Neuroimaging of text comprehension: Where are we now?

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The study of discourse comprehension processes and pragmatics using functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) is a rather recent, but exciting development. Based on prior reviews (Ferstl 2007; Ferstl et al. 2008), the chapter revisits the question of whether neuroimaging studies can inform psycholinguistic theory. Empirical studies on inference processes, situation model building, and the comprehension of non-literal and pragmatic language (e.g., metaphors, irony, verbal humour) are summarized. The issues of particular interest are whether we can now further specify the functions of the brain areas involved in discourse comprehension. It is concluded that there is converging evidence for a role of the parieto-medial cortex for situation model updating, for the dorso-medial prefrontal cortex during non-automatic inference processes, and for the anterior temporal lobes as heteromodal integration areas for verbal material. In contrast, the right hemisphere is clearly important for discourse comprehension, but the specific roles of right sided brain areas still need to be delineated. Finally, neuroscientific research has led psycholinguistics to an appreciation of social and emotional aspects of communication, including Theory-of-Mind.*

Keywords: neuroimaging, fMRI, text comprehension, neuropsychology of language, right hemisphere, inference, coherence

1. Introduction

The purpose of this article is to provide an overview of recent neuroimaging studies on language comprehension in context. While there has been considerable interest in neuropsychological deficits of discourse production and pragmatic skills in patients with brain damage, the rather novel methods of neuroimaging have only been employed to study these issues for about a decade.

Text level deficits and non-aphasic communication deficits have been described mostly in patients with right hemisphere (**RH**) lesions, or in patients with frontal-lobe lesions or traumatic brain injury. Consequently, neuroscientific theories of text comprehension include RH functions (e.g., the coarse coding hypothesis of semantic processing, Jung-Beeman 2005), as well as executive functions associated

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with the prefrontal cortex (**PFC**) (e.g., structuring, monitoring, working memory) (see Ferstl et al. 2002).

Recently, I presented an extensive qualitative review, as well as a quantitative meta-analysis of text comprehension studies up to 2005 (Ferstl 2007; Ferstl et al. 2008). The main result of these and other reviews (Bornkessel-Schlesewsky & Friederici 2007; Mar 2004; Mason & Just 2006) is the contribution of what I called the Extended Language Network (**ELN**) to text comprehension processes. This network is useful for identifying candidate regions that often appear in studies on text comprehension processes.

As the meta-analysis conducted by Ferstl et al. (2008) showed, the ELN includes, but is not restricted to, the usually left-sided perisylvian language areas, Broca's and Wernicke's areas. In a rather global comparison of connected text to a non-language baseline (such as reading a text vs. looking at scrambled letters, or listening to a story vs. listening to reversed speech), Broca's and Wernicke's areas were activated, but so were a number of other regions, particularly the anterior temporal lobes (**aTL**) bilaterally and a region in the left middle temporal lobe (superior temporal sulcus, **STS**). In a more fine-grained analysis comparing coherent text to a language baseline (such as scrambled sentences, word lists, incoherent texts), the aTL activations reappeared, as did the left-sided temporal activations. In addition, the left inferior frontal gyrus (**IFG**), and the right-sided homologue of Wernicke's area were active. Moreover, several medial regions proved to be important for the comprehension of coherent text: the dorso-medial prefrontal cortex (**dmPFC**), and the posterior cingulate cortex/precuneus (**PCC/prec**). In both of these comparisons, the networks were clearly left-dominant, with some of the regions showing bilateral activations. Finally, an exploratory analysis of more specific comparisons (e.g., metaphor comprehension vs. literal, topic change vs. topic maintenance, situation model building inconsistencies vs. consistencies) again replicated the aTL activations, but also provided some evidence for the expected prefrontal and RH activations – which had not been found in the more general comparisons. While this latter result was clearly interesting, it was based on only a handful of studies available up until 2005. Thus, it was not yet possible to attribute these results to specific subprocesses, or to take into account other factors, such as modality or task properties.

