global and local visual processing was first introduced by Navon (1977): Navon showed that reaction times for global processing were faster than reaction times for local processing, indicating that the processing of global properties precedes that of local properties in visual perception. According to Han and colleagues frontal regions may act as a top-down selector, which allows subjects to switch from more global to more local hierarchical levels.

In general, these studies suggest a human-specific capacity for visuospatial processing of symbol sequences with a hierarchically complex structure. The neural structures subserving such visuospatial hierarchical processing seem to differ, at least partially, from those dedicated to the processing of linguistic hierarchical structures. The significance of these results however remains tentative, as a more precise taxonomy of the existing hierarchical structures in the visuospatial domain and their level of complexity needs to be established (see section 4.2).

### 2.3.5 MATHEMATICAL OPERATIONS

Research on mathematical intuition and on the neural substrates of numeric representations and calculation has provided evidence for two different systems subserving mathematical operations in humans, one for exact arithmetic knowledge and one for quantity manipulation and approximation. An investigation of normal subjects combining behavioral measures with fMRI and ERP techniques, showed that each of these two mathematical systems is associated with a specific pattern of neural activity (Dehaene et al., 1999). Exact calculation proved to be encoded in a linguistic format and elicited more activity in brain regions implicated in language processing, in particular the left inferior frontal regions, the cingulate gyrus and, bilaterally, the angular gyrus. Approximate calculation, on the other hand, was shown to be language-independent and probably dependent on linear visuospatial estimates. Activation elicited by approximate calculation were found, in particular, in the parietal lobes and precentral areas, bilaterally, and also in the dorso-lateral prefrontal cortex. This neural circuit had previously been shown to subserve visuospatial working memory and attention (e.g. Corbetta et al., 1995; Nobre et al., 1997). A more recent experiment using fMRI also found results consistent with a similar dissociation between linguistically and non-linguistically based calculation: linguistically based calculation involving the angular gyrus in the left inferior parietal lobe, and non-linguistically based calculation involving the lateral bank of the intraparietal sulcus, bilaterally (Simon et al., 2002). The two systems for exact and approximate calculation can be differentially damaged in adult patients with brain lesions (Dehaene and Cohen, 1995). Furthermore, dyscalculia – a selective deficit of mathematical abilities – is frequently found in children born preterm (Klein et al., 1989); dyscalculic children born preterm have been recently shown by analysis of volumetric brain morphometry to have reduced grey matter in the left inferior parietal lobe compared to normal controls (Isaacs et al., 2001).

The preverbal numerical abilities that play a role in approximate arithmetics have been identified also in several non-human species (Brannon and Terrace, Science 1998; Dehaene et al.,

1998) and in human infants (Wynn, 1998). On the other hand, exact arithmetics seems to be a specific achievement of human culture, which depended on the development of a mathematical language (Ifrah, 1994)<sup>24</sup>. Also, developmental studies show that children learning exact arithmetics – such as multiplication tables – actively reorganize mathematical entries in a highly structured format that makes information easier to retrieve (Butterworth, 1999).

Given that exact arithmetics appears to be human specific, dependent on the language system and having a rule-based structured representation, one can speculate that exact arithmetics is governed by hierarchical organization principles, numbers and mathematical notions being combined into discrete correspondences of increasing complexity (in contrast to approximate arithmetics which may be non-hierarchically organized). Such a hypothesis has not been forwarded explicitly in the literature, but several observations appear to support it. First, some acalculic patients that are impaired in their knowledge of numerical quantities and their relations as a consequence of lesions in the left inferior parietal cortex, have spared algebraic knowledge (Pessoa and Desimone, 2003), which is a form of exact arithmetics. Algebraic knowledge, such as in equations (e.g.  $(a+b)^2 = a^2 + 2ab + b^2$ ), involve arranging of mathematical algebraic symbols into distinct, nested hierarchical levels, whereas knowledge of numerical quantities is non-hierarchically organized and coded. Second, for problem solving, hierarchical structuring may be essential (Newell and Simon, 1972). Third, exact mathematical operations such as adding, multiplying, etc. are not freely associative (e.g. (4+5)\*2 is not equivalent to 4+(5\*2)) and the positional order of numbers and symbols is strictly rule-based (e.g. 4+\*5214= is a meaningless expression).

It must be emphasized, however, that, although hierarchical structuring is a common property of language, gestures and exact arithmetics, the acquisition of these properties differs in the various domains: while the acquisition of language and gestures is spontaneous, the acquisition of exact arithmetics depends on the exposure to an explicit system of rules (cf. Moro, 1996).

<sup>24</sup> Whether elementary exact arithmetics in young infants (such as constructing a list of symbolic representations of integer natural numbers) develops independently, or instead dependently on the development of analog (approximate) mathematical abilities, such as knowledge of numerosity, is unclear (see Ansari and Karmiloff-Smith, 2002 for a review).

# 2.3.6 MUSIC

Just like language, music is certainly governed by structural hierarchical principles (Raffman D. 1993). It has been claimed that the closest analogue to the syntactic structure of language is perhaps found in music (Balzano, 1986; Clynes, 1982; Lerdah and Jackendoff, 1983; Sloboda, 1977). Nonetheless, important differences in the syntactic structures of language and music are found (Patel, 1998). In music, syntactic dependencies are not obligatory (as they are in language), but probabilistic (Meyer, 1956; Narmour, 1990). Syntactic conventions in language are used to signal "who-did-what-to-whom" (thematic relations), while in music syntax participates in the dynamic articulation of mobility vs. closure, or "tension-resolution", and in harmonic relations (Swain J, 1997). On a different structural level, musical performance — a domain closely related to action and gesture execution — calls for complex hierarchic-rhythmic skills, required both for motor coordination and for processing musical syntax (Givon, 1998).

As pointed out in the introduction, hierarchical relations among basic processing units provide the basis for a culturally particularly relevant human capacity: recursive computation. The ability to generate an infinite number of constructions from a finite set of elements depends on such a capacity. Recursiveness, in addition to language and possibly also other human activities such as games and social structures, has been tentatively implicated also in music (Hauser et al., 2002).

Analogies between language and music suggest common or shared neural substrates. In particular, it has been demonstrated in an ERP study that the detection of violations in musical syntax (i.e. harmonically inappropriate chords) elicits responses that are rather similar both in temporal and topographical distributions to those elicited by violations of linguistic syntactic structures (Maess et al., 2001): of particular significance is that the detection of syntactic violations in both domains

activated Broca's area<sup>25</sup>. Similar electrophysiological responses have been found when musically educated subjects are asked to detect incongruities in musical syntactic phrase structures (Patel et al., 1998). Such findings appear to reflect commonalities between music and language with respect to their hierarchical syntactic structuring.

In the acquisition of perceptual musical skills, children have been shown to be able to detect and use transition probabilities between musical tones in a comparable manner to that observed in segmenting sequences of speech sounds (Saffran et al., 1999). Infants, but not adults, can learn the statistical (non-hierarchical) distribution of individual tones in a continuous string of musical sounds (Saffran and Griepentrog, 2001). It remains to be seen whether the learning mechanisms underlying the acquisition of hierarchical musical structures are analogous to those involved in the acquisition of hierarchical structures in language (see for instance Peña and colleagues' work in section 2.1.1).

#### **2.3.7 SUMMARY**

In all the different behavioral domains examined in this section, elementary units of processing having a physical or symbolic value are combined, forming higher-order levels that are hierarchically organized. During the course of development, human infants modify their processing skills and progressively master more complex hierarchical structures. It seems reasonable to assume that the organization of processes and routines in a hierarchical manner contributes to their increasing efficiency in terms of computational demands, storage and retrieval. Indeed, such an organization of behavior presents two important advantages for the organism. First, complex behavioral sequences do not need to be learned or planned as whole entities; the computational process can instead be chunked into simple routines that operate on elementary units, thus significantly reducing the memory load for each operation. Simple routines can be recursively

<sup>25</sup> These data may reinforce the view that Broca's area is a 'supramodal processor of hierarchic structures' (but see above and section 4.2).

combined, producing complex behaviors with minimal computational costs. Second, abstract hierarchical structuring helps the organism in organizing the many discrete entities constituting its environment and the repertoire of its own actions. In the absence of a powerful structural organizing principle, as for example in the presence of brain dysfunctions, a disorganized behavior is observed.

Non-linguistic hierarchical structures have certain commonalities with linguistic ones, especially at lower complexity levels; as hierarchical complexity increases, analogies become less apparent. Nonetheless, analyzing structural commonalities between various cognitive and behavioral domains, could guide the identification of existing links at the computational and representational level. Such links can in turn be used to formulate empirically testable inferences pertaining to the existence and location of neural resources shared by different domains – or conversely, to the existence of distinct neural systems (see also section 4.2).

"Some insinuated that each letter could influence the following one and that the value of MCV in the third line of page 71 was not the one the same series may have in another position on another page, but this vague thesis did not prevail."

Jorge Luis Borges, "The Library of Babel"

"The proposition is not a mixture of words (just as the musical theme is not a mixture of tones).

The proposition is articulate."

Ludwig Wittgenstein, "Tractatus logico-philosophicus"

3. EMPIRICAL STUDIES

# 3.1 STUDY 1. Syntax and the brain: disentangling grammar by selective anomalies<sup>26</sup>

## 3.1.1 ABSTRACT

Many paradigms employed so far with functional imaging in language studies do not allow a clear differentiation of the semantic, morphological and syntactic components, as traditionally defined within linguistic theory. In fact, many studies simply consider the brain's response to lists of unrelated words, rather than to syntactic structures, or do not neutralize the confounding effect of the semantic component. In the present PET experiment, we isolated the functional correlates of morphological and syntactic processing. The neutralization of the access to the lexical-semantic component was achieved by requiring the detection of anomalies in written sentences consisting of pseudo-words. In both syntactic and morphosyntactic processing, the involvement of a selective deep component of Broca's area and of a right inferior frontal region was detected. In addition, within this system, the left caudate nucleus and insula were activated only during syntactic processing, indicating their role in syntactic computation. These findings provide original in vivo evidence that these brain structures, whose individual contribution has been highlighted by clinical studies, constitute a neural network selectively engaged in morphological and syntactic computation.

<sup>26</sup> Moro et al., 2001.

#### 3.1.2 INTRODUCTION

Modern linguistics has succeeded in decomposing the complexity of grammars in the interaction of independent modules. More specifically, for any given sentence in any language three abstract levels of representation converge to give the associated structure; the phonological level (where the possible sequences of sounds are checked), the syntactic level (where words are combined yielding the proper hierarchical structures), the semantic level (where the meaning of the whole sentence is computed on the basis of the meaning of each lexical item). Thus, for example, an English native speaker knows that such expressions as "remnantzry", "dog a barks" and "happiness broke his arm" are not acceptable at the phonological, syntactic and semantic level, respectively.

Such a modular architecture, which is claimed to reflect the implicit knowledge of grammar that every human being is endowed with genetically, raises many empirical questions. A crucial one is whether this threefold abstract partition is actually isomorphic to some neurophysiological process, and more specifically whether these three levels of representation are subserved by distinct neural correlates. Of course, although the rules governing each level are independent, there is no direct way to test each of them in isolation, since by definition they are activated simultaneously. Several experiments have shown that semantic information as expressed by the lexicon is independently represented in the brain (Martin et al., 1995; Martin et al., 1996; Perani et al., 1999a; Vandenberghe et al., 1996); nevertheless, the fundamental question remains as to whether syntactic operations can be associated with some dedicated neural networks. Indeed, it must be highlighted that many neuroimaging experiments on human language have used as stimuli lists of words, rather than full sentences, which are in fact the actual units of spontaneous speech (Price, 1998).

Along with such an abstract model of the knowledge of grammar, the actual process of interpretation of a sentence of course requires assigning each element of the sentence to the proper slots in the actual mental representation-grid; this in turn implies the memory load capacity to keep phrases in an activated state. Syntactic processing during sentence reading has been addressed by

several functional neuroimaging investigations focusing specifically on syntactic complexity, which showed consistent activations in Broca's pars opercularis, during an on-line acceptability-judgment task (Caplan et al., 1998; Stromswold et al., 1996) and during a post-sentence presentation judgment task (Just et al., 1996). In the latter paper, Just and colleagues, in addition to left Broca's and Wernicke's regions, found activations also in right hemispheric homologue areas. The reported activations were indeed interpreted as being due to increasing syntactic complexity and, concerning Broca's area specifically, to augmented memory and computational load. Similar findings were reported for sentences presented in the auditory modality (Caplan et al., 1999): however, in contrast to the above mentioned studies, the pars triangularis and not the pars opercularis of the inferior frontal gyrus was activated. Caplan and colleagues (1998), in addition to Broca's area, found activations in the anterior cingulate gyrus and in the right medial frontal gyrus (similar finding are reported in Stromswold et al. (1996). This pattern, in the authors' opinion, correlates with phonological encoding and subvocal rehearsal, an hypothesis that is supported by other imaging studies (Paulesu et al., 1993; Zatorre et al., 1992). Subvocal rehearsal might be used for assigning the head of the sentence its thematic role, as in relative clauses (Swinney and Zurif, 1995; Swinney et al., 1996; Zurif et al., 1993).

A recent fMRI experiment (Dapretto and Bookheimer, 1999) used a sentence comprehension task, in which different relative weights for syntactic and lexico-semantic processing had been introduced. Subjects were asked to decide whether a certain pair of sentences had the same meaning. Such pairs were constructed by either changing one single word in the same sequence, called "semantic condition", or changing the full sequence, called "syntactic condition". The subjects were requested to give "same" or "different" judgments. For example, in the syntactic condition, sentences such as "The policeman arrested the thief" or "The thief was arrested by the policeman" were judged as "same" whereas "West of the bridge is the airport" or "The bridge is west of the airport" as "different". Again, a selective activation in Broca's pars opercularis on the lateral brain surface was found to be associated with syntactic processing. Clearly, such a task was crucially

centered on a major, although implicit, assumption, namely that changing the syntactic structure of a sentence does not affect the semantic component. So, the transformation of an active sentence like "the policeman arrested the thief" into a passive sentence like "the thief was arrested by the policemen" is considered not to affect the semantic interpretation. Although the transformation from active to passive construction is surely a syntactic phenomenon, one cannot be sure that this is not affecting also the semantic component. Indeed, since at least Jackendoff (1968), it is well-known that passive constructions do not preserve the semantics content of their active counterparts. Famous examples, often quoted in the linguistic literature are the pairs like: "many arrows didn't hit the target" and "the target wasn't hit by many arrows". Clearly, the state of affairs which are compatible with the two sentences differ, since the target could still be hit by many arrows, if the first sentence is true, whereas this cannot be the case if the second one is. Indeed, these kind of observations lead Chomsky to formulate the so called "Extended Standard Theory" -see for example, Chomsky (1975) contra Chomsky (1965) based on Katz and Postal (1964)-, and have never been dismissed ever since that time.

The Dapretto and Bookheimer (1999) experiment represents an advancement with respect to previous works in the field. In the present study, we have adopted an alternative strategy, which allows to disentangle grammar and isolate syntax from semantics. The innovative strategy we pursued, was suggested on the basis of some crucial problematic aspects of the previous work in the field. Indeed, all previous neuroimaging experiments, either using words or sentences, left the access to semantics unaltered. To avoid these problematic issue, we have designed a paradigm which neutralizes the access to any semantic component. Such a problem was overcome by using non-words, that is invented words which are not related to any meaning in the lexicon, like "staze". Functional words and morphemes, instead, like articles, auxiliaries, prepositions, plural morphemes etc. have been fully preserved. In such a case, any anomaly in the syntactic structure could not influence any semantic interpretation which was missing in the input in the first place. All in all, even if a non-word is in fact assigned a syntactic category on the basis of its morphological structure

and the context where it occurs, it is clearly impossible for it to have a proper semantic status for at least two reasons: first, it is by definition not assigned an extension in any possible world; second, which is crucial, it can by no means contribute to the computation of the semantics of the whole sentence which we take to be its truth functional value (Dowty et al., 1981).

In our experiment we tested the subjects' linguistic knowledge at each level by selectively disrupting one level while maintaining the others intact. More specifically, we have asked the subjects to detect either phonological, morphosyntactic and syntactic anomalies in pseudo-word sentences which contained only one type of anomaly for each level (see Materials and Methods). This in principle allows one to focus selectively on syntactic processing rather than on the different amount of syntactic complexity, as done in cited works. A major problem was also overcome which is implicit in this type of experiment. In fact, when the syntactic level is disrupted, a potential semantic anomaly is also produced; thus, for example, if one says "all the eaten have chickens snakes" the anomalous syntactic structure also disturbs the semantic interpretation which would be impossible to reconstruct.

3.1.3 MATERIALS AND METHODS

3.1.3.1 *Subjects* 

The study was approved by the Ethics Committee of the Scientific Institute H San Raffaele,

and each volunteer gave his written informed consent prior to the admission to the study.

Eleven male volunteer right-handed subjects (mean age 26 years, range 22 to 28 years) entered

the study. All subjects had no history of neurological or psychiatric disorders. Right-handedness was

verified using the Edinburgh Inventory (Oldfield, 1971).

3.1.3.2 Tasks Design

The study consisted of three experimental and one baseline conditions. Subjects were asked to

covertly read sentences presented visually and, for the three experimental conditions only, to make

acceptability judgments at the corresponding sentence-structure levels. The sentences all consisted of

pseudowords only ('pseudosentences'), so as to neutralize the access to semantic components: this

'Quasi-Italian', devoid of any open-class word, but maintaining inflections and function-words, was

employed in order to isolate the correlates of morphosyntactic and syntactic processing (see

Appendix 1). According to the experimental tasks, anomalies either at the phonotactic, the

morphosyntactic or the syntactic level were introduced. Syntactic anomalies presented sentences with

wrong linear order but proper agreements. Morphosyntactic anomalies presented sentences with

proper word order but agreement errors. Phonotactic anomalies presented sentences containing

Italian unlegal consonant strings.

Examples:

Baseline: "Il gulco gianigeva le brale."

$$(D_{\text{m/sing}} \ N\text{-}_{\text{m/sing}} \ V\text{-} \ AGR/T_{\text{3rd sing}} \ D_{\text{f/plur}} \ N\text{-}_{\text{f/plur}})$$

Syntactic anomalies: \* "Gulco il gianigeva le brale."

 $(N_{\text{-m/sing}} D_{\text{m/sing}} (Synt.\text{-anomaly}) V_{\text{-}} AGR/T_{3rd sing} D_{f/plur} N_{\text{-f/plur}})$ 

67

Syntactic anomaly = wrong word order: N- D- instead of D- N-

Morphosyntactic anomalies: \* "Il gulco ha gianigiata questo bralo."

 $(D_{\text{m/sing}} \ N \text{-}_{\text{m/sing}} \ Aux \ PP \text{-} \ AGR/T_{\text{f/3rd sing}} \ (Morph.\text{-}anomaly) \ D_{\text{m/plur}} \ N \text{-}_{\text{m/plur}})]$ 

Morphosyntactic anomaly = -a, fem./sing. instead of m/sing. (-o)

Phonotactic anomalies: \* "Il gulco gianigzleva le brale."

 $(D_{m/sing} N-_{m/sing} V- (Phonot.-anomaly) AGR/T_{3rd sing} D_{f/plur} N-_{f/plur})$ 

Phonotactic anomaly = gzl, string of consonants not present in Italian

For each condition, 3 sets each of 13 pseudosentences were formed, corresponding each to an experimental block. For the three experimental conditions only, 9 of the 13 pseudosentences within a block contained corresponding anomalies, whereas the other 4 were correct. Order of sentence presentation within blocks was fully randomized. All blocks within a condition were balanced for sentence length. Pseudosentences were presented individually on a NEC computer screen (distance from the eyes: 60 cm, angle: 30°), typed in black uppercase characters on a white background. Sentence presentation time was 4000 ms, with an Inter Stimulus Interval of 1000 ms. Subjects read the sentences covertly and, either pressed a response-box button when they had completed sentence reading (for the baseline condition), or pressed the response-box when they detected an anomaly (for the experimental conditions). Reaction times and response accuracy were recorded.

A preliminary dyslexia test battery was administered to all subjects, in order to exclude possible pseudoword processing deficits. All experimental and behavioral subjects included in the analysis performed as normal.

## 3.1.3.3 PET data acquisition and analysis

Regional cerebral blood flow (rCBF) was assessed with positron emission tomography (PET) on each of the eleven experimental subjects, while they were instructed to execute one of the four tasks. Three repetitions of each condition were run for each subject, for a total of 12 PET scans per subject. Condition-presentation order was balanced across subjects (Latin square design).

rCBF was measured by recording the distribution of radioactivity following an intravenous injection of <sup>15</sup>O-labeled water (H<sub>2</sub><sup>15</sup>O) with a GE-Advance scanner (General Electric Medical System, Milwaukee, WI) which has a field of view of 15.2 cm. Data were acquired by scanning in 3D mode. A 5 mCi slow bolus of H<sub>2</sub><sup>15</sup>O, 4 cc in 20 sec, plus 4 cc of saline solution in 20 s, were injected (Silbersweig et al., 1993). After attenuation correction (measured by a transmission scan using a pair of rotating pin sources filled with <sup>68</sup>Ge), the data were reconstructed as 35 transaxial planes by three-dimensional filtered back projection with a Hanning filter (cut-off 4 mm filter width) in the transaxial plane, and a Ramp filter (cut-off 8.5 mm) in the axial direction. The integrated counts collected for 90 s, starting 30 s after injection time, were used as an index of rCBF.

Image transformations and statistical analysis were performed in MATLAB 4.2 (Math Works, Natick, MA, USA) using statistical parametric mapping (SPM-96, Wellcome Department of Cognitive Neurology, London, UK). The original brain images were first realigned and then transformed into a standard stereotactic space (defined by the International Consortium for Brain Mapping project (ICBM) (NIH P-20 grant), and closely approximates the space described in the atlas of Talairach and Tournoux (1988). In order to increase signal to noise ratio and accommodate normal variability in functional gyral anatomy each image was smoothed in three dimensions with a Gaussian filter (16 x 16 x 16 mm). A repeated-measures ANCOVA was used for the comparison of different tasks, in which every subject was studied under all conditions. Global differences in cerebral blood flow were covaried out for all voxels and comparisons across conditions were made using t statistics with appropriate linear contrasts (Friston et al., 1995a; Friston et al., 1995b). The set of t values for each voxel of the image comprise the statistical parametric map (SPM{t}).

The following contrasts were evaluated:

Commonalities: overall main effects masked with each of the individual contrasts:

- 1. (Ph + M + S) B; masked with (Ph B); (M B); (S B).
- 2. (M + S) Ph; masked with (M Ph); (S Ph).

Simple Main effects:

- 3. M -Ph
- 4. S Ph

 $B = baseline \ task; \ Ph = phonotactic \ task; \ M = morphosyntactic \ task; \ S = syntactic \ task.$ 

#### 3.1.4 RESULTS

### 3.1.4.1 Behavioral data

All subjects performed the tasks with high accuracy (range B: 92-100 %; Ph: 92-100 %; M: 77-100 %; S: 69-100 %). A multivariate repeated measure Anova was performed on the accuracy rates (expressed in % of correct answers; correct answer defined as: answer given within time < 4000 ms, and correct anomaly detection). Experimental conditions (Means: B = 99.0 %; Ph = 98.8 %;

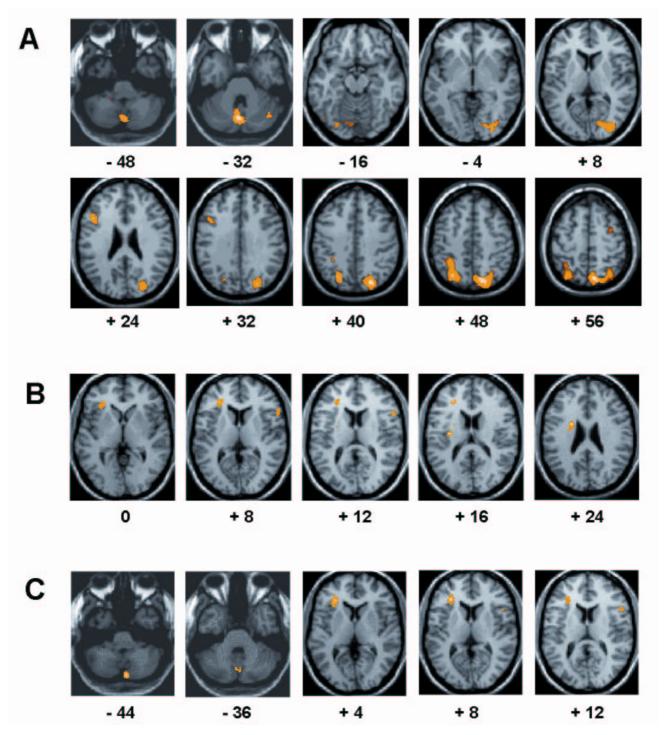
The same analysis was also performed on the Reaction Times (RT) of the 11 experimental subjects and gave the following results: Experimental conditions (Means: B = 1946 ms; P = 1693 ms; P = 1891 ms; P = 1891

# 3.1.4.2 Functional data

The 3 experimental conditions share a common neural network as revealed by the main effect, masked with the individual simple main effects, using the baseline as a reference condition. The common pattern of significant activations included Broca's area pars opercularis (BA 44) and the left inferior parietal lobule (BA 40); on the right hemisphere, the lateral premotor area (BA 6), the cuneus (BA 18) and the middle occipital gyrus (BA 19 and 18). Bilateral activations included the superior

parietal lobule (BA 7), the precuneus (BA 7), the fusiform gyrus (BA 18/37), the cerebellum and the cerebellar vermis (Table 3.1.1A for stereotaxic coordinates and Figure 3.1.1A).

TABLE 3.1.1A $(Ph + M + S)$ - Baseline, masked with simple main effects					
Brain region	X	y	Z	Z	
L inferior frontal gyrus (44)	-46	18	24	4,80	
L inferior parietal lobule (40)	-36	-42	44	3,82	
L superior parietal lobule (7)	-30	-68	48	5,38	
	-34	-50	52	4,57	
	-32	-58	52	4,49	
L precuneus (7)	-26	-70	40	5,03	
L occipital/fusiform gyrus (18/37)	-30	-82	-16	3,97	
	-20	-80	-16	3,30	
	-22	-84	-8	3,19	
L cerebellum	-50	-64	-24	3,99	
	-44	-72	-24	3,77	
	-20	-42	-48	3,36	
R lateral premotor (6)	34	-2	60	4,14	
R superior parietal lobule (7)	30	-64	56	4,52	
R precuneus (7)	10	-72	56	5,99	
	20	-76	48	5,37	
	26	-80	40	5,25	
R cuneus (18)	22	-82	4	4,20	
	14	-78	8	3,87	
R occipital/fusiform gyrus (18/37)	22	-84	-8	4,22	
	16	-80	-20	3,98	
	14	-82	-8	3,80	
R middle occipital gyrus (19)	28	-82	20	4,71	
	30	-94	16	4,36	
	28	-84	12	4,77	
R cerebellum	42	-68	-32	4,02	
cerebellar vermis	-4	-70	-36	5,39	
	-8	-52	-32	3,21	



**Figure 3.1.1.** Foci of significant activation for the corresponding contrast are superimposed on a set of axial slices, derived from a T1 Magnetic Resonance Imaging single-subject image (SPM-96), which has been normalized to the standard stereotactic space (ICBM), closely approximating the space described in the atlas of Talairach and Tournoux (1988). Below each axial slice, the corresponding coordinate level along the z axic is indicated (in mm). (A) (S + M + Ph) - Baseline masked with the individual simple main effects, Z > 3.09 (see Table 3.1.1A); (B) S - Ph, Z > 2.33 (see Table 3.1.1C); (C) M - Ph, Z > 2.33 (see Table 3.1.1D).

