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The structure and dynamics of normal language processing: Insights from neuroimaging

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Review

Abstract. This paper reviews current psycholinguistic and neuroimaging evidence on language processing with particular focus on the relationship between production and comprehension. In the first part, different methods of psycholinguistic research are introduced and examples for psycholinguistic models (production: Levelt et al. 1999; comprehension: Friederici 2002) are sketched. In the second part, the neural correlates of semantic, phonological, and syntactic processing are reviewed. For semantics and phonology there seem to be different fronto-temporal networks which are shared in production and comprehension. The results for the processing of syntactic information are not entirely conclusive. Yet the data reveal that phonological strategies may be used in syntactic tasks. This finding opens the discussion of alternative, phonology-based strategies for language processing. Such strategies are accounted for by dual-route models featuring one direct and one indirect route which often involves phonological processing. This insight leads to some tentative conclusions about remediation strategies in dyslexics with selective (e.g., phonological) deficits.

Key words: language production, language comprehension, functional magnetic resonance imaging, fMRI, phonology, semantics, syntax, gender, reading, dual-route models, strategies

INTRODUCTION

During the past 150 years there have been numerous attempts to identify the neural systems underlying human linguistic abilities. First evidence for a localist approach to mapping different aspects of language to distinct brain regions was reported in the late 19th century by Broca (1861) and Wernicke (1874) on the basis of single case studies. The patient Leborgne described by Broca suffered from a severe production deficit, allowing him only to utter the syllable "tan". However, he could vary the prosody related to the intended meaning. Broca examined the patient's brain post mortem and detected a profound lesion in the left inferior frontal lobe, appearing to cover approximately a region labelled Brodmann's areas (BA) 44 and BA 45 (cf. Fig. 1 for the original illustration by Brodmann (1909) of cortical regions differing in cytoarchitecture. BA 44 and 45 are highlighted).

From these findings, Broca concluded that the lesion site (which later was named Broca's area to honour its discoverer) was somehow related to language production. Thirteen years later, Wernicke presented results from a different patient who, after a lesion in the left superior temporal lobe (later referred to as Wernicke's area), exhibited severe problems in understanding normal speech. Interestingly, his own speaking ability was preserved in the sense that he was able to utter many words in a row; however, this speech stream was meaningless, as the content words were chosen inappropriately. On the basis of this double dissociation, the so-called neurological model of language processing was formulated by Lichtheim (1885) and introduced into the Anglo-Saxon community by Geschwind (1970). This model attributes language production to the motor-related frontal areas and comprehension to Wernicke's area located in the posterior portion of the superior temporal gyrus (pSTG). Additional neural structures such as the angular gyrus and the arcurate fasciculus connecting both regions were included in the model, which for many years was the principal reference for neurologists dealing with language disorders.

With the advent of functional neuroimaging techniques evidence became available from healthy subjects providing insight into the normal functions of the brain regions associated with language processing. These data, in turn, led (at least partially) to dramatical changes in the view of the brain's functionality. Some of the neuroimaging evidence will be presented in this paper. Before doing this, two examples of psycholiguistic models of language production (Levelt et al. 1999) and comprehension (Friederici 2002) are given together with supporting evidence. These models provide a basis for the functional interpretation of the data recorded in positron-emission tomography (PET), functional magnetic resonance imaging (fMRI), electroencephalography (EEG), and magnetoencephalography (MEG). Throughout the paper, the distinction between language production and language comprehension will be made, as the findings in both domains are similar but not identical to each other.

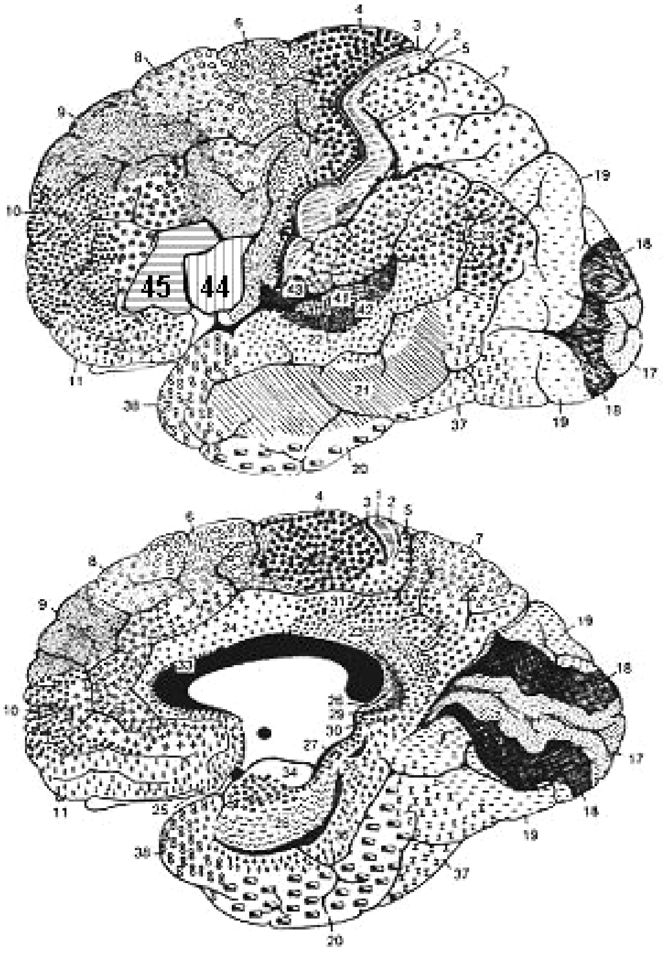

Fig. 1. The original cytoarchitectonic map of Brodmann (1909), showing a lateral (top) and medial (bottom) view of the human brain. The cerebral cortex is parcellated into more than 50 regions. The language-relevant areas 44 and 45 in the left inferior frontal gyrus (known as "Broca's area") are highlighted. Modified from Brodmann (1909).

PSYCHOLINGUISTIC APPROACHES TO LANGUAGE PROCESSING

Psycholinguistic methods

In order to obtain empirical data researchers have to apply some stimulation in order to elicit the process of interest. This stimulation can vary depending on the nature of the process of interest. In the simplest case, some data (e.g., EEG, MEG, fMRI) are recorded while the subject listens to or utters natural speech. In this case, the "regular" processes are tapped; however, it is difficult to draw conclusions about the existence, characteristics, or interactions of underlying sub-processes, unless there is some external criterion by which the processes can be differentiated (such as in the MEG study by Levelt and coauthors (1998). Here, the dipole analysis was guided by prior knowledge from behavioral experiments about the time windows during which semantic, syntactic, and phonological processing takes place). In order to assess sub-processes of which there is no or deficient a priori knowledge, subjects can be instructed to make a metalinguistic decision about some property of a stimulus that is possibly related to the sub-process. For instance, subjects may judge whether two successive stimuli are identical or different, or whether a stimulus matches to some predefined target. Using this rationale, Démonet and coauthors (1992) had their subjects decide whether in a given stimulus the phoneme /b/ occurred after the phoneme /d/. In a study by Burton and coauthors (2000), subjects indicated whether or not two successive CVC syllables were identical. Such tasks lack the naturality of the process under investigation, since the outcome of highly automatic processes such as phoneme identification must be analyzed consciously before any reaction can be made (cf. Wittmann and Fink 2004, for a discussion of methods in phonological processing). Here, the problem is to what extent the results obtained in metalinguistic decision tasks are still related to the natural speech process they were meant to tap. Therefore, other methods have been invented that allow drawing conclusions about particular aspects of natural language processing. By disturbing the natural process very specifically, the resulting differences in the dependent variable (reaction times, response latencies, EEG, BOLD response, etc.) reveal some of the characteristics of the underlying process. In language production, one well-established method is the picture–word interference paradigm (Glaser and Düngelhoff 1984) where a picture has to be named while a distractor word is presented visually on the computer screen or acoustically *via* ear-phones. In such an experiment, the naming latencies increase when the picture and the distractor are semantically related but decrease if they are phonologically related (Schriefers et al. 1990). In comprehension studies, semantic or syntactic violations induce different alterations of the ERP signal (cf. Friederici 2002, for a review).

Another way to obtain information about particular processes is the investigation of deviant or erroneous performance of either healthy subjects (i.e., speech errors), persons with circumscribed impairments (e.g., aphasic patients, children with developmental disorders), or other subjects differing in their performance from the average adult subject with respect to some other variable (such as age, gender, second vs. first language acquisition, etc.). Since the late 19th century, the analysis of patients' data has been a main source of information (e.g., Caramazza et al. 2000). Focussing on the performance of healthy persons, Meringer and Mayer (1895) presented a large corpus of spontaneous speech errors that could serve as a basis for detailed analyses. As a consequence of their analyses, the authors proposed a classification of speech errors that is still accepted today. Meringer and Mayer (1895) made a principle distinction between meaning-related errors ("yours" → "mine") and form-related errors ("train" →"brain") and detected that a great proportion of meaning-related errors are characterized by a close phonological relationship between the exchanged elements (so-called mixed errors). However, the analysis of spontaneous speech errors can be criticized with respect to some biases that are likely to occur during the collection of the corpus. As Bock (1996) demonstrated, the low probability of the occurrence of speech errors requires an enormous amount of utterances to obtain a sufficiently large and representative corpus. Top–down processes such as expectancy can influence the registration of errors (Elman and McClelland 1988, Warren and Warren 1970); the attentional focus of the listener can be either on formal or on semantic aspects (Poulisse 1999); some errors cannot be detected as easily as others (e.g., phonological relative to lexical errors: Cohen 1980; errors that do not change the content of an utterance: Bock, 1996), and the inter-rater reliability is substantially low (Ferber 1991).

In order to circumvent these fallacies, Baars et al. (1975) developed an experimental technique that permitted the controlled induction of a substantial amount of phonological and mixed errors. Still, as in the case of studies relying on decisions on particular properties of language, the use of data related to any kind of violation can be criticized as not revealing the regular processes. Such studies may produce either non-representative performance (in language production) or extra processes such as error detection (and, if requested in the experiment, even repair of the violation during comprehension: Indefrey et al. 2001b, Meyer et al. 2000) that possibly interfere with the processes of interest. Finally, and in general, any psycholinguistic experiment can be conducted in different modalities (i.e., auditorially or visually), with the focus on units of different size (i.e., single words, phrases, sentences, or even larger units such as stories: Indefrey et al. 2001a, Papathanassiou et al. 2000). As the dependent variable, either offline measures (such as error rates, speech errors) or online measures (such as reaction times or neuroimaging data) can be recorded. As a conclusion, none of the many methods available in psycholinguistic research is a perfect instrument; however, the aspects in which they differ from each other can constitute either a problem or an advantage, depending on the focus of interest in each single case. Moreover, as outlined above, there are obvious parallels between the methods applied in production and comprehension research. In some cases as in the picture-word interference paradigm or in overt reading tasks, one cannot distinguish completely to what extent aspects of production and comprehension interact. Therefore, the careful analysis of the processes involved in each task is a prerequisite of each psycholinguistic study.

