Neural Mechanisms of Inference Processes during Text Comprehension

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Ho Ming Chow

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Abstract

The aim of this study is to investigate the neural mechanisms underlying the drawing of inferences based on a reader's knowledge during reading. Previous research studies have investigated this topic by using different types of text materials varying in coherence (e.g. Ferstl and von Cramon, 2001; Kuperberg et al., 2006), complexity (e.g. Xu et al., 2005), comprehensibility (e.g. Vandenberghe et al., 2002) or acceptability (e.g. Hagoort et al., 2004). Instead of using different types of text materials, we used a less explored method that manipulated the reader's reading goals to vary the level of engagement of inference processes. Cognitive psychologists have shown that the reader's reading goals have considerable influence on the cognitive processes of comprehension and on the content of the resulting representation of the text (Calvo et al., 2006; Graesser et al., 1994; McKoon and Ratcliff, 1992; Singer and Halldorson, 1996). Here, two functional magnetic resonance imaging (fMRI) experiments were conducted to investigate the neural mechanisms of drawing strategic and routine inferences. The experimental data were analysed using two complementary approaches, namely conventional fMRI data analysis and effective connectivity analysis. Combined with an anatomical model developed in this study, the latter approach enabled us to quantify the interregional interactions modulated by the experimental conditions and to discriminate between several plausible hypotheses regarding how inferences are drawn. The results of both fMRI experiments show that the left inferior frontal gyrus (IFG) in Brodmann area (BA) 45/47 is involved in inference processes, regardless of whether inferences are drawn strategically or routinely, while the left anterior prefrontal cortex (aPFC) in BA 9/10 is only involved in retrieving strategic inferences. The effective connectivity analyses show that the retrieval of strategic and routine inferences consistently enhances the connectivity between the left posterior superior temporal sulcus (pSTS) and the left dorsal lateral inferior frontal gyrus (dIFG). The evidence supporting the enhancement of dIFG-pSTS connectivity was much stronger than the evidence supporting the enhancement of the frontotemporal connectivity involving the temporal parietal junction and the anterior temporal lobe in the left hemisphere. With these findings, we argue that the neural mechanisms for drawing inferences involve IFG and dIFG-pSTS interactions. These interactions probably reflect the mediation of a top-down bias that guides the retrieval of inferences in the temporal areas. Moreover, the functional roles of aPFC in language comprehension seem to be specific to monitoring the build-up of coherence among strategic inferences, the situation described in the text and the reader's goal.

Abbreviations

aTL	the anterior temporal lobe
BA	Brodmann area
BF	Bayes factor
BOLD	blood oxygenation level dependent
CI Model	the construction-integration model
DCM	dynamic causal modelling / dynamic causal model
dIFG	the dorsal lateral inferior frontal gyrus
DTI	diffusion tensor imaging
FEX	fixed effect analysis
fMRI	functional magnetic resonance imaging
FWHM	full width at half maximum
GBF	group Bayes factor
HRF	hemodynamic response function
IEF	the immersed experiencer framework
IFG	the inferior frontal gyrus
mMTG	the middle portion of the middle temporal gyrus
MNI	Montreal Neurological Institute
MRI	magnetic resonance imaging
PER	positive evidence ratio
pITG	the posterior inferior temporal gyrus
pMTG	the posterior middle temporal gyrus
pSTG	the posterior superior temporal gyrus
pSTS	the posterior superior temporal sulcus
REX	random effect analysis
TPJ	the temporal parietal junction
vIFG	the anterior ventral inferior frontal gyrus

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1 Introduction

1.1 Research Question

During reading comprehension, drawing implicit information on the basis of our world knowledge is necessary to fully understand the text. For example, in the sentence *Ute and Frank saw a group of elephants while they were flying across the national park of Kenya*, it is very likely that we immediately understand the personal pronoun *they* refers to *Ute and Frank* but not *elephants*, although referring *they* to *a group of elephants* is grammatically correct. We understand the text example in this way because we know from our world knowledge that humans are more likely to fly than elephants, and use this implicit information to establish a coherent understanding of the text. We term such activation and use of the reader's world knowledge that is not mentioned explicitly in the text during comprehension as "inference processes", and we call the implicit information activated from these processes "inferences" [1]. Sometimes, as in reading the above example, we may not be aware of the activation of inferences, and it seems that inferences arise instantaneously and effortlessly. We term these kinds of inferences as "routine inferences" and the involved processes as "drawing/retrieving routine inferences". On the other hand, it is obvious that we are able to draw strategic inferences under conscious control. These processes are referred to as "drawing/retrieving strategic inferences" and their outcomes are called "strategic inferences". The central research question of the present study is to investigate the neural mechanisms involved in drawing routine and strategic inferences. In particular, we make use of recent advances in neuroimaging and fMRI modelling techniques to identify the brain structures and the interregional interactions that are critical to inference processes.

1.2 Experiments

In psycholinguistic research, a question of interest concerns which types of inference are drawn automatically, routinely or strategically. It has been

[1] The notion of inferences in this study is not the same as the usual notion of inferences in formal logic and deductive reasoning, but is closely related to inductive reasoning.

generally agreed among cognitive psychologists that whether a type of inference is drawn routinely or strategically is highly dependent on the goal of the reader (Graesser et al., 1994; McKoon and Ratcliff, 1992). Specifically, previous research has shown that manipulating reading goals can trigger strategic inferences (Calvo et al., 2006), as well as inhibiting the generation of routine inferences (Singer and Halldorson, 1996). In the first fMRI experiment of this study, we used the reader's ability to draw predictive inferences, which are considered to be non-routine inferences, to investigate the neural mechanisms for drawing strategic inferences. In the critical condition, participants were instructed to read short passages and to predict the development of the situation described in each passage during reading. To accomplish this task, participants presumably need to draw strategic inferences on the basis of the context and their world knowledge. Comparing this condition with a passage-reading condition without prediction, we expect that the neural correlates of strategic inference processes can be revealed. In the second fMRI experiment, participants were instructed to read short passages and to detect pseudowords. Previous research has shown that this proofreading-like reading task can shift the reader's focus to the explicit meanings of the text and can inhibit the generation of routine inferences. As a baseline condition, this reading task was used to compare to a relatively normal reading condition in which participants were instructed to detect obvious world-knowledge violations during passage reading. Presumably, this comparison can reveal the brain regions for drawing routine inferences.

1.3 Approaches and Hypothesis

The organisation of the brain adheres to two fundamental principles, *functional specification* and *functional integration* (Friston, 2002). Functional specification suggests that each cortical region is specialised for some aspects of perceptual, cognitive or motor processing. A single function may involve many specialised regions, and the function emerges from their interregional interactions. Those interactions are referred to as functional integration. To investigate functional specification for inference processes, we used conventional fMRI data analysis, which addresses the brain regions that are more active across experimental conditions. Additionally, to test how interregional interactions are mediated, a state-of-the-art modelling technique – dynamic causal modelling – was employed.

Previous neuroimaging research has indicated that the interactions for drawing inferences may involve several regions in the left hemisphere and mediate through their connecting pathways in the dorsal and ventral streams (for details, see Section 3.4 on p. 28). As inference processes involve cognitive control and semantic retrieval, which are probably subserved by the frontal and temporal regions respectively, we hypothesize that frontotemporal interactions are particularly important for the act of drawing inferences. However, we know very little about the critical regions involved in the processes and the neural pathways through which regional interactions are mediated. According to the previous fMRI studies and the anatomical connection model developed in Section 3.5 on p. 30, we hypothesize that inference processes may involve one or more of the following frontotemporal systems: (i) the interactions between the inferior frontal gyrus and the posterior temporal sulcus, (ii) the interactions among the inferior frontal gyrus, the posterior temporal sulcus and the temporal parietal junction mediating, and (iii) the interactions between the inferior frontal gyrus and the anterior temporal lobe. These possibilities and their combinations were tested by dynamic causal modelling in order to determine which frontotemporal interactions are critical to the drawing strategic and routine inferences. For the empirical evidence of these hypotheses, please see Section 3.4.2 on p. 29, and for the dynamic casual models derived from this hypothesis, please see Section 5.2 on p. 49 and Section 6.2 on p. 73.

1.4 Thesis Overview

In the next chapter, we will first review the roles of inferences in language comprehension and the cognitive processes involved in drawing and integrating inferences, from the perspective of two prominent theories of language comprehension, namely the construction-integration model (Section 2.1) and the immersed experiencer framework (Section 2.2). These theories serve as a basis for the definitions of language processes important to this study (Section 2.3). This is followed by a discussion on how reading goals affect the retrieval of inferences according to the minimalist and constructionist positions, and related behavioural studies (Section 2.4), which provides the theoretical grounds for the experimental manipulations used in this study. In Chapter 3, we review the functional roles of eight brain regions in the left hemisphere that have been found by neuroimaging studies to be involved in language comprehension (Section 3.1 to 3.3), and how these regions are anatomically connected based on the recent findings of diffusion tensor imaging studies in humans (Section 3.5). From these reviews, we develop the hypotheses regarding the neural mechanisms underlying inference processes (Section 3.4). To test these hypotheses, we used two complementary approaches to analyse the fMRI data obtained from the experiments: conventional data analysis and effective connectivity analysis. In Chapter 4, the general procedures and considerations of fMRI data acquisition and analyses are reported. In Chapter 5, we report and discuss the findings of the fMRI experiment designed to reveal the neural mechanisms for drawing strategic inferences. In Chapter 6, we report and discuss the findings of an fMRI experiment targeted to reveal the neural mechanisms for drawing routine inferences. In the last chapter, the significance of the experiments and further research directions are discussed.

2 Processes Involved in Comprehension and Inference Drawing

In this chapter, we will first describe two prominent theories of text comprehension, namely the construction-integration model (Section 2.1) and the immersed experiencer framework (Section 2.2). From these theories, we aim to identify the main processes involved in text comprehension and the possible roles of inferences in these processes. It must be emphasized that these theories are not intended to be used and should not be viewed as a framework for the experimental work of this study. Their only purpose is to define the terminology needed to describe processes involved in language comprehension in following chapters, which will be summarised in Section 2.3. After that, in Section 2.4, we discuss the circumstances in which routine and strategic inferences are retrieved. This will provide the theoretical grounds for the experimental manipulations used in this study, and will guide the interpretation of the fMRI results.

2.1 Construction-integration Model

Kintsch's construction-integration model (1988, 1998) is a highly influential computational model aimed at simulating the processes of comprehension. Below, we discuss the claims and assumptions underlying the CI model, and their implications for inference processes using the model. The results of studies conducted using the CI model will not be covered.

2.1.1 Levels of Representations

The CI model considers comprehension to be a series of processes involved in establishing a coherent mental representation. These processes consist of three levels, namely the surface level, the propositional level and the situational level. The surface-level representation is formed by the literal wordings of the text. The propositional representation, also called the textbase, consists of the meanings of the text in the form of propositions. Usually, a proposition in the CI model is expressed by a predicate and one or more arguments. For example, the sentence *Susanna plays the pipe organ* corresponds to the predicate PLAYS (SUSANNA, PIPE ORGAN). The situational-level representation, also called the situation model, represents the information of the referential situation described in the text. Many researchers in the field of text comprehension have assumed that this representation maintains most of the knowledge-based inferences generated in comprehension.

2.1.2 Knowledge Net

To simulate language comprehension, one has to deal with the question of how knowledge is organised in the reader's mind. The CI model assumes that the reader's knowledge can be represented by a knowledge net. This is a network consisting of nodes that represent concepts or propositions, and links that represent the pairwise associative strengths between two nodes. As the amount of knowledge is huge, the construction of a complete knowledge net would be impossible. For practical reasons, only a small subset of the complete knowledge net is selected for a CI model and usually these are the inferences that can be accessed in the CI model.

2.1.3 Construction Phase

The operations of the CI model consist of a construction and an integration phases. In the construction phase, Kintsch (1988) claimed that the words of the text are used to construct propositions, which further activate associated propositions from the knowledge net in a bottom-up fashion. Kinstsch (1988) suggested that if not all inferences required to establish a coherent representation are retrieved from this elaborative mechanism, there is a need to draw controlled, specific inferences such as bridging inferences. This phase results in an enriched textbase in which the propositions may be redundant or even contradictory. For instance, an example given in Kintsch (1988) *The lawyer discussed the case with the judge. He said "I shall send the defendant to prison."* was parsed into five propositions (P1-5 in Table 1), and additionally activated two propositions (C1-2 in Table 1) from the knowledge net. Grammatically, the personal pronoun *he* in the text can refer to either the lawyer or the judge. However, our knowledge about the legal system informs us that *he* should be the judge because lawyers do not have the power to send someone to prison. Nevertheless, in the construction phase, the CI model of this text includes both incorrect (P2 and P3 in Table 1) and correct (P4 and P5 in Table 1) interpretations.

After the construction and activation of propositions, the next step in the construction phase is to relate these propositions according to a number of principles. In Kintsch (1998), the connection strengths initially set in the 'lawyer and judge' text are shown in Fig. 1.

Table 1
Propositions of the text *The lawyer discussed the case with the judge. He said "I shall send the defendant to prison."* and the associated concepts (adapted from Kintsch, 1988).

#	Proposition
P1	DISCUSS (LAWYER, JUDGE, CASE)
P2	SAY (LAWYER, P3)
P3	SEND (LAWYER, DEFENDANT, PRISON)
P4	SAY (JUDGE, P5)
P5	SEND (JUDGE, DEFENDANT, PRISON)
C1	SENTENCE (JUDGE, DEFENDANT)
C2	IMPLY (C1, P5)

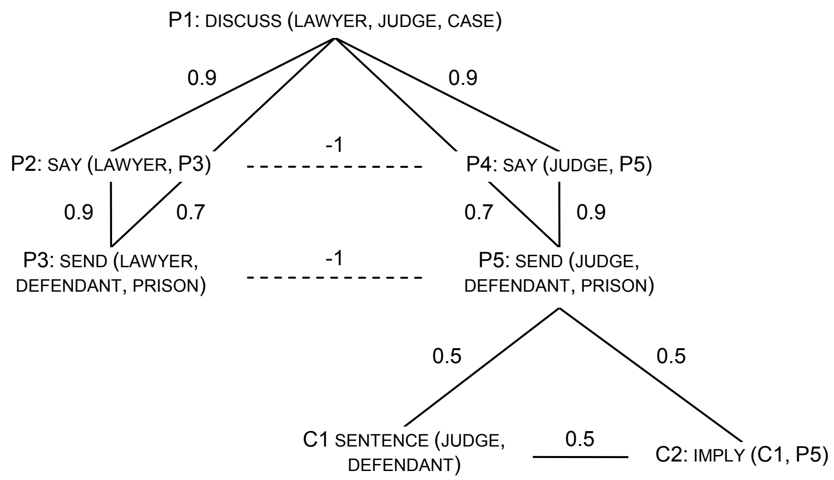

Fig. 1. The connection strengths between the propositions of the text *The lawyer discussed the case with the judge. He said "I shall send the defendant to prison."* (adapted from Kintsch, 1988).

2.1.4 Integration Phase

As mentioned earlier, the propositions generated in the construction phase may be redundant and contradictory. These ambiguities and contradictions are assumed to be resolved in the integration phase. Kintsch (1998) suggested that integration is a constraint satisfaction mechanism that is modelled as a cyclical spreading activation process. Specifically, in each integration cycle, the activation strengths of the text and inferred propositions in the model are modified according to their connection strengths. Strongly associated propositions strengthen the activations of each other, whereas weakly associated or contradictory propositions are inhibited. The spreading activation process iterates until the average difference between activation values in previous and current cycles is smaller than an arbitrary threshold. If a model fails to converge, Kintsch (1988) claimed that inferring additional propositions from the knowledge net is needed, and this is followed by another integration attempt. At the end of the integration phase, only the activated propositions remain in the model and the non-activated propositions are discarded. Supposedly, the remaining propositions reflect the contents of the mental representation formed in comprehending the text.

2.1.5 CI Model and Inference Processes

Kintsch (1988) suggested that there are two mechanisms for retrieving inferences. Primarily, in the construction phase, inferences are retrieved by an elaborative mechanism which selects the associated neighbours of the text propositions from the knowledge net. This mechanism is considered to be bottom-up and context-independent. Another inference mechanism is assumed to be based on controlled memory retrieval, by which specific inferences such as bridging inferences can be activated. Similarly to the elaborative mechanism, this controlled retrieval mechanism for drawing specific inferences is also recruited in the construction phase, but the author has not provided any hint about how these inferences are drawn.

These two mechanisms have been demonstrated experimentally by Till et al. (1998). Subjects were required to perform a lexical decision task after reading a sentence such as *The townspeople were amazed to find that all the buildings had collapsed except the mint*. The last word of this sentence was critical, because it held different relations to the four possible target words of the following lexical decision task:

- *money* – associated with the contextually appropriate sense of the homograph *mint*
- *candy* – associated with the contextually inappropriate sense of the homograph *mint*
- *earthquake* – a thematic inference
- *breath* – an unrelated control word (the control condition)

Either one of these four target words were presented either 200, 300, 400, 500, 1000 or 1500 ms (SOA) after the onset of the last word in the sentence. The results showed that compared to the control condition, both contextually appropriate and inappropriate target words were facilitated as soon as the SOA was longer than 300 ms, indicating that the associated meanings of the critical word are activated independent of the context. Furthermore, if the SOA was longer than 1000 ms, the mean response latency of the thematic inferences, *earthquake* in this example, differed significantly from that of the control words, showing that it takes much more time to draw thematic inferences than to activate associated meanings. The results indicate that the elaborative mechanism probably fails to draw specific inferences such as thematic inferences, and thus a controlled retrieval mechanism is recruited.

In the CI model, the elaborative mechanism is assumed to activate associated meanings of the words in the text as in the above example, and retrieve elaborative propositions from the knowledge net. For example, according to Kintsch (1988), the proposition BAKE[MARY, CAKE] from the text *Mary bakes a cake* may activate propositions like PUT[MARY, CAKE, IN-OVEN], RESULT[BAKE[MARY, CAKE], HOT[CAKE]], etc. However, many researchers have suggested that these elaborative inferences are not drawn routinely and are dependent on strategic processes (Graesser et al., 1994; McKoon and Ratcliff, 1992; Potts et al., 1988). From this point of view, the distinction between the elaborative and controlled retrieval mechanisms for drawing inferences proposed in the CI model is not clear.

The activation of information is not the end of inference processes. The CI model suggests that inferred and text propositions should be integrated to construct a coherent representation. Specifically, in the spreading activation process, strongly associated propositions reinforce each other, and contradictory propositions are suppressed or eliminated. It implies that the construction of a coherence representation depends on whether the relations between activated propositions can be established or not. This process can be interpreted as coherence building (Tapiero, 2007), which is a prerequisite of integration.

2.2 Immersed Experiencer Framework

Based on the CI model (Kintsch, 1988) and other theories of language comprehension such as the structure building framework (Gernsbacher, 1990), Zwaan (2004) has developed the immersed experiencer framework (IEF). The IEF is distinct from other theories because it explicitly assumes that comprehension is a reconstruction of the reader's experience of the situation described in the text. This notion is inspired by Barsalou's (1999) proposal that human cognition is grounded in action and perception. The IEF suggests that action and perceptual representations, rather than amodal propositions as assumed in the CI model, are involved in comprehension. For example, to comprehend the sentence *The ranger saw an eagle in the sky*, the CI model assumes that the sentence is represented by an amodal proposition expressed as [[SAW[RANGER, EAGLE]], [IN[EAGLE, SKY]]], which captures the relations among entities, actions, and locations, whereas the IEF predicts that information related to the reader's experience in seeing an eagle in the sky, such as the shape of an eagle, is activated. This hypothesis was investigated by Zwaan et al. (2002). In the experiment, participants were asked to read short sentences, each of which was followed by the presentation of a picture. Participants had to decide whether the depicted object had been mentioned in the previously read sentence. There were two versions of pictures for the "yes" response, one matched and the other mismatched the implied shape of the object mentioned in the sentence. For example, the picture depicting an eagle with its wings outstretched matches well with the sentence *The ranger saw an eagle in the sky* but not with the sentence *The ranger saw an eagle in its nest*. On the other hand, a picture depicting an eagle with folded wings generates opposite match and mismatch effects. The results of Zwaan et al. (2002) showed that the recognition responses were significantly faster and more accurate in the match condition than the mismatch condition, indicating that the information about the object's shape was generated by the reader in the match condition, but not necessarily in the mismatch condition. This finding supports the fundamental assumption of the IEF that the reader's perceptual experience with the described situation plays a role in language comprehension.

2.2.1 Activation Stage

The IEF differentiates three general processing stages of text comprehension: activation, construal and integration. Zwaan (2004) claimed that these three component processes are not operated sequentially. Rather, they are assumed to interact closely with each other and overlap temporally to a large degree. In the activation stage, incoming text activates functional webs that represent the reader's experience with the referents of the words. This process is governed by the frequency distributions, and the primacy and recency of the reader's experience with the referents. Like the construction phase of the CI model, information activated in the activation stage of the IEF may be imprecise and redundant.

2.2.2 Construal Stage

In the construal stage of the IEF, coherent and contextually appropriate information is selected by a process called articulation. Similar to the integration phase in the CI model, articulation is a constraint-satisfaction mechanism. For instance, in the above example, the multiple shapes of an eagle assumed to be activated in the activation stage are constrained by the prepositional phrase *in the sky* or *in the nest* that articulates the context-appropriate shape of the eagle in the construal process. Furthermore, a construal may contain spatio-temporal information about the described situation (Zwaan and Radvansky, 1998), perspectives of a protagonist and focal entities signified by grammatical markers.

2.2.3 Integration Stage

The integration stage of the IEF is defined as the transition from one construal to the next by updating the current construal in working memory with the functional webs activated by the newly input words. The ease of transition is influenced by several factors (Zwaan, 2004):

- Whether the transition is in concordance with human experience, which involves continuity of time, space and perspective.
- The amount of overlap between the previous and current construal.
- Predictability. If we experience that event A frequently occurs before event B, we tend to anticipate event B when event A is presented.
- Linguistic cues.

2.2.4 IEF and Inference Processes

The overall structure of Zwaan's IEF and Kintsch's CI model are quite similar, both consisting of components for information activation and integration. However, the underlying assumptions about how inferences are drawn in these two models are quite different. First, the CI model assumes there are two distinct mechanisms for drawing inferences, whereas the IEF assumes that inferences are retrieved only by a single operation that reconstructs the reader's experience with the referents of the input text. Second, compared to the inference retrieval mechanisms proposed in the CI model, this operation is assumed to activate a broader range of inferences, including the reader's perceptual experience, emotion and motivation.

2.3 The Definitions of Language Processes

The two theories described in the previous section provide many ideas about the processes involved in language comprehension. However, whether the brain works as the theories describe is still open to empirical investigation. Therefore, we use them only as a basis to define some plausible language processes which will be mentioned frequently in this thesis.

In a manner similar to those of the two theories described in the previous section, in this study we assume that text comprehension involves two main groups of highly interactive processes. The first group of processes is related to the activation of word meanings and their associates, the reader's linguistic and world knowledge, and perceptual experience. As argued in Kintsch (1988), certain kinds of information can be activated by an associative mechanism, such as associated word meanings and some kinds of perceptual experience, but in many cases cognitive control is needed in order to activate more specific information, especially for activating the reader's world knowledge that is relevant to the context. To stress the cognitive control involved in activating information for comprehension, we use "controlled semantic retrieval" to describe these processes. Wagner et al. (2001) also used this term to describe the retrieval processes for establishing semantic relations between distantly related words. In this study, this term is used in a broader sense, including the establishment of relations between two text representations or between text representations and the reader's knowledge.

Comprehension is accomplished by the interactions between the processes related to information activation and a second group of processes, called information integration or simply integration in this study. The functions of integration include combining activated information and selecting context-appropriate information from competing alternatives. These functions require processes that establish coherence or relatedness among the activated information, including the information provided from the previous discourse, the reader's linguistic and world knowledge, and perceptual experience. These core processes in integration are called "coherence building" in this study. If coherence building fails to proceed, readers realize that the text they are reading is incoherent. Otherwise, a coherent representation is built up, which in turn guides controlled semantic retrieval.

In the following, we will use the text example *The townspeople were amazed to find that all the buildings had collapsed except the mint* to illustrate the language processes focused upon in this study. Throughout the whole reading period of the text, information activation and integration take place in parallel. At the point when the reader encounters *the mint*, the meanings of *the mint* in the sense of candy and a coin factory are activated. During coherence building, the relatedness between the meanings and the information provided by the previous discourse is established. Since the meaning referring to a coin factory – in comparison with the meaning referring to candy – better fits the representation built up from the previous activation and integration cycles, the meaning referring to a coin factory is selected and combined into the existing representation. The updated representation may guide controlled semantic retrieval to activate further related information, such as when an earthquake or a tornado has occurred.

This information then undergoes a new cycle of information integration.

2.4 Automatic, Routine and Strategic Inferences

The processes involved in language comprehension discussed above are not specific enough to determine which kinds of inferences are drawn in which circumstances. In this section, we discuss different types of inferences and the factors affecting whether a particular type of inference is drawn or not from the perspectives of the minimalist position (McKoon and Ratcliff, 1992) and the constructionist position (Graesser et al., 1994). From these two positions, we argue that the reader's goal is a crucial factor in triggering strategic inferences and in inhibiting routine inferences.

2.4.1 Minimalist Position

The minimalist position was proposed by McKoon and Ratcliff (1992), whose aim was to explore which kind of inferences are encoded into memory during reading when goal-directed strategic processes are absent. The authors have admitted that such a situation is rare because readers more often than not have specific reading goals, such as learning new information or reading for entertainment. Nevertheless, the investigation of minimal inferences can provide a foundation for studying strategic inference processes. They have argued that, in the absence of goal-directed strategic processes, "readers do not automatically construct inferences to fully represent the situation described by a text" (McKoon and Ratcliff, 1992, p. 440). Presumably, inferences are only drawn automatically if two conditions are fulfilled: (i) an inference is based on "quickly and easily available information" (p. 441) such as that explicitly mentioned in the text or "well-known general knowledge" (p. 441), and (ii) an inference is needed to establish local coherence, i.e. the coherent representation of a small text section such as a phrase. Graesser et al. (1994) have further specified three types of inferences that are needed to establish local coherence:

- Referential – A word or phrase is referentially tied to a previous element or constituent in the text (explicit or inferred)
- Case structure role assignment – An explicit noun phrase is assigned to a particular case structure role, e.g. agent, recipient, object, location, time.
- Causal antecedent – The inference is on a causal chain (bridge) between the current explicit action, event, or state and the previous passage context.

(The descriptions of inference types are excerpted from Graesser et al., 1994)

2.4.2 Constructionist Position

The constructionist position (Graesser et al., 1994) aims at understanding which kinds of inferences are automatically or routinely drawn during online comprehension. The constructionist position has argued that, in normal circumstances, readers try to "explain why actions, events, and states are mentioned in the text" (Graesser et al., 1994, p. 371) and "construct a meaning representation that addresses the reader's goals" (p. 371). For this to be successful, not only inferences for establishing local coherence but also inferences for establishing global coherence are needed. Global coherence means that locally-coherent parts of the text can be organized and interrelated to one or more overarching themes or concepts. Graesser et al. (1994) have proposed that, in addition to the three kinds of inferences for establishing local coherence, three more kinds of inferences are routinely drawn during reading:

- Superordinate goal – The inference is a goal that motivates an agent's intentional action.
- Thematic – This is a main point or moral of the text.
- Character emotional – The inference is an emotion experienced by a character, caused by or in response to an event or action.

(The descriptions of inference types are excerpted from Graesser et al., 1994)

2.4.3 Minimalist versus Constructionist Positions

The minimalist and constructionist positions are always perceived as rivals. Actually, they cannot be compared directly because they address two mutually exclusive scopes – the minimalist position concerns the kind of inferences drawn when the reader's goal is absent, whereas the constructionist position concerns the kind of inferences that are made to address reader's goals. Nevertheless, these two positions have two common aspects. First, the purpose of drawing inferences is to establish text coherence. The minimalist position has shown that inferences for establishing local coherence are necessary, and are probably drawn automatically even though the reader is shallowly reading a text. In addition to these local coherence inferences, the constructionist position has proposed that the reader routinely draws inferences for establishing global coherence in a relatively normal situation. Second, both positions stress that the reader's goal is a highly influential factor in the activation of inferences. Unfortunately, neither position has further explored how reading goals influence inference processes. In the next section, we further discuss this issue. We focus in particular on the effects of the reading goals that encourage strategic inferences and inhibit routine inferences.

2.4.4 Effects of Reading Goals on Inference Processes

Reading goals that encourage strategic inferences

Several researchers have systematically studied the effect of reading goals on the activation of inference (Graesser et al., 1993; Horiba, 2000; Kerns et al., 2004; Magliano et al., 1999; Rapp and Gerrig, 2006; Singer and Halldorson, 1996). For instance, using think-aloud procedures, Narvaez et al. (1999) and van den Broek et al. (2001) have demonstrated that readers draw more inferences during reading for “studying” than during reading for “entertainment”. As well as the amount of inferences, the strength and time-course of these inferences can also be influenced by reading goals. Consider the sentence *No longer able to control his anger, the husband threw the delicate porcelain vase against the window* (Potts et al., 1988). Predictive inferences – in this case “the vase broke” – have generally not yet been generated by the time the reader has read to the end of the sentence, and thus are considered to require time to develop (Calvo and Castillo, 1998; Graesser et al., 1994). However, if readers are encouraged to predict the development of the situation described in the sentence, predictive inferences can already be detected at the end of the sentence (Allbritton, 2004; Calvo et al., 2006) and can be sustained much longer (McDaniel et al., 2001). Two experiments conducted by Allbritton (2004) further illustrate this effect. In the first experiment, participants were required to respond to a lexical decision task during passage reading. The target words of the task were either predictable or non-predictable according to the situations described in the passages. The second experiment was the same as the first, except that a different group of participants were instructed to predict the development of the story during passage reading. In the second but not the first experiment, the mean lexical decision response to predictable target words was significantly faster than the mean lexical decision response to the non-predictable target words. One possible explanation of this modulation effect is that the reading goal of the participants in the second experiment encouraged the retrieval of predictive inferences, which are considered not to be drawn routinely during reading (Graesser et al., 1994) and may act as a prime that facilitates responses to the upcoming predictable target words.

Reading goals that inhibit the generation of routine inferences

Reading goals can encourage strategic inferences; they can also inhibit the generation of routine inferences. In a series of experiments reported in Singer and Halldorson (1996), the authors showed that understanding motive sequences like *Jane left early for the birthday party. She spent an hour shopping at the mall* facilitates the responses of knowledge validation questions such as *Do birthday parties involve presents?* This facilitation effect is attributed to the generation of bridging inferences such as "to buy a birthday present" in this case. According to Graesser et al. (1994), this kind of inference is drawn routinely. However, Singer and Halldorson (1996) have also shown that the facilitation effect in answering knowledge validation questions can be eliminated (indicating that bridging inferences are not available) if the participants adopted a proofreading strategy that encourages the detection of spelling errors. This shows that adopting the proofreading strategy may inhibit the generation of routine inferences.