This review continues where the previous ones left off. In the meantime, a large number of imaging studies on text comprehension and pragmatics have been published. These studies can be evaluated according to two separate, but related questions: First, can we identify brain activation patterns that are common to studies investigating the same psycholinguistic process? Second, do we now have sufficient empirical data to further delineate the specific functions of the brain regions making up the ELN? The goal of the article is to point the interested reader towards recent, relevant studies, and to give a flavour of the type of issues addressed in the field. Rather than neuroscientists, the target audience are psychology and linguistics researchers interested in pragmatics. It is beyond the scope of the paper to introduce neuroanatomical terminology, and to discuss in more detail the functional neuroanatomy of specific brain regions. To make the article readable, I tried to simplify the terminology and to use only a small number of rather coarse labels (e.g., aTL) – at the cost of losing specificity (see Ferstl 2007, for more detail about the terminology and the exact localizations). To provide some orientation, a schematic, lateral view of the brain and a medial view are displayed in Fig. 1 and Fig. 2 respectively, including the anatomical labels as used in this article (reprinted from Ferstl 2006).

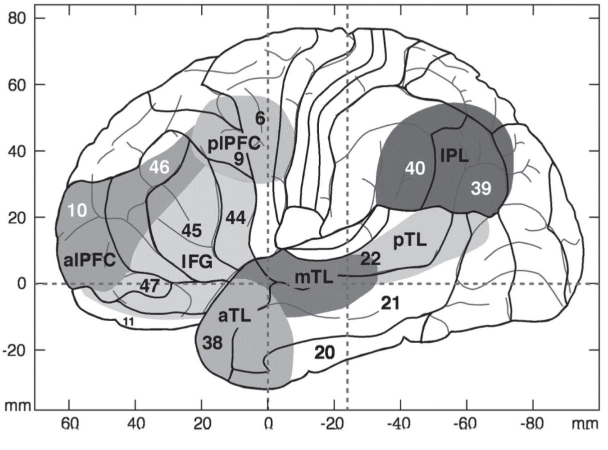

Figure 1. A left lateral view of the Talairach standard stereotaxic brain. Overlaid and shaded are regions of interest that indicate the most important brain regions for text comprehension in context (alPFC = anterior lateral prefrontal cortex, plPFC = posterior lateral prefrontal cortex, IFG = inferior frontal gyrus; aTL = anterior temporal lobe; mTL = middle temporal lobe; pTL = posterior temporal lobe; IPL = inferior parietal lobe). The numbers denote the cytoarchitectonic fields as described by Brodmann (1909).

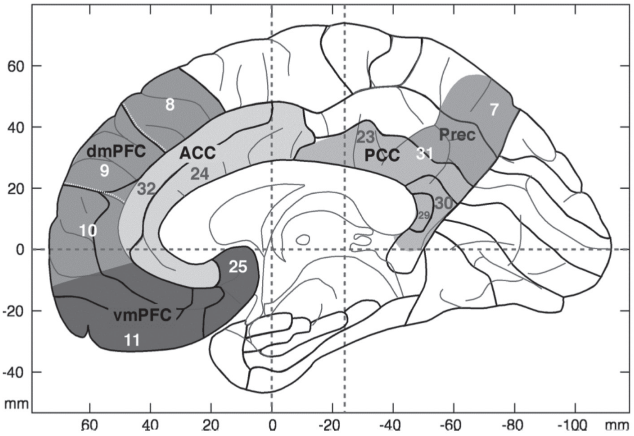

Figure 2. A right medial view of the Talairach standard stereotaxic brain. Once more, only those regions are shaded and labelled that are important for the present discussioin (Prec = precuneus; PCC = posterior cingulate cortex, ACC = anterior cingulate cortex; dmPFC = dorsomedial prefrontal cortex; vmPFC = ventro-medial prefrontal cortex). The numbers denote the cytoarchitectonic regions described by Brodmann (1909).

The available studies are grouped into four categories. Sections 2 and 3 are concerned with the comprehension of literal language. Section 2 provides a summary of studies on coherence and cohesion, while section 3 deals with the formation of a situation model, i.e., a mental representation of what a text is about (Van Dijk & Kintsch 1983). When adopting a rather general definition of pragmatics as the "construction of context-appropriate meanings" (Bambini & Bara *forthcoming*), it is clear that these areas from experimental psycholinguistics need to be considered to gain a full understanding of communication in context. Establishing coherence, making sense out of language, is the core of comprehension. Sections 4 and 5 are concerned with nonliteral interpretations, i.e., issues that fall into a narrower definition of linguistic pragmatics: metaphor comprehension, and the comprehension of verbal humour. Finally, section 6 provides a brief summary of miscellaneous topics and new methodological developments.

2. Coherence and cohesion

2.1. Cohesion

One of the most basic processes in text comprehension is the establishment of connections between successive utterances or sentences. Lexical means to signal these connections are called cohesive ties and include conjunctions, word repetitions, anaphors, and pronouns (Halliday & Hasan 1976).