Psycholinguistic models

In the last decades, a number of models have been proposed for both language production (e.g., Dell 1986, Fromkin 1971, Garrett 1975, 1980, Levelt 1989, Levelt et al. 1999, MacKay 1987, Shattuck-Hufnagel 1979, 1987, Stemberger 1985) and comprehension (e.g., Frazier, 1987, Friederici 2002, Hagoort 2003, Liberman et al. 1967, Marslen-Wilson and Tyler 1980, McClelland 1991, McClelland and Elman 1986). The interaction of these two domains of language processing has just recently moved into the focus of interest (e.g., Garrett 2000; Hickok and Poeppel 2000, Levelt et al. 1999). In more general terms, one major distinction between the different models within one domain concerned e architecture, i.e., the issue of parallelism or seriality of the processes engaged. There has been an ongoing debate about the question whether the different types of core information (i.e., semantics, syntax, and phonology) are accessed simultaneously (production: e.g., Dell 1986; comprehension: e.g., Marslen-Wilson and Tyler 1980) or in some hierarchical order (production: e.g., Levelt et al. 1999; comprehension: e.g., Friederici 1999, 2002). Here, two serial models (Friederici, 2002, Levelt et al. 1999) will be presented as examples of psycholinguistic approaches. Both models are well supported but not undisputed (for an example for an opposing parallel approach to language comprehension cf. Hagoort 2003).

PRODUCTION: THE LEVELT MODEL

On the basis of an earlier and highly detailed version (Levelt 1989) and including new empirical evidence, Levelt and coauthors (1999) put forth a language production model that focuses on single-word utterances. The model consists of five different levels or strata: (i) the lexical concept; (ii) the lemma (i.e., the lexical concept plus syntactic information); (iii) the morpheme; (iv) the phonological word; and (v) the phonetic gestural score level. These strata are connected by unidirectional links pointing from earlier to later processing steps (i.e., from the lexical concept towards articulation). There are no inhibitory connections.

The production process of a single word is assumed to take place as follows (Fig. 2). In a first step of conceptual preparation, the adequate lexical concept (i.e., the idea) is selected out of a number of more or less appropriate concurrents. Depending on the perspective the speaker takes, he/she may refer to an item as “animal”, “dog”, or “beagle”. Related concepts are organized in a network-like structure; thus, any activated node sends some amount of activation to its neighbors. Lexical concepts are represented as units, not as bundles of features that are partially shared by related concepts. This organization principle was chosen to avoid the so-called hyperonym problem, i.e. the fact that each activated concept (here: dog) would automatically activate its superordinate concepts (here: animal, mammal, vertebrate, etc.) which thus should be selected as often as the intended concept itself, which is apparently not the case. Note, however, that there are different solutions to the hyperonym problem compatible with a feature-based representation (Carpenter and Grossberg 1987, cf.

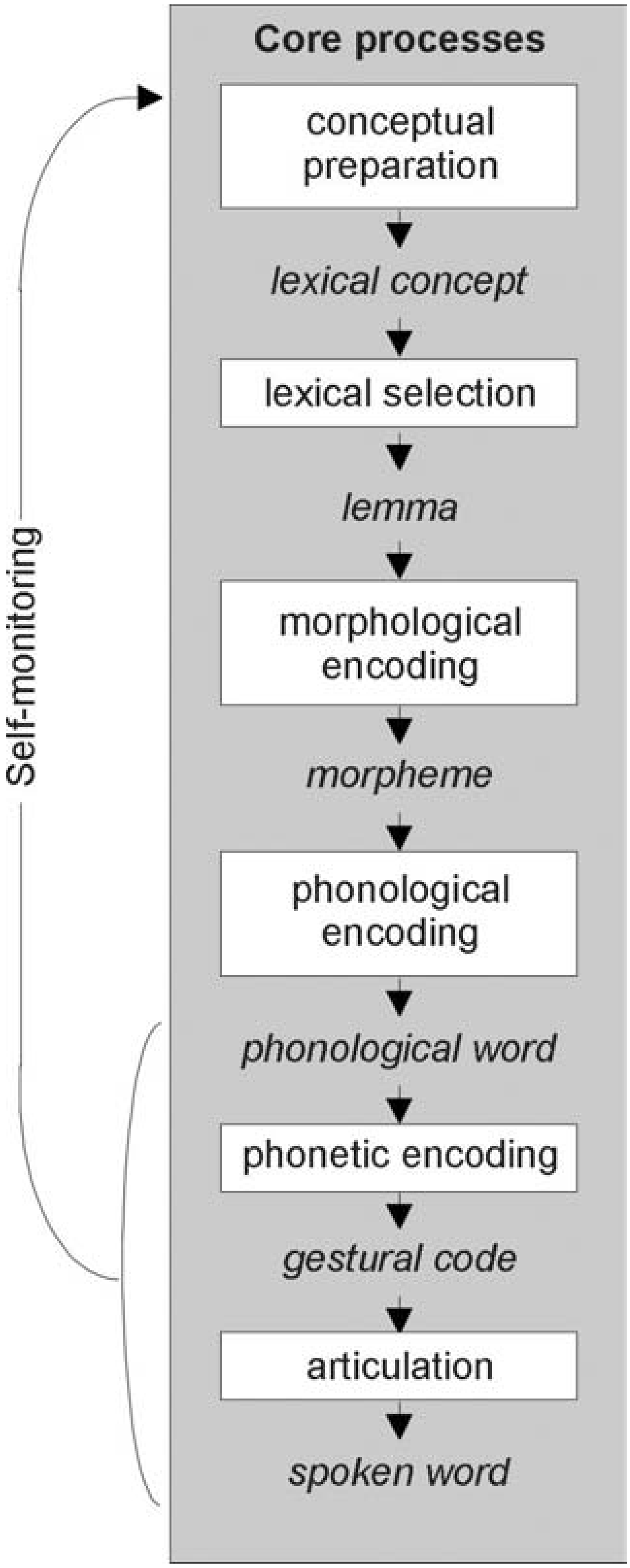

Fig. 2. Schematic outline of the serial two-stage language production model of Levelt and coauthors (1999). Modified from Levelt and coauthors (1999).

Bowers 1999). According to the model, only one lexical concept is finally selected and further processed, with one exception: in the case of synonyms (e.g., couch – sofa), both concepts are selected and further processed (cf. Excursus 1).

In the next step, activation spreads to the lemma level. Here, syntactic information such as word category, gender, case, number, etc. is supposed to be stored in separate nodes (one node for each kind of information). With respect to grammatical gender, there is an ongoing debate whether gender information is activated and accessed any time the corresponding noun is activated (e.g., Caramazza and Miozzo 1997, Roelofs et al. 1998, cf. Schriefers and Jescheniak 1999, for a review). Although put somewhat ambiguously elsewhere (Bock and Levelt 1994), the current model assumptions are such that gender information is activated any time a word is accessed, but is only selected when needed for the retrieval of the phonological code (Roelofs et al. 1998).

With the selection of conceptual-semantic and syntactic information being complete, the processing on the first of two qualitatively different domains is finished. Now, the speaker has to cross the divide between the domain of more content-related information and the form stratum, comprising morpho-phonological and phonetic information. With respect to that rift in the model architecture, the Levelt model is also referred to as a "two stage model".

On the morphological level, three different kinds of information are activated, namely the word's morphological make-up, its metrical shape, and its segmental make-up. However, on this level, there is no syllable information available.

In the next step, the phonological properties of the word are accessed. According to Levelt and coauthors (1999), all phonemes of a word are accessed in parallel. Hereafter, the syllabification is initiated. Note that the syllable structure of a word can differ from the segments retrieved on the morphological level. If the plural form of "horse" is to be produced, the two morphemes "horse" and "iz" (the plural marker) are selected. After the syllabification process, however, the two resulting syllables will be "hor" and "ses". The syllabification follows language-specific rules. The product of the syllabification process is called the phonological word or prosodic word (Levelt et al. 1999, p. 5). Finally, phonetic encoding (i.e., retrieving the phonological word's gestural score) and, in the last step, articulation is initiated. A self-monitoring mechanism located on the phonological code level and onwards guarantees optimum error-free production.

Excursus 1: Selection of one single concept?

In the Levelt model, it is assumed that only one lexical concept is selected, which then undergoes further production processing. Evidence for this notion comes from ERP experiments by Jescheniak and coauthors (2003) who demonstrated that, in the time window of phonological processing, only the phonological code of the target concept, but not that of related concepts, is activated.

There is, however, an exception to this rule in the case of synonyms (e.g., couch – sofa) (Jescheniak and Schriefers 1998, Peterson and Savoy 1998), several competitors may be processed in parallel. Peterson and Savoy (1998) labeled their alternative to the strictly serial approach by Levelt (1989) and Roelofs (1997) "cascaded processing". Synonyms appear to play a unique role in lexical access. Testing antonyms, i.e., concepts with opposite meaning which are closely related to the target, Jescheniak and Schriefers (1999) did not report any phonological coactivation. Levelt and coauthors (1999) account for the available evidence by admitting that, in the case of "contextual appropriateness", more than one concept may be selected.

Excursus 2: From words to phrases: modeling multi-word utterances

Although the Levelt model focuses on single-word utterances, some attempts have been made recently to expand the framework to multi-word utterances (Levelt 2001). Based on evidence from viewing time studies (Meyer and Van der Meulen 2000, Meyer et al. 1998, Van der Meulen et al. 2001) it is assumed that, in the description of scenes containing two objects, the lemmas of both objects are retrieved simultaneously, while the phonological encoding is successive and not overlapping in time. This view is challenged by Costa and Caramazza (2002). Using the picture-word interference paradigm, they had subjects produce phrases in two languages (English: determiner + adjective + noun; Spanish: determiner + noun + adjective) and tested for semantic and phonological effects on the noun in each phrase (i.e., the adjective in the English phrases vs. the noun in the Spanish phrases). The authors obtained both effects in both languages (i.e., independent from word order) and thus argue that the phonological word of the second element of a phrase is already activated before the production of the phonological word of the first element is completed. These results are corroborated by Experiments 2 and 3 in the study by Roelofs (2002). He, too, used the picture-word interference paradigm to test effects of relatedness (distractor did or did not equal the second element of a verb-particle construction, i.e., the particle) and preparation (using sets in which all particle verbs did or did not share the first element, i.e., the verb). Relatedness and preparation yielded significant and additive effects. This demonstrates that the phonological word of the second item (the particle) was already activated when the utterance of the first element was initiated.

COMPREHENSION: THE FRIEDERICI MODEL

Based on the so-called syntax-first model by Frazier (e.g., Frazier 1987, Frazier and Fodor 1978) and integrating the growing amount of electrophysiological evidence, Friederici (1995, 1998, 1999, 2002) proposed a neurocognitive model of language comprehension that focuses on word processing in a phrasal or sentence context. By including not only behavioral studies (which were mostly reading studies), but explicitly relying on online data from EEG and MEG experiments, Friederici (2002) contributed to resolving the controversy between models assuming serial (e.g., Frazier 1987) or parallel (e.g., Marslen-Wilson and Tyler 1980) processing. Her model parallels the Levelt model in implementing a strictly serial order of the first processing steps; however, it assumes interactions in later phases responsible for lexical integration. These processes will now be sketched (Fig. 3).