The <u>common activations for Syntactic and Morphosyntactic</u> conditions, as revealed by the main effect masked with each of the individual contrasts compared to the Phonological condition, were located in the rostral depth of the circular sulcus in the left inferior frontal gyrus (BA 45) and in the right homologue of Broca's area (BA 44) (see Table 3.1.1B for stereotaxic coordinates).

TABLE 3.1.1B $(M + S)$ - Ph masked with simple main effects						
Brain region	X	y	Z	${f z}$		
L inferior frontal gyrus (circular sulcus) (45)	-28	34	8	4,19		
R inferior frontal gyrus lateral (44)	56	18	12	3,12		

The <u>direct comparison of Syntactic vs Phonotactic</u> condition yielded significant activations again in the depth of the circular sulcus in the left inferior frontal gyrus (BA 45), and in the right homologue of Broca's area (BA 44,45); further activations were in the left caudate nucleus and insula (see Table 3.1.1C for stereotaxic coordinates and Figure 3.1.1B).

TABLE 3.1.1C S - Ph				
Brain region	X	y	Z	Z
L inferior frontal gyrus (circular sulcus) (45)	-28	32	4	3,53
L insula	-36	-14	16	2,88
	-36	-22	24	2,52
L caudatus nucleus	-24	-2	20	2,79
R inferior frontal gyrus (44,45)	58	22	8	3,03
	60	14	12	2,71

Comparable activation foci in the depth of the circular sulcus (BA 45) and in the right homologue of Broca's area (BA 44,45) were found in the <u>direct comparison of Morphosyntactic vs</u>

<u>Phonotactic</u> condition. In addition the vermis was also activated (see Table 3.1.1D for stereotaxic coordinates and Figure 3.1.1C).

TABLE 3.1.1D M - Ph				
Brain region	X	y	Z	Z
L inferior frontal gyrus (circular sulcus) (45)	-28	34	8	3,89
R inferior frontal gyrus (44,45)	50	14	12	3,10
	58	22	16	2,59
cerebellar vermis	6	-80	-44	3,21
	6	-36	-36	2,88
	12	-8	-8	3,13

#### 3.1.5 DISCUSSION

The detection of errors in pseudosentences is associated with the activation of an extended network of brain regions, involving the classical language areas as well as several other associative occipito-temporal and parietal areas (Table 3.1.1A). Common to all three experimental conditions was the activation of high-order visual areas, which may reflects aspects of visual processing specific for the error detection task in comparison with the reading condition. In particular, error detection engages more extensive attentional resources than simple reading, and might thus result in stronger parietal activation (Wojciulik and Kanwisher, 1999). The main issue underlying the present investigation was to address sentence processing at the syntactic level, while keeping this component as far as possible disentangled from lexical semantics: we will discuss the activations specifically related to morphological and syntactic processing, which included Broca's area, the caudate nucleus and the cerebellum.

Broca's area has been traditionally associated with morphosyntactic processing. The main basis for this association is the fact that the clinical picture of agrammatism, characterized by morphological errors in production and (inconstantly) by disordered syntactic comprehension (Caplan et al., 1981), is usually part of the symptom complex of Broca's aphasia (see Grodzinsky (2000), for a recent review). The classical syndrome of Broca's aphasia, however, combines the morphosyntactic disorder with impairments in other domains, such as articulation and phonological and lexical-semantic processing. It is common clinical knowledge that the full syndrome of Broca's aphasia actually follows from extensive anterior perisylvian damage extending beyond Broca's area proper. Most patients with this complex syndrome have been affected by extensive lesions, typically centered on Broca's area (BA 44 and 45), but extending towards other brain regions: precentral gyrus, insula, anterior temporal cortex (Déjerine, 1914). There has been a considerable effort in the clinico-pathological literature to "fractionate" the speech and language components of Broca's aphasia, and to associate them with specific neural substrates. The most successful aspect of this endeavor is

probably related to the articulatory disorder, variously labeled as apraxia of speech, cortical dysarthria, aphemia or anarthria. Clinico-pathological studies have indicated a specific role of the precentral gyrus (Lecours, 1976; Tonkonogy and Goodglass, 1981), and in particular of its insular part (Dronkers, 1996). When the lesion spares this area, and is limited to Broca's area proper, the clinical picture is different from typical Broca's aphasia. According to some early CT studies (Mohr et al., 1978), small lesions in Broca's area are associate with mild, transient aphasia. Tonkonogy and Goodglass (1981) reported a case with a clinical picture of anomia. When clinico-radiological correlation studies have attempted to define the relationship between syntactic disorders and lesion location within what we may call the Broca's region, the results have been largely disappointing. Lesions in several areas within the whole left perisylvian cortex, and in rare cases also in the right homologous region, have been shown to be associated with defective syntactic processing (Tramo et al., 1988). An exception is a recent study, which suggested that the effects of Broca's area involvement dissociate from those of a more anterior involvement of the left prefrontal cortex: patients with the latter location of lesions have unimpaired syntactic processing skills, but show pronounced deficits in narrative serial ordering, i.e. in producing temporally coherent sequences of actions (Sirigu et al., 1998).

The results of clinico-anatomical correlation studies must now be reconsidered in the light of the results of functional neuroimaging. The left dorsolateral prefrontal cortex, including Broca's area proper, has been shown to be activated by a variety of tasks involving different kinds of linguistic and cognitive processing. In particular, auditory-verbal short term memory tasks have been shown to be associated with activation of the posterior part of BA 44, which appears to be involved in phonological recoding and rehearsal processes (Paulesu et al., 1993). The same region was shown to be activated also in phonological discrimination tasks (Zatorre et al., 1992). Different areas (BA 45 and 47) appear to be related to memory encoding, as well as by lexical-semantic processing (reviewed in Gabrieli et al. (1998)). A direct contrast between these different regions was shown by a fMRI study of word fluency, in which phonological cueing was associated with activation in the

opercular, semantic cueing with anterior triangular component of Broca's area (Paulesu et al., 1997). The "semantic" area appears to be modulated by specific demands of the task, such as the amount of search required (Thompson-Schill et al., 1997), or the semantic category (Perani et al., 1999b).

The complex contribution of Broca's region to semantic processing, which is underlined by these studies, represents a problem for the interpretation of the few investigations of syntactic processing, which failed to unravel the syntactic from the semantic component (see introduction). Our results, based on a paradigm which aims to disentangle grammar from the semantic component, suggest that it is a specific portion of Broca's area, i.e. BA 45 within the depth of the lateral sulcus in the inferior frontal gyrus, to be activated by both the morphosyntactic and the syntactic task. On the other hand, the common activation for the three experimental conditions in Broca's area was centered within the pars opercularis (BA 44); this activation, observed also by others (Caplan et al., 1998; Dapretto and Bookheimer, 1999; Just et al., 1996; Stromswold et al., 1996), may not thus be specifically related to syntactic processing. A similar area was found to be activated by both syntactic and semantic anomalies in a recent event-related fMR study, in which subject read minimal verb phrases (of the type "forgot made" or "wrote beers") (Kang et al., 1999).

The activation of the right-sided homologue of Broca's area is also interesting. Data from patients who had undergone full or partial callosal section as a treatment for epilepsy suggest two parallel and complementary functions for Broca's area and its right hemispheric homologue. The right hemisphere of split-brain patients, though severely limited in its capacity to use syntactic information in comprehension (Gazzaniga, 1980; Gazzaniga et al., 1984; Zaidel, 1983) is quite capable of judging whether a spoken sentence is grammatical or not (Baynes and Gazzaniga, 1988). It thus seems that, while a deep component of Broca's area is likely to be the preferred locus for syntactic analysis and computation, a right hemispheric region, homologous to Broca's area is capable of conscious abstractions pertaining to the level of metalinguistic knowledge, which are clearly required for acceptability-judgment tasks of the type we have used.

The selective activation we found of the left caudate region for the syntactic anomaly

condition is consistent with the hypothesis that the basal ganglia might be involved in syntactic processing. Agrammatism can be observed in patients with left subcortical lesions. Broca's-like production deficits have been observed, as the result of extensive subcortical damage affecting connections to and from Broca's area, leaving the latter region and more generally the prefrontal cortex intact (Alexander et al., 1987; Mega and Alexander, 1994; Naeser et al., 1982). Further, neuropsychological studies of patients with Parkinson Disease (PD) have shown selective deficits in syntactic judgment tasks as well as in the comprehension of syntactically conveyed discourse meaning (Grossman et al., 1991; Lieberman et al., 1990). It must be underlined, however, that PD patients have also other cognitive disorders, pertaining to abstraction, problem solving and working memory (Cummings and Benson, 1984; Flowers and Robertson, 1985). The problem of the relationship of working memory with sentence comprehension is complex; it has been claimed that a "specialization" exists for assigning the syntactic structure of a sentence and using that structure in determining sentence meaning, separate from the system underlying the use of sentence meaning (Caplan and Waters, 1999). The visual presentation used in the present experiment can be expected to reduce the burden on working memory, as the whole pseudo-sentences were always physically present during the task. It must be however underlined that activations in Broca's area have been observed in association with the processing of both written (Caplan et al., 1998) and auditory (Caplan et al., 1999) sentences. A recent case study of a patient with mild parkinsonism due to anoxic damage to the putamen and the head of the caudate nucleus is indicative of the complex relationship between syntactic complexity and working memory load (Pickett et al., 1998). The patient presented "frontal" deficits: she scored below average in sequencing ability and showed perseverations in rule applications, which required switching from one criterion to the next one; she also showed an impaired comprehension in sentence meaning conveyed by syntax: however, her verbal and visual short-term memory were intact. Interestingly, her sentence comprehension capacity increased proportionally with increasing syntactic complexity. The authors interpret this somewhat striking finding, as an interplay of two cognitive strategies employed by the patient, namely her tendency to perseverate being overcome by her intact verbal short-term memory in more complex sentences. These findings might suggest, that syntactic complexity might in fact relate to an increased verbal memory load. The most probable location to play this role seems to be Broca's area (see introduction), particularly in relation with subvocal rehearsal processes. The left basal ganglia may play an essential role in establishing an interplay with frontal regions of the cortex, Broca's area in particular, that allows sentence word order to be checked, stored and retrieved at the right time, and the appreciation of hierarchical syntactic structure.

The foci of selective cerebellar activation associated with morphosyntactic anomalies detection is also consistent with clinical data. There are now a handful of case reports of production agrammatism after cerebellar damage (Silveri et al., 1994; Zettin et al., 1997), suggesting an involvement of the cerebellum in the production of morphologically correct sentences: whether this represents a genuine disorder of language production, or can be interpreted as a consequence of a highly specific impairment in motor planning and execution requires further investigation.

In conclusion, strong converging evidence appears to be now available, leading to a better understanding of the anatomo-functional structure of the neural network involved in sentence processing at the morphosyntactic and syntactic level. The overall pattern resulting from this experiment suggests that syntactic capacities are not implemented in a single area. Rather, they constitute an integrated system which involves both left and right neocortical areas, as well as other portions of the brain, such as the basal ganglia and the cerebellum, providing independent evidence for the interpretation of clinical data. Furthermore, the lack of a complete overlap between the neurological correlates of the syntactic and the morphosyntactic components of the language faculty fits well with the distinction made in linguistics on theoretical grounds: further experimental work is necessary to clarify this important issue.

# 3.2 STUDY 2. Neural correlates for the acquisition of natural language syntax<sup>27</sup>

# 3.2.1 ABSTRACT

Some types of simple and logically possible syntactic rule never occur in human language grammars, leading to a distinction between grammatical and non-grammatical syntactic rules. The comparison of the neuroanatomical correlates underlying the acquisition of grammatical and non-grammatical rules can provide relevant evidence on the neural processes dedicated to language acquisition in a given developmental stage. Until present no direct evidence on the neural mechanisms subserving language acquisition at any developmental stage has been supplied. We used fMRI in investigating the acquisition of grammatical and non-grammatical rules in the specified sense in 14 healthy adults. Grammatical rules compared to non-grammatical rules specifically activated a left hemispheric network including Broca's area, as shown by direct comparisons between the two rule types. The selective role of Broca's area was further confirmed by time by condition interactions and by proficiency effects, in that higher proficiency in grammatical rule usage, but not in usage of non-grammatical rules, led to higher levels of activation in this area. These findings provide evidence for the neural mechanisms underlying language acquisition in adults.

<sup>27</sup> Tettamanti et al., 2002.

#### 3.2.2 INTRODUCTION

The two major determinants of language acquisition are the characteristics of the linguistic input, such as the structural properties of phrases and the distribution of each linguistic item, and the learner's encounter with such an input (Kuhl, 2000; Saffran et al., 1996). The latter involves primarily the degree of exposure to a language and the age of acquisition. Information on the developmental time course of language acquisition in infancy has been gained from normal and neurologically or developmentally impaired children (Fletcher and MacWhinney, 1995). Clinical studies, together with neuroimaging investigations on bi- and multilinguals, have contributed to the identification of the neuroanatomical correlates of language production and comprehension in languages acquired before and after puberty (Abutalebi et al., 2001). However, no direct evidence concerning the neural mechanisms subserving language acquisition at any developmental stage has been forwarded. An unresolved issue pertains to how the brain regions involved in the acquisition of a second language in adulthood are related to the regions involved in processing the mother tongue.

In adults, specific patterns of neural activity associated with the different language components as defined by linguistic theories have been found. In particular, there is now converging evidence as to the brain areas subserving syntactic processing in the mother tongue. Many non-fluent aphasic patients with a lesion in left inferior frontal cortical areas (BA 44 and 45) display the clinical syndrome of agrammatism. Agrammatism is characterized by the omission of bound and free-standing grammatical morphemes (Kean, 1985). Furthermore, some agrammatic patients are unable to understand the meaning of a sentence, when functional arguments such as subject and direct object have to be identified on the basis of syntactic structure (Grodzinsky, 2000). In agreement with such clinical findings, neuroimaging studies have revealed activations within and around Broca's area, when healthy adult subjects were required to perform tasks calling for syntactic processing. Some studies varied the level of syntactic complexity (Caplan et al., 1998; Stromswold et al., 1996), resulting in differential demands on verbal working memory resources. Other studies used materials

consisting either of syntactically anomalous sentences (Embick et al., 2000; Meyer et al., 2000; Ni et al., 2000) or of sentence pairs with different syntactic structure, which could be same or different in meaning (Dapretto and Bookheimer, 1999). A drawback of the latter studies is that processing of the pertinent syntactic features is tied up with sentential semantic processing.

To eliminate such confounding semantic effects, Moro and colleagues (see section 3.1) also used a syntactic violation detection task but adopted an innovative experimental approach to study syntactic processing. Syntax was isolated from lexical-semantics (i.e. that portion of semantics that has no role in syntax) by replacing lexical word-roots by phonologically legal pseudowords. In this study, syntactic processing was associated with activation in the circular sulcus, a deep component of Broca's area, in the right inferior frontal gyrus, in the left insula and the left caudate nucleus.

A further issue to be considered in studying the mechanisms of language acquisition is that variations among natural grammars are not totally unbound but rather governed by a highly interconnected net of universal principles (Chomsky, 1981; Seiler, 2000). Some syntactic rule formats, albeit simple and logically possible, have never been found in human languages (Dryer, 1992; Greenberg, 1963). For example, in human languages there are no syntactic rules that are based on the number of words occurring in a given sentence or on mirror-reversals of the linear order of all words in a sentence. Accordingly, a rule such as "the auxiliary verb must immediately follow the third word of the sentence", even if it refers to perfectly identifiable lexical items, is to be considered as "non-grammatical", since it has never been found in any human language grammar. Any syntactic relation in any human language must be established on hierarchical syntactic notions such as subject, predicate, etc., rather than on precedence or subsequence of words in a sentence (Chomsky, 1995). The fact that hierarchical structures must be linearized into sequences of words is due to the physical constraints of human linguistic communication and has far reaching consequences on the overall design of grammar and the typology of phrase structure (Kayne, 1994; Moro, 2000).

Given that language rules follow a specific set of principles, what happens if the brain is

confronted with a non-grammatical rule to learn? Functional magnetic resonance imaging (fMRI) was used to investigate the neuroanatomical mechanisms involved in the acquisition of novel syntactic rules in adults, comparing the effects elicited by syntactic rules of a grammatical (G) and of a non-grammatical (NG) type. We hypothesised that the acquisition of G-rules would engage to a significantly greater extent than NG-rules brain regions known to participate in syntactic processing in the mother tongue.

The G-syntactic rules were based on functional relationships among the elements of a sentence, such as subject, predicate, etc. (again, defined in terms of hierarchical phrase structure). The NG-syntactic rules, instead, made use of sequential cues specifying the absolute position of some element within the linear sequence of words. The syntactic manipulations giving origin to the novel G- and NG-rules always amounted to position exchanges of words on a string, whether or not they conformed to the human language grammatical universals. Both the acquisition and usage of these two types of novel rules were studied. During the stage of acquisition a syntactic rule had to be extracted. During the stage of usage it was a matter of detecting syntactic violations of acquired rules.

Following the experimental approach adopted in our previous work (section 3.1), we eliminated lexical-semantics and manipulated the positional level of syntax (Levelt, 1989), selectively. The sole piece of information that had to be acquired consisted of the particular novel syntactic rule introduced, as phonological and the non-manipulated grammatical features were all kept invariant from the volunteers' mother tongue.

#### 3.2.3 MATERIALS AND METHODS

# 3.2.3.1 *Subjects*

14 right-handed volunteer subjects (7 females and 7 males; mean age 27,2 years, range 21-35 years) with a comparable level of education participated in the study. They all were monolingual Italian-speakers from birth, with Italian-speaking parents. None of the subjects had a history of neurological or psychiatric disorders. After receiving an explanation of the procedures, participants gave written informed consent. Right-handedness was verified using the Edinburgh Inventory (Oldfield, 1971).

## 3.2.3.2 Experimental design

Four experimental conditions were designed by combining 2 types of syntactic rule (grammatical (G) vs. non-grammatical (NG)) and 2 types of task (rule acquisition (RA) vs. rule usage (RU)). Two baseline conditions controlled for RA and RU tasks, respectively. The experiment thus comprised the following conditions: (a) RA-baseline: reading sentences following mother tongue syntax; (b) G-RA: reading sentences following a new syntactic rule of a G nature; (c) NG-RA: reading sentences following a new syntactic rule of a NG nature; (d) RU-baseline: detecting violations of mother tongue syntax; (e) G-RU: detecting rule violations using the G-rule knowledge acquired in (b); (f) NG-RU detecting rule violations using the NG-rule knowledge acquired in (c).

Characteristic sentences for the 6 conditions in the experiment are given below (see also Appendix 2):

a)Rule acquisition baseline (RA-baseline):

"Molte tille bilbavano il daffio."

(Dem<sub>fem/plur</sub> N<sub>fem/plur</sub> V-T/AGR past/3rd plur Artmasc/sing N<sub>masc/sing</sub>)

b)Grammatical rule acquisition (G-RA):

"Molte tille bilbavano daffio il."

 $(Dem_{fem/plur}\ N_{fem/plur}\ V-T/AGR_{past/3rd\ plur}\ N_{masc/sing}\ Art_{masc/sing})$ 

Syntactic rule of a grammatical type: The article immediately follows the noun it refers to.

c)Non-grammatical rule acquisition (NG-RA):

"Molte tille il bilbavano daffio."

 $(Dem_{fem/plur}\ N_{fem/plur}\ Art_{masc/sing}\ V-T/AGR_{past/3rd\ plur}\ N_{masc/sing})$ 

Syntactic rule of a non-grammatical type: Articles immediately follow the second word in the sentence.

d)Rule usage baseline (RU-baseline):

Sentences following either mother tongue syntax as in (a) or containing mother tongue syntactic violations as in:

"Tille molte bilbavano il daffio."

 $(N_{\text{fem/plur}} Dem_{\text{fem/plur}} V-T/AGR_{\text{past/3rd plur}} Art_{\text{masc/sing}} N_{\text{masc/sing}})$ 

syntactic violation = wrong word order: N-Dem-V-Art-N instead of Dem-N-V-Art-N.

e)Grammatical rule usage (G-RU):

sentences following either the new grammatical rule as in (b) or containing rule violations as in:

"Molte il tille bilbavano daffio."

(Dem<sub>fem/plur</sub> Art<sub>masc/sing</sub> N<sub>fem/plur</sub> V-T/AGR<sub>past/3rd plur</sub> N<sub>masc/sing</sub>)

rule violation = wrong word order: Dem-Art-N-V-N instead of Dem-N-V-N-Art.

f)Non-grammatical rule usage (NG-RU):

sentences following either the new non-grammatical rule as in (c) or containing rule violations as in:

"Il molte tille bilbavano daffio."

(Art<sub>masc/sing</sub> Dem<sub>fem/plur</sub> N<sub>fem/plur</sub> V-T/AGR<sub>past/3rd plur</sub> N<sub>masc/sing</sub>)

rule violation = wrong word order: Art-Dem-N-V-N instead of Dem-N-Art-V-N.

Glosses:  $Art_{(gender/number)} = article$ ;  $Dem_{(gender/number)} = demonstrative$  or quantifying adjective;  $N_{(gender/number)} = noun$ ;  $V-T/AGR_{(tense/agreement)} = verb$  with agreement and tense inflections.

For each type of syntactic structure (G vs. NG) 2 new rules were introduced. G-rule 1: The article must immediately follow the noun it refers to. G-rule 2: The auxiliary verb must immediately follow the main verb it refers to. NG-rule 1: Articles must immediately follow the second word in the sentence. NG-rule 2: The auxiliary verb must immediately follow the third word in the sentence.

In all sentences open-class word-roots were replaced by pseudowords, so as to eliminate lexical-semantic processing (see section 3.1). Italian phonology (as encoded in graphic form), inflections, function words and grammatical rules (with the exception of the novel syntactic rules introduced) were maintained.

Silent reading was required for all conditions. Subjects were asked to perform the following tasks: in conditions a, b and c to press a response button immediately after having read each sentence. In conditions b and c only, they were additionally told that all sentences followed a new syntactic rule that had to be learned. In d, e and f subjects were required to press the button only if the sentence was correct according to the syntactic structures of a, b and c, respectively. Rules were never made explicit to the subjects before or during scanning sequences. Reaction times and accuracy scores were recorded.

Note that the full variety of Italian articles and auxiliary verbs was used; also note the occurrence of other function words with the same word-lenghth as articles and auxiliaries. This excluded that purely perceptual strategies could have lead to successful rule inference: the linguistic status of the different words forming a sentence had to be identified in order to infer the syntactic regularities.

Four scanning sequences were formed, 2 of which introducing a novel G-rule and 2 introducing a novel NG-rule. Sequences consisted of two parts. The one part (experimental) comprised 4 successive alternations between RA and RU experimental conditions (tasks b/e or c/f), the other (baseline) 4 alternations between baseline conditions (a/d). Each alternation formed a block. Within a block there were two sets of 8 sentences each corresponding to one of the two conditions, thus resulting in a total of 512 sentences (4 sequences x 8 blocks x 16 sentences). Example for a scanning

sequence is: (RA-baseline)<sub>b1</sub>-(RU-baseline)<sub>b1</sub>-(RA-baseline)<sub>b2</sub>-(RU-baseline)<sub>b2</sub>-(RA-baseline)<sub>b3</sub>-(RU-baseline)<sub>b3</sub>-(RA-baseline)<sub>b4</sub>-(RU-baseline)<sub>b4</sub>-(G-RA)<sub>b1</sub>-(G-RU)<sub>b1</sub>-(G-RA)<sub>b2</sub>-(G-RU)<sub>b2</sub>-(G-RA)<sub>b3</sub>-(G-RU)<sub>b3</sub>-(G-RA)<sub>b4</sub>-(G-RU)<sub>b4</sub> (b1-b4 subscripts indicate the 4 blocks in each of the two parts forming a sequence). Each subject underwent all 4 scanning sequences. The order of the two parts (experimental and baseline) within a sequence was balanced over the presentation of the four sequences; the four sequences themselves were also presented in a balanced order across subjects. Sentences were balanced for both average number of syllables and average number of words across conditions, sequences and blocks. A fixed presentation time of 3750 ms was used with no interstimulus interval. Full sentences were displayed on a single line and centered in the subjects' visual field.

To familiarize subjects with the task, a trial sequence for each of the two types of syntactic structure (G vs. NG) was administered before positioning subjects in the magnet; different syntactic rules were used than in the experimental conditions.

# 3.2.3.3 Data acquisition

Data were acquired on a 1.5 T whole body scanner (Signa Horizon, Echo-speed LX General Electric Medical Systems, Milwaukee, WI) equipped with a standard product transmit-receive head coil. Functional whole-brain imaging was conducted using a T2\*-weighted gradient-echo, echoplanar pulse sequence with a repetition time of 2900 ms, an echo time of 58 ms and a flip angle of 85°. Thirty contiguous, axial slices were acquired with a field-of-view of 28x28 cm², a slice thickness of 4 mm and an imaging matrix of 64 by 64 data points, yielding an in-plane resolution of 4.38 mm x 4.38 mm. Series of 205 sequential volumes were acquired for each scanning sequence.

### 3.2.3.4 Data analysis

Repeated measures ANOVA was used to test for behavioral effects between conditions (baseline, G and NG) and condition by block interactions. The data of the 4 scanning sequences were

pooled together for each individual condition.

Functional MRI data processing and statistical analysis were performed with SPM99 (www.fil.ion.ucl.ac.uk). The entire volume set of each subject was realigned to the first volume of the first sequence. The obtained brain images were then normalized to the Montreal Neurological Institute (MNI) standard space (closely approximating the space described by the atlas of Tailairach and Tornoux (Talairach and Tournoux, 1988)) to allow for group analysis: transformation parameters were calculated on a structural spin-echo brain image matched to the fMRI images (TE = 12 ms, TR = 700 ms). Prior to statistical analysis, all images were smoothed using an isotropic Gaussian kernel (full width and half maximum = 8 mm) (Ashburner and Friston, 1999). High-pass filtering was used to remove artefactual contribution to BOLD signal. Global differences in fMRI signal were compensated using proportional scaling. Data were then fitted at every voxel using a linear combination of the effects of interest calculated on least-squares values. Effects of interest included the timing of condition presentation (box-car) convolved with the SPM99 standard hemodynamic response function. Comparisons between conditions were then made using t-Student statistics. The set of T values given by each voxel of the image produced the statistical parametric map (Friston et al., 1995b).

The comparisons between the rule acquisition conditions and the baseline and the direct comparisons between rule acquisition conditions were performed as fixed effect analysis. All the reported activations for these comparisons survived a corrected significance threshold of P<0.05, except for the G-rule vs. NG-rule acquisition comparison where a small volume correction (SVC, sphere of radius 20 mm) was performed (Worsley et al., 1996), centering on the coordinates of BA 44, 6 and 39 identified in the comparison with the baseline. For control, SVC centering on the same locations was performed also in the NG-rule vs. G-rule acquisition comparison.

Time-parametric statistics were performed by convolving the fMRI time series with a linear regressor, which allows the detection of increases and decreases of activation in time. Time-parametric statistics were performed using a random effect analysis (Frison and Pocock, 1992).

Contrasts between the G-rule and the NG-rule acquisition conditions were calculated by one-sample t-tests (n=14) and masked by the corresponding acquisition condition vs. baseline effects (significance threshold for masking was P<0.05 uncorrected). All the reported activations for these comparisons survived an uncorrected significance threshold of P<0.01.