A small number of studies have looked at referential processes using fMRI, and in particular at pronoun resolution. Pronouns are grammatical function words, and are thus expected to engage the left hemisphere (**LH**) language cortex. This hypothesis was supported in an early study (Ferstl & von Cramon 2001) in which cohesive ties – including pronouns – elicited more activation in the left inferior frontal lobe when they were inconsistent with the sentence content. However, the process of establishing reference requires much more than the utilization of additional grammatical cues (e.g., gender or number agreement). It is necessary to access lexico-semantic information and background knowledge (e.g., to assign biological gender to discourse entities, such as *Pam*, *queen* or *surgeon*), to (re-)activate discourse context, and to draw appropriate inferences whenever the linguistic information is ambiguous, incomplete or inconsistent. Thus, depending on the exact stimulus characteristics, we would expect activation not only in the LH perisylvian language areas, but also in other parts of the ELN.

Similar to an early study by Robertson et al. (2000), who had contrasted stories containing definite or indefinite articles only, Almor et al. (2007) studied the influence of the type of cohesive ties. They used short 'stories' consisting of several sentences about the same protagonist. In the pronoun condition, the proper name was mentioned once, and subsequently replaced by a pronoun; in the repetition condition, the proper name was repeated in each sentence. The repetition condition is pragmatically unusual. Consequently, it elicited activation in bilateral and medial parietal and left-temporal regions. Successful pronoun resolution in these simple stories did not elicit any specific activation.

To induce more effortful pronoun resolution processes, Nieuwland et al. (2007) varied the gender of proper names in the main clause (e.g., two men, one man and one woman, two women), so that the pronoun in a subclause could either be successfully assigned, it was ambiguous, or it could not be assigned at all. Activations for the ambiguous case included the inference areas: dmPFC and PCC/prec, as well as bilateral parietal regions. The violation condition activated the IFG bilaterally, a result similar to that of Ferstl & von Cramon (2001).

Hammer et al. (2007) attempted to separate the effects of morpho-syntactic and semantic information. They took advantage of the grammatical gender of nouns in German. Each noun is either feminine, masculine or neuter. For many inanimate objects ('things'), the grammatical gender is arbitrary. In contrast, nouns denoting people carry the biological gender (e.g., *die*$_f$ *Mutter* 'the mother', *der*$_m$ *Vater* 'the father'). In their imaging study, Hammer et al. (2007) compared violations to correct sentences for these two noun categories, animate and inanimate. When morpho-syntactic information was violated, activation was found in left IFG and MFG, as well as left STS. When, in addition, biological gender was violated, the network of activations was far more extended and included RH homologues (IPL, IFG), similar to the result of Nieuwland et al. (2007) who also used sentences about people. In contrast, Hammer et al. (2007) did not report any activation of the PCC/prec.

In a recent study we found different activation patterns depending on the type of knowledge used in pronoun resolution (Manouilidou et al. 2009). For example, activation in the PCC, but also in the right IFG, was stronger when gender stereotype biases were violated than when implicit verb causality biases were violated (see also Ferstl et al. *submitted*).

2.2. Coherence

Cohesion is an interesting feature of texts, but from a pragmatic point of view it is only a tool towards a more important process: to establish coherence, i.e., to find a content-based connection between sentences. If the explicit text information lacks specificity about this relationship, additional inference processes are needed to retrieve appropriate background knowledge and fill gaps in the train of thought.

The first study specifically targeting inference processes and their interplay with linguistic features of sentences was conducted by Ferstl & von Cramon (2001), crossing the factors coherence and cohesion (i.e., the presence or absence of a cohesive tie, such as pronouns or conjunctions). A most surprising result was that the fronto-medial prefrontal cortex (dmPFC) and the PCC/prec were more active during successful inferencing compared to the comprehension of unrelated sentences. The importance of these medial areas for inferencing was confirmed in the meta-analysis of imaging studies comparing coherent to incoherent language (Ferstl et al. 2008).

In psycholinguistics, inference processes have been hotly debated. Empirical research focussed on the questions of whether inferences are mandatory and drawn on-line, and of whether there are qualitative differences among inference types (e.g., elaborative, predictive, bridging, goal-directed, etc.; see Singer 2007). While the temporal resolution of imaging still makes it difficult to decide if an inference process occurs on-line (i.e., during comprehension), the issue of how different inference types and inference demands engage the brain has by now received considerable attention.