During Phase 0 in auditory sentence comprehension (0–100 ms), the primary acoustic analysis is performed, the phonemes are extracted, and the phonological word form is identified. In the next phase (Phase 1: 150–200 ms), word category information is accessed, allowing the formation of an initial syntactic structure. In Phase 2 (300–500 ms), thematic roles are assigned on the basis of lexical-semantic and morpho-syntactic processes. Phase 3 (500–1 000 ms) comprises integration processes, including the re-analysis of elements which are incompatible with the actual syntactic structure.

In the first version of the model, Friederici (1995) focused only on the temporal aspects of the processing steps. With neuroimaging evidence becoming more

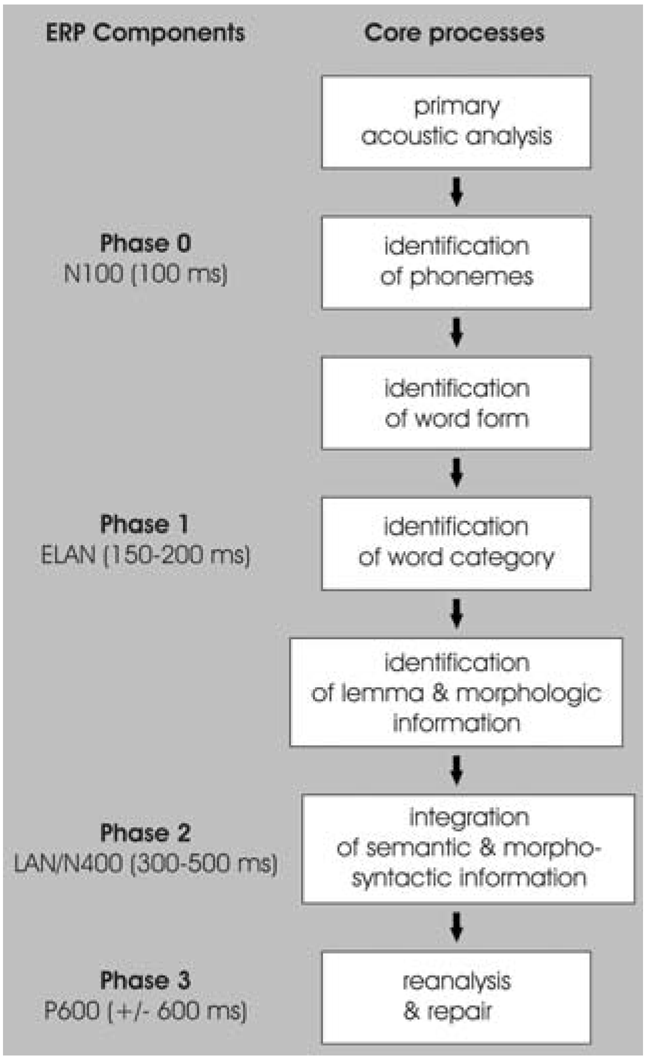

Fig. 3. Schematic outline of the neurocognitive model of language comprehension of Friederici (2002). Modified from Frederici (2002).

available, she included the spatial aspect in the model by integrating available results from PET, fMRI, and MEG. In the most recent version (Friederici 2002), even the interaction with working memory processes is considered (this issue, however, will be excluded from the present discussion of the model).

Excursus 3: The relationship of Phase 0 and Phase 1

In the model architecture, the seriality and independence of the processes in the first phases are assumed. This issue was investigated in a recent study by Hahne and coauthors (2002) which focused on the interaction of physical parameters (processed in Phase 0) and syntactic information (Phase 1). As a physical variable, the authors manipulated whether or not the last word in a sentence was presented from the same location as the previous element. As a syntactic variable, the presence or absence of a word category violation on the final element of the sentence was varied. As a third condition, the combination of a change in the location and a syntactic violation was applied. In the physical condition, a change in the word location elicited mismatch negativity in the EEG, whereas syntactic violations resulted in an early left anterior negativity (ELAN). Both effects had a different topography but were additive, as revealed by the double violation in the third condition. The authors take these results as evidence for the independent and parallel functioning of the two systems. On the one hand, this conclusion contradicts the seriality assumption; on the other hand, however, the independence of the two processing phases is still preserved.

Excursus 4: The relationship of Phase 1 and Phase 2

According to the Friederici model, processing during Phase 1 and Phase 2 should be serial and independent. In terms of the functional relationship of the two phases, this means that processing during Phase 1 can influence processing in Phase 2, but not *vice versa*.

Evidence for this notion can be obtained from experiments including double violations, with one aspect of the violation being processed during Phase 1 and the other in Phase 2. Such a study was conducted by Friederici and coauthors (1999), who investigated phrase structure violations (eliciting an ELAN in Phase 1) and semantic violations (resulting in a negativity around 400 ms, called N400, in Phase 2) together with double syntactic-semantic violations. As expected, in the single violation conditions, the ELAN or the N400 were present. In the double violation condition, there was only an ELAN effect, but no N400. This result is clearly in line with the predictions of the Friederici model.

However, the absence of the N400 might result from differences in the availability of semantic and syntactic information which are due to the construction rules of the stimulus materials. Both violations were realized on a participle, where the word category error could be detected from the affix (ge-), but the semantic information could only be derived from the stem subsequent to the affix. In order to control for such timing differences, Hahne and Friederici (2002) replicated the experiment but reversed the temporal relationship of semantic and syntactic information. In their materials, the authors used nouns and participles sharing the same onset and diverging only in the suffix (noun: -ung; participle: -t). Thus, semantic information could be accessed before word category information. However, in the double violation condition, the same pattern as in the study by Friederici and coauthors (1999) was observed. This means that, although the semantic cohort of the target could have been activated with the availability of the first phonemes, the semantic analysis was only initiated: (i) when the word category analysis was completed; and (ii) if no error was detected in this analysis. Thus, the evidence available at present clearly indicates that processing in Phase 1 influences processing in Phase 2 such that the detection of a word category violation inhibits further semantic processing.

Production and comprehension: Two sides of the same coin?

To communicate means to exchange a message, and in most communications, each member is both sender and recipient. From an economic point of view, one could wonder why anybody even considers the existence of two systems supporting the same action. On the other hand, in order to render communication as efficient as possible, two systems which are working independently from each other and are thus most likely not to interfere could be an attractive solution. Thus, there is no a priori reason to hypothesize one united or two separate language systems.

In fact, most psycholinguistic models only concentrate on one aspect of communication (i.e., production or comprehension) while neglecting the other. With respect to the two models discussed above, this is true for the Friederici model. In the Levelt model, however, the self-monitoring mechanism relates language production to comprehension. By controlling the phonological output, errors in the syllabification progress can be detected and corrected. Levelt and coauthors (1999) assume that production and comprehension share the same systems from the lemma stratum upwards; however, they state explicitly that the phonological system underlying comprehension and the self-monitoring system are different from each other. Evidence for the former statement comes from a study by Pickering and coauthors (2000) who found syntactic priming on the sentence level not only from production to production, but also from production to comprehension. However, the results of Jacobsen (1999) suggest some caution in assuming identical lemma levels for production and comprehension. In this study, subjects had to name pictures or read words in German. Using a paradigm in which a sentence fragment did or did not prime the grammatical gender of the picture or word target, Jacobsen (1999) observed facilitation and inhibition in the picture naming task relative to gender-neutral primes for gender-congruent and incongruent primes, respectively. However, in the reading task, there were only inhibition effects. On the basis of these results, one might conclude that production and comprehension (as operationalized by word reading) share only partly overlapping lemma levels.

In line with the argument of Levelt and coauthors (1999) in favor of partly distinct systems for production and comprehension are the results by Nickels and Howard (1995). They compared the performance of aphasic patients and showed that the input and output deficits differ from each other. The authors conclude that this performance could only be due to separate phonological systems for production and comprehension (on the theoretical as well as on the neural level). However, in a review considering the theoretical implications of several proposed mechanisms for self--monitoring, Postma (2000) pointed out that one central comprehension-based monitor which is supported by some automatic production-based modules provides the best solution for a self-monitoring mechanism. Considering the role of the production network for language comprehension and *vice versa* on the basis of numerous results, Garrett (2000) argued that comprehension may support error-free production, while as, assumed by the motor theory of Liberman et al. (1967) production could serve as an auxiliary for comprehension: "[...] production systems should be viewed as having a functionally similar role with respect to comprehension, namely, that they provide a continual error control mechanism via the production monitoring of partial products of the recognition system. A somewhat broader way of putting this point is to think of the production system as a filter on the generation of multiple analyses by the recognition system." (Garrett 2000, p. 48–49).

To conclude, the exact relationship of the production and the perception system remains subject to further research. This research can take two different perspectives. First, behavioral studies may reveal further similarities and dissimilarities of the architecture of both domains. Moreover, electrophysiological time-sensitive measures, especially EEG and MEG, may provide new insights into the temporal aspects of the sub-processes of production and comprehension. Second, functional neuroimaging studies using fMRI or PET are most likely to reveal evidence about which neural systems in the brain support semantic, syntactic, phonological, and other linguistic processes in both domains, and, in particular, to which extent these systems are identical for both production and comprehension.

The remainder of this paper will focus on the latter subject, i.e., the neural correlates of language processing. In this context, a special focus will be on the shared and unique brain resources involved in comprehension and production.

THE NEURAL CORRELATES OF LANGUAGE PROCESSING

Semantic processing

Among the different sub-domains of language, semantics is one of the most frequently investigated in neuroimaging studies. Accordingly, there is a profound knowledge about the neural networks supporting semantic processing. Since the results presented by Wernicke (1874), there are some hints at the contribution of the temporal lobe to semantic knowledge.

PRODUCTION

In language production, the temporal lobe appears to play an important role in semantic processing. In a picture naming experiment with healthy subjects, Damasio and coauthors (1996) found activation in the middle and inferior temporal lobe. In a baseline task, subjects had to indicate whether unknown faces were presented upright or upside down by saying “up” or “down”. In particular, the authors were able to show category-specific activations in distinct regions of the temporal lobe. While pictures of animals activated the ITG, tools required activation in the posterior aspects of the temporal lobe. Pictures of faces of famous persons evoked activation in the vicinity of the temporal pole. Moreover, pictures of all three categories resulted in activation of the left IFG (BA 45). In a parallel experiment, the authors showed that patients with lesions in these regions exhibited selective naming deficits for pictures belonging to the categories shown to activate the lesioned area.

Further evidence for the specialization of certain regions for the processing of items of a particular semantic class comes from a study by Martin and coauthors (1996). In a silent naming task, subjects were presented with pictures of tools, animals, or non-objects. While both tools and animals (as compared to non-objects) activated the left insula as well as fusiform gyri bilaterally, there was specific activation for tools in prefrontal areas (BA 44/6), whereas pictures of animals activated additionally the visual cortices. These results were replicated by Chao and Martin (2000, Experiment 2).

COMPREHENSION

In language comprehension, comparable results were reported with respect to the distinction between natural and man-made objects (e.g., Kapur et al. 1994, Miceli et al. 2002). Kapur and coauthors (1994) compared a semantic task (“living or non-living”) using written words with a task they called “lexical decision” (detecting the letter “a”) and found activation in left inferior frontal regions (BA 45, BA 46, BA 47, and BA 10). Similarly, Miceli and coauthors (2002) reported the involvement of the left IFG (BA 47) and middle frontal gyrus (MFG; BA 9 and BA 9/46) in an animateness decision task compared to silently reading pseudo-words.