For the analysis of the effects of proficiency, with separate procedures for the G-rule and the NG-rule usage conditions, individual accuracy measures were used to divide the experimental data into a "high proficiency" group, which included the subjects with the highest accuracy scores, and a "low proficiency" group, which included the subjects with the lowest accuracy scores (see Table 3.2.1). Between group comparisons were calculated by two-sample t-tests using a random effect analysis (Frison and Pocock, 1992). All the reported activations for these comparisons survived an uncorrected significance threshold of P<0.001.

	Subject	G	Subject	NG
group	s13	98,4	s1	96,9
gr	s4	96,9	s8	95,3
ncy	s2	95,3	s12	95,3
icie	s10	95,3	s5	95,3
rofi	s9	92,2	s14	93,8
High proficiency	s7	92,2	s10	90,6
Hig	s3	90,6	s4	87,5
dn	s14	89,1	s3	84,4
group	s5	89,1	s11	82,8
ıcy	s11	89,1	s9	78,1
cier	s8	87,5	s7	76,6
proficiency	s12	87,5	s6	73,4
w bi	s6	81,3	s13	73,4
Lov	s1	73,4	s2	70,3

**Table 3.2.1.** *Groups of high and low proficiency in new syntactic rule usage.* 

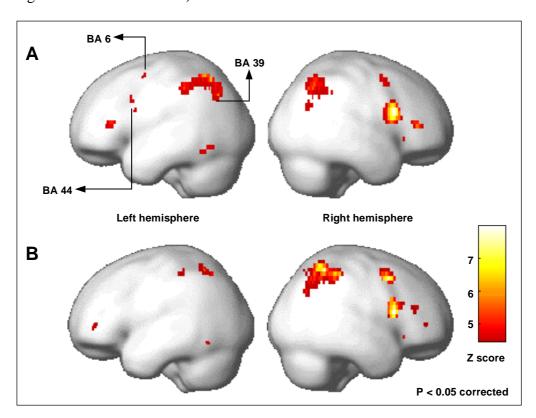
For each subject (s1-s14), accuracy scores averaged over the 4 blocks are given for grammatical rule (G) and non-grammatical rule (NG) usage, respectively (expressed as percentage of correct answers).

### 3.2.4 RESULTS AND DISCUSSION

Our analysis identified specific neural correlates for the acquisition of G-rules as opposed to NG-rules. We then examined how the activity in such areas is modulated in time and reflected in behavioral measures assessing competence in rule usage.

## 3.2.4.1 Rule-type specific neural correlates

Comparisons between the acquisition conditions and their baseline resulted in the identification of the neuroanatomical network participating in the acquisition of G-rules on the one hand and NG-rules on the other. These brain activations are shown in Figure 3.2.1A and Figure 3.2.1B. With both rule types activations in a bilateral fronto-parietal network were found (see Table 3.2.2, for the corresponding stereotaxic coordinates).



**Figure 3.2.1.** Overall main effects of rule acquisition compared to the baseline. Activation maps (in colour) were projected on a rendered view of the smoothed canonical MNI brain template. (A) Regions of significant activation for the acquisition of G-rules. The grammar-specific activations

in the left hemisphere (BA 44, 6 and 39) are indicated by arrows. (B) Regions of significant activation for the acquisition of NG-rules.

	G-rule acquisition				NG-rule acquisition				
	vs. baseline				vs. baseline				
Brain region	X	y	Z	Z		X	y	Z	Z
L inferior frontal gyrus (BA 46)	-50	32	8	5.34	•	-44	46	4	5.06
L inferior frontal gyrus (BA 44)	-46	10	32	4.58	•				
L inferior frontal gyrus (BA 44)	-42	8	24	4.53	•				
L dorsal premotor area (BA 6)	-24	2	48	5.35	•				
L superior parietal lobule (BA 7)	-28	-58	52	7.22	•	-30	-54	60	4.77
L inferior parietal lobule (BA 40)	-40	-42	44	6.03	•	-48	-36	52	4.86
L precuneus (BA 7)	-22	-70	48	6.72	•	-28	-64	40	5.87
L angular gyrus (BA 39)	-30	-64	28	6.47	•				
L fusiform gyrus (BA 37)	-46	-56	-16	4.78		-44	-60	-16	4.69
L/R anterior cingulate gyrus (BA 32)	2	22	40	5.10		6	34	28	5.63
R middle frontal gyrus (BA 46)					•	46	34	20	5.17
R inferior frontal gyrus (BA 46)	48	36	12	5.33	•	44	46	4	4.79
R inferior frontal gyrus (BA 44)	48	14	24	7.37	•	46	14	16	6.33
R inferior frontal gyrus (BA 47)	32	26	-4	4.96	•	36	26	-8	4.65
R dorsal premotor area (BA 6)	38	6	52	5.22		40	10	48	7.00
R superior parietal lobule (BA 7)						26	-58	60	6.95
R inferior parietal lobule (BA 40)	34	-58	40	7.94		34	-58	44	7.30
R precuneus (BA 7)	14	-66	44	6.68		14	-66	40	5.34

**Table 3.2.2.** Anatomical regions of significant activation in the experimental conditions as compared to their baseline. The stereotaxic coordinates (x,y,z) for significant voxels are given in mm together with the corresponding effect sizes (Z = Z scores).

This finding suggests that the activated fronto-parietal network is involved in the acquisition of both hierarchical and non-hierarchical syntactic features. The activation of this network is likely to reflect the participation of multimodal memory systems in learning tasks. Such an interpretation is supported by several neuroimaging studies on learning and memory. Activations in a bilateral fronto-parietal network have been found in an fMRI experiment concerned with learning rules of an

artificial grammar (Fletcher et al., 1999), whose syntactic properties differed from those of human language grammars. Similar activation patterns were also obtained in studies concerned with remembering (Marshuetz et al., 2000) or practicing (Wildgruber et al., 1999) verbal items in a particular order. Parietal and frontal regions seem to support separate functions. Some studies have demonstrated that posterior parietal areas, in association with right dorsal premotor areas, subserve visuo-spatial working memory and attention (Jonides et al., 1993; Nobre et al., 1997). Visuo-spatial functions are indeed thought to be required in forming detailed representations of ordered sequences of symbols, such as words forming written sentences. The activations in the middle and inferior frontal gyri appear to reflect operations related to manipulating and maintaining syntactic information, allowing such information to be synthesized in patterns of regularities. Tasks calling for maintenance and manipulation have indeed been shown to activate prefrontal cortex (Fletcher and Henson, 2001).

Crucially and in agreement with our expectations based on the hierarchical properties of human language grammars, some activation foci were specific for the acquisition of each type of rule: Grules activated the opercular portion of Broca's area (Brodmann area (BA) 44), the left dorsal premotor area (BA 6) and the left angular gyrus (BA 39). NG-rules activated the right middle frontal gyrus (BA 46) and the right superior parietal lobule (BA 7). These findings indicate that different cortical subcomponents in fronto-parietal regions are activated, depending on whether the rules to be acquired are in line with the universal grammatical properties of human languages or not. In particular, the activation in Broca's area specifically found for the acquisition of grammatical rules is in agreement with the syntactic parsing functions attributed to this brain region (see introduction) and it is well known that lesions in the left premotor area can lead to the syndrome of Broca's aphasia (Mohr, 1978). Thus, the acquisition of novel grammatical rules engages the neural network that sustains the processing of the syntactic aspects of language, specifically.

In order to substantiate these differences further, we performed direct comparisons between the acquisition of novel G- and NG-rules. The left inferior frontal gyrus (BA 44/45, coordinates: x=-44,

y=14, z=4, Z score=3.11) and the left ventral premotor area (BA 6, x=-50, y=-4, z=28, Z=3.26) were significantly more activated by G-rules than by NG-rules. Additional activations were found in the left superior temporal and angular gyri (BA 22/39, x=-64, y=-40, z=8, Z=3.99 and x=-34, y=-66, z=20, Z=3.78, respectively). NG-rules, in turn, activated the right inferior frontal gyrus (BA 44/45, x=54, y=18, z=16, Z=3.41) and the right superior parietal lobule (BA 7, x=28, y=-52, z=60, Z=5.75). Such findings confirm the specific role of Broca's area and the lateral premotor area in the acquisition of G-syntactic rules. In addition, higher activation of Wernicke's area (BA 22/39) in the G than in the NG condition is also in agreement with a number of neuroimaging studies investigating syntactic processing (Dapretto and Bookheimer, 1999; Embick et al., 2000; Just et al., 1996).

# 3.2.4.2 Temporal changes during the acquisition of novel rules

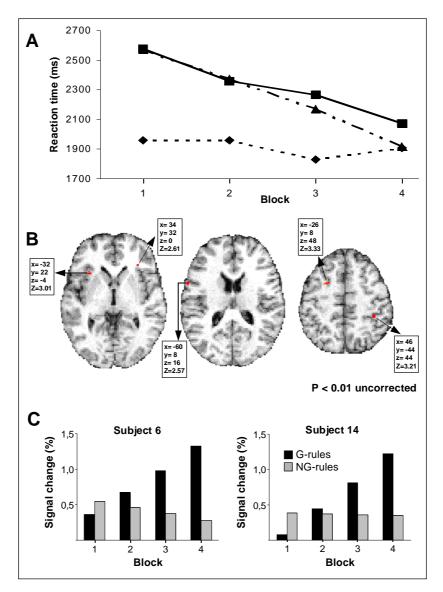
Our experimental paradigm not only allowed us to measure effects over the entire duration of the acquisition tasks, but also to assess significant temporal changes occurring during rule acquisition. The behavioral data analysis showed that the reaction times in the two acquisition conditions (G-RA and NG-RA) differed significantly from the baseline condition (RA-baseline), both as a main effect and as a condition by block interaction. The interaction effects were analysed by post-hoc paired t-test comparisons between experimental and baseline conditions in the first (block 1) and last (block 4) acquisition blocks: significant differences in block 1 were no longer significant in block 4. Most notably, the results of the ANOVA comparing G-RA and NG-RA were not significant (see Table 3.2.3A and Figure 3.2.2A).

(A) Temporal changes during the acquisition of novel rules							
	main effect	condition by	t-test : block 1	t-test : block 4			
		block interaction					
G-RA vs. RA-baseline	F(1,13) = 66.2	F(3,13) = 16.3	P < 0.0001	P = 0.07 *			
	P < 0.0001	P < 0.0001					
NG-RA vs. RA-baseline	F(1,13) = 12.8	F(3,13) = 9.2	P = 0.0004	P = 0.72 *			
	P = 0.003	P < 0.0001					
G-RA vs NG-RA	F(1,13) = 0.35	F(3,13) = 1.08					
	P = 0.56 *	P = 0.37 *					

(B) Effects of proficiency in novel rule usage								
	main effect	condition by	t-test : block 1	t-test : block 4				
		block interaction						
G-RU vs. RU-baseline	F(1,13) = 19.6	F(3,13) = 3.9	P = 0.002	P = 1 *				
	P < 0.0001	P = 0.01						
NG-RU vs. RU-baseline	F(1,13) = 11.3	F(3,13) = 4.4	P < 0.0001	P = 0.26 *				
	P = 0.002	P = 0.006						
G-RU vs NG-RU	F(1,13) = 2.9	F(3,13) = 1.5						
	P = 0.10 *	P = 0.21 *						

**Table 3.2.3.** Behavioral data analysis: summary table. \* = not significant.

While no significant interactions between the acquisition of G-rules and NG-rules were found in terms of behavioral measures, indicating that the acquisition of both rule types was of equal difficulty and took a similar course, the fMRI data analysis revealed significant interaction effects. Time by condition interactions were estimated, revealing brain regions whose activity linearly increased or decreased in time significantly more during the acquisition of G-rules than of NG-rules. These were the opercular portion of Broca' area (BA 44), the left insula, the left superior frontal gyrus (BA 8), the right ventral inferior frontal gyrus (BA 47) and the right inferior parietal lobule (BA 40) (Figures 3.2.2B and 3.2.2C). No brain regions, in turn, were increasingly more activated during the acquisition of NG-rules than of G-rules. These findings give additional support to the hypothesis that Broca's area must be attributed a crucial role in the acquisition of G-rules.



**Figure 3.2.2.** *Temporal changes during acquisition of novel rules.* (A) The four average reaction time measurements corresponding to blocks 1-4 are plotted for the acquisition of G-rules (solid line), NG-rules (dash-dotted line) and the baseline (dotted line). (B) Areas increasingly more activated in time during G-rule than during NG- rule acquisition are superimposed (in red) on a single subject T1 image normalised to the MNI standard space. Stereotaxic coordinates (x, y, z in mm) and effect size (Z = Z score) of the activation peaks (indicated by arrows) are given in boxes. (C) The temporal interaction effect in the opercular portion of Broca's area (BA 44) is shown for two representative subjects. Filled bars indicate BOLD signal change percentage (amplitude of the hemodynamic response curve) in the four blocks for G-rule and NG-rule acquisition.

At first this might appear to be counterintuitive, because as rules get more mastered a decrease

rather than an increase of activation should be expected in perisylvian areas. Indeed, several studies have shown that automatic language tasks typically do not engage perisylvian cortical areas (Bookheimer et al., 2000; Raichle et al., 1994). Presumably, the monitored time interval of acquisition was too brief to allow for an automatization of grammatical rule processing. Thus, although the novel grammatical rules have been successfully acquired their access still relies on the need to perform detailed syntactic parsing. These findings should be considered along with neuroimaging data on syntactic processing in the mother tongue. Moro and colleagues (section 3.1) found activations in a deep component of Broca's area (BA 45), located in the circular sulcus, when examining mother tongue syntactic processing selectively, while controlling for confounds such as complexity and sentential semantics. Stromswold and colleagues (Stromswold et al., 1996) as well as Caplan and colleagues (Caplan et al., 1998), compared processing of syntactic structures of high and low complexity and found activations on the lateral surface of the opercular portion of Broca's area. It is in this location that linear temporal increases are found in the present experiment. Syntactic complexity and non-automatized rule processing presumably necessitate verbal working memory functions. As has been demonstrated (Paulesu et al., 1993; Zatorre et al., 1992) the opercular portion of Broca's area is indeed associated with verbal working memory. Taken together, such evidence suggests that the acquisition of novel syntactic rules in its less automatized stages depends on a more lateral cortical portion of Broca's area than the one dedicated to syntactic processing in the mother tongue.

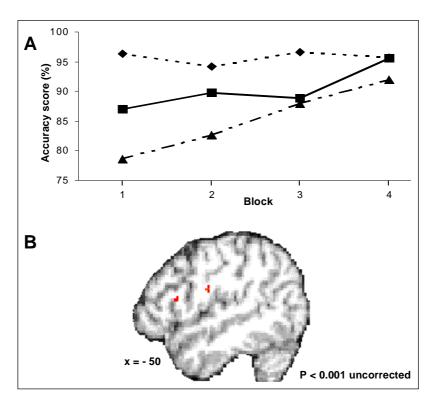
# 3.2.4.3 Effects of proficiency in novel rule usage

Most studies on the neuroanatomical correlates of bi- and multilingualism have highlighted on the significance of such variables of linguistic competence as proficiency level, age of acquisition and degree of exposure to a particular language. These studies show comparable levels of activation in left perisylvian areas elicited by the mother tongue and the second language in highly proficient bilinguals (Chee et al., 1999; Klein et al., 1995; Perani et al., 1998) and significantly different levels

of activation in the same areas in low proficient bilinguals (Dehaene et al., 1997; Kim et al., 1997; Perani et al., 1996). The activation of left perisylvian regions thus seems to be modulated by the level of competence in the second language. This led us to hypothesise that the level at which novel Grules are mastered would modulate the activation of the brain regions found to participate in the acquisition of those rules.

To test for this hypothesis the effects of accuracy in the usage of the new rules were estimated. Changes in rule usage accuracy level during the course of the experiment were significant for both Grules and NG-rules, as revealed by the behavioral analysis. Accuracy scores in the two usage conditions (G-RU and NG-RU) differed significantly from the baseline (RU-baseline). This was true both as a main effect and as a condition by block interaction. The interaction effects were analysed by post-hoc paired t-test comparisons between experimental and baseline conditions in the first (block 1) and last (block 4) acquisition blocks: significant differences in block 1 were no longer significant in block 4. Most notably, the results of the ANOVA comparing G-RU and NG-RU were not significant (see Table 3.2.3B and Figure 3.2.3A).

In the fMRI data analysis, between group statistics comparing high with low proficient subjects in G-rule and NG-rule usage (see Table 3.2.1) were computed. During G-rule usage, the high proficiency group activated Broca's area (BA 44, x=-50, y=16, z=12; Z=3.41) and the left ventral premotor area (BA 6, x=-48, y=-8, z=20; Z=3.82) to a significantly greater extent than the low proficiency group (Figure 3.2.3B). During NG-rule usage, the high vs. low proficiency group comparison revealed a significantly activated focus in the left cerebellar hemisphere (x=-26, y=-68, z=-20; Z=3.49). Thus, competent usage of G-syntactic rules was associated with higher activations in Broca's area and the left ventral premotor area, regions that have been consistently implicated in several aspects of syntactic processing. These findings suggest that, in adulthood, the activity of specific brain areas within the left perisylvian cortex is modulated by the acquisition of linguistic competence for selected linguistic structures.



**Figure 3.2.3.** Effects of proficiency in novel rule usage. (A) The four average accuracy score measurements corresponding to blocks 1-4 are plotted for the usage of G-rules (solid line), NG-rules (dash-dotted line) and the baseline (dotted line). (B) Usage of novel G-rules, comparison between the groups of high and low proficiency subjects: significant activation foci (in red) in Broca's area and the left ventral premotor area, are superimposed on a sagittal slice of a single subject T1 normalised image.

## 3.2.5 CONCLUSIONS

Several conclusions can be drawn from the present study. First, this study demonstrates a selective and robust participation of Broca's area in the acquisition of novel G-rules as opposed to NG-rules. Second, the present data help in clarifying the cerebral mechanisms that underlie adult second language acquisition: the gain of competence for novel and selected linguistic features appears to be tightly associated with variations of activity in exactly those perisylvian brain regions implicated in the processing of the corresponding linguistic aspects. Third, in the early stages of

language acquisition, the processing of novel linguistic structures engages lateral cortical aspects of Broca's area that support less automatic processes.

All these points elucidate the neural processes participating in the acquisition of grammatical language features in adulthood, as the two types of rules to be acquired only differed from each other at the positional syntactic level; all other variables were held invariant. However, while our data show that a neuroanatomical network comprising Broca's area underlies language acquisition in adults, it is possible that such a network is not specific to language acquisition. G-rules and NG-rules differed to the extent that the former were based on hierarchical syntactic notions, whereas the latter were based on absolute positions within the linear sequence of words. Such a distinction is not unique to language. Visuo-spatial perceptual processing or manual object manipulation can also be either hierarchical or linear (Conway and Christiansen, 2001). Behavioral and neural evidence pointing to an homology between the acquisition of hierarchical strategies for manual object combination and the acquisition of language has been supplied in young children (Greenfield, 1991). Both in their developmental time-course and their neural bases language and manual gestures appear to be tightly correlated (Bates and Dick, 2002). Several neuroimaging experiments in adults show that perception, imitation and spontaneous production of language on the one hand and perception, imitation and spontaneous production of gesture on the other hand activate a partially overlapping distributed network (Bates and Dick, 2002). In particular, overlapping activations in Broca's area for language and for gesture execution or observation have been found (Rizzolatti et al., 2001).

To summarize, several pieces of evidence suggest that Broca's area may be a supramodal hierarchical processor. The present study demonstrates that, in adults, the acquisition of linguistic hierarchical syntactic structures depends on a network comprising Broca's area. Our future research will be aimed at showing to what an extent the network including Broca's area overlaps with the neural correlates involved in the acquisition of non-linguistic hierarchical concepts.

3.3 STUDY 3. Sentences describing motor actions activate the visuomotor circuits coding the same actions<sup>28</sup>

### 3.3.1 ABSTRACT

Observing actions made by others activates the cortical circuits that are responsible for the planning and execution of the actions observed. This observation-execution matching system (mirror-neuron system) is thought to play an important role in the understanding of actions made by others. In an fMRI experiment we tested whether this system is also activated by language during the processing of action-related sentences. Participants listened to sentences describing actions performed with the mouth, hand, and leg. Abstract sentences of comparable syntactic structure were used as control condition. The results showed that listening to action-related sentences activates Broca's area and, most interestingly, those sectors of premotor and parietal cortex where the actions described in the listened sentences are coded. These data provide the first direct evidence that listening to sentences describing actions engages visuo-motor circuits subserving action execution.

<sup>28</sup> Tettamanti et al., submitted.

#### 3.3.2 INTRODUCTION

Experiments in monkeys have shown that observing an action made by another individual activates an observation/execution matching system, named mirror-neuron system (Gallese et al., 1996; Rizzolatti et al., 1996a). It has been proposed that this system subserves the understanding of actions made by others. According to this view, observing an action evokes a motor representation coded in fronto-parietal circuits. Because the observer knows the outcome of this motor representation, this activation allows him/her to understand the meaning of the action observed (Rizzolatti et al., 2001).

Electrophysiological studies (Fadiga et al., 1995; Hari et al., 1998; Cochin et al., 1999; Gangitano et al., 2001) and imaging data (Rizzolatti et al., 1996b; Grafton et al., 1996; Grèzes et al., 1998) showed that a mirror-neuron system similar to that described in the monkey also exists in humans. Imaging studies showed also that the human mirror-neuron system consists of a series of parallel premotor-parietal circuits (Iacoboni et al., 1999; Blakemore and Decety, 2001) that show a somatotopic organization (Buccino et al., 2001).

Action observation is not the only condition triggering the activation of the mirror-neuron system. Recently, it has been shown that in monkey's premotor cortex there are mirror neurons that discharge not only when an action is seen or executed, but also when it is heard (bimodal, audiovisual mirror neurons, (Kohler et al., 2002)). This new observation supports the idea that the mirror-neuron system codes action content at an abstract level and that this content can be accessed auditorily.

In humans, action-related knowledge may be retrieved not only by action observation or action sound, but also by sentences describing actions. This language-mediated action knowledge might be supported, at least in part, by the same neural substrate that mediates action recognition during observation and action-related sound listening. If this is the case, one should expect that hearing action-related sentences (e.g. "I am grasping a cup") should produce an activation of those neural

structures that code for the motor representation of the same actions. This implicit, not consciously evoked, motor representation of the action heard may contribute to the understanding of the action content of the sentence. Importantly, implicit motor representations should be distinguished from motor imageries that are voluntarily evoked by an individual. Motor imagery requires effort (Jeannerod, 1997) and is characterized by the activation of mesial cortical areas (Grafton et al., 1996; Stephan et al., 1995; Tyszka et al., 1994; Gerardin et al., 2000). In contrast, no effort is required during listening to simple sentences like those used in the present study.

To address these issues, we tested in an fMRI study seventeen healthy, right-handed native Italian speakers, while they were passively listening to sentences describing actions performed with the mouth (e.g. "Mordo la mela", English: "I am biting an apple"), with the hand, and the leg. As a control condition, participants listened to sentences with an abstract content (e.g. "Apprezzo la sincerità; "I appreciate sincerity"). The participants were naive as to the purpose of the experiment. Data processing and statistical analysis were performed using SPM99, SureFit 4.38 and Caret 4.5.

#### 3.3.3 MATERIALS AND METHODS

# 3.3.3.1. *Subjects*

Seventeen right-handed (Oldfield, 1971) volunteer subjects (12 females and 5 males; mean age 25.3 years, range 19-36 years) with comparable level of education participated in the study. They were all native monolingual speakers of Italian. None of the subjects had a history of neurological or psychiatric disorders. Participants gave written consent after receiving an explanation of the procedures.

#### 3.3.3.2. Stimuli

Sentences were created by matching a transitive verb in the first person singular to a syntactically and semantically congruent object complement. Each verb was paired with different objects each time (see Appendix 3). Subjects heard a total of 40 sentences per experimental condition (mouth, hand, leg), plus 120 baseline sentences (abstract). Verb frequency was balanced across conditions (De Mauro et al., 1993). Stimuli were normed for comprehensibility on 20 normal adults, were digitally recorded by a native speaker of Italian and edited using D-Sound Pro (www.d-soundpro.com). Average stimulus length was ~2.5 seconds. Subjects heard all auditory stimuli via MRI-compatible headphones connected to a personal computer.

### 3.3.3.3. Data acquisition and experimental design

We used a 1.5 T whole body scanner (General Electric Medical Systems, Milwaukee, WI) equipped with a standard quadrature head coil. Functional whole-brain imaging was conducted using a T2\*-weighted gradient-echo, echo-planar pulse sequence (TR=4000 ms, TE=60 ms). Thirty contiguous, slices parallel to the AC-PC line were acquired with a field-of-view of 280 mm x 280 mm, a slice thickness of 4 mm and an in-plane resolution of 4.38 mm x 4.38 mm. Series of 125

sequential volumes were acquired for each scanning sequence.

Scanning sequences consisted of 24 epochs. Epochs of sentences referring to a single body part alternated regularly with epochs of abstract sentences (e.g. [mouth-abstract-hand-abstract-leg-abstract]<sub>n=4</sub>). Each subject underwent 2 of such scanning sequences. The presentation order of the experimental conditions was balanced across subjects. Each epoch lasted for 20 s and consisted of 5 stimuli. Stimuli were presented at a frequency of one stimulus every 4 s. The presentation of each sentence was followed by a varying period of silence, such that the duration of sentence presentation and the subsequent silence period together lasted for 4 s. Once the fMRI data acquisition was completed, subjects were asked to recall the highest number of sentences or part of sentences they could remember. On average they were able to recall 13.20 complete sentences (SD = 5,86). More specifically, they recalled on average 4.77 abstract sentences (SD = 3.52), 3.50 mouth sentences (SD = 2.21), 2.55 hand sentences (SD = 1.37), and 3.93 leg sentences (SD = 2.34). All participants declared being unaware of the grouping of sentences into different experimental conditions.