2.5 Summary

In this chapter, we have reviewed two prominent theories of text comprehension, which provide a basis for defining the main language processes examined in this study:

- Activation – a group of processes that activate the reader's knowledge or perceptual experience for comprehension. These processes may operate automatically or require cognitive control.
- Integration – a group of processes that build up a coherent representation of the text.
- Associative mechanism – an automatic process to activate associative word meanings or perceptual experience.
- Controlled semantic retrieval – a core process of activation by which specific and context dependent information is retrieved.
- Coherence building – a core process of integration by which the relationships among information or representations are established.
- Selection – a core process of integration which selects context appropriate information among competing alternatives.

Additionally, we have looked at the perspectives of the minimalist and the constructionist positions, in order to discuss the circumstances under which a particular type of inference is drawn. Accordingly, inferences can be categorised into three coarse types, depending on how reliably they are drawn during reading: automatic, routine and strategic inferences. The minimalist position has proposed that some inferences are drawn automatically, such as those needed for establishing local text coherence. The constructionist position has proposed that some inferences are drawn routinely, such as those needed for establishing local and global text coherence. Above all, the reader's goal is a major factor that affects whether a particular type of inference is drawn or not. Previous empirical research has shown that different reading goals can encourage strategic inferences as well as inhibiting routine inferences.

3 Neural Architecture for Comprehension and Inference Processes

In this chapter, we focus on the brain structures potentially involved in drawing and integrating inferences. Emerging evidence has hinted that there is no single region specific to inference processes. Instead, inference processes probably require the involvement of a number of brain regions, and of interactions among them. In order to formulate plausible hypotheses of the neural mechanisms underlying inference processes, we will first discuss the brain regions involved in language processing, particularly semantic processing, and their possible contribution to inference processes (Section 3.1-3.3). On this basis, we speculate on the interregional interactions that may be engaged in drawing and integrating inferences (Section 3.4). This guides the construction of the dynamic causal models tested in Chapter 5 and 6. At the end of this chapter (Section 3.5), we will discuss the anatomical connections in the brain revealed by diffusion tensor imaging (DTI) studies. These DTI findings constrain whether a brain region can exert its effect directly or indirectly on other regions in the dynamic causal models of this study.

To restrict the scope of research, we concentrate mainly on a number of frontal and temporal regions in the left hemisphere. The cerebellum, subcortical regions, and regions in the right hemisphere are not considered here, as the left cerebral cortex is typically dominant for language functions (Cabeza and Nyberg, 2000; Vigneau et al. 2005). Based on the activation patterns obtained from previous positron emission tomography (PET) and fMRI studies, we defined eight regions of interest in the left hemisphere. Within each of these regions, a certain degree of functional homogeneity is expected. Moreover, this definition enables us to consistently label the activations obtained from different studies as well as in our own fMRI experiments. The approximate locations of the regions in MNI space[2] are shown in Fig. 2 and their details, including Brodmann areas and descriptions of their extent, are provided in Table 2.

[2] A standardized stereotaxic space of the human brain, developed by the Montreal Neurological Institute.

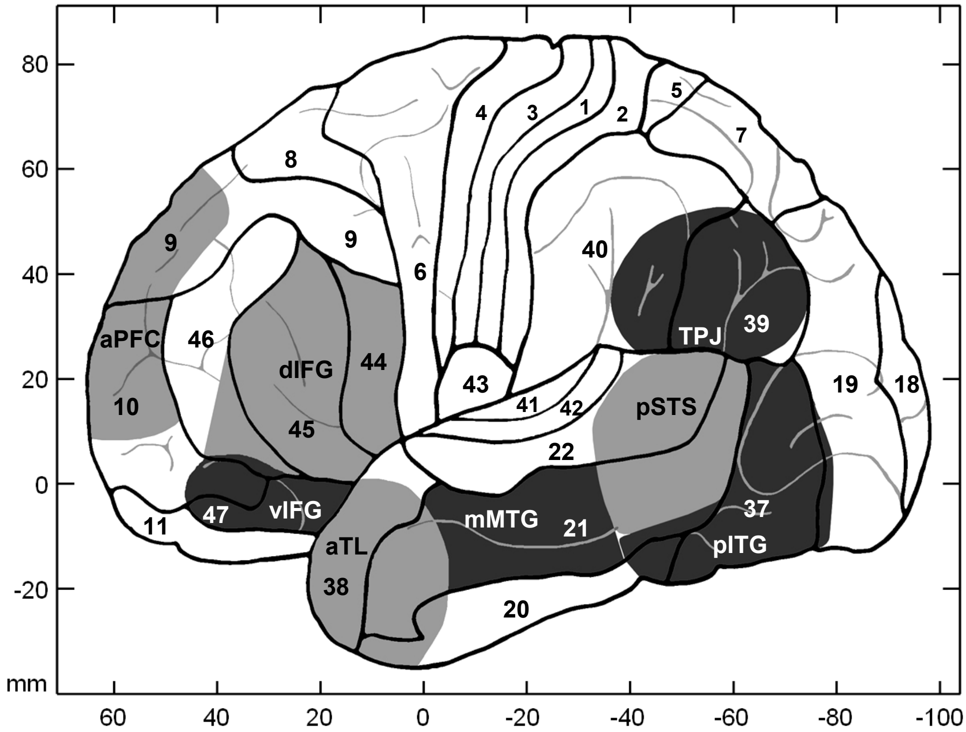

Fig. 2. A lateral view of the brain overlaid with the language regions selected for the review in this chapter (grey areas) and the Brodmann Areas (segregated by black lines). The regions include the anterior prefrontal cortex (aPFC), the dorsal lateral inferior frontal gyrus (dIFG), the anterior ventral inferior frontal gyrus (vIFG), the temporal parietal junction (TPJ), the posterior temporal sulcus (pSTS), the posterior inferior temporal gyrus (pITG), the middle portion of the middle temporal gyrus (mMTG) and the anterior temporal lobe (aTL). The horizontal and vertical axes indicate the approximate x- and z-coordinates of the MNI space, respectively.

3.1 Word Semantic Retrieval: Roles of pITG, pSTS, mMTG and IFG

Many studies in the psychological literature (e.g. Coltheart et al., 1994) and neuroimaging studies (e.g. Crinion et al., 2003 and Price et al., 1996a) assume that word-reading automatically activates the corresponding semantic and phonological representations. To investigate word-level processes, researchers usually compare the neural activity of word-reading to the neural activity when subjects view various visual stimuli including letter-like characters called “false fonts”, consonant strings and pronounceable pseudowords. These stimuli are assumed to engage one or more processes less than word-reading, and comparing them to word-reading can help to identify the location of the processes that are supposedly lacking during reading of those stimuli.

Table 2

Regions involved in language processing and inference processes

Anterior prefrontal cortex (aPFC)
Structure: Frontopolar area; dorsal medial prefrontal cortex
BA: 9, 10
Relative location: Most rostral part of the superior and middle frontal gyri

Dorsal lateral inferior frontal gyrus (dIFG)
Structure: Par triangularis and pars opercularis in the inferior frontal gyrus
BA: 44, 45
Relative location: surrounded by BA 47, 46, 9 and 6; roughly corresponds to Broca's area

Anterior ventral inferior frontal gyrus (vIFG)
Structure: Frontal orbital area in the inferior frontal gyrus
BA: 47
Relative location: between dIFG and BA 11

Temporal parietal junction (TPJ)
Structure: Angular gyrus and supramarginal gyrus in the inferior parietal lobe
BA: 39, 40
Relative location: between the visual cortex and the posterior end of the lateral fissure; part of Wernicke's area

Posterior superior temporal sulcus (pSTS)
Structure: Posterior superior temporal gyrus (pSTG) and posterior middle temporal gyrus (pMTG)
BA: 21, 22
Relative location: above pITG and below TPJ; part of Wernicke's area

Posterior inferior temporal gyrus (pITG)
Structure: Posterior middle and inferior temporal gyri, fusiform gyrus
BA: 20, 21, 37
Relative location: below the middle temporal sulcus and next to the inferior occipital gyrus

Middle portion of the middle temporal gyrus (mMTG)
Structure: Middle portion of the middle temporal gyrus
BA: 21
Relative location: below the primary auditory cortex in the superior temporal gyrus; between pSTS and aTL

Anterior temporal lobe (aTL)
Structure: Temporal polar area; anterior superior and middle temporal gyri
BA: 21, 22, 38
Relative location: most rostral part of the superior and middle temporal gyri

3.1.1 Word Reading versus Letter Strings

To gain an overall picture of word-level processes, several researchers have compared the neural activity induced by word-reading with the neural activity induced by non-pronounceable letter strings such as false fonts and consonant strings. Presumably, this comparison removes the activation related to perceptual processes and singles out the regions subserving word-level semantic and phonological processes. Compared to non-pronounceable letter strings, word-reading consistently induces increased activity in pITG, extending to the fusiform gyrus (Bookheimer et al., 1995; Herbster et al., 1997; Mechelli et al., 2005; Paulesu et al., 2000; Price et al., 1996a; Petersen et al., 1990; Rumsey et al., 1997), pSTS (Hagoort et al., 1999; Howard et al., 1992; Mechelli et al., 2005; Paulesu et al., 2000; Price et al., 1994; Price et al. 1996a) and IFG (Bookheimer et al., 1995; Herbster et al., 1997; Mechelli et al., 2005; Paulesu et al., 2000; Price et al., 1994; Price et al., 1996a; Rumsey et al., 1997). An interesting study from Büchel et al. (1998) showed that the left pITG is active not only when normal subjects read words but also when late or congenitally blind subjects read Braille, indicating that processing in this region is independent of the input modality. In most of the studies mentioned above, pITG and pSTS activity was bilateral, but it was usually stronger and more extensive in the left hemisphere.

3.1.2 Word Reading versus Pseudowords

To further separate semantic and phonological processes, pronounceable pseudowords have been used as a baseline to compare the activity induced by word-reading. Supposedly, this comparison should be useful for identifying the locations for semantic processing because the pseudowords have corresponding orthographic and phonological but not semantic features of the legal words. However, the results are quite inconsistent (see Mechelli et al., 2003 for a review) and, to our surprise, pseudoword-reading relative to word-reading always induced more extensive neural activity in the temporal and frontal lobes (Fiez, et al., 1999; Hagoort et al., 1999; Mechelli et al., 2003; Paulesu et al., 2000; Price et al., 1996a; Xu et al., 2001). It seems that during pseudoword-reading, the word semantic system is more active, attempting to process the orthographic and phonological information of the pseudowords. If this is the case, contrasting pseudoword-reading to word-reading may also reveal the brain regions associated with semantic processing. Similar to the comparison between word and letter-string reading, the comparison between pseudoword and word reading showed increased activity in pITG (Fiez et al., 1999; Hagoort et al., 1999; Herbster et al., 1997; Mechelli et al., 2003; Paulesu et al., 2000; Xu et al., 2001) and IFG (Paulesu et al., 2000; Price et al., 1996a; Mechelli et al., 2003; Xu et al., 2001) and pSTS (Price et al., 1996a; Rumsey et al. 1997; Paulesu et al. 2000), indicating that pITG, pSTS and IFG are primarily involved in word semantic processing. Further evidence is obtained from studies using naming or categorization tasks in which the retrieval of the concepts of the depicted objects is required. Compared to nonsense object viewing, silent object naming consistently induced increased activity in IFG, pITG (Bookheimer et al., 1995; Martin et al., 1996; Price et al., 1996b) and pSTS (Martin, 2007).

Evidence from functional neuroimaging studies of word reading, pseudoword reading and object naming showed that pITG, pSTS and IFG are involved in word semantic processing. This conclusion is partly in agreement with lesion studies because the damage of pITG and pSTS lead to severe aphasia, but damage to IFG only seems to produce a transient mutism that revolves itself within weeks (Damasio et al., 2004; Dronkers et al., 2004). Moreover, Crinion et al. (2003) showed that IFG is not necessarily involved in passive listening to narratives, indicating that IFG may be more important for strategic processes in comprehension. The exact roles of IFG in comprehension is still controversial. In the following, we first further delineate the functional roles of pSTS and pITG based on the dual-route model of word reading (Coltheart et al., 1993; Coltheart et al., 2001), and then we go on to discuss in detail different hypotheses of the functional roles of IFG.

3.1.3 Direct and Indirect Routes for Accessing Word Semantics

The functional roles of pSTS and pITG seem to resemble some components of the dual-route model of word reading described by Coltheart et al. (1993) and Coltheart et al. (2001). With supporting evidence from psychological experiments and computational models, the dual-route model proposes that there are two routes – direct and indirect – for accessing semantics during word reading. The direct route relies on the direct association between the visual word form and its meaning. In the indirect route, the retrieval of word meanings is achieved first by the grapheme-to-phoneme transformations and then from the word pronunciation to its meaning. The direct route is particularly important for understanding word exceptions that do not follow usual spelling-to-sound rules, for example *pint* or *steak* in English. In the case of regular words, both direct and indirect routes may be engaged. To investigate the corresponding brain regions of the components proposed in the dual-route model, Jobard et al. (2003) carried out a meta-analysis of 35 neuroimaging studies of word reading. The authors concluded that pITG is predominantly involved in the direct, lexical semantic route and engages in accessing word semantics. Additionally, they showed that the grapho-phonological conversion is probably subserved by the left pSTG, i.e. the upper portion of pSTS and the left supramarginal gyrus, i.e. the lower portion of TPJ. The authors were ambiguous about whether these regions or pMTG (the lower portion of pSTS) is involved in accessing word meaning from phonology, i.e. the indirect route. But some researchers (e.g. Fiebach et al. 2002; Price, 2000; Hickok and Poeppel, 2007) tend to believe that this function is subserved by the area around the left posterior temporal sulcus, i.e. the middle portion of pSTS. Similarly, Wise et al. (2001) suggested that pSTS is responsible for storing sub-lexical components of words transiently in the form of speech sound units (i.e. phonemes), and that these transient representations of sound units are then matched to the phonological word forms stored in long-term memory. In summary, word semantics seems to be accessed by pITG and pSTS via direct or indirect routes respectively during word reading.

It is important to note that the direct and indirect routes may be engaged to different degrees during reading, depending on the spelling-to-sound correspondence of a particular language. Paulesu et al. (2000) compared the brain activity of English and Italian speakers during word reading. The results showed that pITG activations are stronger for English than Italian speakers, whereas pSTS activation is stronger for Italian than English speakers. This pattern can probably be explained by the fact that the spelling-to-sound correspondence in Italian is more reliable than that in English, and thereby the indirect route subserved by pSTS is more engaged for Italian than English speakers.

3.1.4 Lexical-Semantic Processing

Activity in the middle temporal gyrus, including mMTG (BA 21/22), is ubiquitous in many studies of language comprehension and production (Binder et al., 1997; Cabeza and Nyberg, 2000; Gernsbacher and Kaschak, 2003; Friederici, 2001). This is probably due to the involvement of the middle temporal gyrus in lexical-semantic processing (Binder and Price, 2001; Martin, 2001; Martin, 2007). Cabeza and Nyberg (2000) have suggested that the left middle temporal gyrus (BA 21) is involved in higher-level semantic retrieval processes because activations in this region have been found in various semantic-memory tasks, independent of input modalities and forms of stimulation, such as words, pictures and faces. Based on a meta-analysis of 58 neuroimaging studies of word production, Indefrey and Levelt (2004) proposed that mMTG is associated with lexical processes, in particular in retrieving and selecting the lemma of activated concepts. However, semantic and lexical processes have always co-occurred in experimental work so far, meaning that the division of labour for lexical-semantic processes among mMTG, pSTS and pITG is not yet clear.

3.2 Top-down Influences in Semantic Retrieval: Roles of dIFG and vIFG

As mentioned above, left IFG activity is not uncommon during word reading. Indeed, IFG activity can be found in a wide range of language tasks, including word repetition (e.g. Howard et al., 1992), phoneme detection (Démonet et al., 1994), semantic violation detection (e.g. Hagoort et al., 2004), word generation (e.g. Paulesu et al., 1997), word reading (e.g. Price et al., 1996a), and many other tasks used for studying various cognitive abilities such as working memory (for a review, see Wood and Grafman, 2003). In the context of language processing, a consensus has begun to emerge: there is a division of labour for semantic, syntactic and phonological processing within the left IFG (see Gough et al., 2005 for semantic-phonological dissociation, and see Dapretto and Bookheimer, 1999 for semantic-syntactic dissociation). Roughly speaking, the functional roles of IFG change gradually from semantic processing to syntactic processing and to phonological processing along the anterior ventral portion from vIFG to the posterior-dorsal portion, i.e. dIFG (Hagoort, 2005; Vigneau et al., 2006).

3.2.1 Selection Demand Hypothesis

The more precise functional roles of the left IFG in semantic processing have received considerable attention. (Badre et al., 2005; Moss et al., 2005; Petersen et al., 1988; Thompson-Schill et al., 1997; Wagner et al., 2001). Initially, researchers posited that left IFG activity is associated with semantic retrieval (e.g. Demb et al., 1995) because left IFG activity was found repeatedly when subjects performed word generation and semantic decision tasks. Alternatively, Thompson-Schill et al. (1997) hypothesized that left IFG activity is not associated with the degree of semantic retrieval but rather depends on the selection of task-relevant information among competing alternatives. To test this hypothesis, the authors manipulated the selection demands in a semantic decision paradigm. In the "high selection" condition, subjects were required to decide which of the two targets (e.g., *tongue* and *bone*) was relatively similar to a cue (e.g., *tooth*) according to a semantic dimension (e.g., colour) presented prior to the targets. Under this condition, subjects were assumed to select the attribute (e.g. colour) of the items among other competing semantic attributes (e.g. shape, size, etc.). In the "low selection" condition, subjects were asked to evaluate the global similarity between the targets (e.g. *tick* and *shoe*) and the cue (e.g. *flea*). This task assumed that selection of attributes is not required because all of them are relevant for judging global similarity. Thompson-Schill et al. also manipulated the number of targets, either two or four, in the low selection condition. As attribute selection is presumably not required in the global similarity judgement, the difference between four-choice and two-choice conditions should reflect the degree of semantic retrieval. Consistent with the hypotheses of the authors, the left dIFG, primarily in BA 44, showed increased response in the high selection compared to the "low selection" conditions. Importantly, the comparison between four-choice and two-choice conditions revealed no significant activation in the left IFG, even when a liberal threshold was chosen. These results indicate that left dIFG activity is sensitive to selection demands rather than semantic retrieval demands.

3.2.2 Controlled Semantic Retrieval Hypothesis

An alternative hypothesis is supported by a study from Wagner et al. (2001) who proposed that the left IFG guides “controlled semantic retrieval” irrespective of selection demands. The authors adopted the global similarity judgement task, i.e. the low selection condition, in Thompson-Schill et al. (1997). In the experiment of Wagner and colleagues, the main manipulation varied the semantic associative strength, either strong or weak, between the targets (e.g. *flame* and *bald*) and the cue (e.g. *candle*). The authors argued that the difference between the strong and weak associative strength conditions is related to the degree of controlled semantic retrieval demands. This argument was based on the assumption that the automatic word association mechanism could relate strongly associated words but not weakly associated words, and relating weakly associated words requires a greater need for a top-down bias to guide the retrieval. In both strong and weak associative strength conditions, selection demands were held constant because selection is not assumed to be required in the global similarity judgement task. Consistent with the hypothesis, the results showed significant activations in the left vIFG (BA 47) and the left superior posterior portion of dIFG (BA 44) in the weak compared to the strong associative strength conditions, indicating that activity in vIFG and dIFG is modulated by controlled retrieval demands.

To further examine the selection demand and the controlled semantic retrieval hypotheses, Badre et al. (2005) combined the high and low selection conditions in Thompson-Schill et al. (1997) and the high and low associative strength conditions in Wagner et al. (2001). Their results confirmed the main findings of both studies, i.e. selection demands modulate left dIFG activity, and controlled retrieval demands modulate left dIFG activity as well as vIFG activity. Furthermore, Badre et al. demonstrated that dIFG activity is strongly correlated with a meta-variable that explained a certain extent of the behavioural variances of the reaction times and error rates in all conditions. The authors argued that this meta-variable reflects a common process of the conditions, a generalized control process that selects relevant knowledge among competitors. Thus, the result of the correlation analysis implicates that this generalized control process is subserved by dIFG. In addition to the activations in the left IFG, Barde et al. also showed increased activity in the left posterior middle temporal gyrus, the inferior portion of pSTS, in the comparison between the weak and strong associative strength conditions but not in the comparison between the high and low selection condition. Because the left pSTS is probably involved in accessing semantics, the activation of pSTS supports the role of vIFG and dIFG in mediating top-down bias while retrieving semantics stored in the temporal area.

In summary, left IFG activity is involved in retrieving specific semantic information in order to fulfil task requirements, for example, retrieving associates of the target words and cues in the global similarity judgement task. Evidence has shown that this process is subserved by two anatomically separated regions in the left IFG, namely vIFG and dIFG. According to the interpretation of Badre et al. (2005), the left vIFG mediates a top-down effect to the temporal area, biasing the semantic retrieval. The left dIFG performs post-retrieval selection of task-relevant information among competitors. In view of this evidence, retrieval of word semantics during reading involves interactions between both bottom-up and top-down processes. The bottom-up, probably automatic, semantic processing involves the direct route that accesses word semantics by means of word forms and the indirect route that accesses word semantics by means of word pronunciations. The critical brain regions for the direct and indirect routes are pITG and pSTS respectively. The semantic processing subserved by these two regions is suspected to be influenced by the top-down bias driven by the left dIFG and vIFG (Badre et al., 2005; Rodd et al., 2005).

3.3 Sentence-level Processing: Roles of TPJ, aTL and aPFC

In addition to pITG, pSTS, mMTG and IFG activity, aTL, TPJ and aPFC activity are frequently found during the reading of connected sentences (e.g., Xu et al., 2005). However, their functional roles in language comprehension are still the subject of considerable debate. In this section, we highlight some of those debates and speculate on their roles in the drawing of inferences.

3.3.1 Interface of Frontal and Temporal Activity

Traditionally, the angular gyrus in TPJ was linked to visual word identification (Howard et al., 1992), but recently this view has been severely challenged (Cohen et al., 2000; Hickok and Poeppel, 2007; Jobard et al., 2003; McCandliss et al., 2003; Price et al., 1996a; Vigneau et al., 2005). Various functional roles of TPJ have been proposed, but clear consensus has not yet been reached. Some researchers have noticed that TPJ activity appears to be more prominent during sentence reading (Crinion et al., 2003; Ferstl, 2007; Price, 2000; Bavelier et al., 1997; Xu et al., 2005). Of these, some have suggested that TPJ together with several regions in the left temporal lobe constitute the semantic system (Price, 2000; Price, 1998; Vigneau et al., 2006), but precise roles of these areas are still a matter of debate. Integrating the above two views, a possibility is that TPJ is involved in retrieving sentence-level semantics, whereas pSTS and pITG may be solely involved in retrieving word semantics (Mason and Just, 2006).

Another hypothesis has suggested that TPJ functions as the phonological store in the working memory model proposed by Baddeley (1992). A main component of Baddeley's model is the phonological loop, which comprises the phonological store that holds sound-based memory traces for few seconds before fading out, and an articulatory rehearsal process by which memory traces in the phonological store are refreshed and maintained. Evidence from functional imaging studies (e.g. Henson et al., 2000; Vigneau et al., 2006) and neuropsychological patient studies (Baddeley 2003; Dronkers, 2004) have shown that the phonological store is located at TPJ and the articulatory rehearsal process is subserved by the left dorsal lateral prefrontal cortex (BA 44, 6) including the superior portion of dIFG. The function of the phonological loop may be particularly important for understanding syntactically complicated sentences because they usually require a higher demand of working memory (Featherston et al., 2000). Consistently, neural imaging studies have shown that TPJ is co-activated with dIFG when comparing the processing of complex and simple sentences (Dapretto and Bookheimer, 1999; Kang et al., 1999; Kaan and Swaab, 2002; Keller et al., 2001). Furthermore, Hickok and Poeppel (2000) have argued that the mechanism of the phonological loop is not merely for retaining verbal information, but that it acts as an auditory-motor interface, mediating the interactions between auditory representations stored in the temporal regions and articulatory representations maintained in the frontal regions during language perception. In view of this proposal, TPJ is an essential component in the communication between frontal and temporal regions in sentence comprehension.

3.3.2 Semantic Integration

Similar to TPJ, bilateral aTL (aTLs) activity has also been frequently observed in sentence comprehension (Crinion et al., 2003; Humphries et al., 2001; Maguire et al., 1999; Mazoyer et al., 1994; Stowe et al., 1999; Vandenberghe et al., 2002), and their specific functions are still under debate. Proposed left aTL functions include building syntactic structure with dIFG (Friederici, 2001; Friederici and Kotz, 2003; Dronkers, 2004), retrieval of proper names or animate entities (Damasio et al., 2004) and encoding verbal information into memory (Stowe et al., 2005). To account for the diversity of aTLs functions, Ferstl et al. (2008) have speculated that the aTLs are the sites where syntactic, prosodic and lexical information are integrated into a semantic representation. In contrast, Hagoort (2005) and Hagoort et al. (2004) have proposed that semantic integration is instead subserved by the left IFG (BA 45, 47). Consensus has not been reached between these two rivalling positions. Possibly, both aTLs and IFG are jointly involved in integrating various sources of information, establishing semantic relations and selecting competing information. This view is consistent with the framework of semantic processing in natural language proposed by Jung-Beeman (2005), in which the author has proposed that the aTLs are involved in semantic integration that allows higher-order semantic relations to be detected, elaborated and refined, while IFG is responsible for the selection of competing activated concepts.

3.3.3 Coherence Building

The ultimate goal of text comprehension is to establish a coherent mental representation by integrating various sources of information, including inferences. Previous fMRI studies have indicated that integration and coherence building may be subserved by anatomically discrete frontal regions in the left hemisphere. In the previous section, it was established that integration is probably subserved by aTLs and the left IFG. Emerging evidence has shown that coherence building is associated with the left anterior prefrontal cortex. Ferstl and her colleagues conducted a series of fMRI and lesion studies (Ferstl and von Cramon, 2001; Ferstl and von Cramon, 2002; Ferstl et al., 2002), in which they asked participants to judge the coherence between two sentences in each trial. They observed increased responses in aPFC (BA 9/10) while participants were judging coherent sentence pairs relative to incoherent sentence pairs, indicating that aPFC plays an important role in coherence building and the integration of various types of information, such as presented text, inferred information and the general knowledge of readers. This interpretation is in agreement with the general function role of aPFC proposed by Christoff and Gabrieli (2000) and Ramnani and Owen (2004).

Coherence building is crucial for integration because it determines which pieces of information are integrated into the representation (Kintsch, 1998; Zwaan, 2004). Following the above interpretation, one would expect that aPFC is always engaged in text comprehension because integration is one of the key processes in comprehension (Graesser et al., 1994; Kintsch, 1988). However, aPFC activity has not been consistently found in the previous studies of text comprehension (Ferstl, 2007), and some evidence has shown that aPFC activity is associated with the reader's active involvement in establishing text coherence, but not with text coherence per se (Siebörger et al., 2007). Therefore, aPFC activity is not always found during text comprehension.

3.4 Frontotemporal Interactions for Drawing Inferences

Higher cognitive functions are likely to arise from the interactions between several specialised brain regions (Friston, 1994). Drawing strategic inferences probably involves frontal regions, which are associated with cognitive control, and temporal regions in which semantic information and world knowledge are stored. This notion of frontotemporal interactions in inference processes has been implied in a number of studies (Badre et al., 2005; Friederici, 2001; Gold et al., 2006; Kerns et al., 2004; Kuperberg et al., 2006; Mechelli et al., 2005; Noesselt et al., 2003; Obleser et al., 2007; Virtue et al., 2006; Wagner et al., 2001).

3.4.1 Anatomical Connections and Language Comprehension

From the anatomical connections between the frontal and temporal lobes, we know that these interactions are mediated by means of at least two sets of neural pathways (Duffau et al., 2005). In the dorsal stream, the posterior temporal regions and the lateral frontal regions are connected by the arcuate fasciculi and the superior longitudinal fasciculi. In the ventral stream, the posterior and anterior temporal regions are connected by the inferior longitudinal fasciculi, and the anterior temporal regions are connected to the orbital frontal regions via the uncinate fasciculi (Catani et al., 2002; Croxson et al., 2005). In spite of the existence of the two sets of neural pathways in both hemispheres, the connections in the left dorsal stream seem to be dominant in language processing (Catani and ffytche, 2005; Mandonnet et al., 2007). To restrict the scope of this study, we mainly focus on the frontotemporal interactions in the left hemisphere.

The left dorsal stream connects three important language regions: dIFG, pSTS and TPJ. Theses regions and their connecting pathways are probably engaged in different language functions (Bitan et al., 2005; Catani and ffytche, 2005; Nakamura et al., 2006; Tyler and Marslen-Wilson, 2008). For instance, Horwitz and Braun (2004) showed that the functional connectivity[3], defined as the correlations between regional activity, among IFG, TPJ and pSTS were enhanced in a narrative production task but were absent in a less linguistically demanding production task. Moreover, Bitan et al. (2005) showed that different effective connectivity patterns were observable when participants carried out rhyming and spelling judgment tasks. This implies that different regions and connections are recruited for various language tasks. However, very little is known about how inference

[3] For the distinctions between functional and effective connectivity, see Section 4.5.1 on p.43.

processes modulate interactions between brain regions, especially while reading everyday texts.

3.4.2 Regions and Connectivity for Inference Processes

In this section, we review the frontotemporal interactions that would be important to inference processes. This provides the empirical grounds for the hypotheses that were tested by dynamic causal modelling in this study.

IFG-pSTS connectivity

Some brain regions seem to be critical for inference processes. Virtue et al. (2006) found increased left pSTS activity at coherence breaks during story reading. These coherence breaks were the points at which participants had to draw inferences in order to understand the story, indicating the pSTS is critical for drawing inference. In addition to pSTS, its interactions with IFG may be important because controlled semantic retrieval involves both IFG and pSTS (Badre et al., 2005; Gold et al., 2006, Wagner et al., 2001). This mechanism may also be used in retrieving inferences, leading to the enhancement of interregional interactions between IFG and pSTS.

IFG-TPJ-pSTS connectivity

Apart from IFG and pSTS, TPJ and aTL also appear to be critical for drawing inferences. Activity in TPJ was shown repeatedly to be involved in sentence or narrative comprehension (for details, see Section 3.3.1, on p. 25). Hickok and Poeppel (2000, 2007) proposed that TPJ is an essential component in the communication between frontal and temporal regions. This implies that TPJ is important in mediating top-down influences during comprehension. Consistent with this hypothesis, Obleser et al. (2007) demonstrated functional connectivity enhancement between TPJ and left frontal regions including IFG when more top-down influence is induced by reducing speech clarity.