Besides the decision between animals and artifacts, the decision whether a given word is abstract or concrete has been widely used as a semantic decision task (e.g., Desmond et al. 1995, Friederici et al. 2000b, Gabrieli et al. 1996, Poldrack et al. 1999). There is again unequivocal evidence for the involvement of the IFG in semantic decision-making. Desmond and coauthors (1995) conducted an fMRI study with a case judgment task (upper/lower case) as a baseline. The authors obtained activation in left BA 45, BA 46, and BA 47 for the semantic decision relative to baseline. With the same design, the results were replicated by Gabrieli and coauthors (1996) and by Wagner and coauthors (1997) who also reported activation in left BA 44, BA 45, BA 46, BA 47, and BA 9, as well as in right BA 44, BA 45, and BA 9. Using nouns and prepositions as stimuli, Friederici and coauthors (2000b) also found activation in BA 45 as well as in temporal areas (posterior portion of the left MTG, BA 21/37; posterior portion of the left STG, BA 22) relative to a baseline task in which subjects decided whether a consonant letter string was presented with wide or narrow spacing.

ARE THERE "SEMANTIC MAPS"?

As reported so far, there is compelling evidence that semantic processing in both production and comprehension relies on the contribution of (at least partially) specialized regions within the temporal lobe. In order to test whether the same temporal regions are activated for the processing of semantic information during both production and comprehension, Vandenberghe and coauthors (1996) presented subjects with triplets of items (pictures of objects or their written names) in a PET study. In three tasks, subjects either had to make judgments about the semantic relatedness of the objects, about their natural size, or about the physical size of the items on the computer screen. In the semantic relatedness decision task, Vandenberghe and coauthors (1996) observed activation for both words (comprehension) and pictures (production) in the left MTG (BA 21), the left ITG (BA 20), the left fusiform gyrus (BA 21/37), the left parieto-occipital junction (BA 19/39), the left SOG (BA 19), the left hippocampus, vermis, and the right cerebellum. Moreover, there was frontal activation in the left IFG (BA 45 and BA 11/47). These findings were corroborated by Chee and coauthors (2000) who used the same design as Vandenberghe and coauthors (1996). The authors reported a common semantic network for English words, pictures, and Chinese characters (Kanji) that comprised the left IFG (BA 44 and 45), MFG (BA 9), the left fusiform gyurs, and left posterior temporal regions. This network was activated when subjects decided which of two objects or characters were semantically more closely related to a probe. A perceptual size judgment served as a baseline task.

The present data might suggest that the temporal lobe regions responsible for the processing of semantic information are parceled such that in each single region one particular class of semantic information (such as animals, or dogs, or even terriers) is stored. However, in their meta-analysis of studies claiming to provide evidence for the existence of semantic maps, Devlin and coauthors (2002) concluded that the only valid distinction between semantic classes that result in distinct activation pattern is that between natural objects (medial anterior temporal poles) and man-made objects (left posterior MTG).

A COMMON FRONTO-TEMPORAL NETWORK FOR PRODUCTION AND COMPREHENSION

From the studies discussed so far, it becomes obvious that frontal (in particular inferior frontal) and temporal (in particular middle and inferior temporal) areas are involved in semantic processing. Moreover, it appears as if frontal areas are more often recruited whenever a semantic decision has to be performed, while declarative knowledge (such as semantic categories) is stored in the temporal lobe. This assumption was confirmed by an fMRI study by Thompson-Shill and coauthors (1997) for both production and comprehension. The authors applied a design consisting of a combination of three tasks (word generation (production), classification, and comparison (written words = comprehension)) and three conditions (baseline, "low selection", and "high selection"). In the "low selection" condition, the semantic information was easy accessible, whereas in the "high selection" condition, specific information (such as the price of an object or its weight) had to be retrieved. In all three tasks, the authors obtained evidence that activation in the inferior frontal gyrus (BA 44 and BA 45) varied as a function of the semantic information that had to be accessed in order to perform the task correctly. In other words, the higher the need for selection of particular bits of information, the more pronounced is the inferior frontal activation. In line with these data, another fMRI study by Thompson-Schill and coauthors (1999) provided evidence that, relative to an unprimed word generation task, "correct" priming (i.e., producing the target word in two successive trials) led to a decrease in activation in the IFG (approximately BA 44), while incorrect priming (i.e., producing different target words on successive trials) increased the inferior frontal activation. In contrast, activation in temporal regions (roughly the medial fusiform gyrus) decreased any time a prime occurred before the target, be it identical or different to the target. As a conclusion from both studies, Thompson-Schill and coauthors state that there appears to be a functional differentiation between temporal and frontal areas in processing semantic information, with temporal areas being involved in access to semantic information in general, while activation of inferior frontal regions is required in particular when the need of selection of fine-grained information increases (cf. the study by Burton et al. 2000, for comparable results from phonological processing during comprehension). This notion was further supported by a recent study by Amunts and coauthors (2004) who investigated semantic processing in a verbal fluency task. Compared to a non-demanding task (e.g., continuously repeating overlearned items such as months of a year or day of a week), higher semantic demands (generating examples of semantic categories such as furniture or flowers) elicited activation in BA 45. It should be noted, however, that Swick and Knight (1996) showed that patients with lesions in prefrontal regions (BA 6, 8, 9, 10, 44, 45, and 46) were hardly or not at all affected in a cued recall task and in concreteness judgments.

CONCLUDING REMARKS

From the results of studies of semantic processing reported here, the following pattern emerges: (i) middle and inferior temporal regions (BA 20, 21, 37, and 38) appear to house the semantic aspects of the mental lexicon, exhibiting to some extent specialization to the processing of distinct classes of information (e.g., artifacts and animals); (ii) left inferior frontal areas (BA 45 and 47) are possibly required to select specific semantic information from the lexicon; (3) language production (as operationalized, e.g., by picture naming or word generation) and language comprehension (e.g., concreteness or animateness judgments on words) involve activation of the same frontal and temporal areas. On the basis of this pattern of evidence, it may be presumed that the same holds true for syntactic and phonological processing. These issues are discussed now.

Phonological processing

STRUCTURE

Comprehension

Focusing on activity in the temporal lobe, recent studies of phonological processing in patients and healthy subjects show the contribution of the pSTG (i.e., Wernicke's area) in language comprehension (e.g., Burton et al. 2000). With respect to frontal regions, there is consistent activation in the superior posterior portion of Broca's area (BA 44) when subjects perform phonological decision tasks such as phoneme monitoring, phoneme discrimination, or phoneme sequencing (Burton et al. 2000, Démonet et al. 1992, Fiez and Petersen 1998, Fiez et al. 1995, Poldrack et al. 1999, Zatorre et al. 1992, 1996). A recent meta-analysis by Bookheimer (2002) nicely summarizes many of the available data.

Production

In production, a similar pattern was observed with respect to pSTG activation (Anderson et al. 1999, Benson et al. 2001, Buchsbaum et al. 2001). However, the situation is somewhat different for frontal activations, since there is high variability in the reported data. Price and coauthors (1997) sought to investigate phonological processes during production in particular. They had subjects perform different naming task (objects, colors, letters, and words) together with an articulatory baseline task. The authors calculated the contrasts of each task against baseline and conducted conjunction analyses for pairs of contrasts. As a result, activations related to the processes common to both contrasts in each conjunction analysis showed up. In the conjunction analysis explicitly planned to track phonological processing (Experiment 5: naming objects and colors), no activation of BA 44, but of BA 46 was reported. Phonological processing was again the only cognitive component of interest that was measured by the conjunction analysis in Experiment 4 (although this was not explicitly mentioned by the authors). Again, Price and coauthors (1997) did not report any activation of Broca's area. Two picture naming studies, one by Levelt and coauthors (1998) using MEG and one by Murtha and coauthors (1999) using PET, reported activation of Broca's area that was related to phonological processes. Chao and Martin (2000) presented subjects with pictures of real objects (experimental conditions) or scrambled objects (baseline). When subjects simply looked at the objects, there was no inferior frontal activation (Experiment 1). However, if they had to name these objects silently, this evoked additional activation in Broca's area (Experiment 2). The latter results are corroborated by data of Crosson and coauthors (2001) and Thompson-Schill and coauthors (1997) who reported activation of BA 44 in word generation tasks in which subjects had to produce a semantically appropriate verb in response to a noun. The study by Lurito and coauthors (2000) employed a rhyming task and a „fluency“ task in which subjects had to generate words starting with a particular phoneme and found practically identical activation foci in Broca's area in both tasks.

A common fronto-temporal network for production and comprehension?

The reported results do not permit final conclusions to be drawn about the neural correlates of phonological processing during language production (cf. Fiez 1997, Fiez and Petersen 1998, Indefrey and Levelt 2000, Poldrack et al. 1999 for reviews). This may be due to the different paradigms used in the different studies. Thus, in order to investigate the direct relationship of the neural correlates of phonological processing during language production and comprehension, it is advisable to apply comparable paradigms. The above-mentioned studies of phonological processing during language comprehension employed decision tasks on phonological properties of target words or syllables. In the domain of language production, similar paradigms (e.g., van Turennout et al. 1997) are well established but so far have not been used in studies investigating the neural correlates of language production.

On this basis, Heim and coauthors (2003b) conducted an fMRI study investigating the neural correlates of language production. We used two phonological decision tasks that were performed on the initial phonemes of German picture names (PHON1: Does the picture name begin with the phoneme "b" or not? PHON2: Does the picture name begin with a vowel or not?). Subjects indicated their answers by pressing one of two buttons. In line with the production model by Levelt and coauthors (1999), a semantic decision task (SEM: Is the presented object natural or man-made?) served as the baseline condition (for the use of these and similar tasks, cf. Abdel-Rahman and Sommer 2000, Rodriguez-Fornells et al. 2002, Schmitt et al. 2000, Szatkowska et al. 2000, van Turennout et al. 1997, 1998). In a second baseline condition (BASE), the subjects were required to make a target object decision. In all contrasts (PHON1-SEM; PHON2-SEM; PHON1-BASE; PHON2-BASE) and in the conjunction analyses yielding the common (i.e., task independent) activation caused by phonological processing, we observed foci in the superior portion of BA 44 (Broca's area) and in the pSTG. Thus, our data showed that the same network activated in phonological processing during language comprehension also contributes to phonological processing during production.

DYNAMICS

Comprehension

Considering the temporal dynamics in the fronto-temporal network identified above, an fMRI study by Thierry and coauthors (1999) demonstrated that in a phoneme sequencing task (as used by Démonet et al. 1992) as well as in a fast repetition task, Wernicke's area was activated earlier than Broca's area. In the combined data from both tasks, this time difference was about 3s.

Production

For language production, Heim and Friederici (2003) re-analyzed the time course of the activation reported by Heim and coauthors (2003b) in Broca's area and Wernicke's area. We observed the reverse of the pattern of the data of Thierry and coauthors (1999), i.e., activation in Broca's area preceded that in Wernicke's area by approximately 3 s. To our view, these data (together with those by Burton et al. 2000 and Thierry et al. 1999) suggested that the superior portion of Broca's area plays a significant role in the extraction of phonemes, which happens either after the perception of the speech signal or in preparation for production ("phonological retrieval"). However, it should be kept in mind that the temporal resolution of fMRI is not very satisfactory (i.e., in the range of seconds). Moreover, the actual time-to-peak values depend on the actual modeling. Thus, the reported data must be regarded as preliminary evidence and need further corroboration with different designs and methods.