## 3.3.3.4. Data analysis

Data processing and statistical analysis were performed with SPM99 (www.fil.ion.ucl.ac.uk). The entire volume set of each subject was realigned to the first volume of the first sequence. The brain images obtained were then normalized to the Montreal Neurological Institute (MNI) standard space to allow for group analysis. Prior to statistical analysis, all images were smoothed using an isotropic Gaussian kernel (FWHM = 8 mm). High-pass filtering was used to remove artefactual contribution to BOLD signal. Global differences in fMRI signal were compensated using proportional scaling. Data were then fitted at every voxel using a linear combination of the effects of interest calculated on least-square values. Each condition involving actions by an effector (mouth, hand or leg) was compared by paired t-Student test with the associated control condition at the single-subject level, yielding for each subject one image consisting of the voxelwise difference between the parameter estimates (Friston et al., 1995b). All reported statistics were then computed as

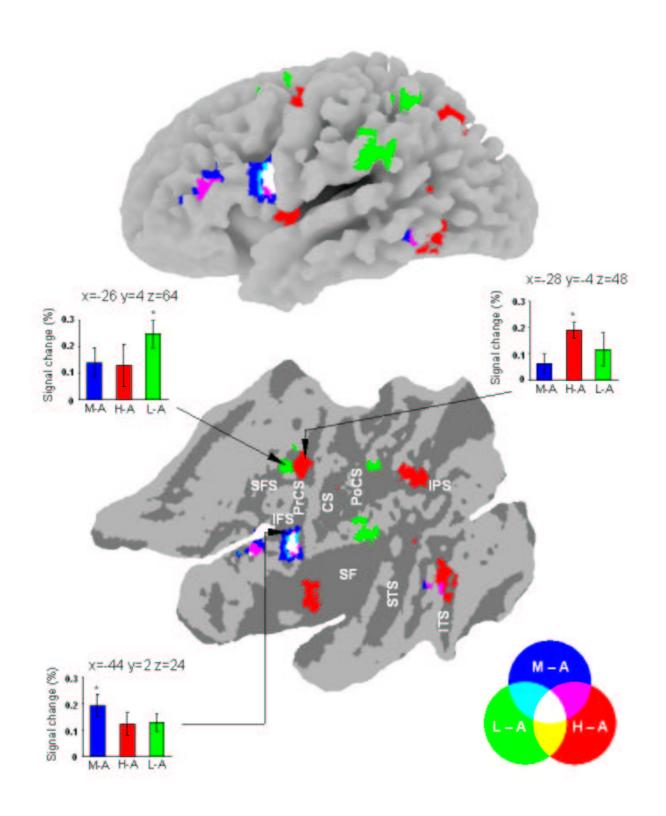
second-level random effects analyses, using a one-sample t-Student test model (n=17). The results of random effects analyses can be generalized at the population-level (Frison and Pocock, 1992). All the reported activations survived an uncorrected significance threshold of p<0.001, except for left parietal lobe and inferior temporal activations, where an uncorrected significance threshold of p<0.005 was used, in order to test for an a-priori hypothesis. For anatomical localization and visualization of brain activations, an average 3D anatomical T1 weighted brain image of the 17 participants (0.98 mm x 0.98 mm x 1.5 mm resolution), priorly normalized to the MNI standard space with SPM99, was automatically segmented with SureFit 4.38 software (Van Essen et al., 2001) to obtain a cortical surface 3D reconstruction with tissue specific image values for sulcal vs. gyral cortex. Cortical reconstructions were further processed with Caret 4.5 software (Van Essen et al., 2001), for cortical surface inflating and flattening. Caret 4.5 was also used to map brain activations obtained with SPM99 onto cortical surface maps.

#### 3.3.4 RESULTS AND DISCUSSION

The results are shown in Figures 3.3.1 and 3.3.2 (see also Table 3.3.1). Sentences describing motor actions, compared to abstract sentences, activated the pars opercularis and the pars triangularis of the left inferior frontal gyrus (Broca's area) and two foci in the premotor cortex.

The activations of Broca's area related to the three action-related sentence types showed a considerable overlap. There was, however, a marked predominance of the activations related to mouth sentences. The activation of Broca's area during presentation of action-related sentences is consistent with previous studies showing the involvement of this area in verb processing (Tranel et al., 2001; Martin et al., 1995; Perani et al. 1999b, Pulvermuller et al, 1999). This involvement may be interpreted as due to the specific role of verbs as determinants of the syntactic structure of a sentence and/or to the semantic content of verbs. Evidence in favor of a role of Broca's area in sentence syntactic processing has been recently provided by brain imaging and electrophysiological studies (Moro et al., 2001; Tettamanti et al., 2002; Shapiro et al., 2001). In the present experiment activation of Broca's area was found for sentences containing action verbs, as compared to sentences containing abstract verbs. Given the invariant syntactic structure of the action-related and abstract sentences used in the present experiment, this indicates that Broca's area also plays a role in the semantic access to actions.

While this explanation accounts for the overlapping activations common to the three body parts in Broca's area, the spatial segregation and large extension of the activations due to mouth-related sentences in this region does not fit a linguistic explanation of the activations. There are no obvious reasons why there should be a richer representation of verbs related to mouth actions than of verbs related to hand and leg actions. In contrast, there is plenty of evidence that mouth motor actions are richly represented in the inferior frontal gyrus and that articulatory deficits follow lesions affecting this brain region (Tonkonogy and Goodglass, 1981). It is therefore likely that this segregated mouth-action activation is determined by the recruitment of motor representations of mouth actions.



**Figure 3.3.1.** Activation foci during listening to mouth, hand and leg action-related sentences. Areas of increased activation (p<0.001 uncorrected) in the experimental conditions compared to the control condition are superimposed (in color: M-A: mouth vs. abstract, blue; H-A: hand vs. abstract, red; L-A: leg vs. abstract, green) on a lateral view of a left-hemisperic cortical surface reconstruction

and on a cortical flat map (sulci are in dark grey), which were derived from the average brain image of the 17 participants (see Materials and Methods). Body part specific activations in the opercular portion of Broca's area and in premotor areas are indicated by arrows. Arrows link brain activations with the corresponding stereotaxic coordinates (x, y, z in mm) and with histograms indicating BOLD signal change percentage (amplitude of the hemodynamic response curve) in each experimental condition compared to the control condition. For each effect, standard error bars are indicated. Asterisks above the histogram bars indicate the significant effects. SFS = superior frontal sulcus; IFS = inferior frontal sulcus; PrCS = precentral sulcus; CS = central sulcus; PoCS = postcentral sulcus; SF = sylvian fissure; IPS = intra-parietal sulcus; STS = superior temporal sulcus; ITS = inferior temporal sulcus.

Congruent with this account of the inferior frontal gyrus activation is the finding of two activation foci located in the premotor cortex and specifically related to hand- and leg-actions. The first of these two activations was located in the precentral gyrus in the same location as the activation described by Buccino and colleagues (2001) in volunteers observing video-clips of reaching-to-grasp hand movements. The second focus was located more dorsally in a position similar, but more rostral, to that described in the same study during the observation of leg actions.

In sum, in the frontal lobe there is a pattern of activations that appear to be related to the linguistic modality in which the stimuli were presented. Other activations are clearly related to the motor representation of the actions described in the heard sentences. These motor representations largely coincide with those found to be active during action observation.

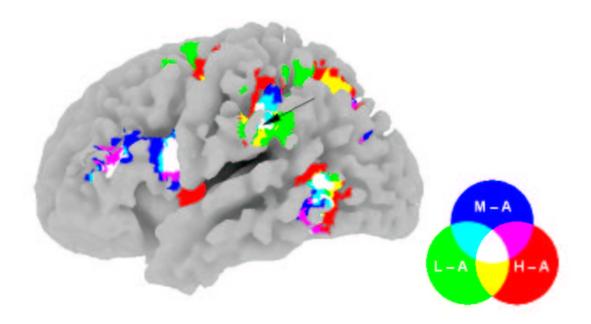
Listening to hand-related sentences also activated a focus in the insula. Given the scanty information on the role of this region in motor control, it is difficult to give a satisfactory explanation for this activation. Note however that the posterior insula, defined as the posterior part of disgranular plus the granular insular sectors, has reciprocal connections with somatosensory and motor areas (Mesulam and Mufson, 1982).

	Mo	uth v	s. abs	tract	На	and vs.	. abstr	act	L	eg vs.	abstr	act
Brain region	X	y	Z	Z	X	y	Z	Z	X	y	Z	Z
L IFG pt	-40	30	16	4.20	-46	34	8	4.21	-42	38	4	3.75
L IFG po	-54	10	16	5.09	-52	8	12	4.12	-50	10	16	3.84
	-44	2	24	3.63								
L PrCG					-28	-4	48	4.44	-26	4	64	3.74
L PoCG	-54	-38	48	2.63 *	-38	-40	48	2.84 *	-36	-48	52	3.25
L IPL	-62	-34	36	3.16 *	-62	-26	36	3.36 *	-64	-32	28	3.89
L IPS	-32	-72	40	3.00 *	-28	-68	48	3.20	-28	-48	36	3.66 *
L IPS/SPL									-34	-56	56	3.84
L pITL	-56	-52	-12	3.55	-50	-58	-16	4.17	-48	-54	-16	2.82 *
L insula					-36	0	4	4.35				
R MTL					40	-62	20	4.19				

**Table 3.3.1.** The stereotaxic coordinates (x, y, z) for significant voxels are given in mm together with the corresponding effect sizes (Z = Z scores; significance threshold: p<0.001 uncorrected; or p<0.005 uncorrected if marked by an asterisk (see also Figure 3.3.2)). IFG pt = inferior frontal gyrus, pars triangularis; IFG po = inferior frontal gyrus, pars opercularis; PrCG = precentral gyrus; PoCG = postcentral gyrus; IPL = inferior parietal lobule; IPS = intra-parietal sulcus; SPL = superior parietal lobule; pITL = posterior infero-temporal lobule; MTL = middle temporal lobule.

Consistent evidence shows that the inferior parietal lobule is part of the observation/execution matching system both in the monkey and humans (Buccino et al., 2001; Gallese et al., 2002). The almost complete lack of activation of the inferior parietal lobule during listening to action related sentences was therefore suprising. In order to test whether this finding really reflects a lack of involvement of the inferior parietal lobule in coding hear sentences with an action-related content, we explored activations in the inferior parietal lobule at a lower significance threshold (p<0.005 uncorrected). The results showed distinct, although partially overlapping activations for sentences describing mouth, hand and leg actions (Figure 3.3.2). In monkeys, the inferior parietal lobule receives its major visual input from the dorsal stream, and in particular from area MT/V5 (Ungerleider and Haxby, 1994). Noteworthy, mouth and hand sentences also activated the posterior

part of the inferior temporal lobe. A corresponding activation was found for leg sentences at p<0.005, uncorrected. These activations, adjacent to area MT/V5, are most likely related to a representation of the movement content of the action (Watson et al., 1993; Tootell et al., 1995; Peigneux et al., 2000).



**Figure 3.3.2.** Activation foci during listening to mouth, hand and leg action-related sentences at p < 0.005 uncorrected. All conventions as in Figure 3.3.1. Inferior parietal activations for all three body parts are indicated by an arrow.

A final observation concerns the distinction made in the Introduction between implicit motor representations and voluntary motor imagery. The activation pattern observed in the present experiment is consistent with this distinciton, in that no activations of mesial cortical areas were observed. This suggests that during listening to action related sentences, implicit motor representations are evoked automatically and are not related to mesial cortical areas activation.

# 3.3.5 CONCLUSIONS

Our results show that listening to sentences describing actions performed by different effectors activates a left-lateralized fronto-parietal system that corresponds anatomically to that activated during action observation and action execution. These data provide the first direct evidence of a common semantic system used by individuals when they act, observe an action or hear its verbal description. In this domain, language does not appear to be detached from the evolutionary ancient sensorimotor systems, but strictly linked to them.

"Within a century, the language was established: a Samoyedic Lithuanian dialect of Guaranì, with classical Arabian inflections. The content was also deciphered: some notions of combinative analysis, illustrated with examples of variations with unlimited repetition."

Jorge Luis Borges, "The Library of Babel"

4.	GENERAL DISCUSSION AND DIRECTIONS OF FUTURE RESEARC	C <b>H</b>

Some implications raised by the three empirical studies reported here will be dealt with in this chapter.

First, the findings of the three studies are to be summarized focussing on Broca's area, a neuroanatomical region which was activated by all the tasks used in these studies. The observed activations of Broca's area will be discussed in the context of cytoarchitectonic analyses which point to a functional parcellation of this region.

Second, aspects related to the processing of linguistic information both during acquisition and during usage of the mother tongue in adulthood will be discussed with respect to models of neuronal connectivity. These models hold that there are specialized clusters of neurons located particularly in the prefrontal cortex and neighboring subcortical structures, which are capable of generating and selecting appropriate rule-based representations of the type required for the processing of not only linguistic syntactic components but of hierarchical structures in general.

Third, some problems posed by the comparison of hierarchical structures across different cognitive domains are to be considered. Evidence coming from neurophysiological and cytoarchitectonic studies in non-human primates, from longitudinal and cross-sectional developmental observations in human infants, and from functional neuroimaging studies, including the third study reported here, suggest that hierarchical linguistic structures, and hierarchical structures in the sensorimotor domain have, at least in part, a common neuronal correlate. A computational model is presented, pointing to problems that must be overcome in order to maintain that hierarchical structures in different cognitive domains are processed by a "supramodal hierarchical neural processor", rather than by distinct neural systems.

## 4.1 BROCA'S AREA: A MULTIMODAL BRAIN REGION

An interesting finding of the three studies reported here is that the different tasks used were all associated with an activation of Broca's area. Broca's area - a brain region in the third frontal circumvolution of the left hemisphere, which has been termed so after the French neurologist Paul Broca, who made the seminal description of a patient that presented with agrammatic speech after a lesion in the left inferior frontal gyrus (1865) - has recently been the object of a detailed cytoarchitectonic analysis (Amunts et al., 1999). This analysis has led to a revision of some common beliefs concering the precise anatomical localization of Broca's area. This study provided evidence that the cytoarchitectonic landmarks corresponding to Brodmann's area (BA) 44 and BA 45 present a pronounced inter-subject variability and do not coincide on average with gross neuroanatomical landmarks, such as the sulcal contours of the opercular and the triangular portions of the left inferior frontal gyrus. As the authors argue, landmark-based anatomic interpretations of functional activations of Broca's area are possible only in those particular cases in which the foci of activation match the free surfaces of the opercular and triangular parts, whereas interpretations become more inaccurate the smaller the distance to a bordering sulcus. Furthermore, Amunts and colleagues found finegrained cytoarchitectonic parcellations within both BA 44 and BA 45, pointing to a possible heterogeneous distribution of functions in Broca's area. In fact, while a multitude of functional neuroimaging studies investigating quite different linguistic, cognitive and sensorimotor tasks have reported activations in a region broadly termed Broca's area, on closer inspection systematic finegrained differences in neuroanatomical localization are found.

In what follows, the activations within Broca's area observed in the three studies reported will be briefly summarized. Each of the three tasks investigated activated different portions of Broca's area, pointing to a parcellation of functions within this brain region. Furthermore, each of the different sub-regions of Broca's area that were activated responded in connection to a specific network of brain areas – compatible with the view that the neuronal populations contained in each

sub-region of Broca's area are connected in a unique manner with other brain regions. Crucially, the recruitement of different brain systems involving different portions of Broca's area seems to play an important role in dynamic processes, such as in the transition from knowledge acquisition to knowledge consolidation.

The first study (3.1) investigated the neural responses evoked by different types of hierarchical relations found in human language, in particular by syntactic relations in the mother tongue of adult subjects. Syntactic processing specifically activated a left hemispheric neuroanatomical system consisting of a deep component of Broca's area (the depth of the circular sulcus), the left posterior insular cortex and the left caudate nucleus. This pattern of activation – a neural correlate of an already consolidated grammatical knowledge – has been subsequently replicated by a study in which event-related fMRI was used to investigate the processing of syntactic anomalies in adults' mother tongue (Ni et al., 2000).

The syntactic component of language was also the focus of the second study reported here (3.2). In this study, however, adult subjects were not confronted with the syntactic structures of their mother tongue, but rather with novel syntactic rules they were unfamiliar with. The neural correlates of the acquisition of these novel syntactic rules was investigated. The results showed that a portion of Broca's area, on the posterior free surface of the left frontal inferior operculum, played a crucial role in the acquisition process; as was shown, the effect size of the activation in this brain region increased over the time of acquisition, in association with a significant improvement of performance. The opercular part of Broca's area was activated together with a widespread system of brain areas: a bilateral fronto-parietal network including the inferior parietal lobule, the dorsal premotor area, and BA 46 – a network which probably plays a role in the initial transcoding of visuo-spatial information into linguistic information – was activated in the early stages of acquisition. Activation was then increasingly observed in a different brain network that included, in addition to the opercular part of Broca's area, the left anterior insula, the left superior frontal gyrus, the right inferior parietal lobule and the right ventral inferior frontal gyrus. This is an entirely different network from the one

activated by the processing of syntactic structures of the mother tongue in the first study, suggesting that, although the subjects' performance in the second study reached native language levels, rule knowledge was not entirely consolidated.

The pattern of activations in Broca's area that emerges when comparing the first and the second study sheds light on the neurophysiological bases that underlie the structuring of grammar in a language. The acquisition of syntactic rules in adulthood is subserved by a lateral portion of Broca's area, namely the free surface of the inferior frontal operculum, a brain region that has been implicated in general verbal working memory (Fletcher and Henson, 2001; Paulesu et al., 1993), and specifically in working memory for syntactic processing (Caplan et al., 1998). Maintaining syntactic information in the verbal working memory buffer, for the purpose of comparing on-line the presented items, identifying and extracting regularities, is a non-automatic and effortful process which crucially depends on neocortical structures. On the other hand, the processing of the fully acquired and consolidated syntactic structures of the mother tongue depends on a deeper component of Broca's area, together with subcortical structures, namely the left posterior insula and the left caudate nucleus. This network is compatible with the observation that automatic language tasks typically do not engage lateral cortical areas (Bookheimer et al., 2000). The processing of the syntactic linguistic component of one's mother tongue is a fully automatized task that requires no effort, and does not depend on neocortical structures. On this view, the full consolidation of grammatical knowledge in the course of language acquisition may thus depend on switching from processing carried out largely by cortical areas to processing subserved largely by subcortical areas.

While activations in the depth of the circular sulcus have been found specifically only for syntactic processing of the mother tongue, the lateral free surface of the opercular part of Broca's area has been implicated in many linguistic, and also non-linguistic, tasks. In the first study reported here, this brain region was found to be active in a statistical comparison performed between the three types of linguistic violations studied (phonological, morphosyntactic and syntactic) averaged together and the baseline (see Figure 3.1.1.A). The violation tasks were specifically designed to disentangle these

three grammatical components from the lexical-semantic component, and the activation of BA 44 can therefore not be ascribed to lexical-semantics. Lexical-semantic processing has indeed been typically associated with activations in the triangular portion of Broca's area (BA 45) and in rostrally adjacent left inferior frontal regions (BA 47) (Gabrieli et al., 1998; Paulesu et al., 1997). A recent meta-analysis conducted on 30 functional neuroimaging studies on verbal working memory showed that the dorsal posterior part of Broca's area (BA 44) is consistently modulated by changes in verbal working memory load, whereas the anterior ventral part (BA 45) is consistently activated by lexical processing demands (Chein et al., 2002). The third study reported here (3.3), however, emphasizes the need to revise, at least partially, the view that BA 44 does not participate in semantic tasks. In the third study, the neural correlates elicited by listening to sentences describing actions performed by different body parts (mouth, hand and leg) were investigated. Action-related sentences were compared to sentences with an abstract content. All the sentences used were formed by combining a transitive verb in the first person singular to a syntactically and semantically congruent object complement (see section 5.3). This was done in order to control for syntactic complexity across conditions, so that only the semantic content of the sentences contributed to residual variance between conditions. The results of the third study showed that listening to action-related sentences evoked body-part specific neural responses in the premotor cortex and in the parietal lobe that were somatotopically organized. Irrespective of body part, however, all action-related conditions activated the opercular and the triangular portions of Broca's area in an overlapping manner. This common activation was located on the free lateral surface of Broca's area and was interpreted as reflecting semantic access to the action content conveyed by the sentences, given that, as pointed out above, the syntactic structure was kept invariant. This finding indicates that, at least in the case of action-related linguistic utterances, the lateral opercular portion of Broca's area (BA 44) also participates in semantic processing.

The third study consistently showed that Broca's area also displays a sensorimotor function, which is not necessarily tied up with linguistic functions. All three action-related conditions recruited

a portion of BA 44, which was located in the infero-posterior bank of the pars opercularis; the hand and leg conditions also recruited each a somatotopically arranged focus in the dorsal premotor area, whereas in the mouth condition a more dorsal portion of area 44 was activated (see Table 3.3.1) besides the commonly activated portion of BA 44 itself. The dorso-posterior bank of the left inferior frontal operculum was thus selectively activated by sentences describing mouth-actions, most likely providing access to premotor representations of the actions performed by the mouth. That this portion of Broca's area serves a premotor function is indeed well-known, as is the fact that mouth motor actions are richly represented in the inferior frontal gyrus (see Rizzolatti et al., 2001 for a review). Furthermore, lesions affecting this brain region cause articulatory deficits (Tonkonogy and Goodglass, 1981).

In sum, the three studies reported here confirm the view that Broca's area is an heterogeneous neuroanatomical region with a fine-grained functional parcellation that is conceptually in agreement with the cytoarchitectonic parcellation observed by others. Different sub-regions of Broca's area seem to subserve specific but also general-domain functions in associations with specific brain networks. Connectivity studies will be needed in order to fully elucidate these aspects.

#### 4.2 NEURONAL NETWORK MODELS OF HIERARCHICAL COMPUTATION

An important question to be addressed in the near future is how specific configurations of connectivity between populations of nerve cells provide the human brain with the capacity of regulating the flow of information within specialized neural structures, such that the specific computational demands posed by linguistic items can be accommodated. Language acquisition, in analogy to basic learning mechanisms known to exist in other living organisms, may be based on the stabilization of synaptic configurations between populations of nerve cells, each with a specialized function. The processing of an already acquired language, in turn, may require accurate tuning among multiple neuronal populations processing information at distinct levels, corresponding to the different linguistic components that have been referred to throughout the preceeding sections. This tuning eventually leads to the integration and temporal sequencing of the various pieces of linguistic information (the result being for example a regular, rhythmic stream of speech).

In the second study (3.2), which investigated language acquisition processes, we described how novel hierarchical linguistic syntactic rules are acquired. At a gross neuroanatomical level, an increased activation of a bilateral cortical network including parietal, premotor and dorsolateral prefrontal areas was observed. Rule extraction is generally taken to be an indicator of prefrontal cortical function. Some forwarded neuronal models of rule extraction are therefore to be discussed and a speculative hypothesis of the regulatory connectivity mechanisms underlying the acquisition of linguistic syntactic rules is to be deducted.

In the rule acquisition task of the second study, subjects were presented with a set of sentences following a particular hierarchical syntactic rule with which they were unfamiliar (i.e. the rules, taken from a language unknown to the participating subjects, specified the position of syntactic elements in phrases in a different order than in their mother tongue). Visual inspection of the input sentences probably led to the formation of a detailed representation of the order of words making up written sentences; these visuospatial representations had to be held online and compared, such that they

could be synthesized into patterns of regularities, i.e. the syntactic rules. In such a two-stage acquisition model – visuospatial analysis followed by the extraction of regularities – each stage is thought to be subserved by a distinct neuroanatomical system, namely a parieto - dorsal premotor system for visuospatial attention and visuospatial working memory, and a prefrontal system, including Broca's area and the anterior cingulate, for syntactic analysis and manipulation. Indeed, both systems were found to be activated in our study.

A closely related two-stage hierarchical<sup>29</sup> model that illustrates how such a rule-learning mechanism might function at the neuronal syntaptic level has been proposed by Dehaene and Changeux<sup>30</sup> (1991; Changeux and Dehaene, 2000). The proposed model consists of two distinct levels of organization: a low level, consisting of a visuo-motor loop, subserved by occipito-parietal visual and frontal premotor areas, and a high level, representing rule-based processing, subserved by the prefrontal cortex. Both levels are composed of clusters of hundreds of synergic neurons with self-sustained activity; the clusters are connected to each other by axon bundles. In order to perform a learning task, some of these connections must be modulated by local synaptic regulations; these in turn are designed according to a synaptic triad configuration: in this particular configuration, the short-term receptiveness of the postsynaptic neuron B to its presynaptic input neuron A is influenced by a modulator neuron C that may act on neuron B to bring it in an active or an inactive state. These regulations provide the neural basis for short-term on-line maintenance of information.

Rules are discovered by rule-coding clusters found at the high level — each cluster coding for a specific dimension (e.g. color or shape); the rule-coding clusters are hierarchically connected to all clusters at the low level, such that they can regulate the low-level connectivities and, by orchestrating the information flow between low-level clusters, allow the organism to extract generalized, abstract

<sup>29</sup> The term 'hierarchical', here, solely refers to a particular configuration of connections between neuronal clusters, influencing both the information flow and its regulation. The use which the authors make of the term 'hierarchical' has no implications whatsoever for the configuration of the functions processed by these neuronal models – the meaning of 'hierarchical' referred to throughout the present work.

<sup>30</sup> This model was designed to solve the Wisconsin Card sorting task, in which a set of cards depicting figures that can vary along several dimensions – e.g. number, shape, position, color – has to be sorted according to a particular rule (e.g according to color) that first needs to be discovered by the person tested. Once a rule is discovered, the cards of the set are presented in a different sequence such that a new sorting rule has to be discovered.

rules from the integration of visual inputs. During the acquisition process, rule-coding neurons at the high level can activate spontaneously one cluster at a time<sup>31</sup>, until that cluster which predicts the target rule-based behavior is selected (e.g. by positive reward).

This simplified neuronal model, at least in principle, may also meet the computational demands in extracting novel linguistic syntactic rules. The transformation of the visual information (gained from reading the stimulus sentences) into visuospatial representations may be carried out by neuronal populations in associative parietal and dorsal premotor areas, structures corresponding to the neuronal model's low level. Drawing inference about the underlying syntactic rules, in turn, might depend on the activity of specialized linguistic syntactic rule-coding neuronal clusters localized in Broca's area and the dorsolateral prefrontal cortex; the clusters in these regions may be activated in an orchestrated sequential order until the proper target syntactic rule is selected (trial and error). A neuroanatomical network that includes the opercular portion of Broca's area, the left ventral premotor area, the left insula, and possibly also Wernicke's area was significantly more activated during the acquisition of hierarchical linguistic rules compared to non-hierarchical, non-linguistic rules. These structures might thus contain a population of neuronal clusters that are specifically sensitive to hierarchically organized syntactic structures.

The first study constituting this thesis (3.1) suggests that when language acquisition, particularly the acquisition of grammatical components, is accomplished (the adult stage), the fronto-parietal network subserving rule-inference gets turned off. Syntactic processing, having become more automatic, is then carried out by subcortical structures such as the deep components of Broca's area, the left insular cortex and the head of the left caudate nucleus.

<sup>31</sup> Because of lateral inhibition, neighboring clusters are not allowed to be synchronously active.

#### 4.3 TOWARD A GENERALIZATION OF HIERARCHY

The third study reported here (3.3) presents results from a fMRI study, showing that the neuroanatomical network that mediates language – at least when processing sentences describing actions – may be linked to the evolutionary older sensorimotor systems subserving action execution and observation. This study was based on neurophysiological and cytoarchitectonic observations in non-human primates – with whom we share common phylogenetic ancestors – and on functional neuroanatomical observations in humans, pointing to the existence of a general-domain mechanism by which sensory perceptions of actions performed by others (gestures, speech, etc.) are internally transcoded into a corresponding motor plan. Such internal transcoding of the observed actions may be the process by which we catch the meaning of the observed actions.

Such transcoding processes are in principle independent of whether the involved domains (language, gestures, etc.) are hierarchically organized or not. On the other hand, as discussed in section 2, language is a hierarchically organized cognitive function. The acquisition of language is highly correlated with that of action-related behaviors (such as object manipulation, tool use and gestures) with respect to increasing hierarchical structural complexity, typology of hierarchical structures, and time course of acquisition. In developing more theory-driven empirical studies that hinge on the question of whether language depends on sensorimotor functions<sup>32</sup>, aspects concerning the typology and complexity of the involved hierarchical structure must be taken into account.

In this section the problems that such studies are confronted with will be discussed and possible solutions proposed.