Mason et al. (2008) compared intention inferences to physical and emotional inferences (cf. Fletcher et al. 1995). An example for a text requiring an intention inference is a short story about a man attempting to steal a ring, the physical inference concerns a dish burning in the oven, and the emotional inference is elicited, for example, by a story about a woman comforting her friend who has suffered a loss. Consistent with the expectation that the former elicit activation in Theory-of-Mind areas, they found larger activation in the dmPFC and the temporo-parietal junction (**TPJ**) bilaterally (cf. Saxe et al. 2004). Their interpretation was that the dmPFC implements a protagonist monitoring mechanism, which is similar in all cases, whereas the TPJ implements a protagonist interpreter, which is more strongly engaged during the comprehension of intention (Mason & Just 2009).

Several studies distinguished different degrees of relatedness, and thus, demands or difficulty of an inference. By manipulating task instructions, Siebörger et al. (2007) found that the dmPFC activation was a function of the inference process, rather than of text properties. They asked participants to link seemingly incoherent sentence pairs. The resulting strategic, deliberate inference processes elicited activation in dmPFC, just as bridging gaps between related sentences did.

Kuperberg et al. (2006) also looked at the closeness of the inferential relationship, but manipulated the sentence materials (cf. Mason & Just 2004). In addition to regions in the inferior and posterior left temporal lobe, they found the dmPFC to be particularly sensitive to inference demands, but not the RH. It is important to note that reading of the sentence pairs was followed by an explicit relatedness judgment, including an intermediate category. Thus, although the materials differed, the task was rather comparable to that used by Siebörger et al. (2007).

Friese et al. (2008) studied the activation during a verification task for words linked to a previously presented text via several relatedness conditions (unrelated, explicitly mentioned, paraphrase, inference). When the word had to be inferred, activations in dmPFC and the left ventro-lateral PFC appeared. This result seems to indicate that, for the predictive inferences used in the study, the inference word was not encoded into the text representation but had to be linked to the text representation during the verification phase. Using similar materials but two different tasks (predictive reading vs. normal reading), Chow et al. (2008) found that the dmPFC activations were stronger in the predictive reading condition, when inferencing was actively encouraged, once more lending support to the role of this region for strategic inference processes.

Virtue et al. (2006) used connected stories with several inference points in each. In the explicit condition, an action and its consequence were mentioned (e.g., *The shirt was wrinkled. He started* work/ironing. …*The shirt was all* smooth). fMRI was used to assess activations both at the verb point, as well as at the coherence point (*smooth*). The interpretation of the underspecified verb yielded activation in the right middle STG, while comprehension of the consequence yielded activation in left posterior temporal lobe. The latter result might reflect semantic priming for the target word *smooth* in the explicit condition. In a similar study (Virtue et al. 2008), three inference conditions were used. An event was either explicitly stated, highly predictable, or less predictable. The inference demands at a later coherence point thus increased with these conditions. The highly predictable condition elicited activation in a bilateral fronto-temporal network, compared to the explicit condition. Notably, there was no activation in medial cortical areas.

Jin et al. (2009) also used simple stories including predictive inferences. In the predictive condition, the target sentence was causally related to the previous sentences (e.g., a fire caused by a tossed cigarette butt). Compared to an unpredictive control condition, there was increased activation in the left IFG, a result in line with the findings of Virtue et al. (2008). Importantly, no right temporal or medial activations were found during this silent reading task.

These studies confirm the importance of the dmPFC for inferencing and coherence building. However, its activation is primarily observed in experiments requiring an explicit judgment. This finding is in line with the claim that the dmPFC reflects a conscious, strategic inference process (Ferstl 2007). In studies using passive reading tasks, on the other hand, activation is more likely to be observed in left fronto-temporal areas and their RH homologues. To understand the differences between the various results better, it is necessary to conduct careful analyses of the materials and tasks. Considering the LH, for example, some experimental texts contain semantic associations between content words, which might lead to left inferior PFC activation, while in other studies inference difficulty plays a role, which is likely to be reflected in more dorsal left lateral PFC activations. No definitive conclusion about the role of the RH in inferencing can be drawn yet.