Syntactic processing

STRUCTURE

Comprehension

On the basis of neuropsychological studies (cf. Grodzinsky 2000) and experiments on healthy subjects using neuroimaging methods, it appears that during language comprehension Broca's area is involved in processing syntactic information. On the sentence level, there is a positive relationship between an increase in syntactic complexity of a sentence and the amount of regional cerebral blood flow in regions supposed to be part of Broca's area (including BA 44, BA 45, and even BA 47; Caplan et al. 1998, 1999, 2000, Just et al. 1996, Stromswold et al. 1996). The mid portion of BA 44 was shown to be activated, in particular, as a function of syntactic memory required to process syntactically complex sentences rather than as a function of syntactic complexity as such (Cooke et al. 2002, Fiebach et al. 2001). Friederici and coauthors (2000a) varied the semantic and syntactic content of sentences independently and found the opercular part of Broca's area (i.e., BA 44) to be activated only in the condition in which the syntactic structure of the sentence was preserved but all content words had been replaced by pseudo-words. A similar activation in a region deep in BA 44 was observed for pseudo-word sentences containing syntactic and morphosyntactic information (Moro et al. 2001). In the domain of single word syntax, Broca's area was involved in the processing of verbs but not nouns in a lexical decision task (Perani et al. 1999). The left BA 44/6 was activated for function words (prepositions) but not for content words (nouns) when subjects performed a detection task on subsequent synonyms (Nobre et al. 1997). Since function words tend to be more abstract than content words, the authors concluded that abstract entries are harder to access and need an extra "motor" representation in the premotor cortex. However, this difference between processing function words and content words disappears if concreteness is counterbalanced between the word categories (Friederici et al. 2000b). In this latter study, subjects were presented with nouns and prepositions. One half of the items of either category was concrete, the other half abstract. In a syntactic task, subjects made a word category decision; in the semantic task they judged the word's concreteness. The result indicated that task requirements rather than word class determined activation differences in the inferior frontal cortex as a function of task: the semantic task (abstract vs. concrete) activated BA 45 whereas the syntactic task (noun vs. preposition) activated BA 44. This finding implies that Broca's area is not the cortical localization site of a particular word class (i.e., function words) but rather supports the underlying processes of word category decision and assignment (for somatotopic activations along the motor strip for action words related to face, arm, or leg, cf. Hauk et al. 2004).

If it is syntactic task or processing requirements that characterizes the role of the inferior tip of BA 44, one may further speculate that not only word category information but any kind of syntactic information is processed here. A language like German that offers different types of syntactic information (namely, word category and gender) is an ideal testing ground for this hypothesis. According to syntax-first models of comprehension only word category information such as noun, verb, article is processed during an initial phase of phrase structure building while lexically bound verb argument structure information and syntactic gender information are processed in a second phase. While word category information is an essential part of every language, this is not true of grammatical gender. Some languages (like German and French) make use of gender information; others (like English or Japanese) do not. Within the group of languages that implement grammatical gender, the gender of the same word may differ among the languages (e.g., the car: *el*$_{\text{masc}}$*coche* (Spanish) vs. *la*$_{\text{fem}}$ *voiture* (French) vs. *das*$_{\text{neut}}$ *Auto* (German)). This indicates that syntactic gender, in contrast to natural gender (s/he) is an idiosyncratic part of the lexical entry for a given noun in a given language.

We directly compared the processing of word category information (SYN1) and grammatical gender information (SYN2) in German (Heim et al. 2003a). A non-lexical task in which subjects had to decide if consonant letter strings were written with wide or narrow spacing served as the baseline (cf. Friederici et al. 2000b). In each single contrast (SYN1-BASE; SYN2-BASE) and the conjunction analysis, we observed activation in the inferior tip of BA 44. In addition, there were task-specific activations in other parts of the left inferior frontal gyrus. This result suggests that the lower portion of Broca's area serves as part of different networks and plays an important role in the processing of several types of syntactic information.

It should, however, be mentioned that there was a second and somewhat surprising effect in our data. As reported in Heim (2003, Experiment 2), our sample actually consisted of two sub-groups that used different strategies for the gender decision task. While one group had direct access to the gender information, the other group used a verbalization strategy, i.e., they produced the definite determiner of the word in order to perform the judgment. Interestingly, Miceli and coauthors (2002) reported that the same strategy was used by their subjects. Verbalizers and non-verbalizers differed significantly in their reaction times (with verbalizers being faster) and showed different patterns of brain activation. The non-verbalizers showed the same activation in the inferior tip of BA 44 that was observed in the word category decision. The verbalizers, however, displayed activation in other cortical areas, among them more anterior parts of the left inferior frontal gyrus and the superior portion of BA 44 similar to that observed in phonological processing, and similar to that reported by Miceli and coauthors (2002), in their verbalizing sample.

These data are in line with a dual-route model of access to grammatical gender including a direct, implicit, lexically-based route and an indirect, explicit, form-based route (Friedmann and Biran 2003, Gollan and Frost 2001). Moreover, Schiller and coauthors (2003) obtained electrophysiological and behavioral facilitation effects in a gender decision task when the stimuli were phonologically marked. I will return to this issue below.

Production

In the field of language production, there is much less knowledge about neural systems supporting syntactic processing. Indefrey and coauthors (2001a) set out to bridge this gap. Having subjects describe scenarios in which coloured objects moved towards and away from one another in different formats, Indefrey and coauthors (2001a) obtained PET evidence for the involvement of Broca's area in syntactic processing. In one condition, subjects had to produce complete sentences (e.g., *Das rote Dreieck jagt den blauen Kreis* – The $_{\text{neut}}$ red triangle is chasing the$_{\text{masc}}$ blue$_{\text{masc}}$ circle). In the second condition, they had to indicate the elements by gender-marked adjective-noun phrases and the action by the infinitive (e.g., *rotes Dreieck, blauer Kreis, jagen* – red$_{\text{neut}}$ triangle, blue$_{\text{masc}}$ circle, to chase), while in the third condition, word lists had to be produced, i.e., the objects were named, and the adjectives as well as the action was referred to in the basic form (*Dreieck, rot, Kreis, blau, jagen* – triangle, red, circle, blue, to chase). Thus, syntactic information in the utterance was varied parametrically, with the sentences containing the full syntactic information (sentential structure information, phrase structure information, gender marking, subject-object differentiation, etc.), the adjective-noun phrases having phrase-structure information and gender marking, and the word lists containing no syntactic information. Indefrey and colleagues reported activation in Broca's area and, predominantly, in the Rolandic operculum (dorsally adjacent to the inferior part of BA 44) that co-varied with the amount of syntactic information required. A replication of their study (Indefrey et al. 2004) yielded comparable results, with slightly more anterior activation (i.e., in the inferior portion of BA 44 proper). In sum, it appears that the inferior portion of Broca's area plays an important role in the explicit and implicit processing of syntactic information.

There are, however, again some additional data that should be considered. As reported above, some evidence suggests a dual pathway scenario for access to grammatical gender in comprehension. The same seems to hold for language production. In one fMRI study (Heim 2003, Experiment 1), subjects had to indicate by button press if the grammatical gender of the German name of a picture was masculine or feminine. Again, many subjects managed this task by silently generating the definite determiner of the picture name before responding. As in the comprehension study (Heim et al., submitted), this group showed activation in the superior portion of Broca's area. Implications of these findings will be discussed in the final section of this paper.

DYNAMICS

There is electrophysiological evidence from studies using violation paradigms that word category information is processed prior to syntactic gender information (e.g., Gunter et al. 2000, Hahne and Friederici 2002). Word category violations elicited an early left anterior negativity (ELAN, ca. 150–200 ms) in event-related potentials (ERPs) (Hahne and Friederici 2002), whereas grammatical gender violations evoked a left anterior negativity in a later time window (350–550 ms). As Friederici and coauthors (2000c) demonstrated by means of dipole localization, the sources of the ELAN signal lay in BA 44 and in the anterior portion of the left superior temporal gyrus, as would have been supposed by the data referred to above.

However, these data concerned the processing of violations of word category or grammatical gender in a sentence context. The reaction time data from the fMRI experiment by Heim and coauthors (2003a) might give some indication about the temporal dynamics of the processing of these two types of syntactic information. In line with the pattern of the ERPs in violation paradigms, the reaction times for a word category decision were significantly shorter than for a grammatical gender decision.

Phonological processing in non-phonological tasks

As reported above, some subjects automatically applied and/or profited from the use of a verbalization strategy, i.e., they produced the definite determiner of a word or picture name in order to gain (explicit) access to the grammatical gender information. Whenever such strategies were reported, the subjects showed activation in the superior portion of Broca's area, resembling the activation observed in phonological processing.

SILENT AND OVERT VERBALIZATION

We thus conducted an event-related fMRI experiment where in one task, the subjects were explicitly instructed to overtly produce the definite determiner of a picture name, while in a control condition, they simply named the picture (Heim et al. 2002). Our results demonstrated that the production of the determiner selectively involved the most superior portion of Broca's area. This activation very much resembles that observed by Heim (2003, Experiments 1 and 2) when the definite determiner was silently produced in a production or in a comprehension task, respectively. Most interestingly, this activation is in a region comparable to that activated in phonological tasks, i.e., the superior portion of BA 44. Moreover, the verbalization strategy draws upon phonological information. Thus, the question arises to what extent the access to the word form, i.e., the phonological code, mediates the performance in linguistic contexts. This issue will be focused on in the following section.

PROSODIC PROCESSING IN SPOKEN AND WRITTEN LANGUAGE COMPREHENSION

First, and instead of answering this question directly, some additional results from the processing of prosody (a sub-domain of phonology: speech melody, rhythm, accents, etc.) will be considered. Using ERPs, Steinhauer and coauthors (1999) investigated the role of intonational phrase (IPh) boundaries, i.e., pauses between two phonological phrases, in the context of syntactically ambiguous (garden path) and normal sentences. The authors observed a positive brain potential (the so-called closure positive shift, CPS) which occurred whenever an IPh boundary was present. Interestingly, Steinhauer and Friederici (2001) were able to demonstrate this CPS also in the visual domain in the presence vs. absence of a comma (instead of the pause in the auditory experiments). The CPS was also found when subjects first heard the (de-lexicalized) sentence melody (without any words), then read the sentence and judged whether the melody was suitable for the sentence. The authors explain this effect by subvocal phonological sentence phrasing, i.e., silent verbalization during the processing of the written stimulus. These results indicate that phonological processing is crucial for the processing of spoken and written language.

THE ROLE OF PHONOLOGICAL PROCESSING IN READING

The data presented so far suggest that phonological processing is essential in language comprehension (Steinhauer and Friederici 2001, cf. Steinhauer 2003, for a comprehensive review). Moreover, for some individuals or particular types of linguistic information (e.g., grammatical gender), the access to phonological cues may facilitate linguistic performance (Heim 2003 – Experiments 1 and 2, Miceli et al. 2002, Schiller et al. 2003).