In brief, the complexity of hierarchical relations can be more readily understood when

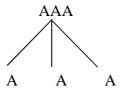
<sup>32</sup> Both during development and in the mature brain.

some internal structural variables such as the number of hierarchical levels underlying a specific item and the number of conformations that a particular structure can take are subjected to a formal analysis. This type of analysis<sup>33</sup> has the potential of being applicable to a wide range of materials across different domains such as linguistic clauses, arrays of physical objects, or gestures. Such a rudimentary analysis provides estimates of hierarchical complexity that may be used in comparisons between different domains (such as language and gestures) with respect to such variables as time course of development, neural substrates, psychometric indices of performance. Using these estimates as confounds in analyses of covariance may reduce residual variance and thus also the risk of overestimating potential cross-domain differences.

The present analysis is based on the assumption that there are boundaries that link elements within a stuctured sequence, as for instance the words in a sentence. The fact that there are boundaries between linguistic elements is a well-established psychological fact and not just a notational convention. These boundaries are hierarchically organized; this hierarchical organization is here taken to be tied up with a computational cost. According to the present view, the higher the number of hierarchical levels underlying a particular abstract structure, the higher the associated computational cost (either in composing or decomposing the structures). Within hierarchical levels, elements may be arranged freely, or have to be arranged in a fixed order (e.g. words in a phrase may have to be in a fixed order to achieve communicative intents, whereas two cups may be placed one above the other, irrespective of which one is above or below). Boundaries linking a certain element to a particular higher-order level can be arranged in a certain number of conformations. Again, as I suggest, the process of fixating one or more well-defined conformations has a computational cost, the higher the number of conformations that need to be discarded from the set of all possible conformations, the higher the computational cost.

<sup>33</sup> I am well aware that this analysis is rudimentary, and other variables may have to be taken in account (such as the degree to which the processing of particular structures is automatized). I am here only concerned with pointing out the direction in which to move.

First consider a set of three identical alphabetic symbols (A, A, A), which are arranged in a non-hierarchical structure  $S_n(A,A,A)$ :

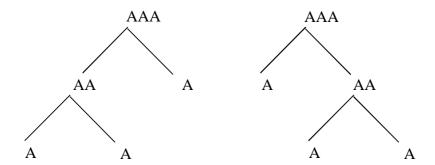


where S stands for structure and the index indicates whether the structure is hierarchical (h) or non-hierarchical (n). The structure  $S_n(A,A,A)$  is mirror-symmetrical: no distinguishable structural conformations can be generated by exchanging structural boundaries across the central, vertical symmetry axis. There is only one structural conformation having this particular complexity, mapping the three elements (A,A,A) onto the higher-order string 'AAA'. We have that the number of distinguishable conformations  $C_s$ =1. By definition:

if 
$$C_s=1$$
, then  $\Gamma=0$ 

where  $\Gamma$  is the computational cost in discarding a particular structural conformation<sup>34</sup>.

Conversely, consider the hierarchical structure  $S_h(A,A,A)$  and its mirror symmetric  $S_h$   $(A,A,A)^\prime$ 



There are two distinguishable, mirror-symmetric, structural conformations that map the three elements (A,A,A) onto the string 'AAA'; therefore  $C_s$ =2. The choice of one particular conformation (i.e. discarding one of the two alternative conformations) is associated, by definition, with a computational cost  $\Gamma$ =1.

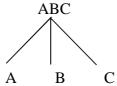
<sup>34</sup> I do not imply that no computational cost is associated with this process. But as the complexity of  $S_n$  (A,A,A) is minimal, I arbitrarily take it here as the null baseline.

In general:

$$\Gamma = C_d$$

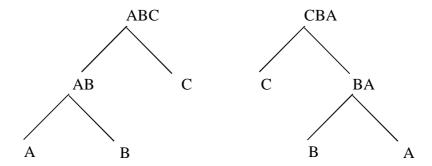
where  $C_d$  is the total number of discarded conformations.

Let us introduce a different case, where a set of three distinct elements (A, B, C) is arranged in a non-hierarchical structure  $S_n$  (A,B,C):



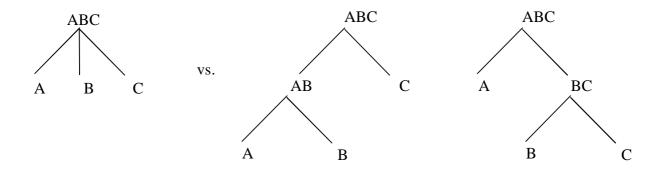
The structure mapping the three elements onto the higher-order unit is per se symmetric. However, each boundary projects from a distinguishable element (either A or B or C), making the conformation asymmetrical. The number of distinguishable conformations  $C_s$  is given by the permutation of the three elements P(3) = 3! = 6. The choice of one and only one particular conformation (i.e. discarding five conformations) is associated with a computational cost  $\Gamma$ =5.

Let us now map the set of three elements (A,B,C) onto the hierarchical structure  $S_h(A,B,C)$  and its mirror symmetric structure  $S_h(A,B,C)$ ':



The number of possible conformations is given by the permutation of the three elements, multiplied by two, to account for the fact that each conformation is associated with its mirror-symmetric; i.e.  $C_s = 2[P(3)] = 2 \cdot 3! = 12$ . Then, the choice of one and only one particular conformation is associated with a computational cost  $\Gamma$ =11.

From these examples it can be seen that the hierarchical organization of elements is a powerful tool to decompose the formation of complex structures into a discrete number of lower-order computations and to instantiate univoque relations that would not be captured by non-hierarchical structures. Compare for instance:

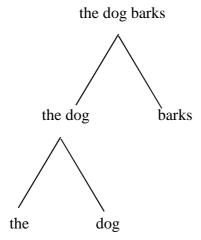


On the other hand, a higher degree of univocity and complexity is associated with a computational cost, which – given a fixed number of elements – is higher for hierarchical than for non-hierarchical structures.

Let us now consider a few practical examples, either of a linguistic or a non-linguistic nature, and see if we can estimate the computational cost associated with each structure.

Let us begin with a string of three English words (the, dog, barks) mapped onto the hierarchical structure  $^{35}$  S<sub>h</sub>(the, dog, barks):

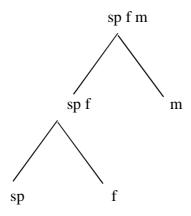
<sup>35</sup> Here and in the following, I leave aside linguistic notations (see e.g. Haegemann, 1994; Levelt, 1989). This simplification helps to illustrate the principles more clearly. The principles discussed here can be extended to meet more refined analyses.



The total number of conformations associated with  $S_h$ (the, dog, barks) is given by the permutation of the three elements, multiplied by two, to account for the mirror transforms implied by the hierarchical structure; i.e.  $C_s = 2[P(3)] = 2 \cdot 3! = 12$ . Many of the conformations thus generated, however, do not conform to the positional syntactic rules of English (e.g. [barks (dog the)] or [(the barks) dog]) and the choice has to converge on only those particular conformations that are legal and possible in English. Since there is only one possible conformation in English (i.e. the one illustrated in the tree-structure above, [(the dog) barks])<sup>36</sup>, 11 conformations have to be discarded. Thus,  $C_d = 11$ , and the associated computational cost is  $\Gamma$ =11.

Let us now turn to a non-linguistic case discussed in section 2.3.2, that is the 'subassembly' strategy achieved by children older than 19-20 months, when a spoon (sp) is first combined with food (f), and together they are put in the mouth (m). We have a set of three elements (sp,f,m), which are hierarchically ordered in the structure  $S_h(sp,f,m)$ :

<sup>36</sup> Contexts can be found, for instance in literature, where the conformation [barks (the dog)] is possible. In this case,  $\Gamma$ =10.

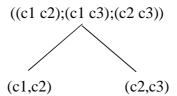


Here too  $C_s = 2[P(3)] = 23! = 12$ . By learning the hierarchical relations governing tool use, the child ends up excluding a number of combinations, such as for instance [(f m) sp] - i.e. picking up food directly with the mouth and then touching the spoon with both<sup>37</sup> – or [(sp m) f] - i.e. taking the spoon to the mouth and then touching food with both. In the original study (Connolly and Dagleish, 1989; Greenfield, 1991), children converge on just the one hierarchical relation depicted above, i.e. [(sp f) m], with a computational cost  $\Gamma$ =11. A second possible combination of the three elements consists in opening the mouth first and then moving the opened mouth toward the food-spoon combination (i.e. [m (sp f)]). If this combination together with the first combination ([(sp f) m]) is considered, then  $\Gamma$ =10.

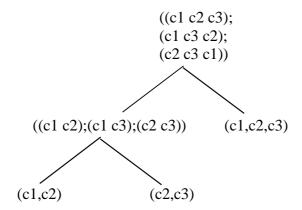
Let us finally turn to another non-linguistic case, originally presented by Greenfield and colleagues (Greenfield PM et al., 1972; Greenfield PM, 1991) and discussed in section 2.3.1. In this case, cups of three different dimensions are hierarchically combined by first putting together two cups, and then putting this higher-order unit together with the third cup (so-called 'subassembly' strategy). We have a set of three cups (c1,c2,c3), where c1 is the small-sized cup, c2 the medium-sized one and c3 the large-sized one. In a subassembly strategy, the three cups are combined hierarchically. As cups are manipulable objects, there is a constraint, i.e. the

<sup>37</sup> While this particular combination is certainly of nutritional relevance, is meaningful in playful contexts and when experimentating, in learning the proper spoon use, the child has to converge on a more appropriate relation between food, mouth and spoon.

combination of two cups to produce the first higher-order unit has to be made by placing a smaller cup in a larger one (such a first-order subassembly can be treated as a single object when pairing it with the third cup). In turn, no higher-order unit is generated, when a larger cup is placed on a smaller cup: indeed, without paying particular attention (i.e. without psychologically treating the cup on top as a separate object), there is a danger of the cup on top to fall down. Therefore:



Three viable first-order combinations can be generated. The first-order assembly generated must then be combined with the third cup. This leads to the set of second order-units  $S_h(c1,c2,c3)$ :



In this type of hierarchical object combination, three out twelve viable second-order hierarchical combinations can be generated ( $C_s = 2[P(3)] = 2 \cdot 3! = 12$ ), and the computational cost is  $C_d = \Gamma = 9$ .

Compared to spoon use, combining cups of three different sizes presents more possibilities of putting elements together, based on their physical shape and dimension. In other words, there are less constraints on the solution to converge on. As a consequence the computational cost associated with this hierarchical organization of elements is lower.

Particular caution is required when comparing hierarchical structures in different domains; despite an equal number of elements combined and an equal number of hierarchical levels, the constraints posed to generate higher-order structures as a whole might well differ. Ignoring this fact can result in false inferences, such as concluding that different neural structures are involved in different modalities or in different tasks, when in fact the same neural structures are engaged, but to a different extent. This is a pitfall when performing developmental or brain activation studies on hierarchical learning. Using an estimate of the computational cost associated with a particular hierarchical structure as a covariate is a potentially powerful method to reveal regional brain modulations as well as existing similarities and differences between modalities.

The present account of hierarchical complexity illustrates the general principle and it has the potential of being applied to simple structures such as those discussed here. As the examples illustrate, the approach allows some other variables to be accounted for, such as the context or the nature of stimuli. On the other hand, more powerful estimates of hierarchical complexity will have to be developed that do not just provide a global measure of the computational costs, but distinguish the costs associated with distinct processing components. Another issue that has been raised above is whether the processes are automatized or not (see footnote 33). Automatic processes are associated with a lower computational cost. To estimate the computational cost of a process which is not automatized, a multiplication factor may be introduced (for instance:  $\Gamma$  (automatic) = 9 and  $\Gamma$ (non-automatic) =  $9^n$ , where n is a factor that needs to be empirically determined by estimation; it accounts for the need of more computational resources).

The approach outlined is in need of empirical testing. Quite specific hypotheses can be formulated and tested. For instance, the learning performances in young children or adults can be predicted by this approach: depending on the estimated computational costs, faster or slower learning should be observed (lower computational costs – i.e. less constraints on learning – should lead to faster learning rates, and/or to a lower percentage or errors). At the time when the

three studies reported here were carried out, such a line of thought was not entertained. Based on the insights gained by taking up this line of thought, it will be possible to design experimental studies along the notions of hierarchical stucturing sketched in this section, leading to a more differentiated view of cognitive processes. "TV is, after all, the modern day roman coliseum

Human devastation as mass entertainment

and now millions sit jeering

collectively cheering

the bloodthirsty hierarchy of the patriarchal arrangement"

Ani DiFranco, "Tamburitza Lingua"

# 5. APPENDICES

## 5.1 APPENDIX 1. STIMULI OF EMPIRICAL STUDY 3.1

# **Baseline condition:**

- 1. Hanno disbato le artine.
- 2. Molte grapotte amionarono.
- 3. Molti celuci furono taffivati.
- 4. Nessun cribaso è stato incenghito.
- 5. Ogni stroidda duccava afflinatamente.
- 6. Nessuna bogganta aveva taccarato ogni safila.
- 7. Ogni ditra ha milenato il fiommo.
- 8. Qualche savapa si è snebiccata.
- 9. Furono amionate le pave
- 10.Qualche clamispo marisce le pode.
- 11.Un tirlitto è stato cutipato.
- 12.Il giappento ha taggalato le tospe.
- 13.è sagoto un migo.
- 14.Gli oprammi nafantavano.
- 15.Il gulco gianigeva le brale.
- 16.Le celucche zuminano.
- 17. Molti lugui sono stati demoggiati.
- 18. Questo lerro non firdò nessuna cota.
- 19.Il lappento non tonce mai.
- 20. Sono icodati gli snebbitti.
- 21. Una mirpa ha trisito lo stoco.
- 22.Le diste sono state tutte tersuerate.
- 23.Il clannino sta batando.
- 24.Lo stoco sta artimando la bodova.
- 25. Molte ciarimbe hanno maipato la bausia.
- 26.Il crombaso si pringò.
- 27. Pochi daffri selaggiano tutte le vibe.
- 28. Quel gonullo fu dibistatto.
- 29.Il sinciaraco accutrina.
- 30. Questa ravitta è stata copidata.
- 31.Si sono vibate le zilie.
- 32. Sono borrettate le rogale.
- 33. Tutti i gorpotti sono stati gasporati.
- 34.Le gorede dirravano le conde.
- 35. Nessun mado è stato mitenato.
- 36. Non si è revigito nessun idoco.
- 37. Ogni daffro sfivvava.
- 38.Quella molmeca non alinava questa frida.
- 39. Nessuno stoco aillò.
- 40. Quelle gittole rappintarono tutte le ravitte.
- 41.Si astipevano tutti gli otrunchi.
- 42. Tutte le spranugie taddeano.
- 43.I linnui fivvavano le diste.
- 44. Una mirpa si è selaggiata.
- 45.Il napirzo egazzò qualche pitanga.

- 46.Le corle furono featite.
- 47.Quei fiomi sono stati naditi.
- 48.Il triaggo fabbisce ogni lustasio.
- 49. Quella gorada ha nagito.
- 50. Scodonnarono le ciaspe.
- 51.Si tasalano molte barne.
- 52.Una gittola ciusì.

# **Phonological condition:**

- 1. Hanno dinsbato le artine.
- 2. Molte grapotrte amionarono.
- 3. Mosnti celuci furono taffivati.
- 4. Nessun cribaso è stgtato incenghito.
- 5. Ogni stroita duccava afflinatznamente.
- 6. Nessuna bogfgata aveva taccarato ogni safila.
- 7. Ogni ditra ha milenaclto il fiommo.
- 8. Il giappento ha tnzgalato le tospe.
- 9. è sazrngoto un migo.
- 10.Gli opradmtmi nafantavano.
- 11.Il gulco giangzleva le brale.
- 12.Le celucche zrsuminano.
- 13. Molti lugui sono stati detymoggiati.
- 14. Questo telero non firdò nessuna cota.
- 15.Il lappento non tonpnce mai.
- 16.Il clannino sta baglntando.
- 17.Lo stodlgnco sta artimando la bodova.
- 18. Molte ciarinzbe hanno maipato la bausia.
- 19.Il crombasrto si pringò.
- 20. Pochi daftfri selaggiano le vibe.
- 21.Quel gonullo fu dibistatro.
- 22.Il sinciatnraco accutrina.
- 23. Tutti i gorpotti sono stati tasdzporati.
- 24.Le gocltrede dirravano le conde.
- 25. Nessun masrdo è stato mitenato.
- 26. Non si è revigiemto nessun idoco.
- 27. Ogni daffro rstfivvava.
- 28. Quella molnrteca non alinava questa frida.
- 29. Nessun srntoco aillò.
- 30.I linnui fintrvvano le diste.
- 31.Una mirtpsa si è selaggiata.
- 32.Il napirzo egazzò qualche pictztanga.
- 33.Le cofrsle furono featite.
- 34.Quei fiomi sono stati nrmaditi.
- 35.Il triaggo fabbisce ogni luszstasio.
- 36.Quella cogzrada ha nagito.

# **Morphosyntactic condition:**

- 1. Hanno disbata le artine.
- 2. Molti grapotti sono stata amionati.
- 3. Molti celuci fu taffivati.
- 4. Nessun cribaso siamo incenghito.
- 5. Ogni stroidda è duccate afflinatamente.
- 6. Nessuna bogganta avevano taccarati ogni saffila.
- 7. Ogni ditra hanno milenata il fiommo.
- 8. I giappenti ha taggalato le tospe.
- 9. Molti migi sono state sagotati.
- 10.Gli oprammi si sono nafantata.
- 11.Il gulco ha gianigiata questo bralo.
- 12.Le celucche è zuminati.
- 13. Molti lugui sono stati demoggiato.
- 14. Questo lerro non hanno firdati nessuna cota.
- 15.Il lappento non hanno tonciate mai.
- 16.Il clannino sono stata batati.
- 17.Lo stoco è artimati la bodova.
- 18. Molte ciarinbe sono maipato la bausia.
- 19.Il crombaso ho pringate.
- 20. Pochi daffri selaggia tutte i vibe.
- 21. Quel gonullo furono dibistatto.
- 22.Il sinciaraco ho accutrinati la mirfa.
- 23. Tutte le gorpotti sono stati gaszporati.
- 24.Le molti gorede dirrava le conde.
- 25. Nessun mado furono stato mitenato.
- 26. Non siamo revigita nessun idoco.
- 27. Ogni daffro ha sfivvata.
- 28.Quella molmeca non ha alinatate questa frida.
- 29. Quelle stoche si sono taillato.
- 30.I linnui fu fivvate le diste.
- 31.La mirpa sono stato selaggiate.
- 32. Tutta il napirzo egazzò qualche pitanga.
- 33.Le corle fu featite.
- 34. Quei fiommi hanno naditate la frunta.
- 35.Il triaggo ha fabbitate ogni lustasio.
- 36.Quella corada è nagiti.

# **Syntactic condition:**

- 1. Hanno disbate artine le con gli ziggoli.
- 2. Grapotte molte amionarono.
- 3. Celuce delle furono taffivate.
- 4. Cribaso è incenghito nessuno a rimbaudo.
- 5. Stroidda ogni duccava afflinatamente.
- 6. Nessuna aveva bogganta taccarato ogni safila.
- 7. Ogni ditra ha milenato fiommo il.
- 8. Giappento il ha taggalato le tospe.

- 9. È sagoto migo un da carampo.
- 10.Soprammi i nafantavano.
- 11.Gulco il gianigeva le brale.
- 12. Celucche delle zuminavano.
- 13.Lugui molti sono stati demoggiati.
- 14. Questo lerro firdò non nessuna cota.
- 15.Lappento il non tonce mai.
- 16. Clannino il sta batando.
- 17.Lo stoco artimando una sta bodova.
- 18. Ciarimbe molte hanno maipato una bausia.
- 19. Crombaso il si pringò.
- 20. Pochi daffri selaggiavano vibe in stripo.
- 21.Gonullo quel fu dibistatto.
- 22. Accutrina sinciaraco ogni.
- 23. Tutti gorpotti i stati sono gasporati.
- 24. Goreda qualche dirava le conde.
- 25. Nessun mado stato è mitenato.
- 26. Non è revigito idoco nessuno.
- 27.Daffri i tutti sfivvavano.
- 28. Molmeca quella alinava una frida.
- 29. Stoda nessuna taillò.
- 30.I linnui fivvavano diste le per funciaco.
- 31. Mirpa una è selaggiata.
- 32. Napirzo il egazzò qualche pitanga.
- 33.Delle furono corle featite.
- 34. Fiommi quelli sono naditi.
- 35.Il triaggo ogni fabbisce lustasio.
- 36.Nessuna lorada è non stata nagita.

# 5.2 APPENDIX 2. STIMULI OF EMPIRICAL STUDY 3.2

### **Baseline:**

- 1. Mizarono le sarille
- 2. Aillò lo stoco
- 3. Snuttava la stimbera.
- 4. Ha mastito la branna.
- 5. Hanno calfiato i saboli.
- 6. Ha torlito un bamo.
- 7. Hanno antocato le gordale.
- 8. Sono gialevati i coransi.
- 9. È fordirgata la bedera.
- 10. Sono alimati i pebari.
- 11.Si sta pivercando lo scaro.
- 12.Si sta comuliando la bilbera.
- 13.Si stanno estemando i nasbini.
- 14. Sono state rogifite le polbe.
- 15.È stato parsolato un redolo.
- 16.Sono stati pegamati i relofi.
- 17.Si farande l'irpenno.
- 18.Si sfivverà il daffro.
- 19.Si dencirono le atrobale.
- 20. Qualche ecamispo non madisce il tervolo.
- 21. Questo lerro non firdò una cota.
- 22. Molti lirpi non lonavano le nibole.
- 23. Alcune ganie margono tutte le crolte.
- 24. Qualche miluno camepì tutte le ciratte.
- 25. Pochi raboli vigognano tutti i crolti.
- 26. Qualche fitania ha ciontito.
- 27. Molti dransi avevano ribogliato.
- 28. Ogni tadero ha trelumito.
- 29. Ogni pamiraco è itinito.
- 30. Alcune varpe furono boregiate.
- 31.Qualche pibuta fu coffronata.
- 32. Molte folucie hanno affepito i loppi.
- 33. Qualche bodalo ha insimito una salpeta.
- 34. Alcune ecorette hanno telmito il cido.
- 35.La mafa non cargì.
- 36.Le grapotte non amionarono.
- 37.Il goncido non cetivò.
- 38.Le stepole hanno demoggiato.
- 39.La fardana ha camepito.
- 40.I renfi avevano derdanato.
- 41.Il berbiso è passuperato.
- 42.I borcisi furono darsiti.
- 43.La sadoga fu riburnata.
- 44.Le pafeole sono rofugate.
- 45.L'arrumpa sta naldando.
- 46.Gli stafi stanno sfogulando.

- 47.Le fideme stanno comenendo.
- 48.I cuspani si dutalevano.
- 49.Le gorante si colciravano.
- 50.La sadona si accavapì.
- 51.Le eggiore si sono pegite.
- 52.Il prideco si era bagunito.
- 53.I biteli si sono stecurnati.
- 54. Tutti i coplasi si safillarono.
- 55. Tutte le fodame si acatravano.
- 56. Tutti i cegri si offuniscono.
- 57. Ogni frento si è bormobato.
- 58. Molte zubore si erano uparite.
- 59. Qualche otelca si era dotenata.
- 60.Il daffio bilbava qualche tilla.
- 61.La molmeca alinava questa frida.
- 62.Le pindole braspinano molti cumi.
- 63. Tutte le stiape pirbarono qualche togno.
- 64. Tutti i macri verpiscono molte nedile.
- 65. Tutte le placine sdagrano qualche dapo.
- 66.La dapostra è stata eulobata.
- 67.La cudocia è stata dimoviata.
- 68.I decli sono stati lominati.
- 69.I cepri sono stati tutti permiccati.
- 70.Le vargucce sono state tutte attisite.
- 71.I meffi sono stati tutti ampaniti.
- 72.La filentra non corange mai.
- 73.Gli erdisi non milesarono mai.
- 74.Le vadise non nisparono mai.
- 75.Gli schevi voncebirono le serle.
- 76.La focisa metisce il bodeto.
- 77.Il tresbo avvupisce i lefri.
- 78.Il chiafo non si irebisce le gufole.
- 79.Le lone non si pernarono il ricero.
- 80.I micoli non si sfivvarono la velza.
- 81.Le partaroghe hanno inuscato i nugli.
- 82.La malusa ha trepito un lendro.
- 83. Una padica ha gertito il nalcio.
- 84.Le miote hanno angibito alcuni dieri.
- 85.Il cifo ha sottrito qualche dancia.
- 86.La becra ha lappato molti murbi.
- 87. Qualche velerono ha coledato ebinamente.
- 88. Molte coravie hanno utenato vesitamente.
- 89. Alcuni panfi hanno verpito milpemente.
- 90.La mandiena si è rivumata balidemente.
- 91.I rebici si sono genivati colsamente.
- 92.Le dege si sono stembite cofamente.
- 93.Non è mecata nessuna megla.
- 94. Non è pontato nessun licero.
- 95.Non è guisita nessuna boga.
- 96.Non è stato celicato nessun fomo.
- 97. Non è stata arebata nessuna fecra.

- 98. Non è stato vorpato nessun despo.
- 99. Non si è intodato nessun vipo.
- 100.Non si è trensita nessuna mibola.
- 101. Non si è saciata nessuna ferla.
- 102.I nedi non hanno mai coledato.
- 103.La beca non ha mai paronato.
- 104.Il grabo non ha mai degizzato.
- 105. Accutrina il sinciaraco.
- 106. Anagiva la bogala.
- 107. Scodonnarono le ciaspe.
- 108. Hanno mobato molti stabri.
- 109. Hanno teriato poche coplase.
- 110.Ha stonfato ogni roveso.
- 111.Ha pidato qualche rifalo.
- 112.Fu argibato ogni blacco.
- 113.È itinito ogni pamiraco.
- 114. Sono rofugate molte pafeole.
- 115.Stanno conendo molte fideme.
- 116.Stanno corbando alcuni fepi.
- 117.Sta firdando qualche corga.
- 118.È stata esbinata la cabla.
- 119.È stato stemmito il carbo.
- 120. Sono stati sirtati i fobari.
- 121. Sono pegamati tutti i relofi.
- 122. Avevano percato tutti i pighi.
- 123. Furono amionate tutte le pave.
- 124. Tutti i celuci furono taffivati.
- 125. Tutti i tredoli furono inurtiti.
- 126. Tutte le artine sono disbate.
- 127.Si voncebì ogni rusaga.
- 128. Si nafantò qualche oprammo.
- 129. Si dernirono molti barmi.
- 130. Questo nabo bilbava la gubra.
- 131.Molte ebalfe costiccano i birasi.
- 132.Qualche manfa farende i paudami.
- 133.Molti ascanti toggiano tutte le ranse.
- 134. Pochi daffri selaggiarono tutte le vibole.
- 135. Ogni rizalo carocca tutte le pelte.
- 136.Lo zemaro arroltì.
- 137.I prelfi agivirono.
- 138.Le sarille mizarono.
- 139.Un rogaro si è sarliato.
- 140.Gli snebbitti si sono icodati.
- 141.Una mirpa si è selaggiata.
- 142.Molti foluci si sono intodati i vipi.
- 143. Molti linnui si sono fivvati le diste.
- 144.Qualche beca si è murnita i dinaci.
- 145. Tutti i faraci si prattiscono.
- 146. Tutte le giarnise si sganivano.
- 147. Tutte le stane si cadoccarono.
- 148.Si safillano tutti i coplasi.