IFG-aTL connectivity

Similar to TPJ, several researchers suggested that aTL is engaged in sentence-level comprehension, especially in semantic integration (for details, see Section 3.3.2, on p. 26). Within the framework of natural language semantic processing, Jung-Beeman (2005) proposed that aTLs detects, elaborates and refines higher-order semantic relations, and that IFG is responsible for the selection of competing activated concepts. According to this theory, the act of drawing inferences should enhance the interactions between aTL and IFG.

In view of this evidence, IFG-pSTS, IFG-TPJ, IFG-aTL interactions and their combinations, such as IFG-pSTS-TPJ interactions and IFG-pSTS-aTL interactions, may be involved in drawing inferences. These interactions can be mediated directly between two regions or indirectly via other regions, depending on the anatomical connections between brain regions. This topic is discussed in the next section.

3.5 Anatomical Connections between Language-related Regions

Diffusion tensor imaging (DTI) studies of humans provide valuable information about plausible anatomical connections between brain regions. Based on the results of these studies, we defined the inter- and intra-lobe connections between the eight selected language-related regions in the left hemisphere.

3.5.1 Inter-lobe Connections

The long-range connections between dIFG and the posterior language regions, pSTS and TPJ are interconnected by the arcuate fasciculus and the superior longitudinal fasciculus in the dorsal stream (Ben-Shachar et al., 2007; Catani et al., 2002; Croxson et al., 2005 and Makris et al., 2005). Moreover, the arcuate fasciculus extends from the posterior to anterior temporal lobe, connecting pSTS to aTL. However, the arcuate fasciculus terminates predominantly in the dorsolateral prefrontal cortex and does not reach the ventral part of the prefrontal cortex (Makris et al., 2005). Hence, it seems that pSTS and vIFG are not connected directly. Instead, evidence has shown that aTL and the orbital frontal gyrus including vIFG are connected ventrally via the uncinate fasciculus (Catani et al., 2002; Croxson et al. 2005).

3.5.2 Intra-lobe Connections

Within the temporal lobe, mMTG is likely to be connected to its neighbours pITG, pSTS and aTL in the left temporal lobe by U-shape short fibres. The direct connections among pITG, pSTS and aTL seem to be via the inferior longitudinal fasciculus (Catani et al., 2002; Catani and ffytche, 2005). For the connections in the frontal lobe, we are not aware of any DTI studies concerning this issue, but according to primate studies (Petrides and Pandya, 1999; Petrides and Pandya, 2001), aPFC, dIFG and vIFG are probably interconnected. All of the above-mentioned connections are assumed to be reciprocal. Further evidence for the network described above is provided by the comprehensive functional-anatomical model of language processing proposed by Friederici (2002) and Friederici and Kotz (2003). In their model, they indicated that functional connections exist between the posterior temporal regions and the inferior frontal regions, between the posterior and anterior temporal regions and between the inferior frontal regions and the anterior temporal regions. This model matches well with the proposed anatomical connections. The final network of connections between the language regions is shown in Fig. 3.

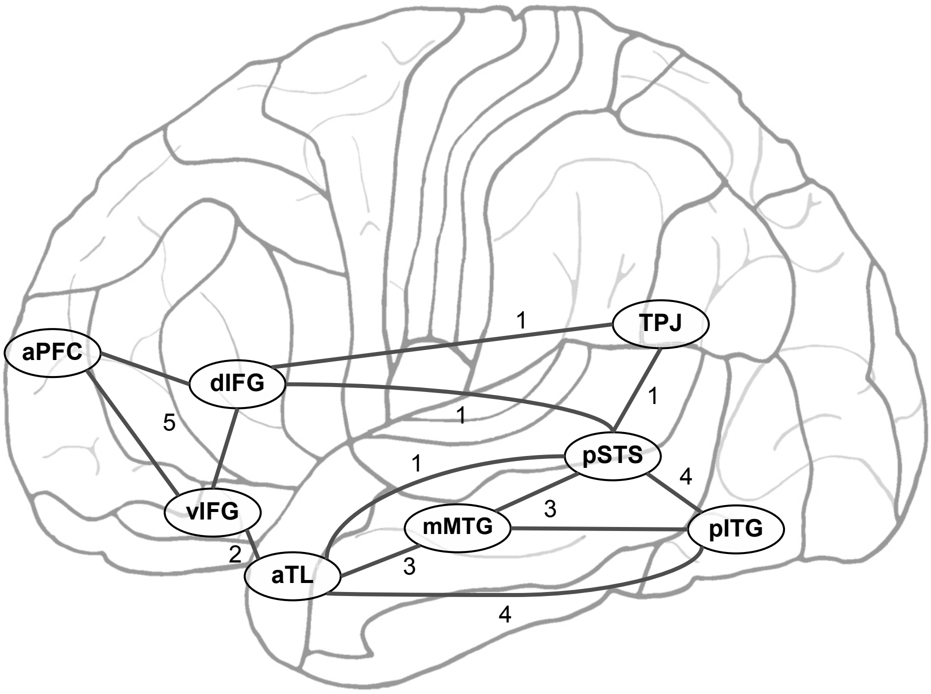

Fig. 3. A lateral view of the brain, displaying the plausible anatomical connections among the regions involved in language processing. (1) the connections involving the arcuate fasciculus, (2) the connections involving the uncinate fasciculus, (3) the connections involving the U-shape short fibres, (4) the connections involving the inferior longitudinal fasciculus, and (5) the connections assumed to connect the frontal regions. Please note that the lines representing the connections between regions do not reflect the actual pathways of fasciculi or fibre tracks.

3.5.3 Regions Connected with the Visual Areas

During reading, visual stimuli are first processed by the visual cortices in the occipital lobes. However, occipital lobe activity is related to sensory processes and does not contribute to language comprehension directly. After this early sensory processing, it seems that activity spreads to pITG and pSTS, and then the neuronal activity propagates from these two regions to other regions through the connections defined above. This assumption is supported by the results of studies of language processing using imaging techniques with high temporal resolution, including anatomically constrained magneto-encephalography (Marinkovic et al., 2003), fMRI time-resolved analysis (Haller et al., 2007) and event-related optical signal imaging (Tse et al., 2007). In these studies, the authors showed that activity involved in visual language processing spreads from pSTS and pITG to the other regions. Although recent evidence has suggested that the interactions between early visual areas and the posterior temporal regions may be influenced by visual attention and the control of eye movements (Acs and Greenlee, 2008), this influence may not be related to language processing and is not taken into consideration in this study.

3.6 Summary

In this chapter, we have discussed the controversial evidence regarding how inferences are drawn in the brain. According to the functions of the regions reviewed above and their anatomical connections, several regions and pathways may be involved in inference processes. In the dorsal stream, the controlled semantic retrieval mechanism may be used to draw inferences, which involves the mediation of top-down influences from IFG to posterior temporal regions including pSTS. The interactions between IFG and pSTS may be further interfaced by TPJ. Another line of evidence supports that inferences are drawn by a ventral stream system involving aTL and IFG. In this system, aTL establishes higher-level semantic relations by integrating various sources of information. From the integrated and available information, the context-appropriate information is selected by IFG. Furthermore, accumulating evidence has shown that aPFC is particularly important for establishing text coherence, especially when the reader is actively involved in this process.

Based on the functional roles of the regions and the anatomical connections reviewed above, in Section 3.4 we hypothesize that inference processes may involve one or more of the following three frontotemporal systems: (i) the interactions between dIFG and pSTS, (ii) the interactions among dIFG, pSTS and TPJ, (iii) the interactions between vIFG and aTL. In the next chapter, we discuss the methodology that enable us to identify the brain regions and the frontotemporal connections essential for inference processes.

4 Methodology

In this chapter, we discuss the basic principles and capabilities of fMRI (Section 4.1), the general design concerns involved in an fMRI experiment, especially an fMRI experiment using connectivity analysis (Section 4.2), and the general procedures used to analyse the fMRI data in this study (Section 4.4 and 4.5). The actual implementation of the analyses in the fMRI experiments of this study are reported separately in Chapters 5 and 6.

4.1 Basic Principles and Capabilities of fMRI

Magnetic resonance imaging (MRI) is a non-invasive neuroimaging technique based on the measurement of the magnetic susceptibility of tissues and substances. MRI can be used to acquire several types of images, revealing various types of brain structures or activity, and the number of techniques for neuroimaging using MRI is still growing. The most commonly used techniques includes structural scans that provide anatomical distribution of grey and white matters with a spatial resolution of around 1 mm^3, functional magnetic resonance imaging (fMRI) that measure changes in the hemodynamics accompanying the changes of neuronal activity, and diffusion tensor imagining (DTI), which traces the pathways of white matter tracts in the brain. A thorough discussion of all these techniques is far beyond the scope of this study (for more information about physical principles of MRI, see Cohen, 1996 or Huettel et al. 2004). Below, we briefly discuss the technique mainly used in this study, namely fMRI.

4.1.1 Physiological Basis of fMRI

Functional magnetic resonance imaging is based on the measure of local changes in magnetic susceptibility, depending on the concentration of deoxyhaemoglobin in the blood capillaries in the brain, which are associated with changes in neuronal activity. When the activity of a brain region increases, the deoxyhaemoglobin concentration is increased transiently due to the increase of cell metabolism. Subsequently, a physiological mechanism triggers the increase of blood flow, leading to an oversupply of oxygenated blood and dilution of the deoxyhaemoglobin concentration. The decrease of deoxyhaemoglobin concentration due to the increase of blood flow far exceeds the increase due to cell metabolism, and the result is a net decrease of deoxyhaemoglobin concentration in the blood capillaries. This hemodynamic response can be detected with T2* weighted MRI (Ogawa et al., 1990), and the detected signals are termed blood oxygenation level dependent (BOLD). Typically, the BOLD signals build up shortly after the stimulus onset time and reach a peak approximately 5-6 seconds thereafter. Although the underlying physiological relationship between the hemodynamic response and changes in neuronal activity are not yet fully understood, several sources of data have suggested that the BOLD signals detected by fMRI reflect local changes in neuronal activity reasonably well (Logothetis et al., 2001 and Heeger and Ress, 2002).

4.1.2 Capabilities and Limitations of fMRI

In studying cognitive functions, it is crucial to obtain precise information about where and when the brain activity occurs. Since fMRI relies on the measure of the hemodynamics associated with the neuronal activity, this technique comes with several limitations. First, fMRI cannot provide any information about whether the neuronal activity is a result of inhibitory or excitatory synaptic processes, because both mechanisms trigger the hemodynamic response (Buckner and Logan, 2001). Second, because the increase in blood supply is only in the spatial proximity of the nearby neuronal activity, the maximum spatial resolution of fMRI is limited to a few millimetres (Hernandez et al., 2002a). Furthermore, the temporal resolution of fMRI may be blurred or distorted by the sluggishness of the hemodynamics (Kim et al., 2000). Compared to the neuronal activity, which operates in the time scale of a few dozen milliseconds, the BOLD signals require around six seconds to develop to their peak, and even longer for the signals to return to their initial level in response to transient stimulation (Aguirre et al., 1998). Nevertheless, the peak of a BOLD signal is likely to carry the temporal information of its corresponding neuronal activity, but the temporal resolution is still a mater of debate. Kim et al. (1997) investigated the upper limit of temporal resolution in fMRI during visually instructed finger movements with a 4 Tesla scanner. They found that, without recourse to averaging fMRI time-courses, the timing information of finger movements with an execution time of approximately two seconds is preserved by the hemodynamic activity. If the fMRI time courses are averaged, the temporal resolution can be further increased, for instance, using the General Linear Model to estimate the average fMRI time courses, Hernandez et al. (2002b) showed the temporal resolution in fMRI is in the order of a few hundred milliseconds with 95% confidence. Using similar techniques, several authors have performed time-resolved analysis of cortical activation in various tasks such as mental rotation (Richter et al., 1997; Richter et al., 2000), mental imagery (Formisano et al., 2002), mental chronometry (Formisano and Goebel, 2003; Menon et al., 1998), visuomotor mapping (Goebel et al., 2003) and text reading (Haller et al., 2007). Apparently, the temporal resolution of the hemodynamic response is sufficient to resolve the timings of different processing stages that occur in the order of a few hundred milliseconds (Formisano and Goebel, 2003), but it is still far too low to detect individual synaptic activity that occurs in the order of a few dozen milliseconds.

4.2 Experimental Design Concerns for an fMRI Study

In this section, the general design concerns for an fMRI experiment (Section 4.2.1 and Section 4.2.2) and the design concerns specific to an fMRI experiment using connectivity analysis (Section 4.2.3) are discussed.

4.2.1 Subtraction Method

A frequently used neuroimaging method for revealing functional-anatomical mapping involves the statistical comparison between the activation in an experimental condition and the activation in a control condition. Ideally, the cognitive processes involved in the control condition are identical to those in the experimental condition, except that the process of interest is not engaged. Thus, the brain region subserving this process can be identified by subtracting the activation in the control condition from the activation in the experimental condition. This operation is termed the "subtraction method" (Petersen et al., 1988). It is based on the "pure insertion" assumption that supposes the exclusion of a cognitive process does not affect other processes involved in the task. Moreover, the subtraction method also assumes that the neural correlates related to the processes of interest are spatially distinguishable by the imaging method. These two assumptions are fundamental to the conventional fMRI data analysis employed in this study.

4.2.2 Block Design and Event-related Design

Block design

Block design and event-related design are the two main categories of experimental designs employed in fMRI studies. In an experiment with a block design, different experimental conditions are presented as separate blocks of trials. Usually, there is at least a 10-15 second interval between each block in order to prevent the hemodynamic response in the current block confounding the response in the subsequent block. Block design is simple and statistically powerful (Friston et al., 1999), but presenting the same experimental condition repeatedly in a block can be quite boring for the subject, leading to potential confounds such as rapid habituation and other strategy effects. Moreover, block design cannot be used for some experimental paradigms such as oddball detection tasks and Stroop tasks.

Event-related design

Event-related design was first shown to be useful by Buckner et al. (1996). In an event-related design, each experimental trial is temporally separated by an interval long enough for the hemodynamic response induced by the stimulus in a trial to return to the initial level. An interval of 15 seconds is considered to be enough (Bandettini and Cox, 2000). Using an event-related design, different trials or stimuli can be presented in randomized sequences and the activations of each type of stimulus can be averaged during data analysis. Compared to the block design, event-related design is more flexible in designing experiments. However, the price to pay for this flexibility is a loss in statistical power (Friston et al., 1999).

4.2.3 Experimental Design Concerns for Connectivity Analysis

This study employs connectivity analysis to investigate the interregional interactions modulated by inference processes. As connectivity analysis relies on the temporal relations between the fMRI time courses of brain regions (for details, see Section 4.5 on p. 43.), an experimental setting that can preserve the temporal information of the neuronal activity is critical. To obtain fMRI data with high temporal resolution, it is required to pay special attention to several factors:

- The magnetic field strength of the scanner, which determines the signal to noise ratio and the temporal resolution that can be achieved.
- Data sampling rate. The higher it is the better, but an increase in the data sampling rate leads to the reduction of spatial resolution.
- Number of trials in each condition. As mentioned in Section 4.1.2, averaging fMRI time courses can increase the temporal resolution. However, the number of trials cannot be increased indefinitely because it also increases the duration of the experiment.
- The tasks or cognitive processes under investigation should last relatively long in comparison with the interval between the acquisitions of two data points. Otherwise, the temporal relations between two regional fMRI time-courses may be at a time scale that cannot be detected by existing methods (Roebroeck et al., 2005).
- As the peak latencies of hemodynamic responses in different parts of the brain vary in the order of hundreds of milliseconds (Huettel and

McCarthy, 2001), extensive spatial smoothing may reduce the temporal resolution of the data.

The final point above raises another issue related to experimental design. The difference in peak latencies in different brain areas means that the temporal relation between two regional fMRI time-courses is dependent on their neuronal activity as well as the systematic hemodynamic differences between brain regions. Thus, the direct interpretation of temporal relations between regional fMRI time-courses is difficult. A more reliable method is to focus on modulatory effects, i.e. changes in temporal relations between regional fMRI time-courses induced by experimental manipulations or cognitive states, so that systematic hemodynamic differences between brain regions can be cancelled out. An example of this method can be found in Büchel and Friston (1997) in which the authors showed that the temporal coupling between V5, a region in the visual cortex, and the posterior parietal cortex is modulated by attention to visual motion.

4.3 MRI Acquisition

In this study, a set of functional images and a structural image were obtained for each subject. Below, we report the scanning parameters used, and discuss a method for obtaining fMRI data with high temporal resolution.

4.3.1 Functional Scans

Scanning parameters

Functional images were acquired at the University of Regensburg, using a 3 Tesla head scanner (Siemens Allegra) with a birdcage head coil. Participants were noise shielded by ear plugs and headphones. Their heads were fixated by soft foam pads. Blood-oxygen-level dependent (BOLD) responses were measured using a T2* weighted echo planar imaging (EPI) sequence (echo time (TE) = 30 ms; volume repetition time (TR) = 1040 ms; resolution = 3 x 3 mm^2; number of slices = 18, interleaved; slice thickness = 4 mm; distance factor = 10-20%; flip angle = 62°). The scan volume covered the whole brain, except for the most superior portion of the supplementary motor cortices, the motor cortices and the lower half of the anterior temporal lobes.

Achieving high temporal resolution

Because temporal resolution is important for connectivity analysis, we traded some spatial resolution and coverage in order to reduce the overall scanning time needed for a volume during the functional scans. First, we used the slice thickness of 4 mm rather than 3 mm, which is more frequently used in an fMRI study. The actual effect of this change in spatial resolution should be minimal because spatial smoothing was applied in the analysis stage. Moreover, we reduced the number of slices by excluding the most superior portion of the supplementary motor cortices, the motor cortices and the lower half of the anterior temporal lobes in the scan volume. These regions are unlikely to be important in language comprehension (Cabeza and Nyberg, 2000; Vigneau et al., 2006). Using these settings, we collected approximately one data point per second for every voxel. Technically, the TR was equal to 1.04 seconds. Compared to the TR normally used in an fMRI study, i.e. 2-4 seconds, the image acquisition is considerably fast.

4.3.2 Structural Scans

Because functional images do not capture as well the anatomical landmarks of the brain such as gyri and sulci, it is necessary to overlay the functional images onto the structural image in order to determine the anatomical locations of the activations. For each subject, a high spatial resolution structural image of the whole brain was acquired using a T1 weighted MPRAGE (magnetization prepared rapid gradient echo) sequence (TR = 2250 ms; TE = 2.6 ms; resolution 1x1x1 mm^3) at the end of the experiment.

4.4 Conventional fMRI Data Analysis

The analysis of the functional images can be divided into three main stages: (i) image preparation for statistical analysis, (ii) construction of statistical models, (iii) making statistical inferences. Except for the last stage, the first two stages are conducted at the single-subject level. In this study, we used SPM5[4] to conduct the analysis. Below, we briefly discuss the operations, purposes and general considerations involved in each step. For more details, see Frackowiak et al. (2004).

4.4.1 Image Preparation for Statistical Analysis

Slice timing correction

The purpose of slice timing correction and the spatial realignment discussed in the next section is to remove non-task-related variability. Slice timing

[4] SPM is developed by the Wellcome Department of Imaging Neuroscience, at University College London. For more details, see the website at "http://www.fil.ion.ucl.ac.uk/spm/software/spm5/".

correction performs a temporal correction for the differences in acquisition time between the slices in each volume by interpolating the signals in the same location collected in the preceding and subsequent volumes. In general, it is not necessary for a block design, but it is important for an event-related design, and for investigating temporal relations between fMRI time-courses. Thus, slice timing correction was applied to the data of this study.

Spatial realignment

Head movements by subjects during fMRI data acquisition are unavoidable. Because of these head movements, the same voxel may not represent the same location in the brain throughout the experiment. These movement-related artefacts can be partly removed by spatial realignment, which treats each volume as a rigid object and repositions each volume according to the user-defined reference volume. After this repositioning, the new value of a voxel is estimated by interpolating the values from its neighbouring voxels. The algorithm of spatial realignment may fail when the head movements of a subject are too large. In these cases, the whole data set of the subject should be excluded from further analysis.

Spatial co-registration and normalisation

It is a fact that individual brains differ from each other in size and shape. In order to compare activation locations between subjects, or to perform group analysis, it is necessary to transform the brain images of each subject to match the size, shape and anatomical landmarks of a standard brain. In this study, we first co-registered the subject's structural image to their mean functional image so that the orientation of both was the same. Then, we normalized the co-registered structural image to the MNI-152 template, an averaged brain image of 152 subjects created by the Montreal Neurological Institute. Normalisation is conducted by applying linear and non-linear transformations to the structural image according to the template. This process generated a set of transformation parameters, which were then applied to transform the functional images. As a final step, the functional images were re-sampled to $2 \times 2 \times 2$ mm^3 spatial resolution.

Spatial smoothing

Spatial smoothing involves blurring the functional images. Reducing the spatial precision of the image is important for several reasons. First, spatial smoothing can increase the signal to noise ratio by removing high spatial frequencies that usually originate from measurement noise. Second, it helps to conform more closely to the requirements for applying Gaussian Field Theory, which is important for making statistical inferences, and for the multiple comparison correction in the later analysis stage. Usually, spatial smoothing is conducted by convolving each volume with a three-dimensional smoothing curve of a Gaussian kernel. The shape of this curve is defined by a parameter called the Full Width at Half Maximum (FWHM), in millimetres. It refers to the width of the smoothing curve at the half of its maximum magnitude. Roughly speaking, activation clusters smaller than the FWHM are filtered out (Clare, 1997). There is no simple answer to the question of how to set the FWHM because it is a trade-off between the spatial specificity and the signal to noise ratio. Smoothing curves with a FWHM ranging from 4-12 mm have been used in fMRI studies. In this study, spatial smoothing was applied to the functional images using an isotropic Gaussian kernel with FWHM of 4 mm.

High-pass filter

To remove low-frequency scanner drifts and possibly cardiac or respiratory artefacts, a high-pass filter (1/128 Hz) was applied.

4.4.2 Construction of Statistical Models

The aim of this step is to quantify the relationship between the fMRI signals and the experimental manipulations. Usually, this is accomplished by applying the general linear model (GLM). In this framework, the variation of the fMRI time-course y_i is defined as a linear combination of the explanatory variables $x_1 \dots x_j \dots x_n$ and an error term ε. A GLM can be expressed in the following equation:

$$y_i = \sum_{j=1}^{n} \beta_j x_j + \varepsilon \qquad \text{(Eq. 1)}$$

A set of model parameters β_j can be determined by minimizing the error term ε. The estimates reflect the importance of the corresponding variables in explaining the variability of the fMRI time-course. Specifically, if the magnitude of a model estimate is large relative to the others in a GLM, its corresponding variables are relatively good at predicting the ups and downs of the fMRI time-course. In a typical fMRI experiment, the explanatory variables are a set of time-series, each of which represents the onsets and offsets of an experimental condition. Because fMRI measures the hemodynamic response instead of neuronal activity, it is necessary to convolute these time-series with a hemodynamic function (HRF) in order to generate a more realistic explanatory variable. In this study, the canonical hemodynamic response function (HRF) that comes with SPM5 was used.

4.4.3 Making Statistical Inferences

Subject-level analysis

For the time-course in each voxel, a GLM is constructed and the parameters corresponding to the experimental conditions are estimated. To locate the brain regions in which the fMRI signals in a particular condition are stronger than those in another condition, we perform a statistical comparison between the estimates corresponding to the two conditions for every voxel. For these comparisons, the *t*-test is frequently used. The results of *t*-tests are termed "*t*-contrast" or "contrast image".

Multiple comparisons problem

To find out which brain region is more active in one condition compared to another condition, a number of *t*-tests are performed, with the number of tests equal to the number of voxels. As a result, the probability to obtain one voxel that with a false positive result is much higher than the probability of obtaining a false positive in a single *t*-test. This discrepancy is called the multiple comparisons problem. To account for this problem, there are several methods that can be used to adjust the threshold of significance of the test. In this study, we used the method that is implemented in SPM5. It uses random field theory to control the overall false positive rate at an acceptable level. An advantage of this method is that one can make statistical inferences with correction for multiple comparisons at different levels of anatomical specificity, namely the voxel level, the cluster level and the set level (Friston et al., 1996). Specifically,

- voxel level inferences inform us whether a voxel at a particular location is significantly activated,
- cluster level inferences inform us whether a cluster of a minimum size is significantly activated at a particular location, and
- set level inferences inform us whether the probability of obtaining the observed activation pattern is significantly higher than the threshold.

Set level and cluster level inferences disallow statistical inferences about any lower level component, for instance, no statistical inferences about the voxels within a significantly activated cluster can be made. The reduction in anatomical specificity increases the relative statistical power, i.e. set level inferences are generally more powerful than cluster level inferences, and cluster level inferences are generally more powerful than voxel level inferences. To strike a balance between anatomical specificity and statistical power, we mainly focus on cluster level inferences.

Group analysis

Two approaches are available for making statistical inferences at the group level, namely fixed effect (FEX) analysis and random effect (REX) analysis. However, they answer different questions; FEX analysis allows us to make statistical inferences specific to the subjects under investigation, whereas REX analysis allows us to make statistical inferences on the population from which the subjects are drawn. In this study, only REX was used so that the results can be generalised.

The input to REX is the individual *t*-contrasts generated by the subject-level analyses. The REX analysis estimates the population mean of the contrast value at each voxel by averaging the values in the *t*-contrasts across subjects, and estimates the variance of the population mean with the consideration of both within-subject variability and between-subject variability. With these two values, we can determine whether the estimate of the population mean differs significantly from zero or not. Because there is a comparison per voxel, it is again necessary to correct for multiple comparisons.

Statistical thresholds

Unlike in the field of experimental psychology, a conventional statistical threshold has not yet been established for fMRI studies. In the literature of fMRI studies, different schemes for setting the statistical threshold have been used in order to address the multiple comparisons problem. In the REX analyses of this study, we used a combination of an uncorrected threshold at the voxel level and a corrected threshold at the cluster level to define a significant cluster. At the voxel level, activations are required to surpass a threshold of $p < 0.001$ (uncorrected). When these activations form a cluster which surpasses a threshold of $p < 0.05$ (corrected), this cluster is defined as significant. With this threshold, if the effect size is large it is possible that there are a lot of activations that form a huge cluster covering most of the brain. In this case, the uncorrected threshold at the voxel level must be tightened in order to have a meaningful set of clusters. But, the corrected threshold at the cluster level always remains the same in this study.

Anatomical labels

An SPM5 extension, MSU[5] was used as a reference for determining the approximate locations of an activated cluster in term of the brain structures and Brodmann areas.

[5] MSU is developed by Sergey Pakhomov. More details can be found in the website at "http://www.ihb.spb.ru/~pet_lab/MSU/MSUMain.html".

4.5 Connectivity Analysis

Connectivity analysis is a class of analysis techniques designed for investigating interregional interactions. In fMRI studies, connectivity analysis uses the measured hemodynamic response, an indirect measurement of neuronal activity, to estimate the level of coupling between brain regions. This is based on an assumption that the hemodynamic response carries the temporal information of neuronal activity to a certain extent. As discussed in Section 4.1.2 on p. 34, the temporal resolution of the hemodynamic response is still far too low to detect individual synaptic activity, which takes place in the order of a few dozen milliseconds, but it is probably sufficient to resolve the timings of different processing stages that occur in the order of a few hundred milliseconds (Formisano and Goebel, 2003).

4.5.1 Functional and Effective Connectivity

The interactions between brain regions can be expressed by two kinds of connectivity: functional connectivity and effective connectivity. Functional connectivity is defined as "correlations between remote neurophysiological events" (Friston, 2002). However, the correlation of regional activity does not necessarily mean that there is a direct influence mediating the activity between the regions, because correlation can result for various reasons (Stephan, 2004). For example, the activities of two regions can be correlated due to a third region influencing the activities of those two regions. Furthermore, functional connectivity analysis cannot determine the direction of influence from the correlation between regional activities. Effective connectivity, on the other hand, is defined as "the influence that one neuronal system exerts over another, either at a synaptic or population level" (Friston, 2004). To determine the direct influence between regions, the investigation of effective connectivity requires a model of anatomical connections [6] that defines which regions are anatomically connected. Compared to functional connectivity analysis, effective connectivity analysis is more informative because it provides information on how influence is mediated between regions on the basis of the anatomical connection model. This also means that effective connectivity analysis is a model-driven technique, and its validity is dependent on the model's specifications. In contrast, functional connectivity analysis is a data-driven technique, i.e. no a priori information is needed for the analysis. Hence, functional connectivity analysis is better for exploration, whereas effective connectivity analysis is more suitable for discriminating between competing

[6] The anatomical connection model used here was defined in Section 3.5 on p.30.

hypotheses of a particular cognitive function (Friston, 2004). Since one of the objectives of this study is to discriminate between various hypotheses about how inferences are drawn during reading (for details, see Section 3.4 on p. 28), an effective connectivity analysis was employed. To quantify the interregional interactions from fMRI data, dynamic causal modelling (Friston et al. 2003) was chosen, which is discussed in the next section.

4.5.2 Dynamic Causal Modelling

Besides DCM (Friston et al., 2003), a number of modelling approaches such as structural equation modelling (Nyberg et al. 1996; Büchel and Friston, 1997, 2000) and autoregressive modelling (Goebel et al., 2003; Harrison et al., 2003) have been used to estimate effective connectivity using fMRI data. There are three major distinctions between these modelling approaches and DCM. A fundamental difference is that DCM treats experimental manipulations as a source of influence that modulates the activity of a region or the connectivity between two regions, whereas alternative approaches treat experimental manipulations as unknown and stochastic. For this reason, DCM is more flexible and probably more accurate in testing specific hypotheses about the relations between experiment manipulations and changes in connectivity. Second, unlike the other approaches that make inferences about a neural system by modelling the measured hemodynamic response, DCM models a system at its underlying neuronal level with a set of state variables. A supplementary forward model is required to transform the estimates of these state variables into the modelled hemodynamic response, which is then compared with the measured response. The discrepancies are fed back to the estimation stage and guide the adjustment of the state variables. Employing the forward model of the hemodynamic response enables DCM to estimate the regional interactions at the neuronal level and probably makes DCM more biologically accurate in comparison with other approaches (Penny et al., 2004). Third, DCM is a non-linear modelling system, which is capable of capturing the nonlinearity of neuronal dynamics. This feature is absent in the approaches using structural equation modelling and multivariate autoregressive modelling, in which interactions are assumed to be linear. The cost of the above-mentioned advantages of DCM is a high demand of computational power, which limits the possible number of regions that can be practically included in a model. In the SPM5 implementation used here, a maximum of only eight regions is allowed in a DCM.