As Frost (1994) reported, subjects reading Hebrew characters tended to wait until the vowel marks were presented with some delay (prelexical phonology) although the Hebrew characters would have provided enough cues to read the words (lexical phonology). Unsworth and Pexman (2003) investigated the relationship between reading skill and three phonological effects (homophone, homograph, and regularity effects. Unskilled but not skilled readers showed regularity effects in a lexical decision task and a phonological task. The authors concluded that the skilled readers made more efficient use of phonological knowledge. Ziegler and coauthors (2000) performed a reading study in Chinese where the characters can be associated with meaning without access to the phonological form. Their results showed, however, that reading times were faster for characters with higher phonological frequencies but not with higher orthographical frequencies. The authors suggest an automatic phonological mechanism involved in reading. In contrast, Hanley and McDonnell (1997) reported the case of patient PS, who had a good understanding of written language, but could not access the second meaning of a written homophone (air/heir). Thus, Hanley and McDonnell (1997) argue that phonological processing can be regarded as helpful, but not obligatory in the understanding of written language.

The facilitative effect of phonological processing has been observed in several contexts by a number of researchers, often as dissociations between spared and impaired performance of patients but also in neuroimaging studies. As a consequence, models have been proposed which share the label "dual route model". As mentioned above, dual route models for access to grammatical gender information were formulated by Friedmann and Biran (2003) and by Gollan and Frost (2001).

Other dual-route models focus on written language comprehension (e.g., Coltheart et al. 2001). They have

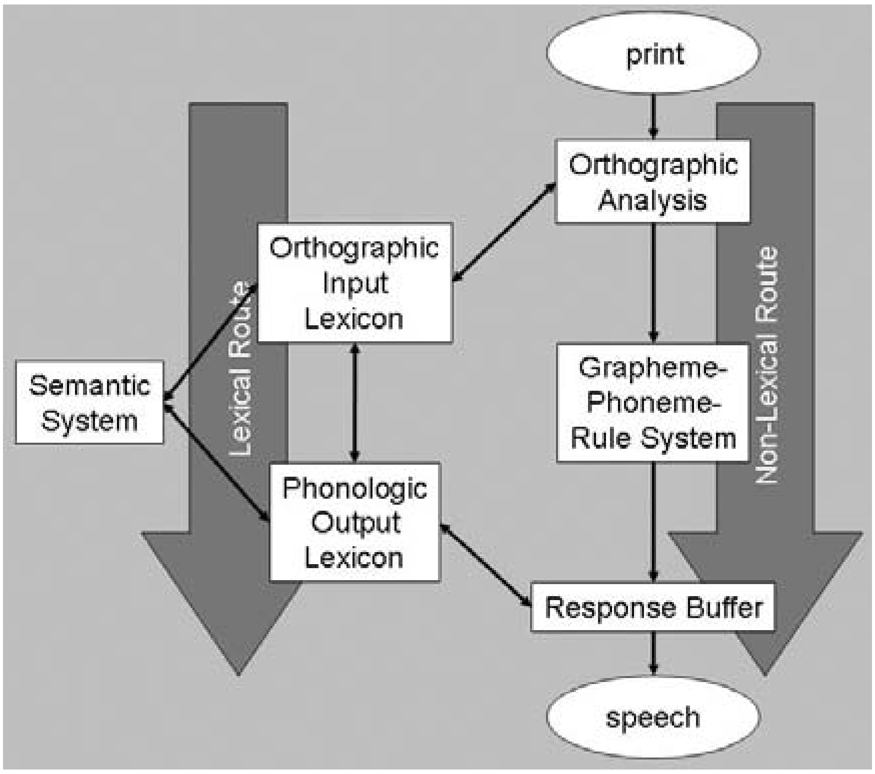

Fig. 4. Schematic outline of the dual-route model of visual word recognition of Coltheart and coauthors (2001). Modified from Coltheart and coauthors (2001).

in common one direct route and another, indirect pathway which is form-related or phonologically mediated. In the direct, fast route, whole words are mapped onto the corresponding word form representations stored in the mental lexicon (addressed phonology). In contrast, in the indirect, non-lexical pathway, written input is translated letter by letter into phonological information (assembled phonology, grapheme-to-phoneme conversion). For an outline of the dual-route model of reading by Coltheart and coauthors (2001), see Fig. 4.

In the literature, there are some imaging studies in accordance with a dual-route account (Fiebach et al. 2002, Fiez et al. 1999, Ischebeck et al. 2004, Rumsey et al. 1997, cf. Mechelli et al. 2003, for a review). Fiez and coauthors (1999) applied a word-naming paradigm and observed activation in BA 44 for low frequency words with inconsistent spelling-to-sound mapping, as well as for non-words. Since this region had been shown to be involved in phonological processing, Fiez and coauthors (1999) interpreted their result as demonstrating rule-based phonological processes in accessing these infrequent and irregular words. Similarly, when investigating the effects of word frequency with fMRI, Fiebach and coauthors (2002) observed activation for pseudo-words and low frequency words compared to high frequency words in BA 44 (but see Chen et al. 2002). The authors suggest that this posterior part of Broca's area might support rule-based grapheme-to-phoneme conversion. The same region was also observed in a study tapping the reverse process, i.e., phoneme-to-grapheme conversion (Omura et al. 2004). However, since all these interpretations were *ex-post-facto*, further imaging studies are necessary to directly demonstrate the relationship of activation in BA 44 and the processes hypothesized by dual-route models.

CONCLUSION

In this paper, the neural correlates of processing semantic, syntactic, and phonological aspects of language in production and comprehension were reviewed. It became evident that phonological processing can have facilitative effects in particular in written language comprehension. This finding may be related to the phonological deficit hypothesis of dyslexia (e.g., Snowling 2001, cf. Ramus 2003, for a recent and comprehensive review). Further research will clarify the extent to which the phonological route can be intentionally chosen as a processing strategy (cf. Miyake et al. 2004). Such a strategic use of this route could then be employed in therapeutic interventions in order to either selectively train phonological abilities or to bypass the direct but impaired processing on the other route.

INDEX OF ANATOMICAL ABBREVIATIONS

aIns	-	Anterior portion of the insula
BA	-	Brodmann's area
CH	-	Head of the caudate nucleus
FG	-	Fusiform gyrus
FO	-	Frontal operculum
GC	-	Cingulate gyrus
IFG	-	Inferior frontal gyrus
IFS	-	Inferior frontal sulcus
ITG	-	Inferior temporal gyrus
ITS	-	Inferior temporal sulcus
LG	-	Lingual gyrus
MC	-	Motor cortex
MFG	-	Middle frontal gyrus
mIns	-	Middle portion of the insula
MOG	-	Middle occipital gyrus
MTG	-	Middle temporal gyrus
pIns	-	Posterior portion of the insula
PMC	-	Premotor cortex
PO	-	Parietal operculum
PrCG	-	Precentral gyrus
PrCS	-	Precentral sulcus
pSTG	-	Posterior portion of the STG
RO	-	Rolandic operculum
SFG	-	Superior frontal gyrus
SFS	-	Superior frontal sulcus
SMG	-	Supramarginal gyrus
SOG	-	Superior occipital gyrus
STG	-	Superior temporal gyrus
STS	-	Superior temporal sulcus

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REFERENCES

Abdel-Rahman R, Sommer W (2000) Parallel access to semantics and phonology in object recognition? J Psychophysiol (Suppl) 14: 124.

Amunts K, Weiss PH, Mohlberg H, Pieperhoff P, Eickhoff S, Gurd JM, Marshall JC, Shah NJ, Fink GJ, Zilles K (2004) Analysis of neural mechanisms underlying verbal fluency in cytoarchitectonically defined stereotaxic space – The roles of Brodmann areas 44 and 45. Neuroimage 22: 42–56.

Anderson JM, Gilmore R, Roper S, Crosson B, Bauer RM, Nadeau S, Beversdorf DQ, Cibula J, Rogish 3rd M, Kortencamp S, Hughes JD, Gonzalez Rothi LJ, Heilman KM (1999) Conduction aphasia and the arcuate fasciculus: A reexamination of the Wernicke-Geschwind model. Brain Lang 70: 1–12.

Baars BJ, Motley MT, MacKay DG (1975) Output editing for lexical status in artificially elicited slips of the tongue. Journal of Verbal Learning and Verbal Behavior 14: 382–391.

Benson RR, Whalen DH, Richardson M, Swainson B, Clark VP, Lai S, Liberman AM (2001) Parametrically dissociating speech and nonspeech perception in the brain using fMRI. Brain Lang 78: 364–396.

Bock K (1996) Language production: methods and methodologies. Psychon Bull Rev 3: 395–421.

Bock K, Levelt WJM (1994) Language production: grammatical encoding. In: Handbook of Psycholinguistics (Gernsbacher MA, ed.). Academic Press, San Diego, CA, p. 945–984.

Bookheimer S (2002) Functional MRI of language: New approaches to understanding the cortical organization of semantic processing. Ann Rev Neurosci 25: 151–188.

Broca P (1861) Remarks on the localisation of the ability of articulated language and a case report of aphasia (in French). Bulletin Des Societés Anatomiques de Paris 2: 330-357.

Brodmann K (1909) Contributions to the histologic localisation of the cerebral cortex. VI. The parcellation of the cortex in human (in German). Journal für Psychologie und Neurologie 10: 231–246

Buchsbaum BR, Hickok G, Humphreys C (2001) Role of left posterior superior temporal gyrus in phonological processing for speech perception and production. Cogn Sci 25: 663–678.

Burton MW, Small SL, Blumstein SE (2000) The role of segmentation in phonological processing: An fMRI investigation. J Cogn Neurosci 12: 679–690.

Caplan D, Alpert N, Waters G (1998) Efects of syntactic structure and propositional number on patterns of regional cerebral blood flow. J Cogn Neurosci 10: 541–552.

Caplan D, Alpert N, Waters G (1999) PET studies of syntactic processing with auditory sentence presentation. Neuroimage 9: 343–351.

Caplan D, Alpert N, Waters G, Olivieri A (2000) Activation of Broca's area by syntactic processing under conditions of concurrent articulation. Hum Brain Mapp 9: 65–71.

Caramazza A, Miozzo M (1997) The relation between syntactic and phonological knowledge in lexical access: Evidence from the "tip-of-the-tongue" phenomenon. Cognition 64: 309–343.

Caramazza A, Chialant D, Capasso R, Miceli G (2000) Separable processing of consonants and vowels. Nature 403: 428–430.

Carpenter G, Grossberg S (1987) A massively parallel architecture for a self-organizing neural recognition machine. Computer Visions, Graphics, and Image Processing 37: 54–115.

Chao LL, Martin A (2000) Representation of manipulable man-made objects in the dorsal stream. Neuroimage 12: 478–484.

Chee MWL, Weekes B, Lee KM, Soon CS, Schreiber A, Hoon JJ, Chee M (2000) Overlap and dissociation of semantic processing of Chinese characters, English words, and pictures: Evidence from fMRI. Neuroimage 12: 392–403.

Chen Y, Fu S, Iversen SD, Smith SM, Matthews PM (2002) Testing for dual brain processing routes in reading: a direct contrast of Chinese character and pinyin in reading using FMRI. J Cogn Neurosci 14: 1088–1098.