- 149.Si acatravano tutte le fodame.
- 150.Si offuniscono tutti i cegri.
- 151.Si sono tasalate le barne.
- 152.Si sono morpiti i titrami.
- 153.Si erano asoriati i viassi.
- 154. Nessun ipallo si è anagibito.
- 155. Nessuna dorla si è bessata.
- 156. Nessun idoco si è revigito.
- 157. Ogni traco si è renibito.
- 158.Qualche antalio si è pernicato.
- 159. Alcune sarse si sono faniate.
- 160.I decli non si sono lominati.
- 161.Le rogale non si sono borrettate.
- 162.Il pauno non si è cobolato.
- 163.Le triagge fabbiscono ogni lustasio.
- 164.I bargi addambirono qualche fedolo.
- 165.Il fiommo ha milenato ogni ditra.
- 166.Le canbre lobarono tutte le pangre.
- 167.I darmi confano tutte le daste.
- 168.Le dime inuscano tutti i dransi.
- 169.La pagula è stata genadita.
- 170.Il doperco è stato tricelato.
- 171.Gli sfegoni sono stati desustati.
- 172.Un cribaso è stato incenghito.
- 173. Molte cetande sono state baclate.
- 174. Ogni ravitta è stata copidata.
- 175. Qualche tirlitto è stato cutipato.
- 176.I gorpotti sono stati tutti gasporati.
- 177.Le vargucce sono state tutte attisite.
- 178.I meffri sono stati tutti ampaniti.
- 179.Le gorne non hanno mai pirbato.
- 180.I nerici non avevano mai surnito.
- 181.La pasulia non ha mai cadoccato.
- 182.Il gulco gianigeva le brale.
- 183.Le gorede diravano la conda.
- 184.Gli schevi voncebirono le serle.
- 185.Il giappento non ha taggalato le tospe.
- 186.La mirpa non ha trisito lo stoco.
- 187.La conorta non ha colindato gli irpenti.
- 188.Ha strebito ogni drelo selbatamente.
- 189. Hanno duccato molte stroidde afflinatamente.
- 190.Ha tasiato qualche cisco ebinamente.
- 191. Sono attociati molti laterbi alivamente.
- 192.È berliata qualche banvia anastemente.
- 193. Sono stembite alcune dege cofamente.
- 194. Sta batando ogni clannino inerpamente.
- 195. Stanno bralando alcune dafe alendamente.
- 196.Sta gizando qualche ghedo silpemente.
- 197.Non è tolata nessuna tella.
- 198.Non è dibistatto nessun gonullo.
- 199. Non è mitenato nessun mado.

- 200. Non si sodigliò nessun dirro.
- 201. Non si govisò nessuna pota.
- 202. Non si pomirava nessun reseglio.
- 203.La desa non è mai gadiata.
- 204.I cesbi non sono mai affantati.
- 205.La corla non fu mai featita.
- 206.I balfi non sono mai stati trascati.
- 207.Il gauco non è mai stato camagito.
- 208.La lugua non è mai stata demoggiata.

## **Baseline – violations:**

- 1. La è stata esbinata cabla.
- 2. Sinciaraco accutrina il.
- 3. Si tanugie taddeano le.
- 4. Triagge ogni le fabbiscono lustasio.
- 5. Nabo questo bilbava la gubra.
- 6. Tutti gorpotti sono i stati gasporati.
- 7. Le tasalate si barne sono lasivamente.
- 8. Poche canbre lobarono le tutte pagre.
- 9. Stabri hanno molti mobato.
- 10.Blacco fu argibato ogni.
- 11. Beca ha murnito qualche i dinaci.
- 12.I faraci si tutti prattiscono.
- 13.Traco ogni si è renibito.
- 14.I bargi non si addambirono fedolo qualche.
- 15. Ogni ha strebito drelo selbatamente.
- 16. Maliafo ha ogni irebito qualche novagia.
- 17.Bogganta ha nessuna taccarato ogni safila.
- 18. Rusaga nessuna si voncebì.
- 19. Gittola ogni si ciusì.
- 20.Il ha bisanno vilcito ogni ebalco.
- 21. Sirondato i hanno demi.
- 22. Non stata bessata è nessuna dorla.
- 23.Il non disillò verpeno.
- 24.Il ha runo tencato le sanfe.
- 25.Branna ha mastito la.
- 26.Si mirpenno farande il.
- 27. Pindole molti braspinano le cumi.
- 28.Lirpi molte lonavano i nibole.
- 29.Lerro questo firdò una cota.
- 30. Tutti cepri sono i stati permiccati.
- 31.I si stecurnati biteli sono.
- 32.Si imigiti molti parpi sono.
- 33.Qualche muno camepì le tutte cratte.
- 34. Qualche ha fitania ciontito.
- 35. Varpe furono boregiate alcune.
- 36.Bodalo ha insimito qualche una salpeta.
- 37.Le fecre si tutte arebiscono.
- 38.Si è taccarata bogganta nessuna.

- 39.Il daffio bilbava tilla qualche.
- 40. Ogni ha coledato velerono ebinamente.
- 41. Bisanno ha vilcito qualche molti ebalchi.
- 42. Non filentra corange la mai.
- 43.Il ha sottrito cinifo qualche dancia.
- 44. Demoggiato i hanno tepoli.
- 45. Non si celicato nessun è fomo.
- 46. Non si vorpicato nessun è despo.
- 47.Il ropiava puno.
- 48.I hanno ciarimbi le maipato bausie.

#### **Grammatical rule 1:**

- 1. Non arroltì zemaro lo.
- 2. Non scodonnarono ciaspe le.
- 3. Non agivirono prelfi i.
- 4. Non ha pergidito banfa la.
- 5. Non hanno disbato artine le.
- 6. Non è pagotato migo un.
- 7. Non furono amionate pave le.
- 8. Sono state baclate cetande le.
- 9. È stato tricelato doperco il.
- 10. Sono stati desustati sfegoni gli.
- 11.Si covilarono besardi i.
- 12.Si astipevano otrunchi gli.
- 13.Si acrotirono boterve le.
- 14. Qualche manfa farende paudami i.
- 15. Qualche clamispo marisce pode le.
- 16.Ogni ditra ha milenato fiommo il.
- 17. Molti ascanti toggiavano tutte ransole le.
- 18. Pochi daffri selaggiarono tutte vibole le. 19. Alcune crampe hanno amedito cangi i.
- 1). Alcune crampe namo amedito cangi
- 20. Nessuna maina ha ceslicato falfe le.
- 21.Getranti i pugerirono.
- 22.Copramo il nafantava.
- 23. Celuci i furono taffivati.
- 24. Corle le furono featite.
- 25. Tredoli i furono inurtiti.
- 26. Pebranto il si asserfò.
- 27. Crombasi i si pringarono.
- 28. Stolerni gli si dernirono.
- 29. Tutti giarnisi i si soganivano.
- 30. Tutti fotanelli i si cadoccarono.
- 31.Boladi i confosano molte sinte.
- 32. Napirze le egazzarono qualche pitanga.
- 33. Mafero il acrosò alcuni prelpi.
- 34. Tutti darmi i si confano alcune daste.
- 35. Tutti dattimi i si inuscarono qualche draniso.
- 36. Ravitta la e' stata copidata.
- 37. Tirlitto un è stato cutipato.

- 38. Cribaso un è stato incenghito.
- 39. Ramude le sono state tutte amefite.
- 40.Disti i sono stati tutti tersuerati.
- 41. Sdarco lo non saferì mai.
- 42.Lappento il non tonciava mai.
- 43. Gulco il gianigeva brale le.
- 44. Gorede le diravano conda la.
- 45. Conorta la non colindò irpenti gli.
- 46. Dustalco il non amecava stada la.
- 47. Conure le non tisennarono neco il.
- 48. Giappento il ha taggalato tospe le.
- 49. Mirpa la ha trisito stoco lo.
- 50. Gittoli i hanno raspigato molte ravitte.
- 51. Massolo il ha trolcito alcune foralfe.
- 52. Giceni i hanno viscato ogni velmo.

## **Violations of Grammatical rule 1:**

- 1. Bogala anagibiva la.
- 2. I hanno pighi percato isiremente.
- 3. È la stata genadita pagula.
- 4. Ogni rizalo tutte petole caroccava le.
- 5. Varalpo è ratermito il.
- 6. I si torgavano prelfi umbovamente.
- 7. Tutti taldi si i cemubano.
- 8. Birasi molte costiccavano i ebalfe.
- 9. Carbo non è stato stemmito il.
- 10.I non trascano mai balfi.
- 11.Bitane matero non il scabbirono le.
- 12. Ciratta ha didanato la i garpi.

#### **Grammatical rule 2:**

- 1. Gli iobatti elfargato avevano.
- 2. Le corade nagito hanno.
- 3. Le celucche zuminato hanno.
- 4. Il tomuro nesicato aveva.
- 5. La corga firdando sta.
- 6. Il clannino batando sta.
- 7. Le dafe bralando stavano.
- 8. Non pomogato hanno i mapli.
- 9. Non pidato hanno le ritafe.
- 10.Non sirtato hanno i fobari.
- 11. Poche coplase teriato hanno.
- 12.Quei fiommi nadito hanno.
- 13. Ogni roveso stonfato ha.
- 14. Molti parpi si imigiti sono.
- 15. Qualche savapa si snebbicata è.
- 16. Alcune salerse si faniate sono.

- 17.Un rogaro si sarliato era.
- 18.Gli snebbitti si icodati sono.
- 19.Una mirpa si selaggiata è.
- 20.Una certima si conaliando sta.
- 21.Gli stanci si colincando stavano.
- 22.Il ghedo si ginizando sta.
- 23.Si asoriati erano i viassi.
- 24.Si vibate sono le zilie.
- 25.Si borrettate sono le rogale.
- 26.Si cobolato era qualche pafuno.
- 27.Si gorcita è ogni smalla.
- 28.Si girsite sono molte ficcoge.
- 29.I ciarimbi maipato hanno le bausie.
- 30.I linnui fivvato hanno le diste.
- 31.Lo spico parsilando stava una siscola.
- 32.Lo stoco artimando sta la bodova.
- 33. Qualche cisco tasiato ha ebinamente.
- 34. Molte stroidde duccato avevano afflinatamente.
- 35.Un conofo si degilato è sfavatamente.
- 36.Una banvia si berliata è anastemente.
- 37.Le parne pemolando stanno sascamente.
- 38.La ferola snebrando sta fodatamente.
- 39. Nessun dirro sodigliato ha.
- 40. Nessuna potena govisato aveva.
- 41. Nessun reseglio pomirato ha.
- 42. Non corlata era nessuna fodeta.
- 43. Non dibistatto è nessun gonullo.
- 44. Non mitenato è nessun mado.
- 45. Non stato camagito è nessun nauco.
- 46. Non stata demoggiata è nessuna lugua.
- 47. Non si bitelata era nessuna bica.
- 48. Non si revigito è nessun idoco.
- 49.I nerici non surnito avevano mai.
- 50.La pasulia non cadoccato ha mai.
- 51.La desa non gadiata è mai.
- 52.I coresbi non affantati furono mai.

#### **Violations of Grammatical rule 2:**

- 1. Non mai coledato il tallo ha.
- 2. La è fasalla vercata.
- 3. Percicato il radalo è blacunemente.
- 4. Corbando i stanno fepi.
- 5. Hanno molte lante intodato.
- 6. Qualche è si antalio pernicato.
- 7. I morpiti si titrami sono.
- 8. Le barroghe non bedando il stanno nirfolo.
- 9. Attociati i sono laterbi alivamente.
- 10.È non nessuna cortolata vatella.
- 11. Non è si angibito fipallo nessun.

#### **Non-Grammatical rule 1:**

- 1. Qualche ecamispo il non madisce tevo.
- 2. Molte stance i non confosano gorlani.
- 3. Alcune gicene il non viscarono velmo.
- 4. Nedile verpiscono le i tutti macri.
- 5. Dapo sdagrò il le tutte placine.
- 6. Ecorette hanno le telmito alcuni cidi.
- 7. Folucie hanno le affepito molti loppi.
- 8. Taro sta il già pivercando.
- 9. Bilberi stanno i già comuliando.
- 10. Tutti demi i si sirondano.
- 11. Tutti varalpi i si ratermirono.
- 12. Hanno intodato le tutte lante.
- 13. Hanno coledato i tutti patalli.
- 14. Stimbera snuttava la.
- 15. Grapotte amionarono le.
- 16. Goncido cetivò il.
- 17. Pibuti coffronavano i.
- 18. Pebari sono i stati alimati.
- 19. Bamo era il stato torlito.
- 20. Daffro non il si sfivverà.
- 21. Atrobale non le si dencirono.
- 22. Tanugie non le si taddeano.
- 23. Si gorciscono le tutte smalle.
- 24. Si girsiscono le tutte ficcoge.
- 25. Si erano i baguniti pridechi.
- 26. Si sono le zilie vibate.
- 27. Boladi confosano i molte sinte.
- 28. Napirze egazzarono le qualche pitanga.
- 29. Mafero acrosò il alcuni prelpi.
- 30. Polbo non il refisce mai.
- 31. Redo non il parsolò mai.
- 32. Doci non i moviarono mai.
- 33. Mibi sono i stati tutti enfriti.
- 34. Ferli sono i stati tutti arciati.
- 35. Verpeni non i disillarono.
- 36. Mafi non i cargirono.
- 37. Disti non i tersuerarono.
- 38. Fecisa metisce la il bodeto.
- 39. Tresbo avvupisce il i lefri.
- 40. Crampe amediscono le i corangi.
- 41. Micoli non i la sfivvarono velza.
- 42. Bitane non le il scabbirono matero.
- 43. Conure non le il tisennarono neco.
- 44. Barroghe stanno le il bedando nirfolo.
- 45. Spico stava lo una parsilando siscola.
- 46. Stoco sta lo la artimando bodova.

- 47. Ciratta ha la i didanato garpi.
- 48. Partaroghe hanno le i inuscato nugli.
- 49. Malusa ha la un trepito lendro.
- 50. Remiloti già i si fanagibiscono.
- 51. Becri già i si lappisavano.
- 52. Foralfo già il si ceslicava.

#### **Violations of Non-Grammatical rule 1:**

- 1. Molmeche alinavano questa le frida.
- 2. I sono gialevati consi.
- 3. Getranti non pugerirono i.
- 4. Dapostra non si la eulobava.
- 5. Pochi raboli tutti crolti vigognano i.
- 6. Fardana ha camepito la.
- 7. I si pringarono crombasi.
- 8. Tutti cretaldi si i cemubano.
- 9. Chiafo non irebisce il le gufole.
- 10. Gli non milesarono mai erdisi.
- 11. Lone ricero non il pernarono le.
- 12. Dustalco il la non ha amecato stada.

## **Non-Grammatical rule 2:**

- 1. Naldando l'arrumpa sta.
- 2. Sfogulando gli stafi stanno.
- 3. Ribogliato molti diransi avevano.
- 4. Trelumito alcuni tamideri hanno.
- 5. Zuminato molte lucche avevano.
- 6. Calfirato i saboli hanno.
- 7. Antocato le gordale hanno.
- 8. Derdanato i relinfi avevano.
- 9. Tutti i barti stanno si elfargando.
- 10. Tutte le corade stanno si nagendo.
- 11. Tutte le sfale sono si vercate.
- 12. Tutti i radali sono si percicati.
- 13. Tutte le ramude sono si amefite.
- 14. Dutalendo i cuspani stanno.
- 15. Colciando la ganta sta.
- 16. Arfendo la sadona sta.
- 17. Non saferito mai è lo sdarco.
- 18. Non tonciato mai è il lappento.
- 19. Non nispate mai sono le vadise.
- 20. Si mariffate alcune sono pode.
- 21. Si raspigorati molti erano gittoli.
- 22. Si trolcicate alcune sono foralfe.
- 23. Si pirobando molte stavano stiape.
- 24. Si irenibendo qualche stava maliafo.
- 25. Non gertito tutte avevano le nalche.

- 26. Non tenicato tutte le hanno sanfe.
- 27. Torgato alcuni peralfi hanno.
- 28. Acrotito alcune terve hanno.
- 29. Covilato alcuni berdi hanno.
- 30. Si bormobato ogni è frento.
- 31. Si uparite molte erano zubore.
- 32. Si dotenata qualche era otelca.
- 33. Utenato le ravie hanno vesitamente.
- 34. Verpicato i panfi hanno milpemente.
- 35. La mandiena non è si rivumata bademente.
- 36. I rebici non sono si genivati colsamente.
- 37. Pemolando le parne stanno sascamente.
- 38. Snebrando la ferola sta fodatamente.
- 39. Non ciusito qualche ha gittola.
- 40. Non pagotato qualche ha migo.
- 41. Non pergito molte hanno banfe.
- 42. Non stiperato i hanno botrunchi.
- 43. Non asserfito il ha pebranto.
- 44. Non nesicato i avevano turi.
- 45. Il berbiso non è si passurato.
- 46. La soga non è si burnata.
- 47. I borcisi non sono si darsiti.
- 48. Non mecato nessuna ha megola.
- 49. Non ponato nessun ha licero.
- 50. Non guisito nessuna ha boga.
- 51. I nedi non sono si coledati mai.
- 52. La beca non è si ronata mai.

# **Violations of Non-Grammatical rule 2:**

- 1. Pomogato un maplo ha.
- 2. Hanno le fordigato badere.
- 3. Non sono snebbicate si le savape.
- 4. Estemando i stanno nasbini.
- 5. Hanno quei nadito fiommi.
- 6. La gania aveva il margito crolo.
- 7. Le pegite si eggiore sono.
- 8. Lo spico colcirando una stava goranta.
- 9. Degilato un è conopo sfavatamente.
- 10. Nessuna era fideta si corlata.
- 11. Non è si gibeca bitelata nessuna.
- 12. Il grabo ha mai degizzato non.

#### 5.3 APPENDIX 3. STIMULI OF EMPIRICAL STUDY 3.3

## **Abstract sentences (baseline):**

## English translation:

Adoro la lealtà.
 Adoro l'ozio.
 Ammiro il coraggio.
 Ammiro la coerenza.
 Ammiro la costanza.
 Ammiro la perseveranza.
 Apprezzo la fedeltà.
 Apprezzo la sincerità.
 Apprezzo l'amicizia.
 Apprezzo le doti.
 Approvo il comportamento.

11.Approvo il comportamento12.Approvo il decreto.13.Approvo la decisione.14.Approvo l'atteggiamento.15.Attendo il congedo.16.Attendo un cambiamento.17.Attendo un chiarimento.18.Attendo una soluzione.

21.Confondo le idee.22.Confondo le storie.23.Considero i fatti.24.Cosidero la possibilità.25.Critico i vizi.

19.Confondo gli eventi.

20.Confondo i ricordi.

26.Critico la scelta.
27.Critico le idee.
28.Critico le ideologie.
29.Deduco il risultato.
30.Deduco la soluzione.
31.Desidero il ritorno.
32.Desidero la felicità.
33.Desidero la gioia.

34.Dimentico la domanda.35.Dimentico la promessa.36.Dimentico l'impegno.37.Esaudisco il desiderio.38.Esaudisco la promessa.39.Esaudisco la richiesta.40.Imagino lo spavento.41.Immagino la collera.

42.Immagino la delusione. 43.immagino la gioia. 44.Ipotizzo una soluzione.

44. Ipotizzo una soluzione. 45. Ipotizzo un'alternativa. I adore loyalty.
I adore laziness.
I admire courage.
I admire coherence.
I admire constancy.
I admire perseverance.
I appreciate faithfulness.
I appreciate sincerity.
I appreciate friendship.
I appreciate talents.
I approve the decree

I approve the decree.
I approve the decision.
I approve of the attitude.
I wait for the discharge.
I wait for a change.
I wait for a clarification.
I wait for a solution.
I confuse the events.
I confuse the memories.
I confuse the ideas.
I confuse the stories.
I consider the facts.
I consider the possibility.
I criticize the vices.

I criticize the choice.
I criticize the ideas.
I criticize the ideologies.
I deduce the results.
I deduce the solution.
I wish for a comeback.
I wish for happiness.
I wish for joy.
I forget the question.

I forget the promise.
I forget the commitment.
I grant the desire.
I grant the promise.
I fulfill the request.
I imagine the fright.
I imagine the rage.

I imagine the disappointment.

I imagine the joy. I hypothesize a solution. I hypothesize an alternative. 46.Perdono il peccato.
47.Perdono il torto.
48.Perdono la colpa.
49.Perdono l'offesa.
50.Ricordo il fatto.
51.Ricordo il passato.
52.Ricordo l'accaduto.
53.Ricordo l'infanzia.
54.Temo la delusione.

55.Temo la prova. 56.Temo la sconfitta. 57.Temo l'indifferenza. 58.Tollero l'offesa. 59.Tollero la povertà. 60.Tollero un inganno. 61.Tollero uno sgarbo. 62.Valuto gli errori.

63. Valuto il comportamento.

64. Valuto il merito.65. Valuto la condotta.

I forgive the sin.
I forgive the wrong.
I forgive the guilt.
I forgive the offense.
I remember the fact.
I remember the past.
I remember the event.
I remember childhood.
I fear a disappointment.

I fear a disappointment.
I fear the trial.
I fear a defeat.
I fear indifference.
I tolerate the offense.
I tolerate poverty.
I tolerate betrayal.
I tolerate an insult.
I evaluate the mistakes.
I evaluate the behavior.
I evaluate the merit.

I evaluate the conduct.

# **Sentences describing mouth actions:**

Addento il panino.
 Addento il torrone.
 Addento una brioche.
 Addento una carota.
 Addento una mela.
 Bacio il bambino.
 Bacio la fronte.

8. Bacio la guancia.9. Bacio le labbra.10.Fischio al cane.11.Fischio la canzone.12.Fischio un motivetto.

13.Inghiotto il boccone.14.Inghiotto la pastiglia.15.Inghiotto lo sciroppo.16.Lecco il cucchiaio.17.Lecco il gelato.

18.Lecco il piatto.
19.Lecco la crema.
20.Mastico il pane.
21.Mastico la cicca.
22.Mastico la focaccia.
23.Mastico la pizza.

24. Mordicchio il cracker. 25. Mordicchio la matita. 26. Rosicchio le unghie.

27.Rosicchio le costine.

I bite into a sandwich. I bite into the nougat.

I bite into the hough I bite the pastry. I bite the carrot. I bite an apple. I kiss the child. I kiss the forehead. I kiss the cheek.

I kiss the cheek.
I kiss the lips.
I whistle at the dog.
I whistle the song.
I whistle the jingle.
I swallow the bite.
I swallow the pill.
I swallow the syrup.
I lick the spoon.
I lick the ice-cream.
I lick the dish.
I lick the cream.
I chew the bread.

I chew the bread.
I chew some gum.
I chew the focaccia.
I chew the pizza.
I nibble the cracker.
I nibble the pencil.
I bite my nails.
I nibble the ribs.

28.Sgranocchio i biscotti. I munch the cookies. 29.Sgranocchio il popocorn. I munch the popcorn. 30.Sgranocchio le mandorle. I munch the almonds. 31.Sgranocchio le noci. I munch the nuts. 32. Soffio sul fuoco. I blow on the fire. 33.Soffio sulla candela. I blow on the candle. 34.Soffio sulla ferita. I blow on the wound. 35. Succhio il biberon. I suck from the baby bottle. 36. Succhio il ciuccio. I suck on a pacifier. I suck my finger. 37. Succhio il dito. 38. Succhio la bibita. I suck from a straw. 39. Succhio una caramella. I suck on hard candy. 40. Succhio una pasticca. I suck on a lozenge.

# **Sentences describing hand actions:**

1. Abbottono il cappotto. I button the coat. 2. Abbottono l'impermeabile. I button the raincoat. 3. Abbottono la camicia. I button the shirt. 4. Abbottono la giacca. I button the jacket. I stroke the hair. 5. Accarezzo i capelli. 6. Accarezzo il cane. I stroke the dog. 7. Accarezzo la bimba. I stroke the child. 8. Accarezzo la guancia. I stroke the cheek. 9. Afferro il pugnale. I grasp the dagger. 10. Afferro la fune. I grasp the rope. I grasp a stick. 11. Afferro un bastone. 12. Afferro un coltello. I grasp a knife. 13.Disegno un albero. I draw a tree. 14. Disegno un paesaggio. I draw a landscape. 15.Disegno una barca. I draw a boat. 16.Disegno una casa. I draw a house.

17.Impugno il volante.I grab the steering wheel.18.Impugno la maniglia.I grab the handle.19.Impugno la matita.I grab the pencil.20.Impugno la penna.I grab the pen.

21. Ricamo un fazzoletto. I embroider a handkerchief.

22.Ricamo un lenzuolo. I embroider a sheet. 23. Ricamo un tovagliolo. I embroider a napkin. I embroider a table cloth. 24.Ricamo una tovaglia. 25.Sfoglio il giornale. I leaf through the newspaper. 26. Sfoglio un catalogo. I leaf through a catalogue. 27.Sfoglio un libro. I leaf through a book. 28.Sfoglio una rivista. I leaf through a magazine. 29. Spalmo il burro. I spread the butter.

29. Spalmo il burro.

30. Spalmo la crema.

31. Spalmo la lozione.

32. Spalmo la nutella.

33. Spezzo il pane.

34. Spezzo il torrone.

I spread the butter.

I spread the cream.

I spread the lotion.

I spread the chocolate.

I break the bread.

I break the nougat.

35. Spezzo un biscotto. 36. Spezzo un grissino.

37. Suono il campanello.

38.Suono il piano. 39.Suono l'arpa.

40. Suono la chitarra.

I break a cookie.

I break a breadstick.

I ring the bell.

I play the piano.

I play the harp.

I play the guitar.

# Sentences describing leg actions:

1. Calcio il pallone.

2. Calcio la palla.

3. Calcio un barattolo.

4. Calcio un sasso.

5. Calpesto gli sterpi.

6. Calpesto il pavimento.

7. Calpesto il tappeto.

8. Calpesto le foglie.

9. Infilo gli zoccoli.

10.Infilo i mocassini.

11.Infilo le ciabatte.

12.Infilo le pantofole.

13.Pesto l'erba.

14.Pesto la coda.

15.Pesto un mozzicone.

16.Pesto una cicca.

17.Pigio il freno.

18.Pigio il pedale.

19.Pigio l'uva.

20.Pigio la frizione.

21.pigio l'acceleratore.

22.Premo il freno.

23. Premo il pedale.

24.Premo l'acceleratore.

25.Premo la frizione.

26. Scalpiccio sul selciato.

27. Scalpiccio sulla ghiaia.

28. Scalpiccio sulla neve. 29. Scalpiccio sulla sabbia.

30. Schiaccio una formica.

31. Schiaccio il fogliame.

32. Schiaccio una lumaca.

33. Schiaccio uno scarafaggio.

34.Sfilo gli zoccoli.

35.Sfilo le ciabatte.

36.Sfilo le pantofole.

37. Spiaccico un verme.

38. Spiaccico una buccia di banana.

39. Spiaccico una formica.

40. Spiaccico una lumaca.

I kick the football.

I kick the ball.

I kick a can.

I kick a stone.

I stamp on the branches.

I stamp on the floor.

I stamp on the carpet.

I stamp on the leaves.

I slip on the clogs.

I slip on the moccasins.

I slip on the slides.

I slip on the slippers.

I step on the grass.

I step on the tail.

I step on the cigarette butt.

I step on the chewing gum.

I press the brake.

I press the pedal.

I press the grapes.

I press the clutch.

I press the accelerator.

I slam on the brakes.

I slam on the pedal.

I slam on the accelerator.

I slam on the clutch.

I pound the pavement.

I pound the gravel.

I pound the snow.

I pound the sand.

I crush an ant.

I crush the leaves.

I crush a slug.

I crush a beetle.

I remove the clogs.

I remove the slides.

I remove the slippers.