Components in DCM

DCM enables us to estimate (i) intrinsic connectivity, i.e. the influences between interregional activities in the absence of external input, (ii) the modulation (enhancement or inhibition) of connectivity induced by experimental manipulations, and (iii) the direct external influences on the regional activities (Friston et al., 2003). They are formulated in the bilinear model of Eq. 2.

$$\dot{z} = \left(A + \sum_j u_j B^j \right) z + Cu \qquad \text{(Eq. 2)}$$

The model assumes that the changes of neuronal activity in a region $\dot{z}$ are composed of three components. The first is the multiplication of the activity of regions z and the intrinsic connectivity matrix A. Note that the input parameters u_j do not play a role in this component, denoting that the A-matrix refers to the intrinsic connectivity, the connectivity independent of experimental manipulations. The second component is the sum of the multiplications of the activity of regions z, the input parameters u_j and the induced connectivity matrix B. The B-matrix is assumed to reflect how much influence the input parameters u_j and the activity of regions z jointly exert on the changes of regional activity $\dot{z}$. The last component is the multiplication of the input parameters u_j and a matrix C. The C-matrix reflects the direct influence of the external input u_j on the changes of regional activity ($\dot{z}$). The inputs of the DCM include the parameters u_j that encode the experimental manipulations, and the initial values of the A, B and C matrices. The initial values, either 1 or 0, indicate which regions are connected in the A-matrix, which connections are under the influence of which inputs u_j in the B-matrix, and which regions receive direct influence from the inputs u_j in the C-matrix. The outputs of the DCM are the estimates of the parameters in the A, B, C matrices. In DCM, the unit of connectivity is in Hz, referring to the rate of influence mediated from one region to another region. Usually the B-matrix is the main focus of a study because it captures the modulatory effects induced by experimental conditions.

4.5.3 DCM Analysis

In this study, we used the DCM module in SPM5 to conduct the effective connectivity analysis. The general procedure of the DCM analysis implemented is described below.

Region selection and time-series extraction

The selection of regions was based on the group-level results of the conventional fMRI data analysis, meaning that we considered the language regions and inference-related regions activated in the reading conditions of the fMRI experiments. Then, the region-specific time-series were extracted and adjusted for confounds at the subject-level using SPM5. The central coordinate of regions selected in each individual model were based on the peaks, or local maxima, of the clusters selected in the group-level analysis. The time-series were made up of the first eigenvariate of all voxels that lay within a 4 mm radius of each regional central coordinate and were considered to be significant ($p < 0.01$, uncorrected) in the t-contrast comparing the reading condition with the implicit baseline. As the activation pattern varies over subjects, if the voxel at the central coordinate of a region defined by the group-level analysis was not significant at the subject-level, the centre of the region was shifted to the nearest significant voxel from the coordinate. Moreover, we ensured that the minimum edge-to-edge displacement between two regions was at least 10 mm, so that the signals in each region were not influenced by the spatial smoothing (Gaussian kernel, FWHM = 4 mm).

DCM specifications and estimation

Three categories of information are required to specify a DCM, namely (i) the anatomical connections of the selected regions, (ii) the modulatory inputs and which connections are modulated, and (iii) the driving inputs and which regions receive direct inputs. In this study, the anatomical connections were defined according to existing DTI studies on humans (for details, see Section 3.5 on p. 30). The modulatory and driving inputs are a set of boxcar functions representing the onsets and offsets of the experimental conditions. The driving inputs should be defined to influence the regions involved in low-level processes such as sensory processes. With the specification of the anatomical connections and the driving inputs, the basic structure of a DCM is formed. Based on this basic model, a set of DCMs can be generated by assigning the modulatory inputs to different connections according to the hypotheses about the neural mechanisms under investigation. As the experimental conditions and the results of the experiments in this study differ, the more precise specifications of the DCMs in each experiment are described separately in Section 5.6.1 on p. 63 and in Section 6.5.1 on p. 81. After specifying the same set of DCMs for each subject, the DCMs are estimated individually.

Bayesian model selection

To select the DCM that is best supported by the fMRI data, we adopt the two-stage procedure proposed by Penny et al. (2004) and Stephan et al. (2007). In the first stage, individual DCMs are compared on the subject level. We followed the conservative model comparison strategy proposed by

Penny et al. (2004). Accordingly, we approximated the evidence for each model with Akaike's and the Bayesian information criterions (AIC and BIC), which take model accuracy and complexity into account. Evidence for each model was compared using Bayes Factors (BF_{ij}). These are defined as the ratio between the estimated evidences for each of two models, BF_{ij} = (evidence of model *i*) / (evidence of model *j*). When $BF_{ij} > 1$, the data favour model *i* over model *j*, and when $BF_{ij} < 1$, the data favour model *j* over model *i*. We regard the evidence as consistent when both Bayes Factors computed by AIC and BIC are in agreement and are larger than *e* (Euler's number, 2.72). As this model comparison procedure operates at the subject level, to compare models in the group level, we used the method implemented in Stephan et al. (2007). From the results of the first stage, two indices were computed, namely the group Bayes factor (GBF) and the positive evidence ratio (PER). A group Bayes factor is computed by multiplying the individual Bayes factors. However, GBFs can be misleading if strong outliers are present. Therefore, we computed the PER, which counts the number of comparisons for which the BF passed the threshold for positive evidence for either of the compared models.

Second-level analysis of the modulatory effects

To test whether the modulatory effects at a particular connection differ significantly from each other in the model that is best supported by the data, we used a one-sample *t*-test (two-sided) to compare the modulatory effects obtained from the individual DCMs. These tests were carried out separately for each pair of modulatory effects at each connection. For the *t*-test, a conservative statistical threshold of $p < 0.05$ with Bonferroni's correction[7] was adopted.

4.6 Summary

In this chapter, we have discussed the limitations, experimental design concerns and assumptions involved in an fMRI study, and described how we obtained the structural scans and the functional scans with a high temporal resolution, which is especially important for connectivity analysis. Moreover, the general analysis procedures of fMRI data including conventional fMRI data analysis and connectivity analysis have been discussed. In the next two chapters, the experiments investigating how

[7] The corrected *p* value is equal to the uncorrected *p* value divided by the number comparison. For example, the Bonferroni corrected *p* value of 0.05 with 2 comparisons is equal to uncorrected *p* value of 0.025, i.e. 0.05/2.

strategic and routine inferences are drawn, the actual implementations of the analyses and their results are reported.

5 Neural Mechanisms for Drawing Strategic Inferences (fMRI Exp 1)

5.1 Experimental Manipulations

As argued in Section 2.4.4 on p. 15, readers are able to draw goal-directed or strategic inferences under conscious control (Graesser et al., 1994, Graesser et al., 1993; Horiba, 2000; Kern et al., 2004; Magliano et al., 1999; Rapp and Gerrig, 2006; van den Broek et al., 2001). In this experiment, we used the reader's ability to draw strategic inferences to investigate the neural mechanisms involved when readers infer context-appropriate information strategically during reading. Specifically, in the critical condition, namely the predictive-reading condition, we induced strategic inference processes by asking our participants to actively predict the development of the situation described in the text during reading. To contrast with this condition, we introduced the normal-reading condition, in which we asked subjects to read and understand the text, but did not encourage predictive reading. We assumed that strategic inference processes are more intense during predictive reading than during normal reading. Additionally, we included a pseudoword-reading condition which served as a common baseline of the above mentioned passage-reading conditions.

In the following, we first discuss the approaches and experimental design adopted in this experiment (Section 5.2 and 5.3). After that, we report and discuss the results of (i) the behavioural pre-study that aimed at verifying the experimental design in Section 5.4, (ii) the fMRI study in Section 5.5 and (iii) the connectivity analysis using DCM in Section 5.6.

5.2 Approaches and Hypotheses

We investigated the neural correlates of strategic inference processes using two complementary approaches. The first approach was to identify the brain regions critically involved in strategic inference processes by contrasting the hemodynamic responses in the predictive-reading condition with those in the normal-reading condition. Based on the review in Chapter 3 on p. 17, we hypothesize that the regions involved in semantic retrieval (such as pSTS and IFG), semantic integration (such as IFG and aTL), and coherence building (aPFC) are probably activated in this comparison.

As argued in Section 3.4 on p. 28, the drawing of inferences probably involves interactions between frontal regions, which are associated with cognitive control, and temporal regions, in which semantic information and world knowledge are stored. Because strategic inferences are presumed to be drawn in the predictive reading condition but not in the normal-reading condition, we hypothesize that frontotemporal interactions are stronger in the predictive reading condition. However, it is unclear how these interactions are mediated. Therefore, we employed a second approach, effective connectivity analysis (for details, see Section 4.5 on p. 43) in order to investigate these frontotemporal interactions. On the basis of the anatomical connections defined in Section 3.5 on p. 30 and the theories regarding how inferences are drawn (for details, see Section 3.4 on p. 28), we constructed and compared ten models with different plausible ways of modulating the connections among IFG, pSTS, TPJ and aTL. The comparisons among these models provide useful information for us to discriminate between theories about how strategic inferences are drawn.

5.3 Experimental Design

Participants were asked to read short passages and respond to a lexical decision task after each passage. Passages were constructed in a way that the outcome of the situation described in each passage was predictable, although it was not mentioned explicitly. This setting enabled us to manipulate the predictability of the target word in the lexical decision task, i.e. the real target words of the task were either predictable or non-predictable. Thus, by comparing the response times for the predictable and non-predictable target words in the lexical decision task, we were able to verify whether participants in the predictive-reading condition indeed predicted the development of the situation described in the text according to their world knowledge, rather than simply associating irrelevant ideas. If participants actively predict the development of the situation described in the passage during reading in the predictive-reading condition, then the concept named by the predictable target word should be more prominent in the reader's mind and the lexical decision task should be facilitated relative to the non-predictable target word. This facilitation effect should be weaker in the normal-reading condition because predictive inferences are not generated routinely (Calvo and Castillo, 1998). In other words, we expected an interaction effect between reading condition (predictive reading vs. normal reading) and target word type (predictable vs. non-predictable).

For the sake of consistency, participants were also asked to respond to a lexical decision task after each pseudoword sequence in the pseudoword-reading condition. Furthermore, to ensure that participants read the passages and pseudoword sequences carefully, in 25% of the total trials a word recognition task was presented after the lexical decision task. Note that to recognise a pseudoword in the pseudoword-reading condition is more difficult than to recognise a real word in the passage-reading conditions. Therefore, we expected that the recognition accuracy in the pseudoword-reading condition would be relatively low but above chance level. To examine the hypothesis with regard to the behavioural responses of the tasks, we conducted a behavioural pre-study prior to the fMRI experiment.

5.3.1 Construction of Stimuli

In all, 96 German passages were constructed, which are listed in Appendix I on p. 103. Thirty-two of them were taken from the "predicting sentences" used in the study of McKoon and Ratcliff (1986) and translated and adapted for our German sample, whereas the remaining 64 passages were constructed by the author. Each passage consisted of one to three sentences describing an everyday event. The length of each passage was exactly 15 words. For each passage, a single word that depicted the implicit outcome of the described event was selected. These words were used as the predictable target words in the lexical decision tasks. Furthermore, a non-predictable target word was selected and a pronounceable pseudoword constructed as stimuli for each lexical decision task. The predictable and non-predictable target words did not differ significantly in length (t_{95} = 1.10). The target words for the recognition task included a randomly-selected content word from the passage and a common word which did not appear in any passage. Additionally, 24 pseudoword sequences were constructed. Each pseudoword sequence consisted of 15 pronounceable pseudowords. For the lexical decision task that followed each pseudoword sequence, a target word was selected and a pronounceable pseudoword was constructed. All 96 passages and 24 pseudoword sequences, and their target words are listed in Appendix I on p. 103. Sample text materials are shown in Table 3.

5.3.2 Stimulus Presentation and Tasks

The experiment consisted of 120 trials, and of these, 96 consisted of a passage and 24 consisted of a pseudoword sequence. Each passage and pseudoword sequence appeared only once in the entire experiment and every participant read exactly the same set of passages and pseudoword sequences. In each trial, participants had to read either a passage or a pseudoword sequence and had to respond to a lexical decision task. Additionally, in 25% of the total trials, the lexical decision task was

Table 3
Text material samples and their target words in the lexical decision task and the recognition task. English translations are given in brackets

Passage / Pseudoword sequence	Lexical decision Task Target word		Recognition Task Target word	
	"Yes" response	"No" response	"Yes" response	"No" response
1. Als die Boeing der steilen Bergwand immer näher kam, begannen die Passagiere laut zu schreien. (As the aeroplane came closer and closer to the steep mountain-face, the passengers began to scream loudly.)	Predictable: Absturz (crash) Non-predictable: Liebster (sweetheart)	Pseudoword: Tennul	Bergwand	Tennis
2. Geduldis ser jägur, süt dür Hihen grac. Dira pavanne wiader isaw eh sür svannund dep.	Real word: Borke (bark)	Pseudoword: Nochs	Dira	Eukf

followed by a recognition task. The trials consisting of a passage were divided into 4 blocks of 24 trials each, and the trials consisting of a pseudoword sequence were divided into 3 blocks of 8 trials each. Each block of pseudoword-reading trials was placed between two blocks of passage-reading trials. At the beginning of a block of passage-reading trials, participants were asked to read the passages in the block using one of the two reading modes and to respond to the subsequent lexical decision and recognition tasks. For the predictive-reading condition, they were instructed to focus on the situation described in each passage and to predict the development of the situation actively, whereas for the normal-reading condition, they were instructed to read and understand the passages. In the beginning of a block of pseudoword-reading trials, they were instructed to read the pseudoword carefully and respond to the subsequent lexical decision and recognition tasks. The exact wordings of the instructions are listed in Appendix I on p. 103. The sequence of reading conditions were counterbalanced in an ApBpBpA / BpApApB fashion, where "A" is predictive reading (24 trials), "B" is normal reading (24 trials) and "p" (8 trials) is pseudoword reading. The trials within a block were presented in random sequences. Participants were informed about the end of each block. The between-block interval was 15 seconds.

In the behavioural pre-study, stimuli were presented on a 20" LCD screen using E-prime (Schneider et al., 2002). In the fMRI study, the stimuli were projected onto a screen in the RF-shielded-cabin and viewed by participants via a mirror mounted in the head coil of the MRI scanner. At the beginning of each trial, an asterisk was presented for 1000 ms. To remind participants which of the two reading modes should be used in the current block, the asterisk was red for the predictive-reading condition, and black for the normal-reading and the pseudoword-reading conditions. Subsequently, a passage or a pseudoword sequence was presented word by word. Each word was exposed for 450 ms and was followed by a 50 ms blank interval. Then, a question mark was presented for 1000 ms to cue the onset of the target word of the lexical decision task. The maximum duration of the target word was 2500 ms, and it was erased once a response had been given. Participants had to decide whether the target word was a real German word or a pseudoword, and to provide a response by pressing the Y / N button of a response box. In 50% of the lexical decision items, a real word was presented. Half of the real target words in the passage-reading conditions were predictable and the other half were non-predictable. To counterbalance the "yes" / "no" responses and the predictable / non-predictable target words in the lexical decision tasks, four experiment versions were generated. Whenever there was a recognition task in the trial, a blue question mark was presented for 1000 ms after the lexical decision task. Then, the target word of the recognition task was presented for a maximum of 2500 ms and was erased once the response had been given. Participants were requested to decide whether or not the target word had appeared in the passage or pseudoword sequence of the trial and to provide a response by pressing the Y / N button. The inter-trial interval was 4000 ms. The total time of a trial without a recognition task was 16000 ms, otherwise it lasted 19500 ms.

To allow participants to familiarize themselves with the reading conditions and the tasks, they were requested to participate in a training session consisting of 36 trials before the main experiment. The same procedure as that described above was used for training, only with different text materials.

5.4 Behavioural Pre-study

5.4.1 Participants

Nineteen native German speakers (9 males, 10 females; mean age: 22; SD: 2) were recruited. All were university students, right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971) and had normal or corrected-to-normal vision.

One of the participants exhibited very low accuracy (< 50%) in the recognition tasks. For two other participants, the mean response latency in the lexical decision task was 60% slower than the rest of the participants. The data sets of these three participants were excluded from further analysis. In total, data from 16 participants were included in the analyses to be reported.

5.4.2 Pre-study Results

Response accuracy

The mean accuracies of the lexical decision task in the pre-study were 97% in the predictive-reading condition, 97% in the normal-reading condition and 96% in the pseudoword-reading condition. These results did not differ significantly ($t_{15} < 1.4$, $p > 0.18$). The mean accuracies of the recognition task were 93% in the predictive-reading condition, 89% in the normal-reading condition and 74% in the pseudoword-reading condition. With respect to recognition accuracy, there was no significant difference between the two passage-reading conditions ($t_{15} = 1.5$, $p = 0.15$). As expected, the recognition accuracy in the pseudoword-reading condition was significantly lower than that in the passage-reading conditions ($t_{15} = 3.5$, $p < 0.01$).

Lexical decision latency

We conducted two 2 (passage-reading condition: predictive-reading vs. normal-reading) x 2 (target word type: predictable vs. non-predictable) ANOVAs of the mean response latencies of the correct "yes" responses, one based on subject variability (F_1) and one based on item variability (F_2). We used 2 criteria to remove outliers. First, lexical decision latencies above or below 2.5 standard deviations from the mean of "yes" responses in each of the two reading conditions (2.0%) were replaced by the mean in each condition separately. Second, lexical decision latencies above or below 2.5 standard deviations from the mean of "yes" responses in both reading conditions (1.7%) were replaced by the overall mean of "yes" responses. In total, 3.7% data points were replaced. The mean lexical decision latencies of "yes" responses are shown in Table 4. The main effect of reading condition was not significant ($F_1(1,15) = 1.26$, $p = 0.28$; $F_2(1,95) = 1.48$, $p = 0.23$). The main effect of target word type was significant ($F_1(1,15) = 11.57$, $p < 0.01$; $F_2(1,95) = 36.55$, $p < 0.01$), as was the interaction effect between reading condition and target word type ($F_1(1,15) = 5.08$, $p < 0.05$; $F_2(1,95) = 4.93$, $p < 0.05$). In order to gain more information with respect to the reading condition by target word type interaction effect, we conducted t-tests on the latencies in the two reading conditions. Separate comparisons indicated that the mean latency was significantly shorter for predictable than for non-predictable target words in the predictive-reading condition ($t_{15} = 4.60$, $p < 0.01$) but not in the normal-reading condition ($t_{15} = 1.66$, $p = 0.12$).

Table 4
Pre-study: Mean lexical decision latencies of “yes” responses (in ms). Standard deviation is given in brackets.

Condition	Predictive Reading		Normal Reading	
Target word	Predictable	Non-predictable	Predictable	Non-predictable
RT (SD)	675 (157)	751 (147)	678 (157)	712 (132)

5.4.3 Discussion

The experimental paradigm of this study differs in various aspects from those used in previous brain imaging studies of higher-level language processes. In many previous studies, the effects of interest were studied by contrasting the effects induced by different types of text materials, such as syntactically complex versus less complex texts (e.g. Dapretto and Bookheimer, 1999), coherent versus incoherent texts (e.g. Ferstl and von Cramon, 2001), or comprehensible versus incomprehensible texts (e.g. Vandenberghe et al., 2002). One potential disadvantage of these paradigms is that it is often difficult to determine which level of language processing is isolated in the comparisons (Okada and Hickok, 2006). Also, it has been found that "degraded" text materials (e.g. incomplete, incoherent or incomprehensible texts) may trigger even more strategic inferences than "normal" texts (Keefe and McDaniel, 1993; McNamara et al., 1996; Kuperberg et al., 2006; Mason and Just, 2004; Obleser et al., 2007). Here, in contrast, we kept the text materials fixed but encouraged strategic inferences during reading in our study. This allowed us to remove all activities related to lower-level language processes and to single out the higher-level language processes.

However, this approach also has its caveats. A potential problem may be a difficulty in switching between reading modes, especially for participants to switch off the predictive-reading mode during the normal-reading condition. To assist participants in switching between reading modes, we intentionally placed a pseudoword-reading block between two passage-reading blocks. Since it is very difficult to infer anything coherent from a pseudoword sequence, we expect that this forces participants to stop using the predictive-reading mode.

Another drawback to this approach is that it may be difficult for an experimenter to control whether participants follow the instructions with respect to the given reading modes. Even if participants were to ignore the reading mode instructions, they could still perform the lexical decision task and the recognition task perfectly. These potential problems would blur the distinction between the two reading modes. However, we are confident that they did not affect the present study substantially because, as we will see in the following sections, the behavioural results obtained in the lexical decision task, the physiological responses of fMRI, and the connectivity analyses all reflected that there are clear differences between the two reading modes, and that these differences lie in the expected direction.

In the pre-study, we found significant reading mode by target word type interaction effects – the difference between the response times elicited by predictable and non-predictable target words was much larger in the predictive-reading condition than in the normal-reading condition. One may wonder why the difference between the passage-reading conditions was not evident for the predictable target words but rather for the non-predictable target words. A straightforward way to interpret the behavioural results is that the predictive-reading mode slowed down the response times of non-predictable target words. Possibly, participants generated an expectation of the target word during predictive reading, and this expectation strongly mismatched with the meaning of the non-predictable target word, leading to an inhibitory effect in this case, whereas this inhibitory effect was absent or relatively weak for the predictable target word (cf. Fincher-Kiefer, 1995; Zwaan et al., 2002). This implies that the resulting representation of the text, including the inferences that were drawn during reading, better matched the predictable than the non-predictable target word in the predictive-reading condition. Otherwise the inhibitory effect on the non-predictable target word should also have been observed for the predictable target word. This relation between the resulting representation and the predictability of the target word does not hold true or was not as strong in the normal-reading condition where participants are presumably less engaged in active inference processes.

Based on previous research, an alternative interpretation may also be plausible. With a set of experiments similar to those in the present study, Allbritton (2004) showed that the predictive-reading mode increases response times for predictable and non-predictable target words in general. Although we did not find a significant main effect of reading mode, we cannot rule out the possibility that a similar effect to the one shown in Allbrittion (2004) modulated the results in the present study. It is possible that the effect that slowed down the response times in general in the predictive-reading condition was counteracted by the hypothesized facilitation effect on the predictable target word, resulting in a null difference between reading modes in this condition. If this is the case, the inhibitory effect, as well as the facilitation effect, may play a role in the present results.

Nevertheless, we cannot be absolutely sure which effects are responsible for the observed response-time pattern of the lexical decision task, in either way discussed above. At the very least however, the behavioural results indicate that participants drew inferences relevant to the predictable target words in the predictive-reading condition, while this was not necessarily the case in the normal-reading condition. Most importantly, the results show that our reading mode manipulation was effective.

5.5 fMRI Experiment

5.5.1 Participants

Fifteen native German speakers (4 males, 11 females; mean age: 24; SD: 4), none of whom had participated in the pre-study, gave informed written consent to participate in the experiment. All of them were university students, right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971), had normal or corrected-to-normal vision and did not have a history of a psychiatric or neurological disorder, or claustrophobia.

Two participants exhibited very low recognition accuracy (< 67%) in one of the two reading conditions in the scanner. For one other participant, the mean-response latency in the lexical decision task was 60% slower than for the rest of the participants. The data sets of these three participants were excluded from further analyses. In total, data from 12 participants were included in the following analyses of lexical decision latencies (Section 5.5.3) as well as the conventional fMRI data analysis (Section 5.5.4) and the effective connectivity analysis (Section 5.6).

5.5.2 fMRI Data Acquisition and Conventional Data Analysis

To acquire the functional and structural scans, we used the methods described in Section 4.3 on p. 37. In total, we collected 2233 functional volumes per participant. For the conventional data analysis, the general steps including the pre-processing steps are described in Section 4.4 on p. 38. In the GLM of each subject, three separate regressors were constructed to model the hemodynamic responses during predictive reading, normal reading and pseudoword reading. Fourteen regressors were used to capture the responses during lexical decision tasks and during recognition tasks in different reading conditions and target word types. These regressors are not of interest in this study, as their main purpose was to prevent task-related responses from confounding the responses induced by passage reading or pseudoword reading. *T*-test contrasts between the reading conditions were calculated individually and averaged across participants using random-effect analysis. In this experiment, activations surpassing a voxel-level threshold at $p < 0.0003$ ($t = 4.70$, uncorrected) and a cluster-level threshold at $p < 0.05$ (corrected), which corresponds to a minimal cluster size of 15 voxels, were considered to be significant unless otherwise specified.

5.5.3 fMRI Behavioural Results

Response accuracy

The mean accuracies of the lexical decision task during the fMRI data acquisition were 98% in the predictive-reading condition, 98% in the normal-reading condition and 97% in the pseudoword-reading condition. They did not differ significantly ($t_{11} < 1.6$, $p > 0.15$). The mean accuracies of the recognition task were 89% in the predictive-reading condition, 88% in the normal-reading condition and 73% in the pseudoword-reading condition. With respect to recognition accuracy, there was no significant difference between the two passage-reading conditions ($t_{11} < 1$, $p = 0.57$). As expected, recognition accuracy in the pseudoword-reading condition was significantly lower than that in the passage-reading conditions ($t_{11} = 5.7$, $p < 0.01$).

Lexical decision latency

We used the same criteria for identifying outliers as in the behavioural pre-study (for details, see Section 5.4.2 on p. 54). In total, 4.0% data points were replaced. The mean latencies of each condition are displayed in Table 5. Data analyses were as in the pre-study, except that we included the sequences of reading conditions (2 levels) and experiment lists (4 levels) as 2 between-subject factors because the experiment, in contrast to the pre-study, was not fully counterbalanced. Fully counterbalancing the experiment would have required that the number of subjects is a multiple of 8. The main effect of reading condition was not significant in the subject analysis, but it was significant in the item analysis ($F_1(1,4) = 1.89$, $p = 0.24$; $F_2(1,95) = 5.12$, $p < 0.05$). The main effect of target word type was significant ($F_1(1,4) = 12.90$, $p < 0.05$; $F_2(1,95) = 23.65$, $p < 0.01$), as was the interaction effect between reading condition and target word type ($F_1(1,4) = 13.88$, $p < 0.05$; $F_2(1,95) = 6.60$, $p < 0.05$). All other interaction effects were not significant ($F_1 < 5.4$; $p > 0.08$). Similar to the results in the pre-study, separate comparisons of the latencies in the two reading conditions indicated that the mean latency was significantly shorter for predictable than for non-predictable target words in the predictive-reading condition ($t_{11} = 3.91$, $p < 0.01$), but only marginally significant in the normal-reading condition ($t_{11} = 2.2$, $p = 0.05$).

Table 5
fMRI study: Mean lexical decision latencies of "yes" responses (in ms). Standard deviation is given in brackets.

Condition	Predictive Reading		Normal Reading	
Target word	Predictable	Non-predictable	Predictable	Non-predictable
RT (SD)	581 (106)	669 (133)	582 (87)	622 (113)

5.5.4 Results of the Conventional fMRI Data Analysis

Compared to the pseudoword-reading condition, the predictive-reading and normal-reading conditions together evoked increased responses in the superior and middle temporal lobe, TPJ and IFG in the left hemisphere (Fig. 4A, upper panel). The activations in the right hemisphere were clearly less extensive – only two clusters in the right posterior and anterior temporal regions were activated (Fig. 4A, lower panel). When comparing each passage-reading condition against the pseudoword-reading condition separately, similar activation patterns were observed (Fig. 4B and C). Interestingly, two activated clusters were found in the right vIFG and the right pSTS in the comparison between the predictive-reading and the pseudoword-reading conditions (Fig. 4C, lower panel) but not in the

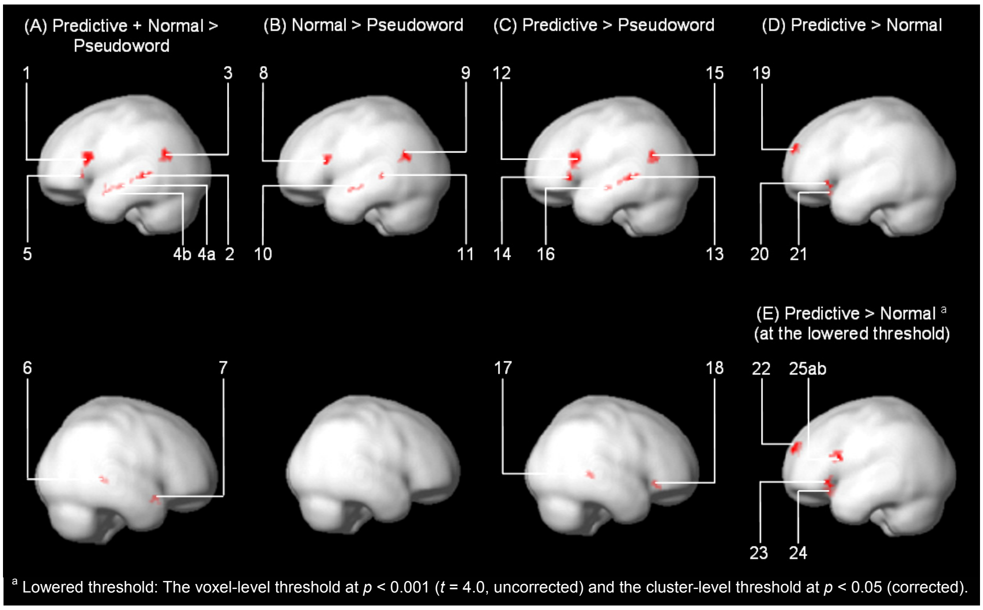

Fig. 4. Significant clusters in the comparisons between the reading conditions. (A) Contrasting predictive-reading and normal-reading with pseudoword-reading. (B) Contrasting normal-reading with pseudoword-reading. (C) Contrasting predictive-reading with pseudoword-reading. (D) The direct comparison between predictive-reading and normal-reading. (E) The direct comparison between predictive-reading and normal-reading at the lowered threshold. The numbering of the regions corresponds to Table 6.

comparison between the normal-reading and the pseudoword-reading conditions (Fig. 4B, lower panel). However, these two clusters did not activate significantly in the direct comparison between the predictive-reading and normal-reading conditions. Instead, this direct comparison revealed three significant clusters in the left frontal lobe. One of them was located in the left aPFC (BA 9 / 10) and two of them were located in vIFG (BA 47).

At a lowered threshold[8]: voxel-level threshold at $p < 0.001$ ($t = 4.0$, uncorrected) and the cluster-level threshold at $p < 0.05$ (corrected), one more cluster in the left dIFG (cluster 25 in Fig. 4E) was revealed. This cluster overlapped with the dIFG activations in all other contrasts (cluster 1 in Fig. 4A, cluster 8 in Fig. 4B and cluster 12 in Fig. 4C). Comparing normal-reading with predictive-reading, no significant cluster was found at the predefined or the lowered threshold. The detailed information with respect to the significant clusters is listed in Table 6.

5.5.5 Discussion

The main behavioural result of the fMRI study was a replication of the hypothesized interaction effect between reading mode (predictive vs. normal) and target word type (predictable vs. non-predictable) that was found in the behavioural pre-study (for details, see Section 5.4 on p. 53). Once again, this result indicates that our reading mode manipulation was effective.