Cohen A (1980) Correcting of speech errors in a shadowing task. In: Errors in Linguistic Performance (Fromkin VA, ed.). Academic Press, New York.

Coltheart M, Rastle K, Perry C, Langdon R, Ziegler J (2001) DRC: a dual route cascaded model of visual word recognition and reading aloud. Psychol Rev 108: 204–256.

Cooke A, Zurif EB, DeVita C, Alsop D, Koenig P, Detre J, Gee J, Pinango M Balogh J, Grossman M (2002) Neural basis for sentence comprehension: Grammatical and short-term memory components. Hum Brain Mapp 15: 80–94.

Costa A, Caramazza A (2002) the production of noun phrases in English and Spanish: Implications for the scope of phonological encoding in speech production. Journal of Memory and Language 46: 178–198.

Crosson B, Sadek JR, Maron L, Gokcay D, Mohr CM, Auerbach EJ, Freeman AJ, Leonard SM, Briggs RW (2001) Relative shift in activity from medial to lateral frontal cortex during internally vs. externally guided word generation. J Cogn Neurosci 15: 272–283.

Damasio H, Grabowski TJ, Tranel D, Hichwa RD, Damasio AR (1996) A neural basis for lexical retrieval. Nature 380: 499–505.

Dell GS (1986) A spreading activation theory of retrieval in sentence production. Psychol Rev 93: 283–321.

Démonet J-F, Chollet F, Ramsay S, Cardebat D, Nespoulous J-L, Wise R, Rascol A, Frackowiak R (1992) The anatomy of phonological and semantic processing in normal subjects. Brain 115: 1753–1768.

Desmond JE, Sum JM, Wagner AD, Demb JB, Shear PK, Glover GH, Gabrieli JDE, Morrell M J (1995) Functional MRI measurement of language lateralization in Wada-tested patients. Brain 118: 1411–1419.

Devlin JT, Moore CJ, Mummery C J, Gorno-Tempini ML, Phillips JA, Noppeney U, Frackowiak RJS, Friston KJ, Price CJ (2002) Anatomic constraints on cognitive theories of category specifity. Neuroimage 15: 675–685.

Elman JL, McClelland JL (1988) Cognitive penetration of the mechanisms of perception: Compensation for coarticulation of lexically restored phonemes. Journal of Memory and Language 27: 143–165.

Ferber R (1991) Slip of the tongue or slip of the ear? On the perception and transcription of naturalistic slips of the tongue. J Psycholinguist Res 20: 105–122.

Fiebach CJ, Schlesewsky M, Friederici AD (2001) Syntactic working memory and the establishment of filler-gap dependencies: Insights from ERPs and fMRI. J Psycholinguist Res 30: 321–338.

Fiebach CJ, Friederici AD, Müller K, von Cramon DY (2002) FMRI evidence for dual routes to the mental lexicon in visual word recognition. J Cogn Neurosci 14: 11–23.

Fiez JA (1997) Phonology, semantics, and the role of the left inferior prefrontal cortex. Hum Brain Mapp 5: 79–83.

Fiez JA, Petersen SE (1998) Neuroimaging studies of word reading. Proc Natl Acad Sci U S A 95: 914–921.

Fiez JA, Raichle ME, Miezin FM, Petersen SE, Tallal P, Katz WF (1995) PET studies of auditory and phonological processing: effects of stimulus characteristics and task demands. J Cogn Neurosci 7: 357–375.

Fiez JA, Balota DA, Raichle ME, Petersen SE (1999) Effects of lexicality, frequency, and spelling-to-sound consistency on the functional anatomy of reading. Neuron 24: 205–218.

Frazier L (1987) Theories of sentence processing. In: Modularity of Knowledge Representation and Natural-Language Processing (Garfield J, ed.). MIT Press, Cambridge, MA.

Frazier L, Fodor J (1978) The sausage machine. A new two-stage parsing model. Cognition 6: 291–325.

Friederici AD (1995) The time course of syntactic activation during language processing: A model based on neuropsychological and neurophysiological data. Brain Lang 50: 259–281.

Friederici AD (1998) The neurobiology of language comprehension. In: Language Comprehension: A Biological Perspective (Friederici AD, ed.). Springer, Berlin, p. 265–292.

Friederici AD (1999) The neurobiology of language comprehension. In: Language Comprehension: A Biological Perspective (2nd ed.) (Friederici AD, ed.). Springer, Berlin, p. 265–292.

Friederici AD (2002) Towards a neural basis of auditory sentence processing. Trends Cogn Sci 6: 78–84.

Friederici AD, Steinhauer K, Frisch S (1999) Lexical integration: Sequential effects of syntactic and semantic information. Mem Cognit 27: 438–453.

Friederici AD, Meyer M, von Cramon DY (2000a) Auditory language comprehension: An event-related fMRI study on the processing of syntactic and lexical information. Brain Lang 74: 289–300.

Friederici AD, Opitz B, von Cramon DY (2000b) Segregating semantic and syntactic aspects of processing in the human brain: A fMRI investigation of different word types. Cereb Cortex 10: 698–705.

Friederici AD, Wang Y, Herrmann CS, Maess B, Oertel U (2000c) Localization of early syntactic processes in frontal and temporal cortical areas: a magnetoencephalographic study. Hum Brain Mapp 11: 1–11.

Friedmann N, Biran M (2003) When is gender accessed? A study of paraphasias in Hebrew anomia. Cortex 39: 441–463.

Fromkin VA (1971) The non-anomalous nature of anomalous utterances. Language, 47: 27–52.

Frost R (1994) Prelexical and postlexical strategies in reading: evidence from a deep and shallow orthography. J Exp Psychol Learn Mem Cogn 20: 116–129.

Gabrieli JDE, Desmond JE, Demb JB, Wagner AD, Stone MV, Vaidya CJ, Glover GH (1996) Functional magnetic resonance imaging of semantic memory processes in the frontal lobes. Psychol Sci 7: 278–283.

Garret MF (1975) The analysis of sentence production. In: The Psychology of Learning and Motivation (Vol. 9) (Brown GH, ed.). Academic Press, New York, p. 133–177.

Garrett MF (1980) Levels of processing in sentence production. In: Language Production: Speech and Talk (Butterworth B, ed.). Academic Press, London, p. 177–220.

Garrett MF (2000) Remarks on the architecture of language processing systems. In: Language and The Brain (Grodzinsky Y, Shapiro LP, Swinney D, eds.). Academic Press, San Diego, CA.

Geschwind N (1970) Organization of language in the brain. Science 170: 940–944.

Glaser MO, Düngelhoff F-J (1984) The time course of picture-word interference. J Exp Psychol Hum Percept Perform 7: 1247–1257.

Gollan TH, Frost R (2001) Two routes to grammatical gender: Evidence from Hebrew. J Psycholinguist Res 30: 627–651.

Grodzinsky Y (2000) The neurology of syntax: Language use without Broca's area. Behav Brain Sci 23: 1–71.

Gunter TC, Friederici AD, Schriefers H (2000) Syntactic gender and semantic expectancy: ERPs reveal early autonomy and late interaction. J Cogn Neurosci 12: 556–568.

Hagoort P (2003) How the brain solves the binding problem for language: a neurocomputational model of syntactic processing. Neuroimage 20 (Suppl): S18–29.

Hahne A, Friederici AD (2002) Differential task effects on semantic and syntactic processes as revealed by ERPs. Cogn Brain Res 13: 339–356.

Hahne A, Schröger E, Friederici AD (2002) Segregating early physical and syntactic processes in auditory sentence comprehension. Neuroreport 13: 305–309.

Hanley JR, McDonnell V (1997) Are reading and spelling phonologically mediated? Evidence from a patient with a speech production impairment. Cogn Neuropsychol 14: 3–33.

Hauk O, Johnsrude I, Pulvermüller F (2004) Somatotopic representations of action words in human motor and premotor cortex. Neuron 41: 301–307.

Heim S (2003) Towards a Common Neural Network Model of Language Production and Comprehension: fMRI Evidence for the Processing of Phonological and Syntactic Information in Single Words. MPI of Cognitive Neuroscience, Leipzig.

Heim S, Friederci AD (2003) Phonological processing in language production: Time course of brain activity. Neuroreport 14: 2031–2033.

Heim S, Opitz B, Friederici AD (2002) Broca's area in the human brain is involved in the selection of grammatical gender for language production: Evidence from functional magnetic resonance imaging. Neurosci Lett 328: 101–104.

Heim S, Opitz B, Friederici AD (2003a) Distributed cortical networks for syntax processing: Broca's area as the common denominator. Brain Lang 85: 402–408.

Heim S, Opitz B, Müller K, Friederici AD (2003b) Phonological processing during language production: fMRI evidence for a shared production-comprehension network. Cogn Brain Res 16: 285–296.

Hickok G, Poeppel D (2000) Towards a functional neuroanatomy of speech perception. Trends Cogn Sci 4: 131–138.

Indefrey P, Levelt WJM (2000) The neural correlates of language production. In: The Cognitive Neurosciences (2nd ed.) (Gazzaniga M, ed.). MIT Press, Cambridge, MA, p. 845–865.

Indefrey P, Levelt WJM (2004) The spatial and temporal signatures of word production components. Cognition 92: 101–144.

Indefrey P, Brown CM, Hellwig F, Amunts K, Herzog H, Seitz RJ, Hagoort P (2001a) A neural correlate of syntactic encoding during speech production. Proc Natl Acad Sci U S A 98: 5933–5936.

Indefrey P, Hagoort P, Herzog H, Seitz RJ, Brown C (2001b) Syntactic processing in left prefrontal cortex is independent of lexical meaning. Neuroimange 14: 546–555.

Indefrey P, Hellwig F, Herzog H, Seitz RJ, Hagoort P (2004) Neural responses to the production and comprehension of syntax in identical utterances. Brain Lang 89: 312–319.

Ischebeck A, Indefrey P, Usui N, Nose I, Hellwig F, Taira M (2004) Reading in a regular orthography: An fMRI study investigating the role of visual familiarity. J Cogn Neurosci 16: 727–741.

Jacobsen T (1999) Effects of grammatical gender on picture and word naming: Evidence from German. J Psycholinguist Res 28: 499–514.

Jescheniak JD, Schriefers H (1998) Discrete serial versus cascaded processing in lexical access in speech production:

Further evidence from the coactivation of near-synonyms. J Exp Psychol Learn Mem Cogn 24: 1256–1274.

Jescheniak JD, Schriefers H (1999) Strictly discrete serial stages and contextual appropriateness. Behav Brain Sci 22: 47–48.

Jescheniak JD, Hahne A, Schriefers H (2003) Information flow in the mental lexicon during speech planning: Evidence from brain potentials. Cogn Brain Res 15: 261–276.

Just MA, Carpenter PA, Keller TA, Eddy WF, Thulborn KR (1996) Brain activation modulated by sentence comprehension. Science 274: 114–116.

Kapur S, Rose R, Liddle PF, Zipursky RB, Brown MG, Stuss D, Houle S, Tulving E (1994) The role of the left prefrontal cortex in verbal processing: semantic processing or willed action? Neuroreport 5: 2193–2196.

Levelt WJM (1989) Speaking: From Intention to Articulation. MIT Press, Cambridge, MA.

Levelt WJM (1998) The genetic perspective in psycholinguistics or where do spoken words come from? J Psycholinguist Res 27: 167–180.