I squash a worm.

I squash a banana peel.

I squash an ant.

I squash a slug.

"I cannot combine some characters 'dhcmrlchtdj' which the divine Library has not foreseen and which in one of its secret tongues do not contain a terrible meaning."

Jorge Luis Borges, "The Library of Babel"

# 6. REFERENCES

- Abutalebi J., Cappa S.F., and Perani D. The bilingual brain as revealed by functional neuroimaging. *Bilingual. Lang. Cogn.* 4(2): 179-190, 2001.
- Alexander M.P., Naeser M.A., and Palumbo C.L. Correlations of subcortical CT lesion sites and aphasia profiles. *Brain* 110(4): 961-991, 1987.
- Amunts K., Schleicher A., Buergel U., Mohlberg H., Uylings H.B.M., and Zilles K. Broca's Region Revisited: Cytoarchitecture and Intersubject Variability. *J. Comp. Neurol.* 412: 319-341, 1999.
- Ansari D. and Karmiloff-Smith A. Atypical trajectories of number development: a neuroconstructivist perspective. *Trends Cogn. Sci.* 6(12): 511-516, 2002.
- Ashburner J. and Friston K.J. Nonlinear spatial normalization using basis functions. *Hum. Brain Mapp.* 7(4): 254-266, 1999.
- Aslin R.N., Saffran J.R., and Newport E.L. Computation of conditional probability statistics by 8-month-old infants. *Psychol. Sci.* 9: 321-324, 1998.
- Atkinson J.R., Woll B., and Gathercole S. The impact of developmental visuospatial learning difficulties on British Sign Language. *Neurocase* 8: 424-441, 2002.
- Balzano G.J. Music perception as detection of pitch-time constraints. In: *Event cognition: An ecological perspective*, ed. McCabe V. and Balzano G.J. Hillsdale, NJ: Erlbaum, 1986.
- Bates E. and Dick F. Language, gesture, and the developing brain. *Dev. Psychol.* 40(3): 293-310, 2002.
- Bauer P.J. and Thal D. Scripts or scraps: Reconsidering the development of sequential understanding. *J. Exp. Child Psychol.* 50(2): 287-304, 1990.
- Bauer P.J., Dow G.A., Bittinger K.A., and Wenner J.A. Accepting and exempting the unexpected: 30-months-olds' generalization of event knowledge. *Cogn. Devel.* 13: 421-452, 1998a.
- Bauer P.J., Hertsgaard L.A., Dropik P., and Daly B.P. When even arbitrary order becomes important:

  Developments in reliable temporal sequencing of arbitrarily ordered events. *Memory* 6(2): 165-198, 1998b.
- Bavelier D., Corina D.P., and Neville H.J. Brain and language: A perspective from sign language.

- Neuron 21: 275-278, 1998.
- Baynes K. and Gazzaniga M.S. Right hemisphere language: insights into normal language mechanisms? *Res. Publ. Assoc. Res. Nerv. Ment. Dis.* 66: 117-126, 1988.
- Beagles-Ross J. and Greenfield P.M. Development of structure and strategy in two-dimensional pictures. *Devel. Psychol.* 15(5): 483-494, 1979.
- Bertoncini J., Morais J., Bijeljac-Babic R., McAdams S., Peretz I., and Mehler J. Dichotic perception and laterality in neonates. *Brain Lang.* 37(4): 591-605, 1989.
- Bickerton D. Language and Species. Chicago: University of Chicago Press, 1990.
- Bickerton D. Syntax is not as simple as it seems. Behav. Brain Sci. 14(4): 552-553, 1991.
- Blakemore S.J. and Decety J. From the perception of action to the understanding of intention. *Nat. Rev. Neurosci.* 2(8): 561-567, 2001.
- Bock K. and Levelt W.J.M. Language Production: Grammatical Encoding. In: *Handbook of Psycholinguistics*, ed. Gernsbacher M.A. San Diego, CA: Academic Press, 1994, p. 945-984.
- Boesch C. Aspects of transmission of tool-use in wild chimpanzees. In: *Tools, language and cognition in human evolution*, ed. Gibson K.R. and Ingold T. Cambridge, MA: Cambridge University Press, 1993, p. 171-184.
- Bookheimer S.Y., Zeffiro T.A., Blaxton T.A., Gaillard P.W., and Theodore W.H. Activation of language cortex with automatic speech tasks. *Neurology* 55(8): 1151-1157, 2000.
- Brannon E.M. and Terrace H.S. Ordering of the numerosities 1 to 9 by monkeys. *Science* 282(5389): 746-749, 1998.
- Broca P. Sur le siège de la faculté du langage articulé. Bull. Soc. Anthropol. 6: 377-393, 1865.
- Buccino G., Binkofski F., Fink G.R., Fadiga L., Fogassi L., Gallese V., Seitz R.J., Zilles K., Rizzolatti G., and Freund H.-J. Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur. J. Neurosci.* 13: 400-404, 2001.
- Butterworth B. A head for figures. Science 284: 928-929, 1999.
- Capirci O., Iverson J., Pizzuto E., and Volterra V. Gestures and words during the transition to two-

- word speech. J. Child Lang. 23: 645-673, 1996.
- Caplan D., Matthei E., and Gigley H. Comprehension of gerundive constructions by Broca's aphasics. *Brain Lang.* 13: 145-169, 1981.
- Caplan D., Alpert N., and Waters G. Effects of syntactic structure and propositional number on patterns of regional cerebral blood flow. *J. Cogn. Neurosci.* 10(4): 541-552, 1998.
- Caplan D., Alpert N., and Waters G. PET studies of syntactic processing with auditory sentence presentation. *Neuroimage* 9(3): 343-351, 1999.
- Caplan D. and Waters G.S. Verbal working memory and sentence comprehension. *Behav. Brain Sci.* 22(1): 77-94, 1999.
- Cartwright T.A. and Brent M.R. Early acquisition of syntactic categories: a formal model. *Cognition* 63: 121-170, 1997.
- Changeux J.P. and Dehaene S. Hierarchical neuronal modeling of cognitive functions: from synaptic transmission to the Tower of London. *Int. J. Psychophysiol.* 35(2-3): 179-187, 2000.
- Chee M.W., Caplan D., Soon C.S., Sriram N., Tan E.W., Thiel T., and Weekes B. Processing of visually presented sentences in Mandarin and English studied with fMRI. *Neuron* 23(1): 127-137, 1999.
- Chein J.M., Fissell K., Jacobs S., and Fiez, J.A. Functional heterogeneity within Broca's area during verbal working memory. *Physiol. Behav.* 77(4-5): 635-639, 2002.
- Cheour M., Ceponiene R., Lehtokoski A., Luuk A., Allik J., Alho K., and Naatanen R. Development of language-specific phoneme representations in the infant brain. *Nat. Neurosci.* 1(5): 351-353, 1998.
- Chomsky N. Aspects in the Theory of Syntax. Cambridge, MA: MIT Press, 1965.
- Chomsky N. Reflections on Languages. New York: Pantheon, 1975.
- Chomsky N. Lectures on Government and Binding. Dordrecht: Foris, 1981.
- Chomsky N. The Minimalist Program. Cambridge, MA: MIT Press, 1995.
- Cleeremans A., Servan-Schreiber D., and McClelland J.L. Finite state automata and simple recurrent

- networks. Neural Comput. 1: 372-381, 1989.
- Clynes M. Music, mind and brain: The neuropsychology of music. London: Plenum, 1982.
- Cochin S., Barthelemy C., Roux S., and Martineau J. Observation and execution of movement: similarities demonstrated by quantified electroencephalography. *Eur. J. Neurosci.* 11(5): 1839-1842, 1999.
- Connolly K.J. and Dalgleish M. The emergence of tool-using skill in infancy. *Devel. Psychol.* 25(5): 894-912, 1989.
- Conway C.M. and Christiansen M.H. Sequential learning in non-human primates. *Trends Cogn. Sci.* 5(12), 2001.
- Corbetta M., Shulman G.L., Miezin F.M., and Petersen S.E. Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. *Science* 270(5237): 802-805, 1995.
- Corina D.P. and Sandler W. On the nature of phonological structure in sign language. *Phonology* 10: 165-207, 1993.
- Corina D.P. Aphasia in users of signed languages. In: *Aphasia in Atypical Populations*, ed. Coppens P., Lebrun Y. and Basso A. Hillsdale, NJ: Erlbaum, 1998, p. 261-309.
- Cummings J.L. and Benson D.F. Subcortical dementia. Review of an emerging concept. *Arch. Neurol.* 41(8): 874-879, 1984.
- Dapretto M. and Bookheimer S.Y. Form and Content: Dissociating Syntax and Semantics in Sentence Comprehension. *Neuron* 24: 427-432, 1999.
- De Mauro T., Mancini F., Vedovelli M., and Voghera M. *Lessico di frequenza dell' italiano parlato*.

  Roma: Etaslibri, 1993.
- Dehaene S. and Changeux J.P. The Wisconsin Card Sorting Test: theoretical analysis and modeling in a neuronal network. *Cereb. Cortex* 1(1): 62-79, 1991.
- Dehaene S. and Cohen L. Towards an anatomical and functional model of number processing. *Math. Cogn.* 1: 83-120, 1995.

- Dehaene S., Dupoux E., Mehler J., Cohen L., Paulesu E., Perani D., van de Moortele P.F., Lehericy S., and Le Bihan D. Anatomical variability in the cortical representation of first and second language. *Neuroreport* 8(17): 3809-3815, 1997.
- Dehaene S., Dehaene-Lambertz G., and Cohen L. Abstract representation of number in the animal and human brain. *Trends Neurosci.* 21(8): 355-361, 1998.
- Dehaene S., Spelke E., Pinel P., Stanescu R., and Tsivkin S. Sources of mathematical thinking: behavioral and brain-imaging evidence. *Science* 284: 970-974, 1999.
- Dehaene-Lambertz G. and Dehaene S. Speed and cerebral correlates of syllable discrimination in infants. *Nature* 370(6487): 292-295, 1994.
- Dehaene-Lambertz G. and Houston D. Faster orientation latency toward native language in two-month-old infants. *Lang. Speech* 41(1): 21-43, 1998.
- Dehaene-Lambertz G., Dehaene S., and Hertz-Pannier L. Functional neuroimaging of speech perception in infants. *Science* 298: 2013-1015, 2002.
- Déjerine J. Semiologie des affections du système nerveux. Paris: Masson, 1914.
- Delis D.C., Kiefner M.G., and Fridlund A.J. Visuospatial dysfunction following unilateral brain damage: dissociations in hierarchical and hemispatial analysis. *J. Clin. Exp. Neuropsychol.* 10 (4): 421-431, 1988.
- Dominey P.F. and Georgieff N. Schizophrenics learn surface but not abstract structure in a serial reaction time task. *Neuroreport* 8(13): 2877-2882, 1997.
- Dominey P.F., Ventre-Dominey J., Broussolle E., and Jeannerod M. Analogical transfer is effective in a serial reaction time task in Parkinson's disease. *Neuropsychologia* 35(1): 1-9, 1997.
- Dominey P.F., Lelekov T., Ventre-Dominey J., and Jeannerod M. Dissociable processes for learning the surface structure and abstract structure of sensorimotor sequences. *J. Cogn. Neurosci.* 10 (6): 734-751, 1998.
- Dowty D.R., Wall R.E., and Peters S. *Introduction to Montague Semantics*. Dordrecht: Reidel Publishing Company, 1981.

- Dronkers N.F. A new brain region for coordinating speech articulation. *Nature* 384(6605): 159-161, 1996.
- Dryer M. The greenbergian word order correlations. Language 68(1): 81-138, 1992.
- Ejiri K. and Masataka N. Co-occurrence of preverbal vocal behavior and motor action in early infancy. *Devel. Sci.* 4(1): 40-48, 2001.
- Ekman P. and Friesen W.V. The repertoire of nonverbal behaviour: Categories, origins and coding. Semiotica 1: 49-98, 1969.
- Elman J.L. Distributed representations, simple recurrent networks, and grammatical structure. *Machine Learn.* 7: 195-224, 1991.
- Embick D., Marantz A., Miyashita Y., O Neil W., and Sakai K.L. A syntactic specialization for Broca's area. *Proc. Natl. Acad. Sci. USA* 97(11): 6150-6154, 2000.
- Emmorey K., Damasio H., McCullough S., Grabowski T., Ponto L.L.B., Hichwa R.D., and Bellugi U. Neural systems underlying spatial language in American Sign Language. *Neuroimage* 17: 812-824, 2002.
- Fadiga L., Fogassi L., Pavesi G., and Rizzolatti G. Motor facilitation during action observation: a magnetic stimulation study. *J. Neurophysiol.* 73(6): 2608-2611, 1995.
- Fink G.R., Halligan P.W., Marshall J.C., Frith C.D., Frackowiak R.S.J., and Dolan R.J. Where in the brain does visual attention select the forest and trees? *Nature* 382: 626-628, 1996.
- Fletcher P. and MacWhinney B. Handbook of child language. Oxford: Basil Blackwell, 1995.
- Fletcher P., Buchel C., Josephs O., Friston K., and Dolan R. Learning-related neuronal responses in prefrontal cortex studied with functional neuroimaging. *Cereb. Cortex* 9(2): 168-178, 1999.
- Fletcher P.C. and Henson R.N. Frontal lobes and human memory: insights from functional neuroimaging. *Brain* 124(5): 849-881, 2001.
- Flowers K.A. and Robertson C. The effect of Parkinson's disease on the ability to maintain a mental set. *J Neurol Neurosurg Psychiatry* 48(6): 517-529, 1985.
- Frison L. and Pocock S.J. Repeated measures in clinical trials: Analysis using mean summary

- statistics and its implications for design. Stat. Med. 11: 1685-1704, 1992.
- Friston K.J., Ashburner J., Poline J.B., Frith C.D., Heather J.D., and Frackowiak R.S.J. Spatial resistration and normalization of images. *HuM. Brain Map.* 2: 165-189, 1995a.
- Friston K.J., Holmes A.P., Worsley K.J., Poline J.B., Frith C.D., and Frackowiak R.S.J. Statistical parametric maps: confidence intervals on p-values. *Hum. Brain Mapp.* 2: 189-210, 1995b.
- Gabrieli J.D.G. The role of left prefrontal cortex in language and memory. *Proc. Natl. Acad. Sci. USA* 95: 906-913, 1998.
- Gallese V., Fadiga L., Fogassi L., and Rizzolatti G. Action recognition in the premotor cortex. *Brain* 119(2): 593-609, 1996.
- Gallese V., Fogassi L., Fadiga L., and Rizzolatti G. Action representation and the inferior parietal lobule. In: *Common mechanisms in perception and action: Attention and Performance, Vol. XIX*, ed. Prinz W. and Hommel B. Oxford, UK: Oxford University Press, 2002, p. 334-355.
- Gangitano M., Mottaghy F.M., and Pascual-Leone A. Phase-specific modulation of cortical motor output during movement observation. *Neuroreport* 12(7): 1489-1492, 2001.
- Gazzaniga M.S. The role of language for conscious experience: observations from split-brain man. *Prog. Brain Res.* 54: 689-696, 1980.
- Gazzaniga M.S., Smylie C.S., Baynes K., Hirst W., and McCleary C. Profiles of right hemisphere language and speech following brain bisection. *Brain Lang.* 22: 206-220, 1984.
- Gerardin E., Sirigu A., Lehericy S., Poline J.B., Gaymard B., Marsault C., Agid Y., and Le Bihan D. Partially overlapping neural networks for real and imagined hand movements. *Cereb. Cortex* 10(11): 1093-1104, 2000.
- Gibson K.R. Tool use, language and social behavior in relationship to information processing capacities. In: *Tools, language and cognition in human evolution*, ed. Gibson K.R. and Ingold T. Cambridge, MA: Cambridge University Press, 1993, p. 251-270.
- Givon T. Toward a neurology of grammar. Behav. Brain Sci. 21(1): 154-155, 1998.
- Goldin-Meadow S. and Mylander C. Spontaneous sign systems created by deaf children in two

- cultures. Nature 391: 279-281, 1998.
- Golestani N., Paus T., and Zatorre R.J. Anatomical correlates of learning novel speech sounds.

  Neuron 35: 997-1010, 2002.
- Goodson B.D. and Greenfield P.M. The search for structural principles in children's manipulative play. *Child Devel.* 46: 734-746, 1975.
- Grafton S.T., Arbib M.A., Fadiga L., and Rizzolatti G. Localization of grasp representations in humans by positron emission tomography. 2. Observation compared with imagination. *Exp. Brain Res.* 112(1): 103-111, 1996.
- Greenberg J.H. Some Universals of Grammar with Particular Reference to the Order of Meaningful Elements. In: *Universals of Language*, ed. Greenberg J.H. Cambridge, MA: MIT Press, 1963, p. 73-113.
- Greenfield P.M., Nelson K., and Saltzman E. The development of rulebound strategies for manipulating seriated cups. *Cogn. Psychol.* 3: 291-310, 1972.
- Greenfield P.M. and Schneider L. Building a tree structure. The development of hierarchical complexity and interrupted strategies in children's construction activity. *Devel. Psychol.* 13: 299-313, 1977.
- Greenfield P.M. Structural parallels between language and action in development. In: *Action, symbol, and gesture: The emergence of language*, ed. Lock A. New York: Academic Press, 1978.
- Greenfield P.M. Language, tools and brain: The ontogeny and phylogeny of hierarchically organized sequential behavior. *Behav. Brain Sci.* 14: 531-595, 1991.
- Greenfield P.M. Language, tools, and brain revisited. Behav. Brain Sci. 21(1): 159-163, 1998.
- Grèzes J., Costes N., and Decety J. Top-down effect of strategy on the perception of human biological motion: a PET investigation. *Cogn. Neuropsychol.* 15: 553-582, 1998.
- Grodzinsky Y. The neurology of syntax: Language use without Broca's area. *Behav. Brain Sci.* 23: 1-71, 2000.

- Grossman M. A central processor for hierarchically structured material: Evidence from Broca's aphasia. *Neuropsychologia* 18: 299-308, 1980.
- Grossman M., Carvell S., Gollomp S., Stern M.B., Vernon G., and Hurtig H.I. Sentence comprehension and praxis deficits in Parkinson's disease. *Neurology* 41(10): 1620-1626, 1991.
- Haegemann L. Introduction to Government and Binding Theory. Oxford: Blackwell, 1994.
- Han S., Fan S., Chen L., and Zhuo Y. Modulation of Brain Activities by hierarchical processing: a high-density ERP study. *Brain Topogr.* 11(3): 171-183, 1999.
- Hari R., Forss N., Avikainen S., Kirveskari E., Salenius S., and Rizzolatti G. Activation of human primary motor cortex during action observation: a neuromagnetic study. *Proc. Natl. Acad. Sci. USA* 95(25): 15061-15065, 1998.
- Hauser M.D., Chomsky N., and Fitch W.T. The faculty of language: what is it, who has it, and how did it evolve? *Science* 298: 1569-1579, 2002.
- Hildebrandt U. and Corina D. Phonological similarity in American Sign Language. *Lang. Cogn. Processes* 17(6): 593-612, 2002.
- Hirsh-Pasek K., Kemler Nelson D.G., Jusczyk P.W., Cassidy K.W., Druss B., and Kennedy L. Clauses are perceptual units for young infants. *Cognition* 26: 269-286, 1987.
- Iacoboni M., Woods R.P., Brass M., Bekkering H., Mazziotta J.C., and Rizzolatti G. Cortical mechanisms of human imitation. *Science* 286: 2526-2528, 1999.
- Ifrah G. Histoire Universelle des Chiffres. Paris: Robert Laffont, 1994.
- Isaacs E.B., Edmonds C.J., Lucas A., and Gadian D.G. Calculation difficulties in children of very low birthweight: a neural correlate. *Brain* 124(9): 1701-1707, 2001.
- Iverson J.M. and Goldin-Meadow S. *The nature and functions of gesture in children's communication*. San Francisco, CA: Jossey-Bass, 1998.
- Jackendoff R. X-bar Syntax: A Study of Phrase Structure. Cambridge, MA: MIT Press, 1977.
- Jackendoff R. Parallel constraint-based generative theories of language. *Trends Cogn. Sci.* 3(10): 393-400, 1999a.

- Jackendoff R. Possible stages in the evolution of the language capacity. *Trends Cogn. Sci.* 3(7): 272-279, 1999b.
- Jackendoff R.S. An Interpretive Theory of Negation. Foundation of Language 5: 218-241, 1968.
- Jeannerod M. The Cognitive Neuroscience of Action. Oxford, UK: Blackwell, 1997.
- Johnson-Pynn J., Fragaszy D.M., Hirsh E.M., Brakke K.E., and Greenfield P.M. Strategies used to combine seriated cups by chimpanzees (Pan troglodytes), bonobos (Pan paniscus) and capuchins (Cebus apella). *J. Comp. Psychol.* 113: 137-148, 1999.
- Jonides J., Smith E.E., Koeppe R.A., Awh E., Minoshima S., and Mintun M.A. Spatial working memory in humans as revealed by PET. *Science* 363: 623-625, 1993.
- Jusczyk P.W., Friederici A.D., Wessels J.M.I., Svenkerud V.Y., and Jusczyk A.M. Infants' Sensitivity to the Sound Patterns of Native Language Words. *J. Mem. Lang.* 32(3): 402-420, 1993.
- Jusczyk P.W. The Discovery of Spoken Language. Cambridge, MA: MIT Press, 1997.
- Just M.A., Carpenter P.A., Keller T.A., Eddy W.F., and Thulborn K.R. Brain activation modulated by sentence comprehension. *Science* 274(5284): 114-116, 1996.
- Kang A.M., Constable R.T., Gore J.C., and Avrutin S. An event-related fMRI study of implicit phrase-level syntactic and semantic processing. *Neuroimage* 10: 555-561, 1999.
- Katz J. and Postal P. An Integrated Theory of Linguistic Descriptions. Cambridge, MA: MIT Press, 1964.
- Kayne R. *The Antisymmetry of Syntax*. Cambridge, MA: MIT Press, 1994.
- Kean M.L. Agrammatism. New York: Academic Press, 1985.
- Kim K.H., Relkin N.R., Lee K.M., and Hirsch J. Distinct cortical areas associated with native and second languages. *Nature* 388(6638): 171-174, 1997.
- Klein D., Milner B., Zatorre R.J., Meyer E., and Evans A.C. The neural substrates underlying word generation: a bilingual functional-imaging study. *Proc. Natl. Acad. Sci. USA* 92(7): 2899-2903, 1995.

- Klein N.K., Hack M., and Breslau N. Children who were very low birthweight: development and academic achievement at nine years of age. *J. Dev. Behav. Pediatr.* 10(1): 32-37, 1989.
- Klima E.S. and Bellugi U. The signs of language. Cambridge, MA: Harvard University Press, 1979.
- Kohler E., Keysers C., Umilta M.A., Fogassi L., Gallese V., and Rizzolatti G. Hearing sounds, understanding actions: action representation in mirror neurons. *Science* 297(5582): 846-848, 2002.
- Kuhl P.K. A new view of language acquisition. *Proc. Natl. Acad. Sci. USA* 97(22): 11850-11857, 2000.
- Lane P. and Henderson J. Simple synchrony networks: learning to parse natural language with temporal synchrony variable binding. *Proc. 8th Int. Conf. Artif. Neural Netw.* Springer Verlag, 1998, p. 615-620.
- Langer J. The origins of logic: One to two years. New York: Academic Press, 1986.
- Langer J. Comparative cognitive development. In: *Tools, language, and cognition in human evolution*, ed. Gibson K. and Ingold T. New York: Cambridge University Press, 1993, p. 300-313.
- Langer J. From acting to understanding: The comparative development of meaning. In: *The nature* and ontogenesis of meaning, ed. Overton W.F. and Palermo D. Hillsdale, NJ: Erlbaum, 1994, p. 191-214.
- Langer J., Schlesinger M., Spinozzi G., and Natale F. Developing classification in action: I. Human infants. *Hum. Evol.* 13: 107-124, 1998.
- Lashley K.S. The problem of serial order in behavior. In: *Cerebral mechanisms in behavior: The Hixon Symposium*, ed. Jeffress L.A. New York: Wiley, 1951, p. 112-146.
- Lawrence S., Giles C.L., and Fong S. Natural language grammatical inference with recurrent neural networks. *IEEE Trans. Knowl. Data Eng.* 12(1): 126-140, 2000.
- Lecours A.R. The "Pure Form" of the phonetic disintegration syndrome (pure anarthria); anatomoclinical report of a historical case. *Brain Lang.* 3(1): 88-113, 1976.

- Lelekov-Boissard T. and Dominey P.F. Human brain potentials reveal similar processing of non-linguistic abstract structure and linguistic syntactic structure. *Neurophysiol. Clin.* 32: 72-84, 2002.
- Lerdah F. and Jackendoff R. A generative theory of tonal music. Cambridge, MA: MIT Press, 1983.
- Levelt W.J.M. Speaking: from intention to articulation. Cambridge, MA: MIT Press, 1989.
- Lewedag V.L., Oller D.K., and Lynch M.P. Infants' vocalization patterns across home and laboratory environments. *First Lang.* 14(40): 49-65, 1994.
- Liddell S. American Sign Language Syntax. New York: Mouton, 1980.
- Lieberman P., Friedman J., and Feldman L.S. Syntax comprehension deficits in Parkinson's disease. *J Nerv Ment Dis* 178(6): 360-365, 1990.
- Lillo-Martin D. and Klima E.S. Pointing out differences: ASL pronouns in syntactic theory. In: *Theoretical Issues in Sign Language Research, Vol 1. Linguistics*, ed. Fischer S.D. and Siple P. Chicago: University Chicago Press, 1990, p. 191-210.
- Lillo-Martin D.C. Universal Grammar and American Sign Language: Setting the Null Argument Parameters. Boston, MA: Kluwer Academic Publishers, 1991.
- Locke J.L., Bekken K.E., McMinn-Larson L., and Wein D. Emergent control of manual and vocal-motor activity in relation to the development of speech. *Brain Lang.* 51(3): 498-508, 1995.
- MacDonald M.C., Pearlmutter N.J., and Seidenberg M.S. Syntactic ambiguity resolution as lexical ambiguity resolution. In: *Perspective on Sentence Processing*, ed. Clifton C., L. F. and K. R. Hillsdale, NJ: Erlbaum, 1994, p. 123-153.
- MacSweeney M., Woll B., Campbell R., Calvert G., McGuire P., David A.S., Simmons A., and Brammer M.J. Neural correlates of British Sign Language comprehension: spatial processing demands of topographic language. *J. Cogn. Neurosci.* 14(7): 1064-1075, 2002.
- Maess B., Koelsch S., Gunter T.C., and Friederici A.D. Musical syntax is processed in Broca's area: an MEG study. *Nat. Neurosci.* 4(5): 540-545, 2001.
- Marcus G.F., Vijayan S., Bandi Rao S., and Vishton P.M. Rule learning by seven-month-old infants.