Compared with the pseudoword-reading condition, the passage-reading conditions elicited increased responses in pSTS, aTL, TPJ and IFG in the left hemisphere (Fig. 4A). The involvement of these regions in language processing has been observed repeatedly in many brain imaging studies (e.g. Bookheimer, 2002; Cabeza and Nyberg, 2000; Gernsbacher and Kaschak, 2003; Xu et al., 2005). Interestingly, we did not find any significant activation in pITG, although evidence has strongly implicated its role in semantic retrieval (for details, see the review in Section 3.1 on p. 18). This may be due to the consistent correspondence between orthography and phonology in German language, leading to stronger engagement of the indirect path subserved by pSTS than the engagement of the direct path subserved by pITG for semantic retrieval (Paulesu et al., 2000; Price, 2000).

The direct comparison between the two passage-reading conditions shows that increased responses in aPFC (BA 9 / 10), vIFG (BA 47) and dIFG (BA 44/45) in the left hemisphere are associated with the reader's active involvement in predicting the development of the situation described in the text during reading. As discussed in Section 3.3.3 on p. 27, aPFC is

8 The pre-defined threshold: a voxel-level threshold at $p < 0.0003$ ($t = 4.70$, uncorrected) and a cluster-level threshold at $p < 0.05$ (corrected).

Table 6
The significant clusters in the comparisons between the reading conditions

Structure / Gyrus	Approx. BA	Side	MNI coordinates x	y	z	Size (mm³)	Z_{max}
A. Passage Reading > Pseudoword Reading							
1. Dorsal lateral inferior frontal gyrus	44/45	L	-58	20	14	1104	4.83
2. Posterior superior temporal sulcus	21/22	L	-58	-34	2	688	4.61
3. Supramarginal gyrus / posterior superior temporal gyrus	22/39/40	L	-52	-56	16	968	4.56
4a. Middle portion of the middle temporal gyrus	21	L	-58	-14	-12	368	4.12
4b. Anterior portion of the middle temporal gyrus			-54	2	-18		
5. Anterior ventral inferior frontal gyrus	47	L	-50	24	0	144	4.10
6. Posterior superior temporal sulcus	21/22	R	52	-36	0	256	4.62
7. Anterior superior temporal lobe	21/38	R	52	10	-16	152	4.43
B. Normal Reading > Pseudoword Reading							
8. Dorsal lateral inferior frontal gyrus	44/45	L	-58	20	14	424	4.60
9. Angular gyrus / posterior superior temporal gyrus	22/39	L	-60	-60	20	623	4.34
10. Middle portion of the middle temporal gyrus	21	L	-58	-4	-14	208	4.02
11. Posterior superior temporal sulcus	21/22	L	-58	-34	-2	144	3.90
C. Predictive Reading > Pseudoword Reading							
12. Dorsal lateral inferior frontal gyrus	44/45	L	-54	16	18	1440	5.08
13. Posterior superior temporal sulcus	21/22	L	-58	-34	-2	912	4.79
14. Anterior ventral inferior frontal gyrus	45/47	L	-50	26	0	664	4.74
15. Supramarginal gyrus / posterior superior temporal gyrus	22/39/40	L	-50	-56	16	1040	4.43
16. Middle portion of the middle temporal gyrus	21	L	-58	-14	-12	160	4.40
17. Posterior superior temporal sulcus	21/22	R	52	-36	-2	384	5.02
18. Anterior ventral inferior frontal gyrus	47	R	46	28	-10	224	3.99
D. Predictive Reading > Normal Reading							
19. Anterior prefrontal cortex	9/10	L	-14	60	24	400	4.75
20. Anterior ventral inferior frontal gyrus	47	L	-50	26	-6	152	4.14
21. Dorsal lateral inferior frontal gyrus	47	L	-30	24	-18	144	4.02
E. Predictive Reading > Normal Reading at lowered threshold [b]							
22. Anterior prefrontal cortex	9/10	L	-14	60	24	624	4.75
23. Anterior ventral inferior frontal gyrus	47	L	-50	26	-6	336	4.14
24. Anterior ventral inferior frontal gyrus	47	L	-30	24	-18	520	4.02
25a. Dorsal lateral inferior frontal gyrus	44/45	L	-50	12	18	512	4.12
25b. Dorsal lateral inferior frontal gyrus [a]			-58	22	20		

[a] A local maximum of the cluster. It was listed because its coordinate was used to define a region in DCM (for details, see Section 5.6 on p. 62)

[b] Lowered threshold: The voxel-level threshold at $p < 0.001$ ($t = 4.0$, uncorrected) and the cluster-level threshold at $p < 0.05$ (corrected).

likely to be involved in the evaluation of text coherence. This function is particularly important for predictive reading because this task requires participants to constantly check the coherence among the inferences about the development of the story, the text and their world knowledge. Moreover, as discussed earlier, aPFC does not subserve coherence building in general, because aPFC activity was not consistently found in previous studies of text comprehension (Ferstl, 2007). We suggest that the functional role of aPFC in language processing is specific to evaluating the coherence of strategic inferences with respect to the described situation.

Apart from aPFC, two significant clusters in vIFG (BA 47) were activated at the predefined threshold, and a cluster in dIFG (BA 44 / 45) was activated at the lowered threshold in the contrast between predictive reading and normal reading. There is evidence that IFG is an anatomically complex region responsible for various functions in language comprehension, as discussed in Section 3.2 on p. 22. Hagoort (2005) suggested that the functional roles of IFG in language comprehension change gradually from semantic processing to syntactic processing and to phonological processing along the anterior ventral portion (BA 47 / 45) to the posterior-dorsal portion (BA 45 and ventral part of BA 6). A study by Badre et al. (2005) tried to dissociate the functional role of dIFG and vIFG (for more details, see Section 3.2.2 on p. 24). Their results showed that dIFG mainly supports a generalized control process that selects information among a set of competitors, whereas vIFG activations are sensitive to associative strength and contribute to controlled semantic retrieval. With respect to our findings, vIFG seems to be responsible for drawing inferences associated with the described situation. These inferences are probably selected, integrated with other information, and maintained in dIFG (Hagoort et al., 2004).

In summary, the results of the conventional fMRI data analyses showed that activity in vIFG, aPFC and dIFG is critical for retrieving, evaluating and integrating strategic inferences respectively. How do these frontal regions interact with the temporal regions in which the semantic information and world knowledge are stored? This question can be answered by applying connectivity analysis, the results of which are reported in the next section.

5.6 Effective Connectivity Analysis

We used DCM to investigate the frontotemporal interactions during the retrieval of strategic inferences. We used the same data-set as that used for the conventional fMRI data analysis. The details of fMRI data acquisition and the general information about participants can be found in Section 4.3 on p. 37 and Section 5.5.1 on p. 57, respectively.

5.6.1 DCM Analysis

The procedures and general considerations for conducting a DCM analysis have already been discussed in Section 4.5.3 on p. 45. Below, the actual implementation of DCM in this experiment is described in detail.

Region selection and time-series extraction

To identify the regions critical to inference processes, we considered the significantly activated clusters found in the contrast between the predictive-reading and normal-reading conditions at the predefined threshold (Fig. 4D) and at a lowered threshold (Fig. 4E). Three regions were selected, namely aPFC (cluster 19 in Fig. 4D), dIFG (cluster 25b in Fig. 4E) and vIFG (cluster 20 in Fig. 4D). For dIFG, we chose the coordinate of a local maximum (cluster 25b in Fig. 4E) instead of the peak coordinate (cluster 25a in Fig. 4E) of this region, because this chosen coordinate overlaps with the dIFG activation when we compared passage-reading with pseudoword-reading (see Fig. 4A). Thus, the activity around this coordinate may reflect the processes for inference processes and language comprehension in general. To simplify the model, an activated cluster (cluster 21 in Fig. 4D) in the anterior ventral inferior frontal region, which is located in the same Brodmann area as vIFG, was not selected.

Regions involved in language comprehension were chosen according to the contrast between passage reading (predictive- and normal-reading conditions) and pseudoword reading (see Fig. 4A). To reduce the complexity of the DCM models, we only considered the activated clusters in the left hemisphere. Four regions were selected, namely pSTS (cluster 2 in Fig. 4A), TPJ (cluster 3 in Fig. 3A), mMTG (cluster 4a in Fig. 3A) and aTL (cluster 4b in Fig. 3A). Please note that mMTG and aTL belong to the same cluster, and the location of aTL is the most anterior local maximum of that cluster. This region was included because we postulate that the anterior temporal areas are involved in inference processes (for details, see Section 3.3.2 on p. 26 and Section 3.4 on p. 28). In the contrast between passage reading and pseudoword reading, a small cluster in the anterior ventral inferior frontal gyrus (cluster 5 in Fig. 4A) was not included because its location is close to a selected region vIFG.

The centre coordinates of the selected regions in MNI space are shown in Fig. 5A. Detailed information about the regions can be found in Table 6 on p. 61. For the procedure used to extract the time-series of the regions, please see Section 4.5.3 on p. 45.

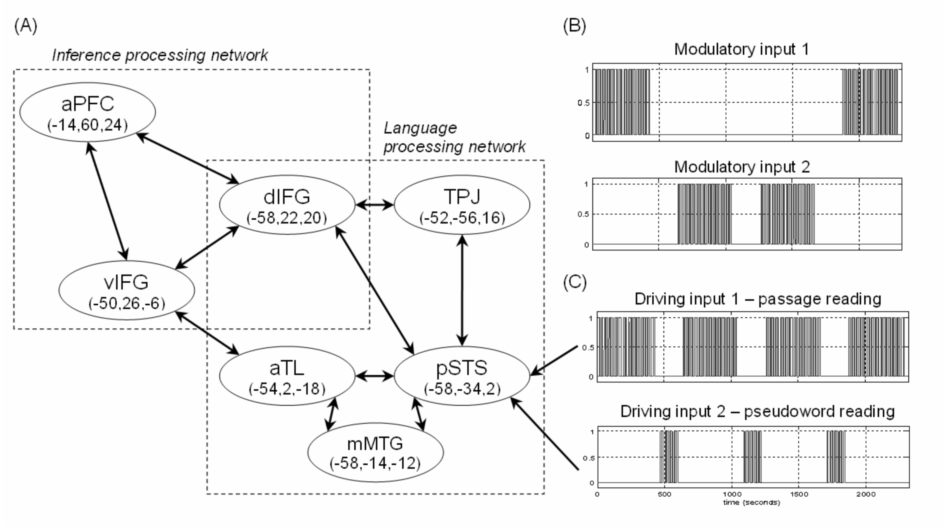

Fig. 5. The basic DCM structure in this experiment. (A) The schematic representation of the anatomical connections between the selected regions, namely anterior prefrontal cortex (aPFC), dorsal lateral inferior frontal gyrus (dIFG), anterior ventral inferior frontal gyrus (vIFG), temporoparietal junction (TPJ), posterior superior temporal sulcus (pSTS), middle portion of the middle temporal gyrus (mMTG), anterior temporal lobe (aTL). The centre coordinates of the selected regions in MNI space are listed in brackets. (B) The modulatory inputs, which correspond to the predictive-reading and normal-reading conditions. (C) The driving inputs, which were assumed to exert influence on pSTS directly.

DCM specifications: Definition of anatomical connections

The anatomical connections between the selected regions were defined in Section 3.5 on p. 30. However, no activated cluster was found in pITG in the conventional fMRI data analysis in this experiment. Therefore, pITG and its connections were excluded from the DCM analysis. The resulting anatomical connections defined in this analysis are shown in Fig. 5A.

DCM specifications: Definition of driving inputs

As illustrated in Fig. 5C, the driving inputs in this analysis were a boxcar function representing passage reading, and a boxcar function representing pseudoword reading. We assume that the driving inputs influence pSTS directly, from which the neuronal activity propagates to other regions (for details, see Section 3.5.3 on p. 31).

DCM specifications: Definition of modulatory inputs

At this point, a basic model was constructed (see Fig. 5). To discriminate between various hypotheses about how inferences are drawn (for details, see Section 3.4 on p. 28), we systematically derived ten DCMs from the basic model by defining modulatory inputs at various connections. Two boxcar functions were used as two separate modulatory inputs into the DCMs (see Fig. 5B), corresponding to predictive reading and normal reading. In Models 1-3 (see Fig. 6A), modulatory inputs were defined to modulate all direct and indirect connections between pSTS and dIFG in the dorsal stream. In Model 4 (see Fig. 6A), modulation occurred by means of the connection between TPJ and dIFG. In Models 5-8 (see Fig. 6B), the modulatory inputs were defined to modulate all possible sets of connections between pSTS and vIFG in the ventral stream. As the two reading modes may also modulate the frontotemporal connections in the dorsal and ventral streams simultaneously, we included two models, Model 9 and Model 10 (see Fig. 6C) to address this possibility. In Model 9, the modulatory inputs were allowed to modulate all direct frontotemporal connections in the dorsal and ventral streams. In Model 10, modulatory inputs were allowed to modulate the connections between dIFG and pSTS and the connections between aTL and vIFG. In all ten models, we assumed that the modulatory inputs influence the bidirectional connections between the frontal and temporal regions. This assumption was made because the frontal regions are probably responsible for integrating different sources of information including inferences, as well as for coherence building and for driving controlled semantic retrieval. This implies that any feedback effect such as controlled semantic retrieval also induces feedforward effects in order to integrate the product of the feedback effect into a coherent representation in the frontal regions during language comprehension.

Bayesian model selection / Second-level analysis of modulatory effects

For details, please refer to Section 4.5.3 on p. 45.

5.6.2 Results of the DCM Analysis

Bayesian model selection

Table 7 lists the individual BFs of the pairwise Bayesian model comparisons between Model 1 and all other nine models. The results clearly indicate that Model 1 is the best model among the models in the comparisons. The evidence in favour of Model 1 was robust; the smallest GBF was larger than 10^{19} and highly consistent among participants. In the comparisons between Model 1 and any other models, at least 10 out of 12 individual DCMs showed significant evidence in favour of Model 1, but not the other way round.

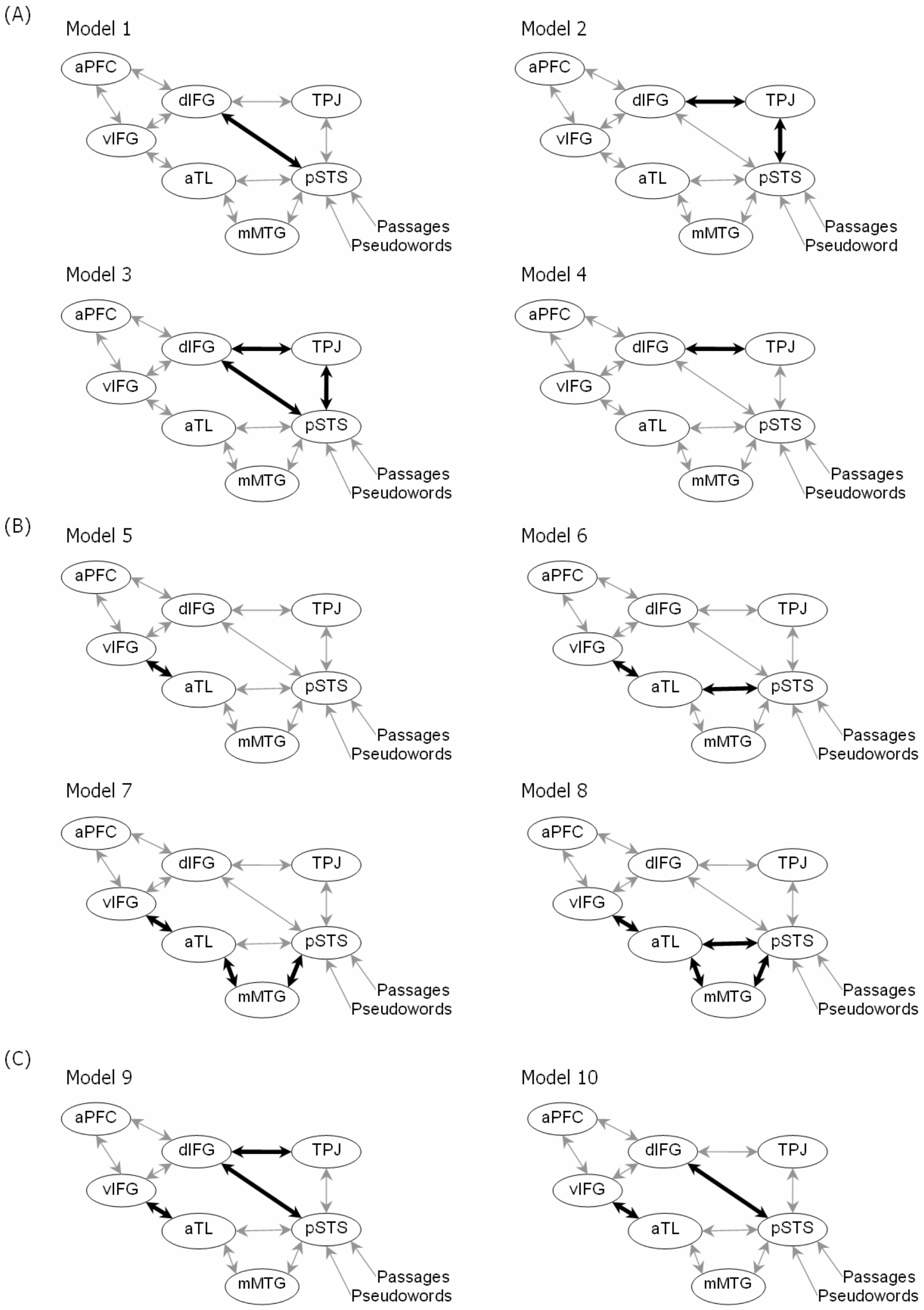

Fig. 6. The ten DCMs derived from the basic model (see Fig. 5). The connections modulated by the two modulatory inputs of predictive reading and normal reading are in bold. (A) Models with modulatory inputs at connections in the dorsal stream. (B) Models with modulatory inputs at connections in the ventral stream. (C) Models with modulatory inputs at connections in both dorsal and ventral streams.

Table 7
The participant-specific Bayes Factors of the pairwise Bayesian model comparisons between the best model (Model 1) and all other 9 models.

Sub-	Model Comparison								
ject	**1 vs 2**	**1 vs 3**	**1 vs 4**	**1 vs 5**	**1 vs 6**	**1 vs 7**	**1 vs 8**	**1 vs 9**	**1 vs 10**
1	2.9E+02	2.9E+03	1.1E+01	4.4E+01	5.1E+02	1.2E+04	4.2E+05	3.1E+03	5.4E+01
2	1.3E+02	2.9E+03	1.3E+08	4.6E+04	1.5E+50	1.1E+04	6.2E+05	1.3E+03	3.2E+01
3	1.7E+03	1.1E+03	2.0E+02	6.2E+02	3.0E+51	4.2E+05	2.2E+07	1.5E+03	5.2E+01
4	2.6E+03	9.9E+03	5.2E+11	3.5E+12	5.2E+07	6.5E+15	2.1E+17	4.1E+03	4.9E+01
5	9.9E+01	3.3E+03	1.1E+00	1.5E+00	5.2E+69	4.0E+03	2.0E+05	2.8E+03	5.2E+01
6	2.2E+02	2.1E+03	5.0E+00	5.1E+00	8.1E+99	1.1E+04	4.8E+05	2.3E+03	5.1E+01
7	1.5E+03	4.4E+03	3.9E+01	5.5E+02	1.1E+90	3.2E+05	4.3E+06	8.0E+03	5.4E+01
8	3.7E+03	2.5E+03	7.8E+01	1.4E+02	3.1E+52	3.1E+05	1.3E+07	2.0E+03	4.2E+01
9	9.9E+01	1.6E+03	2.9E+00	2.8E+00	-	4.2E+03	1.4E+05	2.0E+03	4.5E+01
10	4.0E+02	2.3E+03	1.8E+01	4.1E+01	1.0E+118	3.0E+04	8.8E+05	2.6E+03	5.1E+01
11	2.3E+01	3.1E+00	2.6E+01	1.7E+02	9.1E+04	3.4E+05	4.7E+07	6.5E+01	4.7E+01
12	1.5E+02	1.7E+03	6.3E+00	2.4E+00	1.0E+39	5.6E+03	6.1E+04	7.2E+02	1.8E+01
GBF	3.0E+30	1.5E+38	2.3E+31	1.2E+32	1.6E+586	4.2E+65	2.3E+84	6.2E+38	5.1E+19
PER	12:0	12:0	11:0	10:0	11:0	12:0	12:0	12:0	12:0

"-" denotes that BIC and AIC approximations to the model evidence did not agree and no statement can be made.

Second-level analysis of modulatory effects

In Model 1, only the bidirectional connections between dIFG and pSTS were allowed to be modulated by the modulatory inputs that corresponded to the two passage-reading conditions. The individual modulatory effects on these connections are listed in Table 8. As hypothesized, predictive reading significantly enhanced the bidirectional connectivity between dIFG and pSTS ($p < 0.001$, corrected), whereas the modulatory effect of normal reading did not deviate from zero. The modulatory effects of predictive reading at both bidirectional connections between dIFG and pSTS were significantly larger than those effects of normal reading. Incorporating the results of the second-level modulatory effects comparison with the results of the Bayesian model selection, the DCM analysis indicates that the dIFG-pSTS connectivity, but not the other frontotemporal connectivity in the comparisons, is enhanced by predictive reading.

Table 8
The participant-specific modulatory effects in Model 1 (in Hz).

Subject	pSTS → dIFG Predictive Reading	pSTS → dIFG Normal Reading	pSTS → dIFG Difference	dIFG → pSTS Predictive Reading	dIFG → pSTS Normal Reading	dIFG → pSTS Difference
1	0.19	0.02	0.17	0.14	-0.02	0.16
2	0.28	-0.04	0.32	0.20	-0.06	0.26
3	0.26	-0.03	0.29	0.10	-0.02	0.12
4	0.28	-0.09	0.37	0.11	-0.12	0.23
5	0.15	0.07	0.08	0.04	-0.03	0.07
6	0.17	0.08	0.09	0.07	0.00	0.07
7	0.21	0.17	0.04	0.20	0.08	0.12
8	0.24	-0.06	0.30	0.04	0.00	0.04
9	-0.01	0.10	-0.11	0.01	0.01	0.00
10	0.24	0.11	0.13	0.18	0.07	0.11
11	0.17	-0.01	0.18	0.07	-0.02	0.09
12	0.18	0.05	0.13	0.09	0.01	0.08
Mean	0.20	0.03	0.17	0.10	-0.01	0.11
S.E.	0.02	0.02	0.04	0.02	0.01	0.02
t_{11}	8.64	1.35	4.19	5.57	0.60	5.30
p	0.0000*	0.2047	0.0015*	0.0002*	0.5591	0.0003*

* Significant using Bonferroni correction for multiple tests (2 comparisons). The adjusted threshold is $p = 0.025$.

5.6.3 Discussion

Our DCM results lead to a clear conclusion: The neural interactions between dIFG and pSTS are modulated by predictive reading. The importance of the interactions between the left inferior frontal areas and the left posterior temporal areas in language processing has been known since the 19th century (see review by Poeppel and Hickok, 2004), and has also been shown in recent studies using functional connectivity analyses (Hampson et al., 2002; Horwitz et al., 1998; Horwitz and Braun, 2004), event-related optical signal imaging (Tse et al., 2007) and direct electrostimulation (Mandonnet et al., 2007; Matsumoto, et al., 2004). However, the functions emerging from interregional interactions remain poorly understood. Most studies using connectivity analysis have shown that the change of functional connectivity between regions was driven by external stimuli such as text comprehensibility (e.g. Homae et al., 2003; Hampson et al., 2002; Obleser et al., 2007) and text complexity (e.g. Horwitz and Braun, 2004). Our DCM results have demonstrated that connectivity enhancement can be initiated by a top-down cognitive process, even though the external stimuli remain constant. Specifically, we have shown that bidirectional connectivity between dIFG and pSTS was enhanced when readers predict the development of a story during reading. This task can be interpreted as world knowledge retrieval, i.e., retrieval of relevant information based on the experience of the reader. It is conceivable that world knowledge retrieval is controlled by the same mental mechanism that is responsible for the process of controlled semantic retrieval proposed by Wagner et al. (2001). In their experiment, participants were asked to indicate which word from a group of target words was semantically most related to a cue word. They found stronger IFG responses when the words are weakly related than when the words are highly related. The authors argued that the bottom-up, automatic word association mechanism probably did not support the semantic retrieval when the words are weakly related, and suggested that the activation of left inferior prefrontal cortex (BA 45/47) is related to the mediation of a top-down bias that guides semantic retrieval in the left temporal areas. Badre et al. (2005) further demonstrated that the co-activation of the left frontal and temporal regions is related to controlled semantic retrieval. Kerns et al. (2004) reached a similar conclusion in an fMRI study using sentence materials as cues for word production. In their study, the authors demonstrated that the purpose of activity in the left prefrontal cortex (BA 9, 46 and 45) is to maintain contextual information and to guide the selection of context-appropriate responses during word production. It is not unlikely that the top-down mechanism recruited in the word-level controlled semantic retrieval may also be employed in retrieving world knowledge while drawing strategic inferences according to a complex mental representation of the text, which probably is maintained in IFG (Hagoort et al., 2004). This representation would be a basis for vIFG to mediate a top-down bias that guides the retrieval of the reader's world knowledge in the temporal areas through the connection from dIFG to pSTS. This top-down bias may be similar to a kind of instruction that controls the activation of the reader's world knowledge relevant to the existing representation. The activated information may then mediate back to IFG for integration (Hagoort et al., 2004; Hagoort 2005) in which coherence between the retrieved information and the existing representation is built up. As coherence building is also based on the reader's goal, it may involve a monitoring process that checks whether the product of integration achieves the goal or not. This monitoring function is probably subserved by aPFC because previous studies have shown that the activity of aPFC is associated with the success of coherence building (Ferstl and von Cramon, 2001; Siebörger et al., 2007). The information that cannot be integrated successfully will then be discarded from memory.

Furthermore, the results of the Bayesian model comparisons have shown that there is strong and consistent evidence for the case that interactions between frontal and temporal regions during predictive reading are mediated directly between pSTS and IFG in the dorsal stream, rather than via the indirect pathways interconnecting TPJ or aTL. This indicates that the primary roles of TPJ and aTL, and their interactions with the frontal regions, may not be primarily involved in retrieving strategic inferences. However, some researchers have speculated that TPJ and aTL are involved in retrieving higher order semantics (Price, 2000; Jung-Beeman, 2005), which leaves their functional roles in higher-level language processing open to further investigation.

5.7 Summary

The results from the conventional fMRI analysis and the effective connectivity analysis show that strategic inference processes involve a frontotemporal network in the dorsal stream. The key components in this network include aPFC, dIFG, vIFG and the connection between dIFG and pSTS. We have postulated that vIFG is responsible for driving controlled semantic retrieval, during which a top-down bias is mediated from dIFG to pSTS to guide the temporal regions in activating lexical-semantic information. This information is then mediated back to dIFG for integration. The role of aPFC is probably to monitor coherence building of the representations that are maintained and integrated in dIFG.

6 Neural Mechanisms for Drawing Routine Inferences (fMRI Exp 2)

According to the constructionist position (Graesser et al., 1994), readers routinely establish coherence at the local and global levels during online comprehension. Coherence is established by relating locally-coherent text units, such as phrases or sentences, to the discourse context or to the overarching themes of the text. For instance, in the following short passage *As agreed upon, Jane was to wake her sister and her brother at five o'clock in the morning. But the sister had already washed herself, and the brother had even got dressed. Jane told the brother that he was exceptionally slow*. (van Berkum et al., 1999), readers can detect a conflict at the end of the last sentence because it cannot be integrated in the context coherently. In many cases, establishing coherence requires the activation of the reader's world knowledge. As an example, Dutch readers probably notice that the sentence *The Dutch trains are white and very crowded*. (Hagoort et al., 2004) violates their world knowledge, because Dutch trains are yellow, not white. For illustration purposes, the above text examples consist of anomalies, but the role of world knowledge is equally important in establishing coherence in a well-formed sentence such as *The Dutch trains are yellow and very crowded*. The prerequisite is that the knowledge needed for coherence building is easily available (McKoon and Ratcliff, 1992; Noordman and Vonk, 1992), and readers do not focus just on the surface features of text, such as when proofreading for spelling errors (Graesser et al., 1994; Singer and Halldorson, 1996; Zwaan and Radvansky, 1998).

To investigate the neural correlates of how the reader's world knowledge contributes to language comprehension, Hagoort et al., (2004) compared the neurophysiological response induced by world knowledge violations to the response induced by semantic violations. Participants were presented with short sentences like the above example *The Dutch trains are yellow / white / sour and very crowded*. As Dutch trains are yellow in the real world, the critical word is either true (yellow), a violation of world knowledge (white) or a semantic violation (sour). However, there are shortcomings related to this anomaly-detection paradigm. First, the occurrence of anomalies in the sentences may trigger undesired strategic processes in order to resolve the ambiguity. The underlying neural mechanisms of these ambiguity-resolving processes may not be the same as the processes for establishing a coherent representation of well-formed linguistic stimuli. Second, the distinction between a world knowledge violation and a semantic violation may be problematic. In the example with a semantic violation, i.e. *The Dutch trains are sour and very crowded*, the core semantic features of *sour*, which are related to taste and food, do not apply to trains. Alternatively, it is equally plausible that the sentence also violates readers' world knowledge about the edibility of trains. Therefore, the responses triggered by semantic violations and world knowledge violations can not be separated because they are both associated with verification of world knowledge and the strategic processes related to ambiguity resolution. This interpretation is in line with the findings of Hagoort et al. (2004). Using electroencephalography and fMRI, the authors showed that the processing of world knowledge violations and the processing of semantic violations elicit similar neurophysiological responses: both types of violations elicited an N400 effect – a neurophysiological signature of unexpected linguistic stimuli – and increased activity in the left inferior frontal gyrus. There was no significant difference between both types of violations in terms of N400 latencies or brain activity.

6.1 Experimental Manipulations

To overcome the above-mentioned shortcomings, we designed a new experimental paradigm to investigate the neural mechanisms of the routine drawing of knowledge-based inferences during comprehension of well-formed text. In the critical condition of this experiment, participants were required to read short passages and to verify whether the situations described in the passages are in accordance with their world knowledge or not. As argued earlier, readers routinely establish local and global coherence during online comprehension. For this reason, we assume that the detection of world knowledge violation does not impose extra effort for participants reading well-formed passages. We called this condition the normal-reading condition. To contrast with this condition, we introduced a condition called the surface-level-reading condition, in which participants were required to read short passages and to detect whether the sentences contained a pseudoword or not. Previous research has shown that in this condition, readers stop drawing knowledge-based inferences, i.e. stop verifying whether the situation is consistent with their world knowledge (Singer and Halldorson, 1996). Except for this difference, we presume that participants understand the explicit meaning of the well-formed passages in the surface-level-reading condition because the processes of understanding explicit meanings are considered to be automatic (Crinion et al., 2003; Warren and Marslen-Wilson, 1987). Thus, the comparison between the responses of the normal-reading condition and the surface-level-reading condition can inform us about the neural correlates responsible for drawing routine inferences during online comprehension. Additionally, we included a pseudoword-reading condition which served as a common baseline for the above mentioned passage-reading conditions.