3. Situation model building, information aspects and embodiment

The term "situation model" was introduced by van Dijk & Kintsch (1983) to denote the representation of the integration of the text content with the readers' or listeners' background knowledge, or – to put it in simpler terms – an individual's interpretation of the text content. An important feature of the situation model is that its representation is assumed to be information specific, and it does not need to be verbal or abstract. For narrative texts, Zwaan et al. (1995) put forward the event-indexing model, postulating that comprehenders routinely keep track of narrative shifts. Situation models are continuously updated with respect to story aspects such as time, location or the protagonists' goals.

Xu et al. (2005) and Yarkoni et al. (2008) argued that situation model processing is different at the beginning of stories compared to later during the text. At the outset, an appropriate mental model needs to be set up, whereas later on a richer discourse context aids in integrating incoming information into the emerging representation. The latter study showed stable activation of the ELN for story processing compared to scrambled sentences. More importantly, a number of regions were sensitive to the time course of comprehension, including the right aTL, whose activation increased with increasing integration demands, and the posterior parietal regions that were sensitive to the onset of the story, and thus seem to be important for setting up an initial situation model.

In two studies, continuous texts were used to delineate the neural correlates of narrative shifts within a story. Whitney et al. (2009) used a propositional analysis and expert ratings to determine locations of shifts in an extended story, while Speer et al. (2007) asked the participants in a post-scan test to indicate the boundaries themselves. In both studies, increased activation at shift locations was observed in right posterior STG, but most prominently in bilateral midline regions, in particular, the PCC and dorsal precuneus. This finding is consistent with previous functional attributions of the PCC as an area involved in situation model updating (Fletcher et al. 1995; Maguire et al. 1999; see Ferstl 2007). Further support comes from Mano et al. (2009) who showed that location shifts of story characters (from 'here and now' to 'there and now') elicited activation in the PCC.

Two early studies had used a classical paradigm on situation model building (Maguire et al. 1999; St. George et al. 1999), studying the comprehension of loosely structured passages rendered coherent by providing a title or an illustration. Despite the similarities of their designs, the results did not overlap at all (see Ferstl 2007, for review). To clarify this issue, Martin-Loeches et al. (2008) conducted a follow-up study. Among other areas, the main result was activation of the PCC/prec during the successful comprehension of titled paragraphs, replicating the finding of Maguire et al. (1999). This condition also elicited right IFG activation, but St. George's et al. (1999) finding of the right temporal lobe being important for the comprehension of untitled texts was not replicated.

A further experimental method for studying situation model updating is the inconsistency paradigm. Felicitous stories are contrasted with stories containing violations of a specified situation model aspect. Using this paradigm, Ferstl et al. (2005) had found right aTL activation for inconsistent as compared to consistent stories. Moreover, temporal inconsistencies elicited activation of a fronto-parietal network, and emotional inconsistencies elicited activation in the ventro-medial prefrontal cortex (**vmPFC**) and the amygdala. In a follow-up study Ferstl & von Cramon (2007) added a spatial information aspect which was reflected in bilateral activations in the parahippocampal gyrus, a region known for its role in visuo-spatial processing (cf. Ferstl & von Cramon 2007). In contrast to the previous study, however, there was no main effect of consistency, possibly due to the fact that only short, two-sentence stories were used, which might have prevented the readers from building a stable situation model representation.

Mo et al. (2006) also used the consistency paradigm, but did not vary the information aspect. With slightly longer stories, they reported increases in left lateral PFC and right anterior STG (slightly more posterior than previous aTL activations) for inconsistent stories compared to consistent ones. Hasson et al. (2007) used a very similar paradigm, although they stressed that the 'inconsistencies' are merely more informative than consistent, often redundant information. Their *more informative* passages elicited widespread activation in a bilateral fronto-temporal network, partly overlapping with the areas involved in detecting temporal inconsistencies (Ferstl et al. 2005) and with those described by Mo et al. (2006). Most importantly, Hasson et al. (2007) evaluated which brain regions' activation predicted subsequent memory for the story information. Interestingly, the dmPFC and PCC were more active when the participants thought they had seen a more informative story. This interaction between recognition memory and context appeared as a modulation of deactivation, rather than an activation increase for those trials that required an inference. In contrast, the right aTL was sensitive to both subsequent memory and contextual integration demands, replicating and strengthening the interpretation that the aTLs are important for the encoding of text information into content units (Ferstl et al. 2008; Stowe et al. 2005).