- Science 283(5398): 77-80, 1999.
- Marshuetz C., Smith E.E., Jonides J., De Gutis J., and Chenevert T.L. Order information in working memory: fMRI evidence for parietal and prefrontal mechanisms. *J. Cogn. Neurosci.* 12(2): 130-144, 2000.
- Martin A., Haxby J.V., Lalonde F.M., Wiggs C.L., and Ungerleider L.G. Discrete cortical regions associated with knowledge of color and knowledge of action. *Science* 270(5233): 102-105, 1995.
- Martin A., Wiggs C.L., Ungerleider L.G., and Haxby J.V. Neural correlates of category-specific knowledge. *Nature* 379(6566): 649-652, 1996.
- Matsuzawa T. Nesting cups and metatools in chimpanzees. Behav. Brain Sci. 14(4): 570-572, 1991.
- Mayberry M.R. and Miikkulainen R. Combining maps and distributed representations for shift-reduce parsing. In: *Hybrid Neural Systems*, ed. Wermter S. and Sun R.: Springer Verlag, 2000, p. 144-157.
- McClelland J.L. and Plaut D.C. Does generalization in infant learning implicate abstract algebra-like rules? *Trends Cogn. Sci.* 3(5): 166-168, 1999.
- McGrew W. The intellingent use of tools. Twenty propositions. In: *Tools, language and cognition in human evolution*, ed. Gibson K.R. and Ingold T. New York: Cambridge University Press, 1993, p. 151-170.
- Mega M.S. and Alexander M.P. Subcortical aphasia: the core profile of capsulostriatal infarction.

  Neurology 44(10): 1824-1829, 1994.
- Mehler J., Lambertz G., Jusczyk P., and Amiel-Tison C.R. Discrimination de la langue maternelle par le nouveau-né. *C.R. Acad. Sci. Paris* 303(15): 637-640, 1986.
- Mehler J., Jusczyk P., Lambertz G., Halsted N., Bertoncini J., and Amiel-Tison C. A precursor of language acquisition in young infants. *Cognition* 29: 143-178, 1988.
- Mesulam M.M. and Mufson E.J. Insula of the old world monkey. III: Efferent cortical output and comments on function. *J. Comp. Neurol.* 212(1): 38-52, 1982.

- Meyer L. *The analysis and cognition of basic melodic structures*. Chicago: University of Chicago Press, 1956.
- Meyer M., Friederici A.D., and von Cramon D.Y. Neurocognition of auditory sentence comprehension: event related fMRI reveals sensitivity to syntactic violations and task demands. *Brain Res. Cogn. Brain Res.* 9(1): 19-33, 2000.
- Mohr J.P., Pessin M.S., Finkelstein S., Funkestein H.H., Duncan G.W., and Davis K.R. Broca aphasia. Pathologic and clinical. *Neurology* 28: 311-324, 1978.
- Moro A. La continuita' del modello trasformazionale. In: *La Grammatica Universale*, ed. Cook V.J. and Newson M. Bologna: Il Mulino, 1996, p. 9-18.
- Moro A. Dynamic Antisymmetry. Cambridge, MA: MIT Press, 2000.
- Moro A., Tettamanti M., Perani D., Donati C., Cappa S.F., and Fazio F. Syntax and the brain: disentangling grammar by selective anomalies. *Neuroimage* 13(1): 110-118, 2001.
- Naeser M.A., Alexander M.P., Helm-Estabrooks N., Levine H.L., Laughlin S.A., and Geschwind N. Aphasia with predominantly subcortical lesion sites: description of three capsular/putaminal aphasia syndromes. *Arch. Neurol.* 39(1): 2-14, 1982.
- Narmour E. *The analysis and cognition of melodic complexity*. Chicago: University of Chicago Press, 1990.
- Navon D. Forest before trees: The precedence of global features in visual perception. *Cogn. Psychol.* 8: 353-383, 1977.
- Newman A.J., Bavelier D., Corina D., Jezzard P., and Neville H.J. A critical period for right hemisphere recruitment in American Sign Language processing. *Nat. Neurosci.* 5(1): 76-80, 2001.
- Newport E.L. and Supalla T. The structuring of language: clues from the acquisition of signed and spoken language. In: Signed and Spoken Language: Biological Constraints on Linguistic Form
   Dahlem Konferenzen, ed. Bellugi U. and Studdert-Kennedy M. Weinheim: Verlag Chemie GmbH, 1980, p. 187-211.

- Ni W., Constable R.T., Mencl W.E., Pugh K.R., Fulbright R.K., Shaywitz S.E., Shaywitz B.A., Gore J.C., and Shankweiler D. An event-related neuroimaging study distinguishing form and content in sentence processing. *J. Cogn. Neurosci.* 12(1): 120-133, 2000.
- Nobre A.C., Sebestyen G.N., Gitelman D.R., Mesulam M.-M., Frackowiak R.S.J., and Frith C.D. Functional localisation of the system for visuospatial attention using positron emission tomography. *Brain* 120: 515-533, 1997.
- Nowak M.A., Plotkin J.B., and Jansen V.A.A. The evolution of syntactic communication. *Nature* 404: 495-498, 2000.
- Nowak M.A. and Komarova N.L. Towards an evolutionary theory of language. *Trends Cogn. Sci.* 5 (7): 288-295, 2001.
- Oldfield R.C. The assessment and analysis of handedness: the Edinburgh inventory.

  \*Neuropsychologia 9(1): 97-113, 1971.
- Oshiba N. Memorization of serial items by Japanese monkeys, a chimpanzee, and humans. *Jap. Psychol. Res.* 39: 236-252, 1997.
- Palmer-Brown D., Tepper J.A., and Powell H.M. Connectionist natural language parsing. *Trends Cogn. Sci.* 6(10): 437-442, 2002.
- Patel A.D. Syntactic processing in language and music: Different cognitivie operations, similar neural resources? *Music Perception* 16(1): 27-42, 1998.
- Patel A.D., Gibson E., Ratner J., Besson M., and Holcomb P.J. Processing syntactic relations in language and music: An event-related potential study. *J. Cogn. Neurosci.* 10(6): 717-733, 1998.
- Paulesu E., Frith C.D., and Frackowiak R.S. The neural correlates of the verbal component of working memory. *Nature* 362(6418): 342-345, 1993.
- Paulesu E., Goldacre B., Scifo P., Cappa S.F., Gilardi M.C., Castiglioni I., Perani D., and Fazio F. Functional heterogeneity of left inferior frontal cortex as revealed by fMRI. *Neuroreport* 8(8): 2011-2017, 1997.
- Peigneux P., Salmon E., van der Linden M., Garraux G., Aerts J., Delfiore G., Degueldre C., Luxen

- A., Orban G., and Franck G. The role of lateral occipitotemporal junction and area MT/V5 in the visual analysis of upper-limb postures. *Neuroimage* 11(6/1): 644-655, 2000.
- Peña M., Bonatti L.L., Nespor M., and Mehler J. Signal-driven computations in speech processing. Science 298: 604-607, 2002.
- Perani D., Dehaene S., Grassi F., Cohen L., Cappa S.F., Dupoux E., Mehler J., and Fazio F. Brain processing of native and foreign languages. *Neuroreport* 7: 2439-2444, 1996.
- Perani D., Paulesu E., Sebastian Galles N., Dupoux E., Dehaene S., Bettinardi V., Cappa S.F., Fazio F., and Mehler J. The bilingual brain. Proficiency and age of acquisition of the second language. *Brain* 121: 1841-1852, 1998.
- Perani D., Schnur T., Tettamanti M., Gorno-Tempini M., Cappa S.F., and Fazio F. Word and picture matching: a PET study of semantic category effects. *Neuropsychologia* 37(3): 293-306, 1999a.
- Perani D., Cappa S.F., Schnur T., Tettamanti M., Collina S., Rosa M.M., and Fazio F. The neural correlates of verb and noun processing: a PET study. *Brain* 122: 2337-2344, 1999b.
- Perlmutter D.M. Sonority and Syllable Structure in American Sign Language. *Linguistic Inquiry* 23 (3): 407-442, 1992.
- Pessoa L. and Desimone R. From humble neural beginnings comes knowledge of numbers. *Neuron* 37: 4-6, 2003.
- Petitto L.A. On the autonomy of language and gesture: evidence from the acquisition of personal pronouns in American Sign Language. *Cognition* 27(1): 1-52, 1987.
- Petitto L.A. and Marentette P.F. Babbling in the manual mode: evidence for the ontogeny of language. *Science* 25: 1493-1496, 1991.
- Petitto L.A., Zatorre R.J., Gauna K., Nikelski J., Dostie D., and Evans A.C. Speech-like cerebral activity in profoundly deaf people processing signed languages: implications for the neural basis of human language. *Proc. Natl. Acad. Sci. USA* 97(25): 13961-13966, 2000.
- Petitto L.A., Katerelos M., Levy B.G., Gauna K., Tétreault K., and Ferraro V. Bilingual signed and spoken language acquisition from birth: implications for the mechanisms underlying early

- bilingual language acquisition. J. Child Lang. 28: 453-496, 2001a.
- Petitto L.A., Holowka S., Sergio L.E., and Ostry D. Language rhythms in baby hand movements.

  Nature 413: 35-36, 2001b.
- Piaget J. The construction of reality in the child. New York: Ballantine, 1954.
- Pickett E.R., Kuniholm E., Protopapas A., Friedman J., and Lieberman P. Selective speech motor, syntax and cognitive deficits associated with bilateral damage to the putamen and the head of the caudate nucleus: a case study. *Neuropsychologia* 36: 173-188, 1998.
- Pinker S. How could a child use verb syntax to learn verb semantics? *Lingua* 92: 377-410, 1994.
- Pinker S. Survival of the clearest. Nature 404: 441-442, 2000.
- Plooij F.X. Some basic traits of language in whild chimpanzees. In: *The emergence of language*, ed. Lock A.J. New York: Academic Press, 1978, p. 111-131.
- Plunkett K. Language acquisition and connectionism. In: *Language and cognitive processes*, ed. Plunkett K. Hove: Psychology Press, 1998, p. 97-104.
- Poizner H. Perception of movement in American Sign Language: Effects of linguistic structure and linguistic experience. *Perception and Psychophysics* 33(3): 215-231, 1983.
- Poizner H., Klima E.S., and Bellugi U. What the Hands Reveal about the Brain. Cambridge, MA: MIT Press, 1987.
- Pollard C. and Sag I. *Head-Driven Phrase Structure Grammar*. Chicago: University of Chicago Press, 1994.
- Price C.J. The functional anatomy of word comprehension and production. *Trends Cogn. Sci.* 2: 281-288, 1998.
- Pulvermuller F., Lutzenberger W., and Preissl H. Nouns and verbs in the intact brain: evidence from event-related potentials and high-frequency cortical responses. *Cereb. Cortex* 9(5): 497-506, 1999.
- Raffman D. Language, music, and mind. Cambridge, MA: MIT Press, 1993.
- Raichle M.E., Fiez J.A., Videen T.O., MacLeod A.M.K., Pardo J.V., Fox P.T., and Petersen S.E.

- Practice-related changes in human brain functional anatomy during non-motor learning. *Cereb.*Cortex 4: 8-26, 1994.
- Rizzolatti G., Fadiga L., Gallese V., and Fogassi L. Premotor cortex and the recognition of motor actions. *Brain Res. Cogn. Brain Res.* 3(2): 131-141, 1996a.
- Rizzolatti G., Fadiga L., Matelli M., Bettinardi V., Paulesu E., Perani D., and Fazio F. Localization of grasp representations in humans by PET: 1. Observation versus execution. *Exp. Brain Res.* 111(2): 246-252, 1996b.
- Rizzolatti G. and Arbib M.A. Language within our grasp. Trends Neurosci. 21(5): 188-194, 1998.
- Rizzolatti G., Fogassi L., and Gallese V. Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat. Rev. Neurosci.* 2(9): 661-670, 2001.
- Saffran J.R., Aslin R.N., and Newport E.L. Statistical learning by 8-month-old infants. *Science* 274 (5294): 1926-1928, 1996.
- Saffran J.R., Johnson E.K., Aslin R.N., and Newport E.L. Statistical learning of tone sequences by human infants and adults. *Cognition* 70(1): 27-52, 1999.
- Saffran J.R. The use of predictive dependencies in language learning. *J. Mem. Lang.* 44: 493-515, 2001.
- Saffran J.R. and Griepentrog G.J. Absolute pitch in infant auditory learning: evidence for developmental reorganization. *Dev. Psychol.* 37(1): 74-85, 2001.
- Saffran J.R., Senghas A., and Trueswell J.C. The acquisition of language by children. *Proc. Natl. Acad. Sci. USA* 98(23): 12874-12875, 2001.
- Seidenberg M.S. and Elman J.L. Networks are not 'hidden rules'. Trends Cogn. Sci. 3(8): 288, 1999.
- Seidenberg M.S., MacDonald M.C., and Saffran J.R. Does grammar start where statistic stop? Science 298: 553-554, 2002.
- Seiler H. Language universals research: a synthesis. Tübingen: Narr, 2000.
- Senghas A. and Coppola M.E. Children creating language: How Nicaraguan Sign Language acquired a spatial grammar. *Psychol. Sci.* 12(4): 323-328, 2001.

- Shallice T. Specific impairments of planning. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 298(1089): 199-209, 1982.
- Shapiro K.A., Pascual-Leone A., Mottaghy F.M., Gangitano M., and Caramazza A. Grammatical distinctions in the left frontal cortex. *J. Cogn. Neurosci.* 13(6): 713-720, 2001.
- Shi R., Werker J.F., and Morgan J.L. Newborn infants' sinsitivity to perceptual cues to lexical and grammatical words. *Cognition* 72: B11-B21, 1999.
- Shore C., O'Connell B., and Bates E. First sentences in language and symbolic play. *Devel. Psychol.* 20(5): 872-880, 1984.
- Shore C., Bates E., Bretherton I., Beeghly M., and O'Connell B. Vocal and gestural symbols: similarities and differences from 13 to 28 months. In: *From gesture to language in hearing and deaf children*, ed. Volterra V. and Erting C. Berlin: Springer, 1990, p. 79-91.
- Silbersweig D.A., Stern E., Frith C.D., Cahill C., Schnorr L., Grootoonk S., Spinks T., Clark J., Frackowiak R.S.J., and Jones T. Detection of thirty-second cognitive activations in single subjects with positron emission tomography: a new low-dose H2(15)O regional cerebral blood flow three-dimensional imaging technique. *J. Cereb. Blood Flow Metab.* 13(4): 617-629, 1993.
- Silveri M.C., Leggio M.G., and Molinari M. The cerebellum contributes to linguistic production: a case of agrammatic speech following a right cerebellar lesion. *Neurology* 44: 2047-2050, 1994.
- Simon O., Mangin J.-F., Cohen L., Le Bihan D., and Dehaene S. Topographical layout of hand, eye, calculation, and language-related areas in the human parietal lobe. *Neuron* 33: 475-487, 2002.
- Sirigu A., Cohen L., Zalla T., Pradat-Diehl P., Van Eeckhout P., Grafman J., and Agid Y. Distinct frontal regions for processing sentence syntax and story grammar. *Cortex* 34(5): 771-778, 1998.
- Sloboda J.A. Phrase units as determinants of visual processing in music reading. *British J. Psychol.* 68(1): 117-124, 1977.
- Spinozzi G., Natale F., Langer J., and Schlesinger M. Developing classification in action: II. Young chimpanzees (Pan troglodytes). *Hum. Evol.* 13: 125-139, 1998.

- Spinozzi G. and Langer J. Spontaneous classification in action by a human-enculturated and language-reared bonobo (Pan paniscus) and common chimpanzees (Pan Troglodytes). *J. Comp. Psychol.* 113(3): 286-296, 1999.
- Stephan K.M., Fink G.R., Passingham R.E., Silbersweig D., Ceballos-Baumann A.O., Frith C.D., and Frackowiak R.S. Functional anatomy of the mental representation of upper extremity movements in healthy subjects. *J. Neurophysiol.* 73(1): 373-386, 1995.
- Stevenson S. Competition and recency in a hybrid network model of syntactic disambiguation. *J. Psychol. Res.* 23: 295-322, 1994.
- Stromswold K., Caplan D., Alpert N., and Rauch S. Localization of syntactic comprehension by positron emission tomography. *Brain Lang.* 52(3): 452-473, 1996.
- Studdert-Kennedy M. and Lane H. Clues from the differences between signed and spoken language.

  In: Signed and Spoken Language: Biological Constraints on Linguistic Form Dahlem Konferenzen, ed. Bellugi U. and Studdert-Kennedy M. Weinheim: Verlag Chemie GmbH, 1980, p. 29-40.
- Summerfield A.Q., Cutting J.E., Frishberg N., Lane H., Lindblom B.E.F., Runeson J.S., Shaw R.E., Studdert-Kennedy M., and Turvey M.T. The structuring of language by the requirements of motor control and perception. In: *Signed and Spoken Language: Biological Constraints on Linguistic Form Dahlem Konferenzen*, ed. Bellugi U. and Studdert-Kennedy M. Weinheim: Verlag Chemie GmbH, 1980, p. 89-114.
- Swann P. Greenfield on language, tools, and brain. Behav. Brain Sci. 21(1): 155-159, 1998.
- Talairach J. and Tournoux P. Co-planar stereotaxic atlas of the human brain. Stuttgard: Thieme, 1988.
- Tanenhaus M. and Trueswell J. Sentence comprehension. In: *Speech, Language, and Communication*, ed. Miller J. and Eimas P. San Diego: Academic Press, 1995, p. 217–262.
- Taraban R. and McClelland J.L. Parsing and comprehension: a multiple constraint view. In: *Comprehension Processes in Reading*, ed. Balota D.A., Flores d'Arcais G.G. and K. Rayner K.

- Hillsdale, NJ: Erlbaum, 1990, p. 231-263.
- Tettamanti M., Alkadhi H., Moro A., Perani D., Kollias S., and Weniger D. Neural correlates for the acquisition of natural language syntax. *Neuroimage* 17: 700-709, 2002.
- Tettamanti M., Buccino G., Saccuman M.C., Gallese V., Danna M., Scifo P., Perani D., Cappa S.F., Fazio F., and Rizzolatti G. Sentences describing motor actions activate the visuomotor circuits coding the same actions. Submitted.
- Théoret H. and Pascual-Leone A. Language acquisition: do as you hear. *Curr. Biol.* 12: R736-R737, 2002.
- Thompson-Schill S., D'Esposito M., Aguirre G.K., and Farah M.J. Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. *Proc. Natl. Acad. Sci. USA* 94: 14792-14797, 1997.
- Tomasello M. and Akhtar N. Two-years-olds use pragmatic cues to differentiate reference to objects and actions. *Cogn. Devel.* 10: 201-224, 1995.
- Tomasello M. Do young children have adult syntactic competence? Cognition 74: 209-253, 2000.
- Tonkonogy J. and Goodglass H. Language function, foot of the third frontal gyrus, and rolandic operculum. *Arch. Neurol.* 38(8): 486-490, 1981.
- Tootell R.B., Reppas J.B., A.M. D., Look R.B., Sereno M.I., Malach R., Brady T.J., and Rosen B.R. Visual motion aftereffect in human cortical area MT revealed by functional magnetic resonance imaging. *Nature* 375: 139-141, 1995.
- Tramo M.J., Baynes K., and Volpe B.T. Impaired syntactic comprehension and production in Broca's aphasia: CT lesion localization and recovery patterns. *Neurology* 38(1): 95-98, 1988.
- Tranel D., Adolphs R., Damasio H., and Damasio A.R. A neural basis for the retrieval of words for actions. *Cogn. Neuropsychol.* 18: 655-670, 2001.
- Tyszka J.M., Grafton S.T., Chew W., Woods R.P., and Colletti P.M. Parceling of mesial frontal motor areas during ideation and movement using functional magnetic resonance imaging at 1.5 tesla. *Ann. Neurol.* 35(6): 746-749, 1994.

- Ullman M.T. A neural dissociation within language: evidence that the mental dictionary is part of declarative memory, and that grammatical rules are processed by the procedural system. *J. Cogn. Neurosci.* 9: 266-276, 1997.
- Ullman M.T. A neurocognitive perspective on language: the declarative/procedural model. *Nat. Rev. Neurosci.* 2: 717-726, 2001a.
- Ullman M.T. The neural bais of lexicon and grammar in first and second language: the declarative/procedural model. *Bilingual. Lang. Cogn.* 4(1): 105-122, 2001b.
- Ungerleider L.G. and Haxby J.V. 'What' and 'where' in the human brain. *Curr. Opin. Neurobiol.* 4(2): 157-165, 1994.
- Van Essen D.C., Dickson J., Harwell J., Hanlon D., Anderson C.H., and Drury H.A. An Integrated Software System for Surface-based Analyses of Cerebral Cortex. *J. Am. Med. Inform. Assoc.* 8 (5): 443-459, 2001.
- Vandenberghe R., Price C., Wise R., Josephs O., and Frackowiak R.S. Functional anatomy of a common semantic system for words and pictures. *Nature* 383(6597): 254-256, 1996.
- Volterra V., Bates E., Benigni L., Bretherton I., and Camaioni L. First words in language and action:

  A qualitative look. In: *The emergence of symbols: cognition and communication in infancy*, ed.

  Bates E., Benigni L., Bretherton I., Camaioni L. and Volterra V. New York: Academic Press, 1979, p. 141-222.
- Vygotsky L. The collected works of L.S. Vygotsky, Vol. I: Problems of general psychology. New York: Plenum, 1987.
- Watson J.D., Myers R., Frackowiak R.S., Hajnal J.V., Woods R.P., Mazziotta J.C., Shipp S., and Zeki S. Area V5 of the human brain: evidence from a combined study using positron emission tomography and magnetic resonance imaging. *Cereb. Cortex* 3(2): 79-94, 1993.
- Wildgruber D., Kischka U., Ackermann H., Klose U., and Grodd W. Dynamic pattern of brain activation during sequencing of word strings evaluated by fMRI. *Brain Res. Cogn. Brain Res.* 7 (3): 285-294, 1999.

- Wojciulik E. and Kanwisher N. The generality of parietal involvement in visual attention. *Neuron* 23: 747-764, 1999.
- Worsley K.J., Marrett S., Neelin P., Vandal A.C., Friston K.J., and Evans A.C. A unified statistical approach for determining significant signals in images of cerebral activation. *Hum. Brain Mapp.* 4: 58-73, 1996.
- Wynn K. Psychological foundations of number: numerical competence in human infants. *Trends Cogn. Sci.* 2(8): 296-303, 1998.
- Zaidel E. A response to Gazzaniga. Language in the right hemisphere, convergent perspectives. *Am. Psychol.* 38: 542-546, 1983.
- Zatorre R.J., Evans A.C., Meyer E., and Gjedde A. Lateralization of phonetic and pitch discrimination in speech processing. *Science* 256(5058): 846-849, 1992.
- Zettin M., Cappa S.F., D'Amico A., Rago R., Perino C., Perani D., and Fazio F. Agrammatic speech production after a right cerebellar hemorrhage. *Neurocase* 3: 375-380, 1997.

# 7. CURRICULUM VITAE

Marco Dante Plinio Tettamanti

Born in Bellinzona, TI, Switzerland on October 30, 1972.

Married, 1 son.

2003

1978-1983	Primary School in Bellinzona.
1983-1987	Middle School in Bellinzona.
1987-1991	High School: Liceo C (scientific type) in Bellinzona.
1991-1996	Study of molecular biology (Biologie II) at the Biozentrum of the University of Basel,
	BS, Switzerland.
1994-1995	Diploma thesis on the "Development of the Mushroom Bodies of Drosophila
	melanogaster" carried out at the Zoologisches Institut of the University of Basel,
	under the direction of Prof. Heinrich Reichert and Prof. John. G. Nicholls.
1996	Degree in Biologie II with specialization in neurobiology.
1997-2000	Training and Mobility of Reasearchers (TMR) Grant of the Swiss National Science
	Foundation (Nr. 83EU-050204) to work at the Scientific Institute San Raffaele,
	Milano, Italy, in the laboratory of Prof. Stefano F. Cappa and Prof. Daniela Perani.
2000-2003	Research assistant at the Scientific Institute San Raffaele, Milano, Italy, in the
	laboratory of Prof. Stefano F. Cappa and Prof. Daniela Perani (present affiliation).
2000-2003	Ph.D. Neuroscience Program at the Neuroscience Center of the University of Zürich,
	ZH, Switzerland (Beginning on March 2000). Ph.D. Thesis on "Language Acquisition
	and Processing - Hierarchically Organized Cognitive Processes" under the
	supervision of Prof. Rüdiger Wehner, Dr. Dorothea Weniger, Prof. Spyros Kollias and
	Dr. Peter Brugger.

Ph.D. in Natural Sciences (Dr. sc. nat.), University of Zürich, Switzerland.

# **List of publications:**

- Tettamanti M., Armstrong J.D., Yang M.Y., Endo K., Furukubo-Tokunaga K., Kaiser K., Reichert H. Early development of the Drosophila mushroom bodies, brain centres for associative learning and memory. Dev. Genes Evol. 207: 242-252, 1997.
- Cappa S.F., Perani D., Schnur T., Tettamanti M., Fazio F. Semantic Category and Knowledge-Type in Lexical-Semantic access: a PET Study. Neuroimage 8: 350-359, 1998.
- Perani D., Schnur T., Tettamanti M., Gorno-Tempini M., Cappa S.F., Fazio F. Word and Picture Matching: a PET Study of Semantic Category Effects. Neuropsychologia 37: 293-306, 1999.
- Perani D., Cappa S.F., Schnur T., Tettamanti M., Collina S., Rosa M., Fazio F. The neural correlates of verb and noun processing: a PET study. Brain 122 (12): 2337-2344, 1999.
- Moro A., Tettamanti M., Perani D., Cappa S.F., Donati C., Forbice V., Fazio F. Syntax and the brain: disentangling grammar by selective anomalies. Neuroimage 13(1):110-118, 2001.
- Moresco R.M., Tettamanti M., Gobbo C., Del Sole A., Ravasi L., Messa C., Paulesu E., Lucignani G., Perani D., Fazio F. Acute effects of 3-(4-acetamido)-butyrril-lorazepam (DDS2700) on brain function assessed by PET at rest and during attentive task. Nucl. Med. Commun. 22(4): 399-404, 2001.
- Perani D., Brunelli G.A., Tettamanti M., Scifo P., Tecchio F., Rossini P.M., Fazio F. Remodelling of sensorimotor maps in paraplegia: a functional magnetic resonance imaging study after a surgical nerve transfer. Neurosci. Letters 303(1): 62-66, 2001.
- Perani D., Fazio F., Borghese A., Tettamanti M., Ferrari S., Decety J., Gilardi M.C. Different brain correlates for watching real and virtual hand actions. Neuroimage 14(3): 749-758, 2001.
- Tettamanti M., Paulesu E., Scifo P., Maravita A., Fazio F., Perani D., Marzi C.A. Interhemispheric transmission of visuomotor information in humans: fMRI evidence. J. Neurophysiol. 88: 1051-1058, 2002.
- Tettamanti M., Alkadhi H., Moro A., Perani D., Kollias S., Weniger D. Neural correlates for the acquisition of natural language syntax. Neuroimage 17: 700-709, 2002.

- Perani D., Cappa S.F., Tettamanti M., Rosa M., Scifo P., Miozzo A., Basso A., Fazio F. A fMRI study of word retrieval in aphasia. Brain and Language, in press.
- Tettamanti M., Buccino G., Saccuman M.C., Gallese V., Danna M., Scifo P., Perani D., Cappa S.F., Fazio F., Rizzolatti G. Sentences describing motor actions activate the visuomotor circuits coding the same actions. Submitted.

"An n number of possible languages use the same vocabulary; in some of them, the symbol library allows the correct definition 'a ubiquitous and lasting system of hexagonal galleries', but library is 'bread' or 'pyramid' or anything else, and these seven words which define it have another value. You who read me, are You sure of understanding my language?"

Jorge Luis Borges, "The Library of Babel"

"The limits of my language mean the limits of my world."

Ludwig Wittgenstein, "Tractatus logico-philosophicus"