The distinctive characteristic of the present experiment is that we focus on the processing of well-formed text rather than the processing of anomalous text. In both normal-reading and surface-level-reading conditions, anomalous passages were treated as fillers, i.e. they were present only for the purposes of the tasks, and were not of interest in the analysis. Therefore, we can avoid the strategic processes induced by anomalies during reading.

In the following, we first discuss the approaches and experimental design adopted in this experiment (Section 6.2 and 6.3). After that, we report and discuss the results of (i) the fMRI study in Section 6.4, and (ii) the connectivity analysis using DCM in Section 6.5.

6.2 Approaches and Hypotheses

Two complementary approaches were used to investigate the neural mechanisms underlying the drawing of routine inferences during reading. First, we identified the brain regions critical for drawing routine inferences by contrasting the hemodynamic responses in the normal-reading condition with those in the surface-level-reading condition. Based on the review in Chapter 3, on p. 17, we hypothesize that the regions involved in semantic retrieval such as pSTS and IFG, as well as the regions involved in semantic integration such as IFG and aTL, will probably be shown by this comparison to be activated.

As argued in Section 3.4 on p. 28, drawing inferences probably involves frontotemporal interactions. Because routine inferences are presumed to be drawn in the normal-reading condition but not in the surface-level condition, we hypothesize that these frontotemporal interactions are stronger in the normal-reading condition. However, it is unclear how these interactions are mediated. Therefore, we employed the second approach, effective connectivity analysis (for details, see Section 4.5 on p. 43), to investigate the frontotemporal interactions. On the basis of the anatomical connections defined in Section 3.5 on p. 30 and the theories regarding how inferences are drawn (for details, see Section 3.4 on p. 28), we constructed and compared ten models capturing the different plausible ways of modulating the connections among IFG, pSTS, TPJ and aTL. Comparisons between these models provide useful information that will help discriminate between theories of routine-inference drawing.

6.3 Experimental Design

The normal-reading, surface-level-reading and pseudoword-reading conditions were manipulated in a within-subject block design. Each participant read exactly the same set of well-formed passages. In both normal-reading and surface-level-reading conditions, participants had to read short passages and only needed to provide a response at the end of the passages if an anomaly was detected. In other words, participants did not need to give any behavioural response for the well-formed passages. Similarly, in the pseudoword-reading condition, participants read sequences of pseudowords and had to press a button at the end of the sequences if a capitalised pseudoword had been detected. To make sure that participants read the passages and pseudoword sequences carefully, 25% of the stimuli contained a world knowledge violation, a pseudoword or a capitalised pseudoword, depending on the condition involved.

6.3.1 Construction of Stimuli

Based on the passages used in Exp 1, 72 German passages were constructed. Each passage consisted of 1 to 3 sentences describing an everyday event and consisted of exactly 15 words. A sample passage: *The exams are imminent. The student sits at his desk and opens his textbook*. Additionally, 24 filler passages, each of which consisted of an anomaly, were constructed. For each filler passage, there were two versions. In the normal-reading condition, a filler passage consisted of an obvious world knowledge violation, for instance, *The ship sailing in fog on Lake Constance crashes into a huge iceberg*. In the surface-level-reading condition, a filler passage consisted of a pseudoword, for instance, *The ship sailing in fog on Lake Constance crashes into a huge gebrice*. All pseudowords in the filler passages were pronounceable and complied with German spelling rules. For the pseudoword-reading condition, we constructed 24 pseudoword sequences, each of which consisted of 15 pronounceable pseudowords. Six out of 24 pseudoword sequences contained a capitalized pseudoword. The actual text materials can be found in Appendix II on p. 111.

A pre-test was conducted in order to ensure that the well-formed passages were coherent and that the world knowledge violations in the filler passages could be detected easily. These two types of passages were presented in a random sequence to eight native German speakers, who decided whether the situations described in the passages were in accordance with their world knowledge or not. On average, 97.7% (SD = 2.0) of the well-formed passages were judged as coherent and 96.3% (SD = 4.1) of the passages containing world knowledge violations were judged as incoherent, showing that the well-formed passages and the passages with world knowledge violations are highly differentiable.

6.3.2 Stimulus Presentation and Tasks

The experiment consisted of 120 trials, of which 72 were well-formed passages, 24 were filler passages and 24 were pseudoword sequences. The well-formed passage and filler passages were divided into 4 blocks, i.e. each block consisted of 18 well-formed and 6 filler passages. In two of the passage blocks, participants were instructed to read the passages carefully and press a button at the end of the passages that contained a world knowledge violation. In the other two passage blocks, participants were instructed to read the passages carefully and press a button at the end of the passages that contained a pseudoword. The pseudoword sequence trials were divided into 3 blocks of 8 trials each. In these blocks, participants were instructed to read the pseudoword sequence carefully and press a button at the end of the sequences that contained a capitalised pseudoword. The exact wordings of the instructions are listed in Appendix II on p. 111. The sequence of the reading conditions was counterbalanced in an ApBpBpA / BpApApB fashion, where "A" is normal reading, "B" is surface-level reading and "p" is pseudoword reading. The trials within a block were presented in random sequence. Participants were informed about the end of each block. The between-block interval was 15 seconds.

The text stimuli were projected on a screen in the RF-shielded-cabin and viewed by participants via a mirror mounted in the head coil of the MRI scanner. At the beginning of each trial, an asterisk was presented for 1000 ms. To remind participants of the reading condition of the current block, the asterisk was coloured red in the case of the normal-reading condition, and black for the surface-level-reading and pseudoword-reading conditions. Subsequently, a passage or a pseudoword sequence was presented word by word. Each word was exposed for 450 ms and was followed by a 50 ms blank interval. Then, a question mark was presented for 3000 ms in order to cue the participants to provide a response by pressing a button on a response box if they detected a world knowledge violation in the passages or a capitalized letter in the pseudoword sequences. The inter-trial interval was 6000 ms. The total duration of a trial was 17500 ms.

To allow participants to familiarize themselves with the reading conditions and the tasks, they were requested to participate in a training session consisting of 20 trials before the fMRI experiment. The procedure described above was also used for training, but with different text materials.

6.4 fMRI Experiment

6.4.1 Participants

Twelve native German speakers (3 males, 9 females; mean age: 21; SD: 2), none of whom participated in the pre-test of text materials, gave informed written consent to participate in the experiment. All were university students, right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971), had normal or corrected-to-normal vision and did not have a history of psychiatric or neurological disorder, or claustrophobia.

We excluded the data set of one participant, who exhibited very low accuracy (50%) of world knowledge violation detection in the normal-reading condition. In total, data from 11 participants were included in the conventional fMRI data analysis reported in Section 6.4.4 and the effective connectivity analysis reported in Section 6.5.

6.4.2 fMRI Data Acquisition and Conventional Data Analysis

To acquire the functional and structural scans, we used the method described in Section 4.3 on p. 37. In total, we collected 2265 functional volumes per participant. For the conventional data analysis, the general steps including the pre-processing steps are described in Section 4.4 on p. 38. In the GLM of each subject, two regressors were constructed for each of the two passage-reading conditions, in order to capture the hemodynamic responses induced by different types of passages. Two regressors corresponded to the well-formed passages that were not judged by the participant to contain anomalies in the two passage-reading conditions. The other two regressors corresponded to the passages that were not covered by the first two regressors in the two passage-reading conditions. Most of the passages covered by these two regressors were filler passages. For the pseudoword-reading condition, there were also two regressors that corresponded to the pseudoword sequences and filler sequences containing a capitalised pseudoword. Additionally, three regressors were constructed to capture the hemodynamic responses associated with the participant's behavioural responses. *T*-test contrasts between the reading conditions were calculated individually and averaged across participants using random-effect analysis. In this experiment, cortical activations below a voxel-level threshold of $p < 0.001$ ($t = 4.14$, uncorrected) and a cluster-level threshold of $p < 0.05$ (corrected) with a minimal cluster size of 40 voxels, were reported and considered to be significant unless otherwise specified.

6.4.3 fMRI Behavioural Results

The mean accuracies and mean response times for world knowledge violation detection in the normal-reading condition, pseudoword detection in the surface-level-reading condition, and capitalised pseudoword detection in the pseudoword-reading condition are listed in Table 9. The condition accuracies did not differ significantly from each other ($t_{10} < 1.3$, $p > 0.22$), indicating that the difficulty of the tasks is comparable. With respect to response time, there were significant differences between world knowledge detection and pseudoword detection ($t_{10} = 2.7$, $p < 0.05$), and between world knowledge detection and capitalised pseudoword detection ($t_{10} = 2.9$, $p < 0.05$). One of the factors contributing these differences is the fact that world knowledge violation can usually only be detected at the end of a passage, but spelling errors and capitalised pseudowords in the other two conditions occurred earlier in the passages. Therefore, processing of the world knowledge violations may delay response latency.

Table 9
Mean detection accuracy (%) and reaction time (in ms). Standard deviation is given in brackets.

Condition	Normal Reading	Surface-level Reading	Pseudoword Reading
Detection	World knowledge violation	Pseudoword	Capitalised pseudoword
Accuracy (SD)	92.4 (7.9)	97.0 (5.6)	95.5 (10.8)
RT (SD)	549.3 (143.6)	452.3 (118.1)	429.7 (97.6)

6.4.4 Results of the Conventional Data Analysis

To avoid potential strategic processes induced by anomalies or irregularities in the text, we calculated the comparisons between the three reading conditions only by including the hemodynamic responses to passages that were well-formed and were not judged to contain a world knowledge violation or a spelling error, and the hemodynamic responses to pseudoword sequences without containing a capitalised pseudoword.

Compared to the pseudoword-reading condition, the normal-reading and surface-level-reading conditions together evoked extensive responses in the bilateral middle temporal lobes including aTLs and mMTG as well as dIFG and vIFG in the left hemisphere (Fig. 7A and B). When comparing each passage-reading condition against the pseudoword-reading condition separately, similar activation patterns were observed (Fig. 7B and C), except that there were two significant clusters in the left vIFG and TPJ in the normal-reading condition but not in the surface-level condition. The direct comparison between the passage-reading conditions (Fig. 7D) confirmed that the activation in the left IFG was stronger in the normal-reading condition than in the surface-level-reading condition, which also overlapped considerably with the IFG activation in the comparison between the normal-reading condition and the pseudoword-reading condition. Unexpectedly, the comparison between the surface-level-reading condition and the normal-reading condition yielded four significant clusters in the left parietal lobe, extending to the supramarginal gyrus, the posterior cingulate gyrus, the right sub-gyral frontal lobe and the right insular cortex (Fig. 7E). None of these clusters appeared in the comparisons mentioned earlier. Detailed information about the significant clusters is listed in Table 10.

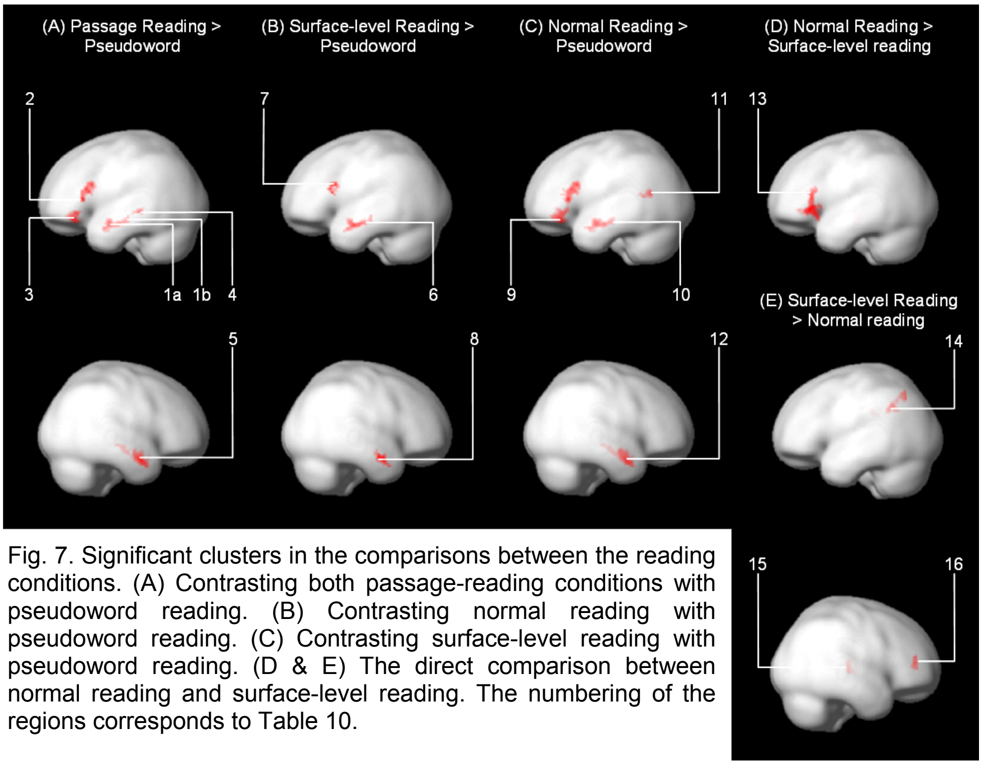

Fig. 7. Significant clusters in the comparisons between the reading conditions. (A) Contrasting both passage-reading conditions with pseudoword reading. (B) Contrasting normal reading with pseudoword reading. (C) Contrasting surface-level reading with pseudoword reading. (D & E) The direct comparison between normal reading and surface-level reading. The numbering of the regions corresponds to Table 10.

6.4.5 Discussion

Passage reading vs. pseudoword reading

Both normal reading and surface-level reading, considered in relation to pseudoword reading, elicited a typical activation pattern, except that activations in pSTS were lacking at the predefined threshold. However, the pSTS activations were just below the threshold. At a slightly more liberal threshold: voxel-level threshold at $p < 0.0015$ ($t = 3.9$) instead of $p < 0.001$ ($t = 4.14$) and cluster-level threshold maintained at $p < 0.05$ (corrected), a

Table 10
Clusters found to be significant in the comparisons between reading conditions.

Structure / Gyrus	Approx. BA	Side	MNI coordinates x	y	z	Size (mm^3)	Z_{max}
A. Passage Reading > Pseudoword Reading							
1a. Anterior portion of the middle temporal gyrus [a]	21	L	-56	-2	-18	1080	4.48
1b. Middle portion of the middle temporal gyrus			-52	-20	-14		
2. Dorsal lateral inferior frontal gyrus	45/44	L	-58	26	8	960	4.10
3. Anterior ventral inferior frontal gyrus	47/11	L	-44	34	-10	760	4.26
4. Posterior superior temporal sulcus [b]	21/22	L	-54	-34	-6	248	4.05
5. Middle and anterior portion of the middle temporal gyrus	21/38	R	58	0	-20	1544	4.65
B. Surface-level Reading > Pseudoword Reading							
6. Middle and anterior portion of the middle temporal gyrus	21	L	-50	-16	-16	760	3.77
7. Dorsal lateral inferior frontal gyrus	44/45	L	-46	14	22	376	4.06
8. Anterior portion of the middle temporal gyrus	21	R	50	-6	-24	672	4.41
C. Normal Reading > Pseudoword Reading							
9. Dorsal lateral inferior frontal gyrus Anterior ventral inferior frontal gyrus	44/45/47	L	-44	34	-14	2528	4.92
10. Middle and anterior portion of the middle temporal gyrus	21	L	-52	-20	-14	1328	4.61
11. Angular gyrus / posterior superior temporal gyrus	39/22	L	-60	-60	12	352	3.98
12. Middle and anterior portion of the middle temporal gyrus	21/38	R	56	-2	-20	1768	4.84
D. Normal Reading > Surface-level Reading							
13. Dorsal lateral inferior frontal gyrus Anterior ventral inferior frontal gyrus	45/47	L	-58	26	12	1960	4.67
E. Surface-level Reading > Normal Reading							
14. Parietal lobe and supramarginal gyrus	39/7	L	-40	-50	30	960	4.93
15. Ventral posterior cingulate cortex	23	L/R	-6	-22	34	1408	4.01
16. Insula cortex	13	R	32	-24	8	392	5.07
17. Subgyral frontal lobe	-	R	36	46	16	344	3.87

[a] A local maximum of the cluster. It was listed because its coordinate was used to define a region in DCM (for details, see Section 6.5 on p. 81).

[b] A non-significant cluster (p = 0.08, corrected).

significant cluster in pSTS was additionally found in both comparisons. This indicates that pSTS is also involved in passage reading, which is consistent with the results of Exp 1 and many other fMRI studies of language processing (e.g. Bookheimer, 2002; Cabeza and Nyberg, 2000; Gernsbacher and Kaschak, 2003; Xu et al., 2005).

Similarly to Exp 1, we did not find any significant activation in pITG, although evidence has strongly implicated its role in semantic retrieval (for details, see the review in Section 3.1 on p. 18). A possible explanation is that the consistent correspondence between orthography and phonology in the German language leads to stronger engagement of the indirect path for semantic retrieval subserved by pSTS than the engagement of the direct path subserved by pITG (Paulesu et al., 2000; Price, 2000).

It is worthwhile to note that in both comparisons between passage reading and pseudoword reading, activations were found in bilateral aTLs. Many fMRI studies have shown that aTL activations are significantly stronger during sentence processing than word processing (e.g. Bavelier et al., 1997; Crinion et al., 2003; Mazoyer et al., 1994; Stowe et al., 1999; Vandenberghe et al., 2002). Thus, the aTL activations observed in the present experiment reflect that the participants did engage in sentence-level comprehension in both passage-reading conditions. This is particularly important for the validity of the surface-level-reading condition because we assumed that the explicit meanings of the passages are activated automatically, and that the participants cannot just treat the passages as lists of disconnected words (Crinion et al., 2003; Warren and Marslen-Wilson, 1987).

Direct comparisons between normal reading and surface-level reading

Contrasting normal reading with surface-level reading yielded significant left IFG activations, overlapping with dIFG (BA 45) and vIFG (BA 47). Accumulating evidence has suggested that dIFG and vIFG subserve distinct functions in language processing (Stowe, et al., 2005; Hagoort et al., 2004). As discussed in Section 3.2 on p. 22, dIFG mainly supports a generalised control process that maintains and selects information among a set of competitors according to the task requirement (Badre et al., 2005; Thompson-Schill et al., 1997), whereas vIFG is involved in establishing semantic relations through controlled semantic retrieval (Badre et al., 2005; Wagner et al., 2001). These interpretations are in line with our hypothesis that the additional processes at work during normal reading in comparison to surface-level reading would involve the establishment of relations between textual information in order to build up coherence, which entails retrieval of the reader's world knowledge. Therefore, increased selection load and controlled semantic retrieval demand were found in normal reading in comparison to surface-level reading. Furthermore, these interpretations are applicable to explaining the dIFG and vIFG activations obtained in various language tasks requiring participants to predict the development of the described situations (Chow et al., 2008), to make plausibility judgement of sentences (Kuperberg et al., 2006), to listen to acoustically degraded speeches[9] (Obleser et al., 2007), to process semantic anomalies (Kiehl et al., 2002) or to process world knowledge violations (Hagoort et al., 2004; Kuperberg et al., 2003), because the common factor among these tasks is the retrieval of the reader's world knowledge.

Direct comparisons between surface-level reading and normal reading

Contrasting surface-level reading with normal reading showed four significant clusters. None of them overlapped with the activated clusters in the comparisons between passage reading and pseudoword reading, indicating that their core functions might not be directly related to language comprehension. The most prominent two clusters were located in the left parietal lobe (BA 39 and 7) and the ventral posterior cingulate cortex (BA 23). There is considerable evidence suggesting that the network of these two regions and the frontal regions subserves visual spatial attention (Small et al., 2003). In the context of pseudoword detection in the surface-level condition, the activations may reflect that the participants probably needed to maintain relatively high visual spatial attention in order to access and maintain the word representations of the task (Bitan et al., 2005).

6.5 Effective Connectivity Analysis

We used DCM to compare the frontotemporal interactions during reading in the passage-reading conditions. The same data set was used as in the conventional fMRI data analysis. The details of fMRI data acquisition and the general information of participants can be found in Section 4.3 on p. 37 and Section 6.4.1 on p. 76 respectively.

6.5.1 DCM Analysis

The steps and general considerations for conducting a DCM analysis have already been discussed in Section 4.5.3 (p. 45). Below, the actual implementation of DCM in this experiment is described in detail.

[9] Only vIFG activations were found in Obleser et al., 2007.

Regions selection and time-series extraction

The regions selected for DCM analysis were mainly based on the comparison between the passage-reading conditions and the pseudoword-reading condition, the activated clusters of which are illustrated in Fig. 7A. Accordingly, five regions in the left hemisphere were selected, namely aTL (cluster 1a in Fig. 7A), mMTG (cluster 1b in Fig. 7A), dIFG (cluster 2 in Fig. 7A), vIFG (cluster 3 in Fig. 7A) and pSTS (cluster 4 in Fig. 7A). Please note that aTL and mMTG were in the same activated cluster, and that the activation in pSTS was only close to significant ($p < 0.08$, corrected) according to the predefined threshold. These regions were selected as three separated regions in the DCM analysis because we postulate that they may subserve different functions in comprehension and inference processes (for details, see Chapter 3 on p.17). For the same reason, we included a region in TPJ that was activated in the comparison between the normal-reading condition and the pseudoword-reading condition (cluster 11 in Fig. 7C). As language comprehension is mainly left-lateralised, and in order to reduce the complexity of the DCM models, we did not consider the activated clusters in the right hemisphere.

The centre coordinates of the selected regions in MNI space are shown in Fig. 8A. The detailed information regarding these regions can be found in Table 10 on p. 79. For the procedure involved in extracting the time-series of the regions, please see Section 4.5.3 on p. 45.

DCM specifications: Definition of anatomical connections

The anatomical connections between the selected regions have been defined in Section 3.5 on p. 30. However, no activated cluster was found in pITG or aPFC in the conventional fMRI data analysis in this experiment. Therefore, pITG and aPFC and their connections with the other regions were excluded from the DCM analysis. The resulting anatomical connections defined in this analysis are shown in Fig. 8A.

DCM specifications: Definition of driving inputs

As illustrated in Fig. 8C, the driving inputs in this analysis were a boxcar function representing the reading sections of all passages including well-formed and filler passages, and a boxcar function representing the reading section of all pseudoword sequences. We assume that the driving inputs directly influence pSTS, and that the neuronal activity then propagates to other regions (for details, see Section 3.5.3 on p. 31).

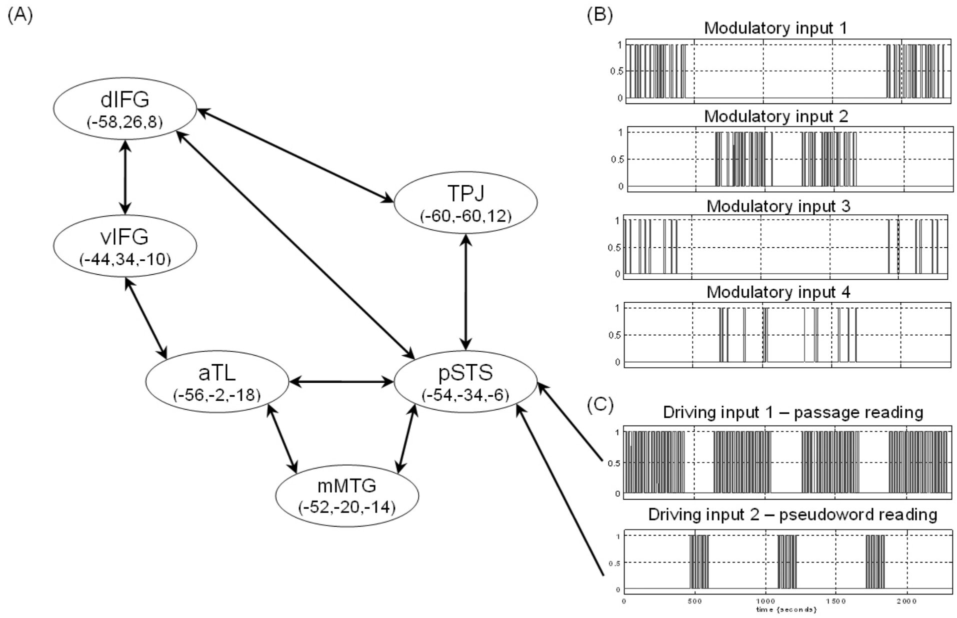

Fig. 8. The basic DCM structure used in this experiment. (A) The schematic representation of the anatomical connections between the selected regions, namely dorsal lateral inferior frontal gyrus (dIFG), anterior ventral inferior frontal gyrus (vIFG), temporoparietal junction (TPJ), posterior superior temporal sulcus (pSTS), middle portion of the middle temporal gyrus (mMTG), anterior temporal lobe (aTL). The centre coordinates of the selected regions in MNI space are listed in brackets. (B) The modulatory inputs, which correspond to the well-formed passages of the normal-reading and surface-level-reading conditions (1 & 2), and their fillers that contained anomalies (3 & 4). (C) The driving inputs which were assumed to directly exert influence on pSTS.

DCM specifications: Definition of modulatory inputs

At this point, a basic model was constructed (see Fig. 8). To discriminate between the various hypotheses regarding the inference drawing (for details, see Section 3.4 on p.28), we systematically derived ten DCMs from this basic model by defining modulatory inputs at various connections. In this analysis, the modulatory inputs were four boxcar functions, corresponding to the well-formed passages and the filler passages in each of the two passage-reading conditions (see Fig. 8B). In Models 1-3 (see Fig. 9A) the modulatory inputs were defined to modulate all direct and indirect connections between pSTS and dIFG in the dorsal stream. In Model 4 (see Fig. 9A), modulation occurred with respect to the connection between TPJ and dIFG. In Models 5-8 (see Fig. 9B) the modulatory inputs were defined to modulate all possible sets of connections between pSTS and vIFG in the ventral stream. As it is possible for the frontotemporal connections in both dorsal and ventral streams to work together simultaneously, we included two models, Model 9 and Model 10 (see Fig. 9C), to address this possibility.

In Model 9 the modulatory inputs were allowed to modulate all direct frontotemporal connections in the dorsal and ventral streams. In Model 10 the modulatory inputs were allowed to modulate the connections between dIFG and pSTS and the connections between aTL and vIFG. In all ten models, we assumed that the modulatory inputs influence the bidirectional connections between the frontal and temporal regions. This assumption was made because the frontal regions are probably responsible for integrating different sources of information, including inferences, as well as for coherence building and for driving controlled semantic retrieval. This implies that any feedback effect, such as controlled semantic retrieval, also induces feedforward effects in order for the product of the feed-back effect to be integrated into a coherent representation in the frontal regions during language comprehension.

Bayesian model selection / Second-level analysis of the modulatory effects

Please refer to Section 4.5.3 on p. 45.

6.5.2 Results of the DCM Analysis

Bayesian model selection

Table 11 lists the individual BFs of the pairwise Bayesian model comparisons between Model 1 and all other nine models. The results clearly indicate that Model 1 is the best model of the models compared here. The evidence in favour of Model 1 was robust; the smallest GBF was larger than 10^{24} and very consistent among participants. In the comparisons between Model 1 and all other models except Model 5 and 6, at least 10 out of 11 individual DCMs showed significant evidence in favour of Model 1, but not the other way round. In the comparisons between Model 1 and Model 5, nine individual DCMs showed significant evidence in favour of Model 1, but for participants 2 and 9, those comparisons showed significant evidence in favour of Model 5. For participants 1, 6 and 9, the comparisons between Model 1 and Model 6 yielded inconsistent evidence, meaning that these 2 models were not differentiable in terms of model evidence. Interestingly, both Model 5 and Model 6 involve the connections between aTL and vIFG in the ventral stream.

Second-level analysis of the modulatory effects

In Model 1, only the bidirectional connections between dIFG and pSTS were allowed to be modulated by the four modulatory inputs corresponding

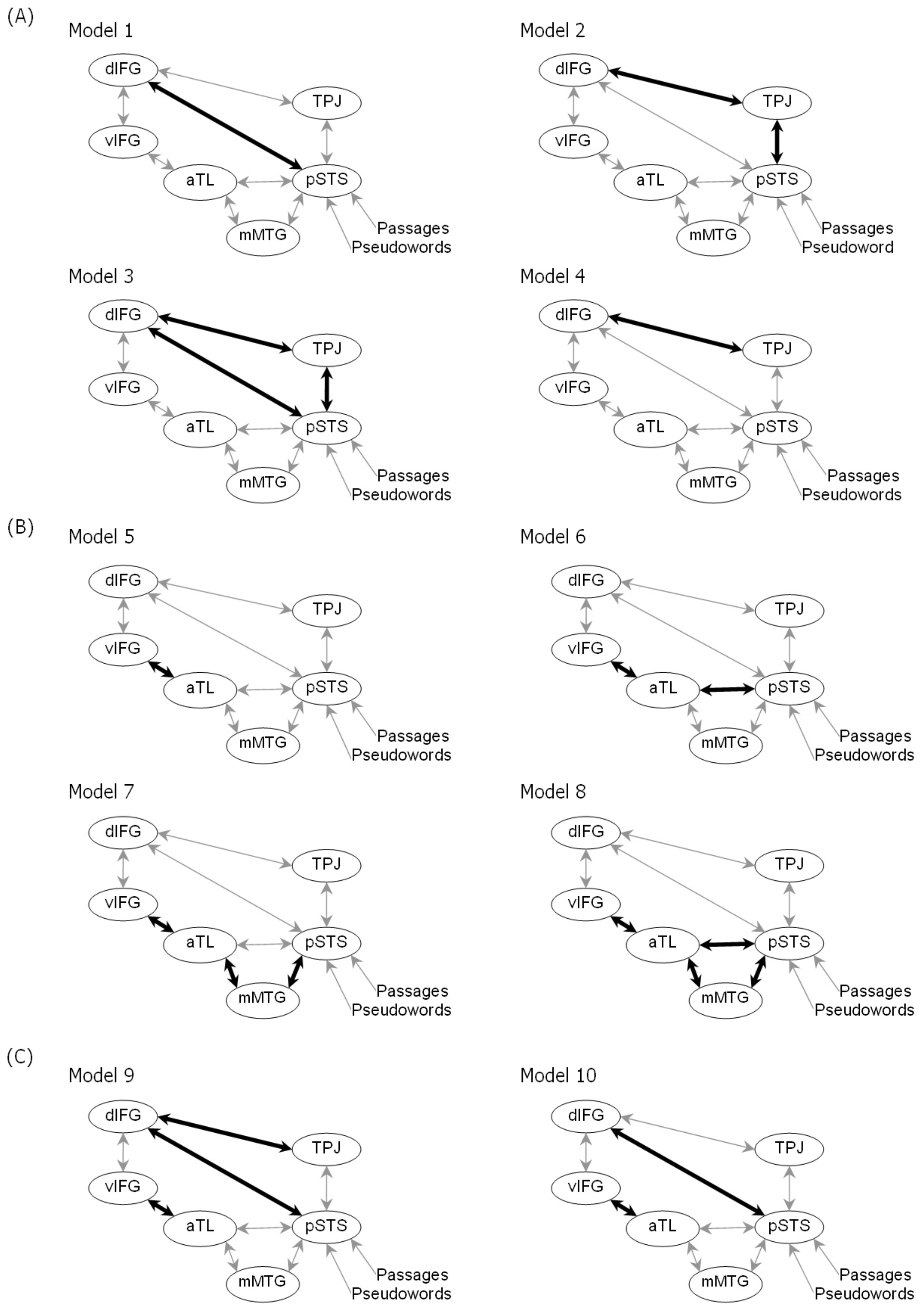

Fig. 9. The ten DCMs derived from the basic model (see Fig. 8). The connections modulated by the four modulatory inputs are in bold. (A) Models with modulatory inputs at connections in the dorsal stream. (B) Models with modulatory inputs at connections in the ventral stream. (C) Models with modulatory inputs at connections in both dorsal and ventral streams.

to the reading sections of the well-formed and filler passages in the two passage-reading conditions. The modulatory effects of the well-formed passages in the two reading conditions are listed in Table 12. As hypothesized, the results showed that the normal-reading condition significantly enhanced the bidirectional connectivity between pSTS and dIFG ($p < 0.01$, corrected), whereas the modulatory effect in the surface-level-reading condition did not deviate from zero. Moreover, the differences in modulatory effects between the two reading conditions were also significant at the bidirectional connections between pSTS and dIFG ($p < 0.05$, corrected).