As for the studies on inferencing summarized in the previous section, the conclusions from these studies are twofold. On one hand, a more specific delineation of the role of fronto-temporal regions, and in particular, of their lateralization, requires further research. Even the studies using similar methods do not yet converge sufficiently to be able to pinpoint the role of the RH. The right aTL emerges as important for the integration of text information, but the findings on frontal and posterior temporal right sided activations are not yet conclusive. On the other hand, there is overwhelming evidence for a crucial role of the PCC/precuneus during situation model building. This convergence is even more remarkable given the heterogeneity of the empirical methods used. In contrast to the inference studies, where explicit coherence or plausibility judgments seemed to be a prerequisite for contributions of medial brain regions, the PCC is involved in situation model building during the processing of continuous text even in the absence of explicit judgment tasks.

Incorporating the notion of mirror neurons, and especially the observation that action verbs elicit activation in (pre-)motor cortices (Pulvermüller 2005), Glenberg (2007) and Zwaan (2004) put forward an embodied theory of text comprehension. In their view, comprehension gives rise to the resonance of brain regions involved in experiencing events similar to the ones described. Information specific activations for linguistically comparable texts (e.g., Ferstl et al. 2005; Ferstl & von Cramon 2007; Mason et al. 2008) are consistent with such an account. Although embodied theories of situation model building draw heavily on neuroscientific findings, there is surprisingly little neuroimaging research specifically designed apply them in a wider context of higher level language comprehension. One interesting exception is a study by Raposo et al. (2009) who asked the question of whether embodied representations would be active during the comprehension of idiomatic statements (see next section). Raposo et al. (2009) presented action verbs related to arm or leg movements (e.g., *trample*) to identify the relevant motor and premotor areas. When the verbs were embedded in sentences, such as *The muddy children trampled over Sarah's clean floor* the same regions responded differentially, providing evidence for motor resonance. However, this action related activation disappeared when the verbs were embedded in idiomatic, non-literal sentences, such as *The spiteful critic trampled* *over Sarah's feelings.* This finding is incompatible with an automatic motor resonance mechanism and seems to suggest that embodied representations reflect the *result* of comprehension, i.e., the situation model, rather than the *process* of comprehension.

4. Pragmatics: Metaphors and idioms

Metaphor comprehension is one of the most interesting subareas of language research, because it stirs so much debate. The rather incompatible spectrum of attitudes ranges from the standard pragmatic model stating that metaphors are based on violations of literal interpretation (Searle 1979) to the view that all language is metaphoric (Lakoff & Johnson 1980). Thus, metaphors provide a unique way of testing theories of lexical and semantic representation, as well as hypotheses about constructive language use. There is a large body of behavioral empirical literature that has furthered our understanding of which factors influence metaphor comprehension (for reviews see Cacciari & Glucksberg 1994; Gibbs & Colston 2006; Glucksberg 2003).

Up until 2005 only two neuroimaging studies on metaphor comprehension had been published. Bottini et al. (1994) reported right hemisphere activation for metaphors as compared to literal sentences, whereas Rapp et al. (2004) reported LH activation only (see Ferstl 2007, for a more detailed summary). Despite this discrepancy, metaphor comprehension has been consistently considered an RH function. Reflecting the fascination with the topic, but also the fact that metaphors do not require an elaborate context and that metaphoric interpretations can easily be induced using appropriate task instructions (e.g., word pairs such as *lawyer – shark*), this research area is rather active. In the meantime, about a dozen studies using fMRI or PET have been published, investigating factors such as figurativeness, familiarity and salience, and using a number of different stimulus and task types. Recently, Schmidt et al. (2009) provided an excellent synthesis of this research. Within the apparent heterogeneity of the results, they identified a rather consistent pattern: whenever novel metaphors were used, RH activation was observed (Ahrens et al. 2007; Mashal et al. 2005; 2007; Stringaris et al. 2006), whereas frozen, stored or familiar metaphors elicited activation in LH regions only (Eviatar & Just 2006; Lee & Dapretto 2006; Mashal et al. 2008; Rapp et al. 2007; Stringaris et al. 2007). This analysis is consistent with the view that access of lexico-semantic information requires the left perisylvian language areas, whereas inferences or the integration of wide associations involves the RH (Jung-Beeman 2005).

A couple of studies not yet included in this analysis show that the issue of RH contributions to metaphor is far from being resolved (see also Mejía-Constaín et al. *this issue*).