Levelt WJM (2001) Spoken word production: A theory of lexical access. Proc Natl Acad Sci U S A 98: 13464–13471.

Levelt WJM, Meyer AS (2000) Word for word: Multiple lexical access in speech production. European Journal of Cognitive Psychology 12: 433–452.

Levelt WJM , Praamstra P, Meyer AS, Helenius P, Salmelin R (1998) A MEG study of picture naming. J Cogn Neurosci 10: 533–567.

Levelt WJM , Roelofs A, Meyer AS (1999) A theory of lexical access in speech production. Behav Brain Sci 22: 1–75.

Liberman AM, Cooper FS, Shankweiler DS, Studdert-Kennedy M (1967) Perception of the speech code. Psychol Rev 74: 431–461.

Lichtheim L (1885) On aphasia. Brain 7: 433–484.

Lurito JT, Kareken DA, Lowe MJ, Chen SH A, Mathews VP (2000) Comparison of rhyming and word generation with FMRI. Hum Brain Mapp 10: 99–106.

MacKay DG (1987) The organization of perception and action: A theory for language and other cognitive skills. Springer, New York.

Marslen-Wilson WD, Tyler LK (1980) The temporal structure of spoken language understanding. Cognition 8: 1–71.

Martin A, Wiggs CL, Ungerleider LG, Haxby JV (1996) Neural correlates of category-specific knowledge. Nature 379: 649–652.

McClelland JL (1991) Stochastic interactive processes and the effect of context on perception. Cogn Psychol 23: 1–44.

McClelland JL, Elman JL (1986) The TRACE model of speech perception. Cogn Psychol 18: 1–86.

Mechelli A, Gorno-Tempini ML, Price CJ (2003) Neuroimaging studies of words and pseudoword reading: consistencies, inconsistencies, and limitations. J Cogn Neurosci 15: 260-271.

Meringer R, Mayer K (1895) Speech Errors and Reading Errors (in German). Göschener, Stuttgart.

Meyer AS, van der Meulen F (2000) Phonological priming effects on speech onset latencies and viewing times in object naming. Psychon Bull Rev 7: 314–319.

Meyer AS, Sleiderink AM, Levelt WJM (1998) Viewing and naming objects: Eye movements during noun phrase production. Cognition 66: B25–B33.

Meyer M, Friederici AD, von Cramon DY (2000) Neurocognition of auditory sentence comprehension: Event related fMRI reveals sensitivity to syntactic violations of task demand. Cogn Brain Res 9: 19–33.

Miceli G, Turriziani P, Caltagirone C, Capasso R, Tomaiuolo F, Caramazza A (2002) The neural correlates of grammatical gender: An fMRI investigation. J Cogn Neurosci 14: 618–628.

Miyake A, Emerson MJ, Padilla F, Ahn JC (2004) Inner speech as a retrieval aid for task goals: The effects of cue type and articulatory suppression in the random task cuing paradigm. Acta Psychol (Amst) 115: 123–142.

Moro A, Tettamanti M, Perani D, Donati C, Cappa SF, Fazio F (2001) Syntax and the brain: Disentangling grammar by selective anomalies. Neuroimage 13: 110–118.

Murtha S, Chertkow H, Beauregard M, Evans A (1999) The neural substrate of picture naming. J Cogn Neurosci 11: 399–423.

Nickels L, Howard D (1995) Phonological errors in aphasic naming: Comprehension, monitoring and lexicality. Cortex 31: 209–237.

Nobre AC, Price CJ, Turner R, Friston K (1997) Selective processing of nouns and functions words in the human brain. Neuroimage 5: 53.

Omura K, Tsukamoto T, Kotani Y, Ohgami Y, Yoshikawa K (2004) Neural correlates of phoneme-to-grapheme conversion. Neuroreport 15: 949–953.

Papathanassiou D, Etard O, Mellet E, Zago L, Mazoyer B, Tzourio-Mazoyer N (2000) A common language network for comprehension and production: A contribution to the definition of language epicenters with PET. Neuroimage 11: 347–357.

Perani D, Cappa S, Schnur T, Tettamanti M, Colina S, Rosa MM, Fazio F (1999) The neural correlates of verb and noun processing. A PET study. Brain 122: 2337–2344.

Peterson RR, Savoy P (1998) Lexical selection and phonological encoding during language production: Evidence for cascaded processing. J Exp Psychol Learn Mem Cogn 24: 539–557.

Pickering MJ, Branigan HP, Cleland AA, Steward AJ (2000) Activation of syntactic information during language production. J Psycholinguist Res 29: 205–216.

Poldrack RA, Wagner AD, Prull MW, Desmond JE, Glover GH, Gabrieli JDE (1999) Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. Neuroimage 10: 15–35.

Postma A (2000) Detection of errors during speech production: A review of speech monitoring models. Cognition 77: 97–131.

Poulisse N (1999) Slips of the Tongue. John Benjamins Publishing Company Amsterdam–Philadelphia.

Price CJ, Moore CJ, Friston KJ (1997) Subtractions, conjunctions, and interactions in experimental design of activation studies. Hum Brain Mapp 5: 264–272.

Ramus F (2003) Developmental dyslexia: specific phonological deficit or general sensorimotor dysfunction? Curr Opin Neurobiol 13: 212–218.

Rodriguez-Fornells A, Schmitt BM, Kutas M, Münte TF (2002) Electrophysiological estimates of the time course of semantic and phonological encoding during listening and naming, Neuropsychologia 40: 778–787.

Roelofs A (1997) A case for nondecomposition in conceptually driven word retrieval. J Psycholinguist Res 26: 33–67.

Roelofs A (2002) Spoken language planning and the initiation of articulation. Q J Exp Psychol 55: 465–483.

Roelofs A, Meyer AS, Levelt WJM (1998) A case for the lemma/lexeme distinction in models of speaking: Comment on Caramazza and Miozzo (1997). Cognition 69: 219–230.

Rumsey JM, Horwitz B, Donohue BC, Nace K, Maisog, .JM, Andreason P (1997) Phonological and orthographic components of word recognition. Brain 120: 739–759.

Schiller NO, Münte TF, Horemans I, Jansma BM (2003) The influence of semantic and phonological factors on syntactic decisions: An event-related brain potential study. Psychophysiology 40: 869–877.

Schmitt BM, Münte TF, Kutas M (2000) Electrophysiological estimates of the time course of semantic and phonological encoding during implicit picture naming. Psychophysiology 37: 473–484.

Schriefers H, Jescheniak JD (1999) Representation and processing of grammatical gender in language production: A review. J Psycholinguist Res 28: 575–600.

Schriefers H, Meyer AS, Levelt WJM (1990) Exploring the time course of lexical access in language production: Picture-word interference studies. Journal of Memory and Language 29: 86–102.

Shattuck-Hufnagel S (1979) Speech errors as evidence for a serial ordering mechanism in sentence production. In: Sentence Processing: Psycholinguistic Studies Presented to Merrill Garrett (Cooper WE, Walker ECT, eds.). Erlbaum, Hillside, NJ, p. 295–342.

Shattuck-Hufnagel S (1987) The role of word-onset consonants in speech production planning: New evidence from speech error patterns. In: Motor and Sensory Processes of Language (Keller E, Gopnik M, eds.). Erlbaum, Hillsdale, NJ, p.17–51.

Snowling MJ (2001) From language to reading and dyslexia. Dyslexia 7: 37–46.

Steinhaurer K (2003) Electrophysiological correlates of prosody and punctation. Brain Lang 86: 142–164

Steinhauer K, Alter K, Friederici AD (1999) Brain potentials indicate immediate use of prosodic cues in natural speech processing. Nat Neurosci 2: 191–196.

Steinhauer K, Friederici AD (2001) Prosodic boundaries, comma rules, and brain responses: The closure positive shift in ERPs as a universal marker for prosodic phrasing in listeners and readers. J Psycholinguist Res 30: 267–295.

Stemberger JP (1985) An interactive activation model of language production. In: Progress in Psychology of Language (Vol. 1) (Ellis A, ed.). Erlbaum, London, p. 143–186.

Stromswold K, Caplan D, Alpert N, Rauch S (1996) Localization of syntactic comprehension by positron emission tomography. Brain Lang 52: 452–473.

Swick D, Knight RT (1996) Is prefrontal cortex involved in cued recall? A neuropsychological test of PET findings. Neuropsychologia 34: 1019–1028.

Szatkowska I, Grabowska A, Szymańska O (2000) Phonological and semantic fluencies are mediated by different regions of the prefrontal cortex. Acta Neurobiol Exp (Wars) 60: 503–508.

Thierry G, Boulanouar K, KherifF, Ranjeva JP, Démonet JF (1999) Temporal sorting of neural components underlying phonological processing. Neuroreport 10: 2599–2603.

Thompson-Schill SL, D'Esposito M, Aguirre GK, Farah MJ (1997) Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. Proc Natl Acad Sci U S A 94: 14792–14797.

Thompson-Schill SL, D'Esposito M, Kan IP (1999) Effects of repetition and competition on activity in left prefrontal cortex during word generation. Neuron 23: 513–522.

Unsworth SJ, Pexman PM (2003) The impact of reader skill on phonological processing in visual word recognition. Q J Exp Psychol A 56: 63–81.

Van der Meulen FF, Meyer AS, Levelt WJM (2001) Exe movements during the production of nouns and pronouns. Mem Cognit 29: 512–521.

van Turennout M, Hagoort P, Brown CM (1997) Electrophysiological evidence on the time course of semantic and phonological processes in speech production. J Exp Psychol Learn Mem Cogn 23: 787–806.

van Turennout M, Hagoort P, Brown CM (1998) Brain activity during speaking: From syntax to phonology in 40 milliseconds. Science 280: 572–574.

Vandenberghe R, Price C, Wise R, Josephs O, Frackowiak RSJ (1996) Functional anatomy of a common semantic system for words and pictures. Nature 383: 254–256.

Wagner AD, Desmond JE, Demb JB, Glover GH, Gabrieli JDE (1997) Semantic repetition priming for verbal and pictorial knowledge: A functional MRI study of left inferior prefrontal cortex. J Cogn Neurosci 9: 714–726.

Warren RM, Warren RP (1970) Auditory illusions and confusions. Sci Am 223: 30-36.

Wernicke C (1874) The Complex of Aphasic Symptoms (in German). Cohn and Weigart, Breslau.

Wittmann M, Fink M (2004) Time and language – critical remarks on diagnosis and training methods of temporal-order judgment. Acta Neurobiol Exp (Wars) 64: 341–348.

Wojciulik E, Kanwisher N, Driver J (1998) Covert visual attention modulates face-specific activity in the human fusiform gyrus: fMRI study. J Neurophysiol 79: 1574–1578.

Zatorre RJ, Evans AC, Meyer E, Gjedde A (1992) Lateralization of phonetic and pitch discrimination in speech processing. Science 256: 846–849.

Zatorre RJ, Meyer E, Gjedde A, Evans AC (1996) PET studies of phonetic processing in speech: Review, replication, and reanalysis. Cereb Cortex 6: 21–30.

Ziegler JC, Tan LH, Perry C, Montant M (2000) Phonology matters: the phonological frequency effect in written Chinese. Psychol Sci 11: 234–238.

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