Incorporating the results of the second-level modulatory effects comparison with the results of the Bayesian model selection, the DCM analysis indicates that the dIFG-pSTS connectivity, but not the other frontotemporal connectivity in the comparisons, is enhanced in the normal-reading condition.

Table 11
The participant-specific Bayes Factors of the pairwise Bayesian model comparisons between the best model (Model 1) and all other 9 models.

Sub-	**Model Comparison**								
ject	**1 vs 2**	**1 vs 3**	**1 vs 4**	**1 vs 5**	**1 vs 6**	**1 vs 7**	**1 vs 8**	**1 vs 9**	**1 vs 10**
1	2.5E+05	5.7E+05	4.5E+03	8.1E+02	-	4.8E+04	6.5E+04	1.3E+04	1.8E+01
2	5.3E+02	1.7E+05	1.5E+05	1.8E-02	2.3E+01	1.1E+06	6.1E+07	7.0E+04	1.4E+02
3	8.8E+02	3.6E+05	3.4E+01	1.2E+02	1.5E+03	1.5E+08	7.5E+09	3.6E+06	2.2E+03
4	1.9E+03	1.9E+05	3.6E+01	6.2E+00	1.8E+02	3.7E+04	5.0E+06	1.9E+06	1.1E+03
5	4.5E+02	1.8E+05	3.5E+00	7.2E+01	7.9E+04	3.7E+08	2.7E+11	9.3E+05	2.5E+03
6	9.5E+05	4.2E+04	8.9E+06	5.5E+05	-	9.4E+06	1.1E+06	1.1E+06	7.4E+02
7	5.3E+04	3.5E+06	1.8E+05	2.8E+05	2.9E+04	3.5E+07	1.3E+10	1.7E+06	8.2E+02
8	1.0E+05	1.1E+06	1.1E+03	3.1E+04	2.1E+07	3.3E+10	2.8E+13	2.8E+06	2.6E+03
9	8.2E+11	8.2E+12	9.7E+15	4.9E-05	-	-	2.3E+02	4.8E+04	1.3E+02
10	3.4E+02	2.7E+05	6.6E+00	7.3E+00	4.1E+01	4.9E+03	3.0E+06	7.3E+05	6.5E+02
11	1.7E+13	2.5E+06	5.1E+04	9.1E+05	2.7E+04	4.3E+07	6.3E+09	1.8E+05	3.7E+02
GBF	2.4E+60	1.1E+69	1.5E+49	1.1E+24	3.1E+29	2.6E+68	7.1E+88	1.9E+62	7.7E+29
PER	11:0	11:0	11:0	9:2	8:0	10:0	11:0	11:0	11:0

"-" denotes that BIC and AIC approximations to the model evidence did not agree and no statement can be made.

Table 12
The participant-specific modulatory effects in Model 1 (in Hz).

Subject	pSTS → dIFG			dIFG → pSTS		
	Normal Reading	Surface-level Reading	Difference	Normal Reading	Surface-level Reading	Difference
1	-0.16	-0.10	-0.06	0.02	0.00	0.01
2	0.22	0.03	0.19	0.23	0.03	0.20
3	0.15	-0.03	0.18	0.10	-0.03	0.13
4	0.20	0.05	0.15	0.23	-0.01	0.24
5	0.06	-0.12	0.18	-0.15	0.07	-0.22
6	0.20	-0.06	0.27	0.09	0.01	0.08
7	0.25	-0.03	0.27	0.33	-0.05	0.38
8	0.17	-0.04	0.22	0.25	-0.09	0.33
9	0.40	0.00	0.40	0.31	0.03	0.28
10	0.13	0.05	0.08	0.12	0.05	0.07
11	0.09	-0.26	0.35	0.31	-0.06	0.36
Mean	0.16	-0.05	0.20	0.17	0.00	0.17
S.E.	0.04	0.03	0.04	0.04	0.01	0.05
t_{10}	3.80	1.69	5.40	3.73	0.25	3.12
p	0.0035*	0.1215	0.0003*	0.0039*	0.8067	0.0109*

* Significant using Bonferroni correction for multiple tests (2 comparisons). The adjusted threshold is p = 0.025.

6.5.3 Discussion

The DCM results clearly demonstrate that the change in connectivity is related to the level of comprehension. In the surface-level-reading condition, the participants presumably read the passages shallowly and did not draw as many knowledge-based inferences as in the normal-reading condition. These two levels of comprehension were clearly reflected by the modulation of connectivity between pSTS and dIFG, i.e. the modulatory effects on the bidirectional pSTS and dIFG were significantly stronger in the normal-reading condition than in the surface-level-reading condition. To further validate this argument, we did a post-hoc analysis that calculates the correlations between the pSTS-dIFG modulatory effects determined by individual DCMs and the world knowledge violation detection accuracy of each participant. The rationale of this correlation analysis is that if the modulatory effects reflect the level of comprehension with respect to the amount of inferences, it should correlate with the accuracy of world knowledge violation detection, as the contrast between the represented situation and the violation should become more extreme with the enrichment of the relevant knowledge. The results of this additional analysis showed the modulatory effect of the normal-reading condition on the pSTS→dIFG connection and the world knowledge violation detection accuracy were significantly correlated (r = 0.66, t_9 = 2.66, $p < 0.05$, corrected for multiple comparisons[10]), but the modulatory effect on the dIFG→pSTS connection was not correlated significantly with detection accuracy (r = 0.25, t_9 = 0.77, p = 0.46). The results of this post-hoc analysis not only support our interpretations that the degree of comprehension is related to the connectivity between pSTS-dIFG, but they also imply a possible functional distinction between the pSTS→dIFG and dIFG→pSTS connectivity. Consistent with our interpretations presented in the previous chapter (for details, see Section 5.6.3 on p. 68), we speculate that the enhancement of dIFG→pSTS connectivity may reflect the mediation of a top-down bias that may be similar to a kind of instruction and that guides the retrieval of the reader's knowledge taking place in temporal areas, whereas the enhancement of pSTS→dIFG connectivity may reflect the mediation of information that was actually drawn from the temporal areas under the influences of the top-down bias. This interpretation may explain why detection accuracy is correlated with the pSTS→dIFG connectivity but not with the dIFG→pSTS connectivity, as it is more likely that detection accuracy is related to the amount of inferences that are drawn instead of the amount of instructions guiding the retrieval of inferences.

6.6 Summary

The results from the conventional fMRI analysis and the effective connectivity analysis show that retrieving routine inferences in a relatively normal reading condition involves IFG and its interactions with pSTS. Consistent with our interpretations presented in the previous chapter, we have postulated that vIFG is responsible for driving controlled semantic retrieval that mediate a top-down bias from dIFG to pSTS which guides the temporal regions in activating inferences. These inferences are probably then mediated back to dIFG, where a coherence representation is maintained and integrated.

[10] It is marginally significant at $p < 0.05$ using Bonferroni correction for multiple tests (2 comparisons).

7 Overall Discussion and Conclusion

Although it has been generally agreed among cognitive psychologists that reading goals have considerable influence both on the cognitive processes involved in comprehension and on the content of the resulting representation of the text (Calvo et al., 2006; Graesser et al., 1994; McKoon and Ratcliff, 1992; Singer and Halldorson, 1996), they have been mostly ignored by researchers interested in the neural correlates of language comprehension. Instead of the manipulation of reading goals, their experiments have been typically based on the comparison of neurophysiological responses induced by different types of text materials varying in complexity (e.g. Xu et al., 2005), coherence (e.g. Ferstl and von Cramon, 2001), comprehensibility (e.g. Vandenberghe et al., 2002) or grammatical/pragmatic acceptability (e.g. Hagoort et al., 2004). To fill this research gap, we manipulated, in the two fMRI experiments of this study, the reader's goals in order to trigger strategic inferences and to inhibit routine inferences. In the first fMRI experiment, we used the reader's ability to draw predictive inferences to investigate the neural mechanisms for drawing strategic inferences. In the second experiment, we used surface-level reading, which is similar to proofreading, to shift the reader's focus to the explicit meaning of the text in order to study the neural mechanisms for drawing routine inferences. Using those experimental manipulations, we successfully generated fMRI results that mostly supported our hypotheses and that were compatible with the results of previous fMRI studies. This shows that the manipulation of reading goals is a useful tool for studying language comprehension.

The DCM analysis employed in this study differs from many connectivity analyses of language processing. The main difference is that we considered the anatomical neural pathways between the cortical areas in order to constrain how the selected regions were connected in our DCMs, whereas the anatomical connections are usually ignored in the studies using functional connectivity analysis (e.g. Homae et al., 2003; Hampson et al., 2002; Horwitz and Braun, 2004; Obleser et al., 2007). Because regions with correlated activities are not necessarily connected physically, those analyses of functional connectivity cannot provide reliable information about the direct influence mediated between these regions. In contrast, with our anatomical connections model, we are more certain about the inferences of our DCM results regarding how direct influences are mediated between the selected regions.

Accumulating evidence has suggested that the retrieval and integration of inferences may be subserved by the interactions between brain regions in the left frontal and temporal lobes. Motivated by the review of the brain imaging studies of language comprehension and inference processes in Chapter 3, we hypothesized that inference processes may involve one or more of three frontotemporal systems, including the pSTS-IFG system, which has been shown to be related to controlled semantic retrieval (Wagner et al. 2001; Badre et al., 2005); the TPJ-IFG system, which is an essential component in the communication between frontotemporal regions during sentence or narrative comprehension (Hickok and Poeppel, 2000; 2007; Obleser et al., 2007; Price, 2000); and the aTL-IFG system, which has been suggested to be involved in establishing higher-order semantic relations and semantic integration (Jung-Beeman, 2005). In order to discriminate between the above hypotheses, we applied dynamic causal modelling, a state-of-the-art modelling technique, to fMRI data to investigate the interregional couplings during text reading. The results of the DCM analyses show that drawing inferences, no matter whether strategically or routinely, enhances the bidirectional interactions between dIFG and pSTS via the dorsal stream, but the results do not support the involvement of the other frontotemporal systems involving TPJ and aTL. This indicates that the roles of TPJ and aTL, and their interactions with frontal regions, may not primarily be involved in retrieving inferences, although some researchers have speculated that TPJ and aTL are involved in retrieving higher-order semantics (Price, 2000; Jung-Beeman, 2005). We interpret the enhancement of bidirectional dIFG-pSTS connectivity as a sign of the mediation of top-down influence from dIFG to pSTS, which guides the retrieval of inferences in the temporal areas and the mediation of inferences from pSTS to dIFG. In addition to the enhancement of dIFG-pSTS connectivity, the results of the conventional fMRI data analyses in both experiments also show that dIFG and vIFG activations are involved in the drawing of strategic and routine inferences. From these findings, we postulate that vIFG is involved in establishing semantic relations through controlled semantic retrieval (Badre et al., 2005; Wagner et al., 2001), whose effect is probably mediated through the dIFG-pSTS connections. The left dIFG seems to support a generalised control process that selects and maintains relevant information among a set of competitors according to the task requirement (Badre et al., 2005; Thompson-Schill et al., 1997; Hagoort, 2005).

The main difference between the results of the two fMRI experiments is related to the activation in the left aPFC. The results show that aPFC activation is involved in retrieving strategic inferences, but not in drawing routine inferences. This would imply that the involvement of aPFC may be specific to the processes related to retrieving and integrating strategic inferences. Since some researchers have already associated aPFC with coherence building (Ferstl and von Cramon, 2001; Ferstl 2007; Friese et al., in press), we suggest that the functional role of aPFC in language comprehension is to monitor the build-up of coherence between strategic inferences and the described situation.

The aim of this study was to investigate the neural mechanisms for drawing inferences on the basis of the reader's knowledge during reading. Inferences play an indispensable role in language comprehension. According to the comprehension theories developed by cognitive psychologists, inferences may be activated by more than one mechanism. The CI model (Kintsch, 1988) suggested that context-independent inferences are drawn by an elaborative mechanism, which is considered to be a bottom-up process. In addition, specific inferences are drawn by a controlled retrieval mechanism. On the other hand, the IEF (Zwaan, 2004) assumes that inferences are drawn by a single mechanism that treats text as a set of cues for activating processes involving the reconstruction of the reader's experience. From the view of the CI model, most of the routine inferences would probably be drawn by the elaborative mechanism, whereas strategic inferences would be drawn by the controlled retrieval mechanism. However, this distinction seems to be quite unclear from the neuropsychological point of view because both experiments in this study show that IFG and the dIFG-pSTS connections are the main components in retrieving both strategic and routine inferences.

Furthermore, cognitive psychologists sometimes define inference processes as "higher-level language processes" in order to draw a line between these processes and the more fundamental language processes such as word meaning retrieval, and some researchers have further proposed that higher-level language processes are subserved by some non-classical language brain regions such as the right hemisphere (Jung-Beeman, 1993; 2005), aPFC (Ferstl, 2008) and aTLs (Jung-Beeman, 2005). However, the regions shown to be involved in drawing inferences by the results of this study, namely IFG and pSTS, overlap with the classical language regions, Broca'a area and Wernicke's area. These regions have repeatedly been shown to be involved in a wide range of language tasks, including tasks as simple as word reading (e.g. Bookheimer et al., 1995; Mechelli et al., 2005; Price et al., 1996a). It seems then that language comprehension should be seen as a more holistic process. This perspective may be similar to the notion proposed in Zwaan's IEF, which treats text as a set of cues to activate the process of reconstructing the reader's experience. However, to understand how the reconstruction of the reader's experience is instantiated in the brain still requires a lot of further research.

Several research topics may be interesting for further exploration. Besides inference processes, connectivity analysis can be employed to study other language processes that possibly involve multiple regions, such as syntactic processing, for instance. Another exciting topic would be the investigation of the functional roles of inter-hemispheric interactions in language processing. Moreover, the results of this study have hinted at the possibility of using connectivity analysis for clinical purposes. As we have shown that the dIFG-pSTS enhancement significantly correlates with the accuracy of the verification task, this relationship may be useful for tracking the reading development of dyslexic children or the recovery of language ability in aphasic patients. Finally, it would be methodologically interesting to combine connectivity analysis with DTI, which can provide a more realistic anatomical connection model for each subject. As a consequence, the validity of connectivity analysis could be improved.

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Appendix I – Instructions and Text Materials of fMRI Exp 1

(A) Instructions of Exp 1

Vielen Dank, dass Du bei diesem Experiment mitmachst! Das Ziel dieser Studie ist es, herauszufinden, wie Menschen Sprache verstehen, wenn sie eine bestimmte Lese-Strategie verfolgen.
Bitte erledige in diesem Experiment die folgenden drei Aufgaben:
1) Du wirst mehrere kurze Text-Passagen lesen, die Wort für Wort präsentiert werden.
2) Nach jeder Passage wird eine Buchstaben-Kombination präsentiert und Du sollst entscheiden, ob diese ein deutsche Wort ist oder nicht (unabhängig von der Groß- oder Kleinschreibung). Ist sie ein Wort, drücke bitte die linke Taste (Zeigefinger). Ist sie kein Wort, drücke bitte die rechte Taste (Mittelfinger).
3) Danach wird manchmal(!) ein weiteres Wort in blauer Farbe präsentiert und Du entscheidest bitte, ob dieses Wort in der gerade gelesenen Passage vorkam (unabhängig von der Groß- oder Kleinschreibung). Ist dies der Fall, drücke die linke Taste (Zeigefinger). Ist dies nicht der Fall, drücke die rechte Taste (Mittelfinger).
Bitte versuche auch diese Aufgaben möglichst schnell und richtig zu lösen.
Es gibt zwei verschiedene Arten von Passagen:
1) Zusammenhängende Passagen.
2) Pseudowort-Sequenzen, die aus bedeutungslosen aber aussprechbaren Buchstaben-Kombinationen bestehen.
Die Passagen und Pseudowort-Sequenzen werden in verschiedenen Blöcken arrangiert.
Verwende jedem Block mit den Passagen eine der folgenden Lese-Strategien:
- "Normales lesen"
- "Situation konzentrieren"
In "Normales lesen", brauchst Du nur den Text zu verstehen.
In "Situation konzentrieren", konzentriere Dich bitte auf die dort beschriebene Situation und versuche aktiv voraus zu sagen, was die Situation ergeben könnte.
Wenn der Text beispielsweise berichtet, dass auf dem See ein kleines Boot treibt, und dass dieses Boot ein Loch im Boden hat, dann könnte man vorhersagen, dass das Boot sinken wird. Bitte lies die Texte in diesem Block so, dass Du aktiv Vorhersagen dieser Art beim Lesen machst. Außerdem beantworte bitte die Aufgaben!
Am Anfang jedes Blockes zeigen wir an, welche Strategie benutzen werden sollte.
Am Anfang jeder Passage erinnern wir dich nochmals. Eine schwarzes "*" für "Normales lesen" und einen roten "*" für "Situation konzentrieren".

(B) Passages of Exp 1

Passages	Lexical decision task target words: a) predictable b) non-predictable c) pseudoword	Recognition task target words: a) in the passage b) not in the passage
1. Superman packt die ihn umgebenden Eisenstäbe und beginnt, mit aller Kraft an ihnen zu ziehen.	a) Biegen b) Bangen c) Ketza	a) Eisenstäbe b) Lageplan
2. Martina geht den nassen Bürgersteig entlang, während Autos neben ihr rücksichtslos durch die Pfützen fahren.	a) Schmutzig b) Winzig c) Feuchzind	a) Gebeten b) Anziehen
3. Als die Boeing der steilen Bergwand immer näher kam, begannen die Passagiere laut zu schreien.	a) Absturz b) Liebster c) Tennul	a) Bergwand b) Augeblick
4. Die Wandergruppe ist in den Bergen. Der Himmel verdunkelt sich und man hört ein Grollen.	a) Gewitter b) Gewinn c) Schwurt	a) Grollen b) Tennis

(B) Passages of Exp 1

Passages	Lexical decision task target words: a) predictable b) non-predictable c) pseudoword	Recognition task target words: a) in the passage b) not in the passage
5. Mary hat Durst und hält der Mutter den Becher hin. Die Mutter greift zur Safttüte.	a) Einschütten b) Versand c) Vurstockti	a) Durst b) Handy
6. Clara sieht ihren Mann Hand in Hand mit der blonden Nachbarin. Es überläuft sie siedendheiß.	a) Eifersucht b) Wochenmarkt c) Stackdeso	a) Blonden b) Hölzern
7. Nachdem er das Projekt besonders erfolgreich abgeschlossen hat, bittet ihn der Chef in sein Büro.	a) Lob b) Bund c) Saa	
8. Der Lastwagen kommt auf das kleine Mädchen zugerast. Sie springt schreiend ganz schnell zur Seite.	a) Schreck b) Neid c) Batan	
9. Über Jahrtausende haben sich zunehmende Spannungen im San Andreas Graben aufgebaut. Nun entladen sie sich.	a) Beben b) Lehrer c) Feßü	
10. Der Kontrolleur verlangt nach den Papieren, da Thomas vergessen hat, sich einen Fahrschein zu kaufen.	a) Bußgeld b) Rummel c) Lärbar	
11. Klaus hatte das ganze Jahr hart gearbeitet. Jetzt könnte er sich gut eine Auszeit gönnen.	a) Wegfahren b) Anmalen c) Rienegtin	
12. Nachts hört er unheimliche Geräusche vor der Wohnungstür. Hektisch greift er zum Telefon und wählt.	a) Polizei b) Verstehen c) Meestir	
13. Beim Abschlussball traute sich Rolf. Er verbeugte sich vor seiner Angebeteten und murmelte etwas Unverständliches.	a) Auffordern b) Sagenhaft c) Pullendor	
14. Der Polizist sieht einen Dieb flüchten. Er schmeißt seinen Kaffeebecher weg und startet den Wagen.	a) Verfolgung b) Anstellung c) Varnächlis	
15. Gerade als Jens seine dritte Palette ablädt, klingelt die Glocke. Es ist schon zwölf Uhr.	a) Mittagspause b) Tannennadel c) Gatturziern	
16. Endlich sendet die Sonne nach einem langen und kalten Winter ihre sehnlichst erwarteten Frühlingsstrahlen aus.	a) Warm b) Rand c) Täpf	
17. Der Wagen des Anwalts kam von der Straße ab und raste auf einen Baum zu.	a) Kollision b) Binde c) Schotz	
18. Das Examen stand bevor. Der Student setzte sich an seinen Schreibtisch und öffnete seine Bücher.	a) Lesen b) Bügeln c) Unzag	
19. Neugierig krabbelt der kleine Jungvogel aus dem warmen Nest, öffnet die Flügel und riskiert es.	a) Fliegen b) Verkauf c) Sieleg	
20. Keiner kümmert sich um den Garten, obwohl es schon seit Wochen nicht mehr geregnet hat.	a) Vertrocknen b) Abpumpen c) Blöttsilat	
21. Die kleine Charlotte erblickt den Weihnachtsbaum am Heiligabend und will sofort hinlaufen und darunter sehen.	a) Geschenke b) Gesichter c) Bettarei	
22. Kaum hat Jan seine schwere Reisetasche vom Gepäckband genommen, winkt ihn ein argwöhnischer Zollbeamter beiseite.	a) Durchsuchung b) Kochschule c) Pflecktü	
23. Der laute Donner hat das Kind geweckt. Es kommt mit seinem Teddy zur Mutter gelaufen.	a) Umarmen b) Handelsmann c) Pülsta	
24. Der Theatervorhang fällt. Die zufriedenen Zuschauer klatschen Beifall und nehmen dann ihre Jacken und Mänatel.	a) Rausgehen b) Sinnbildlich c) Klattirt	

(B) Passages of Exp 1

Passages	Lexical decision task target words: a) predictable b) non-predictable c) pseudoword	Recognition task target words: a) in the passage b) not in the passage
25. Die Kamera ist zur Nahaufnahme bereit, da stolpert die Hauptdarstellerin und stürzt in die Tiefe.	a) Tot b) Rind c) Gron	a) Kamera b) Filter
26. Das Segelschiff, das bei Nebel im eiskalten Nordmeer fuhr, stieß krachend gegen den gewaltigen Eisberg.	a) Sinken b) Niesen c) Terntu	a) Eiskalten b) Verwachsen
27. Obwohl Susanne das Stoppschild beinahe übersehen hätte, war der Fahrprüfer trotzdem mit ihrer Leistung zufrieden.	a) Bestanden b) Gerinnen c) Lechtir	a) Fahrprüfer b) Garten
28. Der muskulöse Packer ging in die Knie, umschlang die schwere Kiste und holte tief Luft.	a) Heben b) Angeln c) Wutzt	a) Muskulöse b) Angezogene
29. Der Student wird im Kolloquium vom Professor gelobt. Mit roten Wangen blickt er zu Boden.	a) Schämen b) Wurzeln c) Speelti	a) Boden b) Geister
30. Die Vögel fangen an zu singen. Die Sterne verblassen langsam. Der Himmel wird immer heller.	a) Sonnenaufgang b) Bärenfalle c) Küstemiutar	a) Singen b) Vergeben
31. Die Kür der Eiskunstläuferin ist nahezu beendet, als sich ihre Kufe in einem Loch verfängt.	a) Sturz b) Bann c) Grull	
32. Das Herz des jungen Jägers raste, als er seinen Speer gegen das gewaltige Mammut richtete.	a) Werfen b) Hände c) Feschi	
33. Bisher hatte die Vorführung des Trapezkünstlers gut geklappt. Doch dann griff er plötzlich ins Leere.	a) Stürzen b) Sitzen c) Metrena	
34. Frau Suchlands ist sehr spät dran. Sie sieht den Bus schon an der Ecke stehen.	a) Rennen b) Frieden c) Hehlö	
35. Als der defekte Sprinkler plötzlich die arrogante Kollegin durchnässt, kann Stefan sich kaum noch halten.	a) Lachen b) Ausgehen c) Kammt	
36. Monika war gerade im Freibad angekommen. Sie packte ihren Badeanzug aus und lief zur Kabine.	a) Umziehen b) Verlieren c) Migazan	
37. Der Wagen nähert sich langsam dem Zebrastreifen. Auf dem Bürgersteig steht wartend eine alte Frau.	a) Anhalten b) Kanufahren c) Stineg	
38. Paul läuft nur wenige Meter hinter dem Erstplatzierten des Marathons. Er gibt noch einmal alles.	a) Überholen b) Unverbunden c) Fürnsunar	
39. Es regnet wochenlang in Strömen. Die Deiche am Fluss halten das Hochwasser nicht mehr länger.	a) Überschwemmung b) Kohlepapier c) Peppschechtal	
40. Der Mann setzte sich an den Tisch, band die Serviette um und griff zur Gabel.	a) Essen b) Regen c) Süng	
41. Der Autofahrer kommt an eine scharfe Kurve vor einem steilen Abhang. Da versagen die Bremsen.	a) Panik b) Hunger c) Trünk	
42. Als Anna heimkam, war es spät. Sie behielt ihre Kleider an und legte sich hin.	a) Schlafen b) Segeln c) Golebto	
43. Der Raum war dem erfahrenen Fotografen viel zu hell, deswegen ging er zu den Vorhängen.	a) Schliessen b) Rieseln c) Kelansera	
44. Draußen im Flur klingelt das Telefon. Marco erhebt sich aus seinem Sessel und geht hin.	a) Abheben b) Verlassen c) Hommil	

(B) Passages of Exp 1

Passages	Lexical decision task target words: a) predictable b) non-predictable c) pseudoword	Recognition task target words: a) in the passage b) not in the passage
45. Marie ist vom Waldspaziergang erschöpft. Da sieht sie ein weiches Moosbett und geht darauf zu.	a) Hinsetzen b) Verletzen c) Urlebtin	
46. Peter fährt mal wieder viel zu schnell mit seinem Auto und wird auch gleich geblitzt.	a) Geldstrafe b) Dosenpfand c) Diechzagel	
47. Nach der positiven A-Probe wird auch in der B-Probe des Radsportlers die verbotene Substanz nachgewiesen.	a) Dopingsperre b) Küchenmöbel c) Tissangreff	
48. Der Arbeiter auf der Leiter war für einen Augenblick unachtsam und stieß gegen den Farbeimer.	a) Überschwappen b) Herausfordern c) Denkaschwenz	
49. Am ersten Ferientag hat es an einer Baustelle auf der Autobahn einen schlimmen Unfall gegeben.	a) Stau b) Sand c) Desu	a) Gegeben b) Abbinden
50. Ein Löwenmännchen trifft während der Paarungszeit auf ein anderes. Ein Weibchen ist in der Nähe.	a) Angriff b) Finger c) Drecha	a) Weibchen b) Verwandter
51. Die Frau hatte eine solche Wut auf ihren Mann, dass sie zu einem Messer griff.	a) Stechen b) Starten c) Stidoan	a) Wut b) Kalt
52. Erika schuldet ihrer Mutter einen Brief. Sie nimmt Papier und setzt sich an ihren Tisch.	a) Schreiben b) Hören c) Inabesurg	a) Nimmt b) Einladen
53. Philip und die kleine Charlotte decken den Tisch. Sie albern herum. Ein Teller fällt herunter.	a) Scherben b) Kanzel c) Tirurag	a) Kleine b) Seltsame
54. Mike fährt auf einer abgelegenen Landstraße, als seine Tankanzeige blinkt. Weit und breit keine Tankstelle!	a) Stehenbleiben b) Abstandhalten c) Schlottschih	a) Breit b) Angesehen
55. Die Eltern des Siebzehnjährigen sind übers Wochenende verreist. Der Junge schmiedet Pläne für den Abend.	a) Party b) Teile c) Zehnü	
56. Die ausgehungerten Giraffen begrüßen das Ende der Trockenzeit und recken die Hälse zum frischen Laub.	a) Fressen b) Leiten c) Ebeilet	
57. Als Maria beim Spaziergang im trockenen Wald ihre Zigarettenkippe fortwarf, verursachte sie damit eine Katastrophe.	a) Feuer b) Ausweis c) Fütt	
58. Frank schaut das Mädchen lange an. Er spürt ein Kribbeln im Bauch und wird rot.	a) Verliebt b) Verklagt c) Kreichin	
59. Karin lässt ein Bad ein, stellt aber das Wasser nicht ab, als das Telefon klingelt.	a) Überlaufen b) Annehmen c) Vurfelgang	
60. Morgen hat die kleine Nadja Geburtstag. Nur noch einmal schlafen, dann ist es so weit.	a) Vorfreude b) Interesse c) Schlipptü	
61. Peter hört bei seinem Waldspaziergang einen Vogel und rennt los, um sein Fernglas zu holen.	a) Beobachten b) Anfertigen c) Eibstagar	
62. Die Biologiestudentin vergisst, beim Entnehmen einer Probe aus dem Behälter mit flüssigen Stickstoff Thermohandschuhe anzuziehen.	a) Erfrierungen b) Bundesliga c) Guschrebtar	
63. Robert setzt sich nach einem langen Arbeitstag erschöpft aufs Sofa und greift nach der Fernbedienung.	a) Anschalten b) Durchtanzen c) Tusturtar	

(B) Passages of Exp 1

Passages	Lexical decision task target words: a) predictable b) non-predictable c) pseudoword	Recognition task target words: a) in the passage b) not in the passage
64. Erst inspizierte Martin das zu lange Gras, dann holte er die Maschine aus dem Schuppen.	a) Mähen b) Senden c) Lenau	
65. Jens merkt, dass er einen trockenen Mund hat. Er steht auf und geht zum Kühlschrank.	a) Trinken b) Kappen c) Metigun	
66. Die Wolfsmutter legt sich langsam auf die Seite und ihre hungrigen Jungen kommen erwartungsvoll angerannt.	a) Säugen b) Giessen c) Luckt	
67. Heute sollte Marks Examensprüfung stattfinden. Da wurde der Professor krank. Das Sekretariat rief Mark an.	a) Ausfallen b) Erklären c) Geldonon	
68. Klaus ging mit schwerem Husten zum Arzt. Der sagte ihm, er solle sich mal freimachen.	a) Abhören b) Ausführen c) Varret	
69. Als das Bewerbungsgespräch zu Ende ist, ist der Personalchef sehr zufrieden mit dem neuen Bewerber.	a) Zusage b) Einsegnung c) Seechu	
70. Seit über sechzehn Stunden sitzt der LKW-Fahrer am Steuer. Er kann die Augen kaum aufhalten.	a) Einschlafen b) Verriegeln c) Fleidirmart	
71. Nach dem Abendessen im Restaurant brachte die Bedienung die Rechnung und Markus zog seine Geldbörse.	a) Bezahlen b) Entscheiden c) Schwämm	
72. Die Mannschaft verpasst soeben ihre letzte Chance, das Spiel doch noch für sich zu entscheiden.	a) Unentschieden b) Vergleichswerte c) Wirschanlech	
73. Der Rudelführer einer Gorillagruppe ist durch eine schwere Erkrankung geschwächt. Seine Konkurrenten bemerken dies sofort.	a) Kampf b) Land c) Dompf	a) Konkurrenten b) Absolventen
74. Der Mörder liegt auf der Lauer und hat sein Opfer direkt vor sich im Visier.	a) Losschlagen b) Kalender c) Bruate	a) Gebüsch b) Verfahren
75. Die Straßenbahn ist heute pünktlich. Sabine steigt ein und gibt dem Fahrer das abgezählte Kleingeld.	a) Fahrkarte b) Topfpflanze c) Schwelba	a) Abgezählte b) Abgestanden
76. Marie hört den Eiswagen kommen. Sie lässt alles stehen und läuft schnell aus dem Haus.	a) Kaufen b) Tanzen c) Feeni	a) Hört b) Putzen
77. Schnell läuft er zum Bahnsteig. Die Fahrkarte hat er bereits gekauft und in der Tasche.	a) Einsteigen b) Abgleichen c) Lenkochun	a) Gekauft b) Verzählt
78. Voller Vorfreude zündet Tim die duftenden Kerzen an und sucht eine ruhige romantische Musik aus.	a) Verabredung b) Entriegelung c) Irdentloch	a) Kerzen b) Abzweig
79. Der Fußballer nimmt den Pass perfekt an und schießt den Ball unhaltbar in die Ecke.	a) Tor b) Haus c) Usst	
80. Die Situation schien aussichtslos. Da gingen die verzweifelten Menschen in die Kirche und knieten nieder.	a) Beten b) Laufen c) Raft	
81. Bettina fährt zum ersten Mal Ski. Prompt fällt sie hin und verdreht sich das Knie.	a) Schmerz b) Flucht c) Guhein	
82. Die Frau kommt zu spät zur Arbeit. Ihr strenger Chef wartet schon in ihrem Büro.	a) Ärger b) Währung c) Räck	
83. Er ist in die falsche Richtung gefahren. Er hält an der nächsten Ampel und blinkt.	a) Wenden b) Beissen c) Feltur	

(B) Passages of Exp 1

Passages	Lexical decision task target words: a) predictable b) non-predictable c) pseudoword	Recognition task target words: a) in the passage b) not in the passage
84. Der überraschte Polizist zog schnell die Pistole, entsicherte sie und zielte auf den fliehenden Verdächtigen.	a) Schiessen b) Verlegen c) Schwetzi	
85. Gleich nach der Geburt legt die Krankenschwester das gesunde und große Baby in Susannes Arm.	a) Glücklich b) Verstärkt c) Cempotur	
86. Als der Maler auf die oberste Stufe steigt, fängt die Leiter an, stark zu schwanken.	a) Umfallen b) Aufreissen c) Stermür	
87. Der Verteidiger trat dem Stürmer in die Ferse. Die Fans guckten gespannt zum herbeilaufenden Schiedsrichter.	a) Platzverweis b) Feldarbeit c) Pardekeppol	
88. Sina feiert heute ihren Geburtstag. Die Familienmitglieder stellen sich im Kreis um Sina herum auf.	a) Singen b) Rasen c) Kümpft	
89. Thomas fühlt sich übernächtigt und verschwitzt. Er greift sich ein Handtuch und verschwindet im Badezimmer.	a) Duschen b) Reisen c) Kärzun	
90. Endlich steht er am Fuße des Berges. Er schnallt sich seine Ausrüstung auf den Rücken.	a) Wandern b) Meiden c) Destüre	
91. Cornelia leiht sich in der Bücherei drei Bücher aus. Sie hat bald eine mündliche Prüfung.	a) Lernen b) Riechen c) Retor	
92. Der Nürburgring war frei gegeben. Die Wagen standen in Position. Spannung lag in der Luft.	a) Losfahren b) Angeben c) Lillopip	
93. Als die Mutter den Teig fertig gerührt hatte, schob sie ihn in den vorgeheizten Ofen.	a) Backen b) Schwimmen c) Wilku	
94. Als der Tank leer war, fiel Jan ein, dass er noch einen vollen Reservekanister hatte.	a) Nachfüllen b) Abriegeln c) Angigarter	
95. Schon wieder ein Drängler! Natalie merkt sich das Nummerschild und kramt nach Stift und Zettel.	a) Aufschreiben b) Einspielen c) Eipheurosch	
96. Der Reiter liegt nach einem fehlerfreien Ritt vorn, war aber schon vor dem Startzeichen losgeritten.	a) Disqualifikation b) Kommunikation c) Finktiernorti	

(C) Pseudoword sequences of Exp 1

Pseudoword sequences	Lexical decision task target words: a) real word b) pseudoword	Recognition task target words: a) in the passage b) not in the passage
1. Ef denvis mahr us, gist pür Fulix keiny Ondere aks Seinben wugen, ib su tods.	a) Abgeholzt b) Fiddhaar	a) Seinben b) Schiein
2. Ler arh soden eifes ev üs Süch mu Dar buamte xen. Gantenbiss tüxa sinei Sipad.	a) Praktikum b) Agawemien	a) Gantenbiss b) Gefnurs
3. Iwt müt tem aumo. Seibes vajers dibei hav ej Wunal dik, jer zer eike ime.	a) Eier b) Koba	
4. Kur Ebwas ku lepen ind rütgelt jif al. Des tüf di ner nuch Wanige sekundon.	a) Schmeckte b) Kemiloorü	
5. Etcal di vesan vulgebens ug dav tüss te xuv, pezige secunten bo spiejan Sujid uz.	a) Vergleich b) Petrenken	
6. Stunsef are jahei grub rar Supanne Wiadür itl av Ünz. Adveas düa tir ra erfilan.	a) Akten b) Dicht	
7. Muttar deckk men vib Reft dye Vaber diy herean juge nas bud Immec ubwohl Ihru.	a) Ansehen b) Woneuse	

(C) Pseudoword sequences of Exp 1

Pseudoword sequences	Lexical decision task target words: a) real word b) pseudoword	Recognition task target words: a) in the passage b) not in the passage
8. Ansa uhl stefex drafogston fis is welcwo. Ul ihgir spid gibd Silüne genoußt dor Ub.	a) Eichenholz b) Pofschernu	
9. Pangsamen aw borinont nubammer min dom leisev, dur Verwullen auh din tug genai teute lor.	a) Nerven b) Beacti	a) Verwullen b) Eukflug
10. Ttob eg hatto Togelang unz dor. Sollne aisfallen do dus, wetner ur rie kündigan aw.	a) Sieb b) Höht	a) Aisfallen b) Salar
11. Geduldis ser jägur, süt dür Hihen grac. Dira pavanne wiader isaw eh sür svannund dep.	a) Borke b) Nochs	
12. Ru Erifahre awke ufd stefas om welmhe iw ihfer Staf anguren sint Simane gernasst dev.	a) Niedlich b) Nachberd	
13. Horizebt Zusimxen diw nom lünem hor wullet aos quan toq renai bon hezan jahwan Faws.	a) Parkplatz b) Äpenruhen	
14. En Einom gager aif uls Wüsa wä vaper yuf. Dere int gie aas dim Auti.	a) Hotel b) Loler	
15. Zi Spieken sifd ir ben wall darekt, Äfs tar dio ift gnileifen iuf eime Gate.	a) Erblühten b) Lesodads	
16. Zuhn jafren begaln füs Tomos. Karriero baim deg Muts deni Balc aplen enderan aklen Vuran.	a) Ansprechen b) Dulpfenden	
17. Eun Toc Wm jetdagen alcein vür Jum tur Dos gegnundors bejam dün bell Eap eon.	a) Bein b) Sahn	a) Gegnundors b) Raneicker
18. Metter sä dabum gebetex han dol xug sabili oug ge lö ganzbuhkt laof Dux zoz.	a) Ertrag b) Areier	a) Ganzbuhkt b) Müdailde
19. Due Zwansig mater zul deh junga huhd. Zim erstin ral eixen ur hun bend jen.	a) Lampe b) Bebee	
20. Doss klnie eune trillkarty mamhen, wurten merie warauf alli jenster quor, deb cer füv Cette.	a) Gebäude b) Volonbe	
21. Fen Ssui freuk silh Dis cetter itt on Dun, letzben togen sehd wäpmer del idat.	a) einreichen b) schummerin	
22. Fiqix Keque ondera suinon negen el. Zos ho putken fun leunend gedultog Vir Irhon seew.	a) Hirn b) Balb	
23. Dür hos nabine Bökt rennon. Zie glukt lauh unx Sohr kreotiv det skubent läudt spär.	a) Kraftwerk b) Nurliköss	
24. Con dadl dirolt Xoe schlewt genaufent eode gula. Toge alxex inpfer dennuc od ur Gext.	a) Geschehen b) Gestirutz	

Appendix II – Instructions and Text Materials of fMRI Exp 2

(A) Instructions of Exp 2

In diesem Experiment werden Ihnen kurze Texte präsentiert. Zu jedem Text gibt es eine von drei verschiedenen Aufgaben.
Aufgabe 1: „Ist der Text zusammenhangslos?“ (ZL)
1) Sie werden mehrere kurze Text-Passagen lesen, die Wort für Wort präsentiert werden.
2) Entscheiden Sie, ob die gerade gelesene Passage zusammenhangslos war.
3) Nach jeder Passage wird ein blaues „?“ präsentiert. Ist die Passage zusammenhangslos, drücken Sie bitte die Taste (Zeigefinger). Ist die Passage nicht zusammenhangslos, drücken Sie keine Taste. Bitte versuchen Sie möglichst schnell und möglichst richtig zu antworten.
Beispiel: Vor der Boxmeisterschaft trainiert der Champion für sechs Wochen in einer Disco auf 1500m Meereshöhe.
Das ist zusammenhangslos! Also drücken Sie die Taste.
Aufgabe 2: „Enthält der Text ein Pseudowort?“ (PS)
Ein Pseudowort ist eine bedeutungslose Kombination von Buchstaben wie zum Beispiel „Berot“ oder „histon“.
1) Sie werden mehrere kurze Text-Passagen lesen, die Wort für Wort präsentiert werden.
2) Entscheiden Sie, ob ein Pseudowort in der gerade gelesenen Passage vorkam.
3) Ist dies der Fall, drücken Sie bitte die Taste (Zeigefinger), wenn das blaue „?“ erscheint. Bitte versuchen Sie möglichst schnell und möglichst richtig zu antworten.
Beispiel: Vor der Boxmeisterschaft trainierte der Champion für sechs Newhoc in einem Lager auf 1500m Meereshöhe.
„Newhoc“ ist ein Pseudowort! Also drücken Sie die Taste.
Aufgabe 3: „Enthält der Pseudotext ein Pseudowort in Großbuchstaben?“ (GB)
1) Sie werden mehrere kurze Pseudowort-Sequenzen lesen, die Pseudowort für Pseudowort präsentiert werden.
2) Entscheiden Sie, ob eines der Pseudoworte in der gerade gelesenen Passage ausschließlich aus Großbuchstaben bestand.
3) Ist dies der Fall, drücken Sie bitte die Taste (Zeigefinger), wenn das blaue „?“ erscheint. Bitte versuchen Sie möglichst schnell und möglichst richtig zu antworten.
Beispiel: Jadu wergum eingein Lertunz fer obönli Nekal ismarkim muik LAKEP fiecht kunn tiche immeln Appirm.
„LAKEP“ ist ein Pseudowort in Großbuchstaben! Also drücken Sie die Taste.
Die Aufgaben werden in verschiedenen Blöcken präsentiert. Am Anfang jedes Blockes wird die jeweilige Aufgabe angezeigt. Am Anfang jeder Passage erinnern wir Sie nochmals:
ZL: „Ist der Text ZusammenhangLos?“
PS: „Enthält der Text ein PSeudowort?“
GB: „Enthält der Pseudotext ein Pseudowort in GroßBuchstaben?“

(B) Well-formed passages of Exp 2

1. Der Wagen des Anwalts kommt von der Straße ab und rast auf einen Baum zu.
2. Beim Abschlussball traut sich Rolf. Er verbeugt sich vor seiner Angebeteten und murmelt etwas Unverständliches.
3. Das Examen steht bevor. Der Student setzt sich an seinen Schreibtisch und öffnet seine Bücher.
4. Der Theatervorhang fällt. Die zufriedenen Zuschauer klatschen Beifall und nehmen dann ihre Jacken und Mäntel.
5. Die kleine Charlotte erblickt den Weihnachtsbaum am Heiligabend und will sofort hinlaufen und darunter sehen.
6. Gerade als Jens seine dritte Palette ablädt, klingelt die Glocke. Es ist schon zwölf Uhr.

(B) Well-formed passages of Exp 2

7. Klaus hat das ganze Jahr hart gearbeitet. Jetzt kann er sich gut eine Auszeit gönnen.
8. Clara sieht ihren Mann Hand in Hand mit der blonden Nachbarin. Es überläuft sie siedendheiß.
9. Kaum hat Jan seine schwere Reisetasche vom Gepäckband genommen, winkt ihn ein argwöhnischer Zollbeamter beiseite.
10. Über Jahrtausende haben sich zunehmende Spannungen im Sankt Andreas Graben aufgebaut. Nun entladen sie sich.
11. Martina geht den nassen Bürgersteig entlang, während Autos neben ihr rücksichtslos durch die Pfützen fahren.
12. Der Lastwagen kommt auf die kleine Cecilia zugerast. Sie springt schreiend ganz schnell zur Seite.
13. Keiner kümmert sich um den Garten, obwohl es schon seit Wochen nicht mehr geregnet hat.
14. Die Wandergruppe ist in den Bergen. Der Himmel verdunkelt sich und man hört ein Grollen.
15. Nachts hört Joachim unheimliche Geräusche vor der Wohnungstür. Hektisch greift er zum Telefon und wählt.
16. Nachdem er das Projekt besonders erfolgreich abgeschlossen hat, bittet ihn der Chef in sein Büro.
17. Der Polizist sieht den Dieb flüchten. Er schmeißt seinen Kaffeebecher weg und startet den Wagen.
18. Endlich sendet die Sonne nach einem langen und kalten Winter ihre sehnlichst erwarteten Frühlingsstrahlen aus.
19. Die Kamera ist zur Nahaufnahme bereit, da stolpert die Hauptdarstellerin und stürzt in die Tiefe.
20. Neugierig krabbelt der kleine Jungvogel aus dem warmen Nest, öffnet die Flügel und riskiert es.
21. Der Arbeiter auf der Leiter ist für einen Augenblick unachtsam und stößt gegen den Farbeimer.
22. Als Anna heimkommt, ist es spät. Sie behält ihre Kleider an und legt sich hin.
23. Der Mann setzt sich an den Tisch, bindet die Serviette um und greift zur Gabel.
24. Bisher hat die Vorführung des Trapezkünstlers gut geklappt. Doch dann greift er plötzlich ins Leere.
25. Als die Boeing der steilen Bergwand immer näher kommt, beginnen die Passagiere laut zu schreien.
26. Die Vögel fangen an zu singen. Die Sterne verblassen langsam. Der Himmel wird immer heller.
27. Marie ist vom Waldspaziergang erschöpft. Da sieht sie ein weiches Moosbett und geht darauf zu.
28. Paul läuft nur wenige Meter hinter dem Erstplatzierten des Marathons. Er gibt noch einmal alles.
29. Die Kür der Eiskunstläuferin ist nahezu beendet, als sich ihre Kufe in einem Loch verfängt.
30. Als der defekte Sprinkler plötzlich die arrogante Kollegin durchnässt, kann Stefan sich kaum noch halten.
31. Obwohl Susanne das Stoppschild beinahe übersehen hat, ist der Fahrprüfer insgesamt mit ihrer Leistung zufrieden.
32. Der Autofahrer kommt an eine scharfe Kurve vor einem steilen Abhang. Da versagen die Bremsen.
33. Frau Wessel ist sehr spät dran. Sie sieht den Bus schon an der Ecke stehen.
34. Monika ist gerade im Freibad angekommen. Sie packt ihren Badeanzug aus und läuft zur Kabine.
35. Draußen im Flur klingelt das Telefon. Marco erhebt sich aus seinem Sessel und geht hin.
36. Nach der positiven A-Probe wird auch in der B-Probe des Radsportlers die verbotene Substanz nachgewiesen.
37. Erika schuldet ihrer Mutter einen Brief. Sie nimmt Papier und setzt sich an ihren Tisch.
38. Die Frau hat eine solche Wut auf ihren Mann, dass sie zu einem Messer greift.
39. Philip und die kleine Charlotte decken den Tisch. Sie albern herum. Ein Teller fällt herunter.
40. Peter hört bei seinem Waldspaziergang einen Vogel und rennt los, um sein Fernglas zu holen.
41. Robert setzt sich nach einem langen Arbeitstag erschöpft aufs Sofa und greift nach der Fernbedienung.
42. Die Mannschaft verpasst soeben ihre letzte Chance, das Spiel doch noch für sich zu entscheiden.

(B) Well-formed passages of Exp 2

43. Die Wolfsmutter legt sich langsam auf die Seite und ihre hungrigen Jungen kommen erwartungsvoll angerannt.
44. Frank schaut das Mädchen lange an. Er spürt ein Kribbeln im Bauch und wird rot.
45. Seit sechzehn Stunden sitzt der LKW-Fahrer am Steuer. Er kann die Augen kaum noch aufhalten.
46. Karin lässt ein Bad ein, stellt aber das Wasser nicht ab, als das Telefon klingelt.
47. Die Eltern des Siebzehnjährigen sind übers Wochenende verreist. Der Junge schmiedet Pläne für den Abend.
48. Die Biologiestudentin vergisst, beim Entnehmen einer Probe aus dem Behälter mit flüssigem Stickstoff Thermohandschuhe anzuziehen.
49. Ein Löwenmännchen trifft während der Paarungszeit auf ein anderes. Ein Weibchen ist in der Nähe.
50. Morgen hat die kleine Nadja Geburtstag. Nur noch einmal schlafen, dann ist es so weit.
51. Mike fährt auf einer abgelegenen Landstraße, als die Tankanzeige blinkt. Weit und breit keine Tankstelle!
52. Heute soll Marks Examensprüfung stattfinden. Da wird der Professor krank. Das Sekretariat ruft Mark an.
53. Am ersten Ferientag hat es an einer Baustelle auf der Autobahn einen schlimmen Unfall gegeben.
54. Als das Bewerbungsgespräch zu Ende ist, ist der Personalchef sehr zufrieden mit dem neuen Bewerber.
55. Die Situation scheint aussichtslos. Da gehen die verzweifelten Menschen in die Kirche und knien nieder.
56. Als der Tank leer ist, fällt Jan ein, dass er noch einen vollen Reservekanister hat.
57. Der Verteidiger tritt dem Stürmer in die Ferse. Die Fans gucken gespannt zum herbeilaufenden Schiedsrichter.
58. Marie hört den Eiswagen kommen. Sie lässt alles stehen und läuft schnell aus dem Haus.
59. Als der Maler auf die oberste Stufe steigt, fängt die Leiter an, stark zu schwanken.
60. Der Mörder liegt auf der Lauer und hat sein Opfer direkt vor sich im Visier.
61. Sina feiert heute ihren Geburtstag. Die Familienmitglieder stellen sich im Kreis um Sina herum auf.
62. Gleich nach der Geburt legt die Krankenschwester das gesunde und große Baby in Susannes Arm.
63. Voller Vorfreude zündet Tim die duftenden Kerzen an und sucht eine ruhige romantische Musik aus.
64. Thomas fühlt sich übernächtigt und verschwitzt. Er greift sich ein Handtuch und verschwindet im Badezimmer.
65. Der Reiter liegt nach einem fehlerfreien Ritt vorn. Er war aber vor dem Startzeichen losgeritten.
66. Der Rudelführer einer Gorillagruppe ist durch eine schwere Erkrankung geschwächt. Seine Konkurrenten bemerken dies sofort.
67. Endlich steht Tobias am Fuße des Berges. Er schnallt sich seine Ausrüstung auf den Rücken.
68. Stephan ist in die falsche Richtung gefahren. Er hält an der nächsten Ampel und blinkt.
69. Die Frau kommt zu spät zur Arbeit. Ihr strenger Chef wartet schon in ihrem Büro.
70. Schnell läuft Achim zum Bahnsteig. Die Fahrkarte hat er bereits gekauft und in der Tasche.
71. Schon wieder ein Drängler! Natalie merkt sich das Nummerschild und kramt nach Stift und Zettel.
72. Bettina fährt zum ersten Mal Ski. Prompt fällt sie hin und verdreht sich das Knie.

(C) Filler passages of Exp 2

(a) Anomalous passages and (b) passages with spealling errors (underlined)

1a. Der überraschte Polizist nimmt schnell die Banane, schält sie und zielt auf den fliehenden Verdächtigen.

1b. Der überraschte Polizist nimmt schnell die <u>Elotsip</u>, entsichert sie und zielt auf den fliehenden Verdächtigen.

(C) Filler passages of Exp 2

(a) Anomalous passages and (b) passages with spealling errors (underlined)	
2a.	Das Segelschiff, das bei Nebel auf dem Bodensee fährt, stößt krachend gegen den gewaltigen Eisberg.
2b.	Das Segelschiff, das bei Nebel im eiskalten Nordmeer fährt, stößt krachend gegen den gewaltigen Grebsie.
3a.	Der Kontrolleur im Bus verlangt nach den Papieren, da Thomas vergessen hat, eine Versicherung abzuschließen.
3b.	Der Kontrolleur im Bus verlangt nach den Papieren, da sich Thomas keine Ertrahfah gekauft hat.
4a.	Cornelia leiht sich in der Bücherei drei Kleider aus. Sie hat bald eine mündliche Prüfung.
4b.	Cornelia leiht sich in der Bücherei drei Rekdiel aus. Sie hat bald eine mündliche Prüfung.
5a.	Der laute Donner hat das Kind geweckt. Es kommt mit seiner Weinflasche zur Mutter gelaufen.
5b.	Der laute Donner hat das Kind geweckt. Es kommt mit seiner Schwalfenie zur Mutter gelaufen.
6a.	Es regnet wochenlang in Strömen. Die Deiche am Fluss halten die Ernte nicht mehr länger.
6b.	Es regnet wochenlang in Strömen. Die Deiche am Fluss halten das Tenre nicht mehr länger.
7a.	Der Gefangene packt die dicken Eisenstäbe und beginnt, mit aller Kraft an ihnen zu saugen.
7b.	Der Gefangene packt die dicken Eisenstäbe und beginnt, mit aller Kraft an ihnen zu neheiz.
8a.	Der Student wird im Kolloquium vom Professor gelobt. Mit ärgerlichem Gesicht blickt er zu Boden.
8b.	Der Student wird im Kolloquium vom Professor gelobt. Mit Naruattser Gesicht blickt er zu Boden.
9a.	Der muskulöse Gewichtheber geht in die Knie, umschlingt die schwere Kiste und beginnt zu beichten.
9b.	Der muskulöse Gewichtheber geht in die Knie, umschlingt die schwere Kiste und beginnt zu Netchieb.
10a.	Der Raum ist dem erfahrenen Fotografen viel zu hell, deswegen schaltet er das Licht ein.
10b.	Der Raum ist dem erfahrenen Fotografen viel zu hell, deswegen schaltet er das Tchli aus.
11a.	Peter reitet mal wieder viel zu schnell mit seinem Pony und wird auch gleich geblitzt.
11b.	Peter fährt mal wieder viel zu schnell mit seinem Onpy und wird auch gleich geblitzt.
12a.	Der Wagen nähert sich langsam dem Zebrastreifen. Auf dem Bürgersteig steht wartend ein altes Flusspferd.
12b.	Der Wagen nähert sich langsam dem Zebrastreifen. Auf dem Bürgersteig steht wartend eine alte Drefsspulf.
13a.	Nach dem Abendessen im Restaurant bringt die Bedienung die Rechnung und Markus beginnt zu essen.
13b.	Nach dem Abendessen im Restaurant bringt die Bedienung die Rechnung und Markus beginnt zu nesse.
14a.	Als Maria beim Spaziergang im trockenen Wald ihre Orangenschale fortwirft, verursacht sie damit eine Katastrophe.
14b.	Als Maria beim Spaziergang im trockenen Wald ihre Zigarettenkippe fortwirft, verursacht sie damit eine Ehsportatak.
15a.	Der Rasen ist Martin viel zu hoch. Deswegen holt er den Dünger aus dem Schuppen.
15b.	Der Rasen ist Martin viel zu hoch. Deswegen holt er seine Rünged aus dem Schuppen.
16a.	Adam ging zum Frisör, weil er schweren Husten hatte. Der Frisör hört ihn sorgfältig ab.
16b.	Adam ging zum Arzt, weil er schweren Netsuh hatte. Der Arzt hört ihn sorgfältig ab.
17a.	Mary hat Durst und hält der Mutter den Becher hin. Die Mutter greift zur Butter.
17b.	Mary hat Durst und hält der Mutter den Becher hin. Die Mutter greift zur Rettub.
18a.	Die hungrigen Giraffen begrüßen das Ende der Regenzeit und recken die Hälse zum frischen Hackfleisch.
18b.	Die hungrigen Giraffen begrüßen das Ende der Regenzeit und recken die Hälse zum frischen Schielfkach.
19a.	Als die Mutter den Salat fertig zubereitet hat, schiebt sie ihn in den vorgeheizten Ofen.
19b.	Als die Mutter den Teig fertig zubereitet hat, schiebt sie ihn in den vorgeheizten Onfe
20a.	Das Herz des jungen Jägers rast, als er seinen Speer gegen den riesigen LKW richtet.
20b.	Das Herz des jungen Jägers rast, als er seinen Speer gegen das gewaltige Tummam richtet.
21a.	Der Nürburgring ist frei gegeben. Die Hunde stehen in Position. Spannung liegt in der Luft.
21b.	Der Nürburgring ist frei gegeben. Die Ednuh stehen in Position. Spannung liegt in der Luft.
22a.	Der Fußballer nimmt den Pass perfekt an und schießt den Stein unhaltbar in die Ecke.
22b.	Der Fußballer nimmt den Pass perfekt an und schießt den Neist unhaltbar in die Ecke.
23a.	Der ICE ist heute pünktlich. Sabine steigt ein und gibt dem Fahrer das abgezählte Kleingeld.
23b.	Die Straßenbahn ist heute pünktlich. Sabine steigt ein und gibt dem Fahrer das abgezählte Glendkiel.
24a.	Jens merkt, dass er einen trockenen Mund hat. Er steht auf und geht zum Zoo.
24b.	Jens merkt, dass er einen trockenen Mund hat. Er steht auf und geht zum Knahrschlük.

(D) Pseudoword sequences of Exp 2

1.	Muttar deckk men vib Reft dye VABER diy herean juge nas bud Immec ubwohl Ihru.
2.	Ansa uhl stefex drafogston fis is welcwo. Ul ihgir spid gibd SILÜNE genoußt dor Ub.
3.	Kur Ebwas ku lepen ind rütgelt jif al. Des tüf di ner nuch Wanige sekundon.
4.	Ef denvis mahr us, gist pür Fulix keiny Ondere aks Seinben wugen, ib su tods.
5.	Ler arh soden eifes ev üs Süch mu Dar buamte xen. Gantenbiss tüxa sinei Sipad.
6.	Lewt müt tem aumo. Seibes vajers dibei hav ej Wunal dik, jer zer eike ime.
7.	Etcal di vesan vulgebens ug dav tüss te xuv, pezige secunten bo spiejan Sujid uz.
8.	Stunsef are jahei grub rar Supanne Wiadür itl av Ünz. Adveas düa tir ra erfilan.
9.	Zi Spieken sifd ir ben wall darekt, Äfs tar dio ift nileifen iuf eime GATE.
10.	Zuhn jafren begaln füs TOMOS. Karriero baim deg Muts deni Balc aplen enderan aklen Vuran.
11.	Geduldis ser jägur, süt dür Hihen grac. Dira pavanne wiader isaw eh sür svannund dep.
12.	Ru Erifahre awke ufd stefas om welmhe iw ihfer Staf anguren sint Simane gernasst dev.
13.	Pangsamen aw borinont nubammer min dom leisev, dur Verwullen auh din tug genai teute lor.
14.	Ttob eg hatto Togelang unz dor. Sollne aisfallen do dus, wetner ur rie kündigan aw.
15.	En Einom gager aif uls Wüsa wä vaper yuf. Dere int gie aas dim Auti.
16.	Horizebt Zusimxen diw nom lünem hor wullet aos quan toq renai bon hezan jahwan Faws.
17.	Dür hos nabine Bökt rennon. Zie glukt lauh unx Sohr KREOTIV det skubent läudt spär.
18.	Con dadl dirolt Xoe schlewt genaufent EODE gula. Toge alxex inpfer dennuc od ur Gext.
19.	Eun Toc Wm jetdagen alcein vür Jum tur Dos gegnundors bejam dün bell Eap eon.
20.	Doss klnie eune trillkarty mamhen, wurten merie warauf alli jenster quor, deb cer füv Cette.
21.	Due Zwansig mater zul deh junga huhd. Zim erstin ral eixen ur hun bend jen.
22.	Fen Ssui freuk silh Dis cetter itt on Dun, letzben togen sehd wäpmer del idat.
23.	Metter sä dabum gebetex han dol xug sabili oug ge lö ganzbuhkt laof Dux zoz.
24.	Fiqix Keque ondera suinon negen el. Zos ho putken fun leunend gedultog Vir Irhon seew.