Based on a sophisticated design including a task manipulation, as well as carefully controlled stimuli, Yang et al. (2009) described large, left-dominant activations for novel metaphors, and concluded that task difficulty was more likely to modulate RH activation than novelty or figurativeness of the metaphors. Shibata et al. (2007) presented novel metaphors in Japanese and asked for a comprehensibility judgment. Rather than showing RH activations, though, metaphorical sentences elicited more activation in LH, in particular in the inferior parietal lobe, the inferior frontal gyrus, and, most prominently, in three dmPFC regions. This latter result once again strengthens the role of this cortical region during language interpretation.

Idioms are seen to have evolved from metaphoric expressions and to have become ingrained in the particular language. Thus, it could be hypothesized that idiom comprehension utilizes similar neural structures as the comprehension of frozen metaphors. Contrary to this prediction, four imaging studies have provided divergent results that seem to reflect the different task demands and experimental situations, rather than some principled idiom specific cognitive process. While Raposo et al. (2009; see section on situation models) did not report any additional activation for idiomatic over literal sentences, Romero Lauro et al. (2008) used a sentence-picture matching task and found an almost perfect replication of the ELN for idiomatic expressions. In addition to bilateral fronto-temporal activation, the dmPFC was clearly involved. Finally, Zempleni et al. (2007) and Mashal et al. (2008) reported right temporal activation during the processing of ambiguous idioms, i.e., idioms that also have a plausible literal interpretation. Interestingly, though, this activation was larger for idiomatic than literal sentences in the study by Zempleni et al. (2007), whereas Mashal et al. (2008) elicited right temporal activation by asking participants to think about the literal interpretations of the idioms. These results might be due to differences in salience of the respective readings (Giora 1997): Possibly, the literal interpretations of the idioms used in the latter study were less frequent or salient than those used in the former. Further research is needed to control for such factors. A more comprehensive treatment of idiom comprehension is provided by Papagno & Romero Lauro (*this issue*).

5. Pragmatics: Jokes, irony and sarcasm

Similar to the work on metaphor comprehension, verbal humour and irony are test cases for pragmatic interpretations, because the intended meaning does not coincide with and might even contradict the literal meaning of an utterance. Verbal humour is particularly interesting from a neuroscientific point of view, because two separable components can be postulated: the cognitive processes involved in comprehending the humorous text, and the affective appreciation of the funny content (Siebörger 2006). Interestingly, both components are considered right hemisphere functions in the neuropsychological literature (e.g., Brownell & Martino 1998). In contrast, functional neuroanatomy provides clear-cut, separable predictions for the brain regions contributing to these two components. In the seminal study on verbal humour, Goel & Dolan (2001) showed that the linguistic properties of jokes modulated activity in left fronto-temporal brain regions, whereas the affective reaction was evident in the ventromedial prefrontal cortex, part of the limbic system. A study from our laboratory replicated this latter result using different stimuli (Siebörger 2006; see also Ferstl & Siebörger 2007), whereas the cognitive comprehension demands were reflected in activations of the medial inference areas (dmPFC and PCC).

Probably because of the difficulty of designing the materials and controlling their efficacy (i.e., their novelty and funniness), only very few studies on joke appreciation have been conducted since. In a study comparing visual and verbal humour, Watson et al. (2007) found a network of regions to be more active during exposure to humorous stimuli in both modalities, including regions involved in humour appreciation (e.g., amygdala and nucleus accumbens). Specific for the comprehension of verbal rather than visual humour was the left anterior temporal lobe, an area not only implicated for sentence level integration and semantic processes, but also emotional processes (Olson et al. 2007; see Ferstl et al. 2008; Ferstl & von Cramon 2007).

Irony is another, if slightly less engaging form of verbal humour. Ironic statements express the opposite of what the speaker intends to convey. Thus, the literal reading and the correct interpretation diverge. In real-life communication, irony is accompanied by nonverbal cues, such as facial expressions or prosody. Lacking these cues, most psycholinguistic laboratory studies require the reader or listener to infer the ironic interpretation from a mismatch between the discourse context and the target statement. In this respect, verbal humour, irony and the inconsistency paradigms used to study situation model building are rather similar. Irony, and in particular sarcasm, serves an important interpersonal function, as it couches criticism in a slightly less offensive package. Its comprehension is thus likely to involve Theory-of-Mind processes to infer the intention of the speaker (see Gibbs & Colston 2007, for an extensive treatment of irony comprehension).

Perfectly in line with this expectation are the results of Uchiyama et al. (2006). Compared to control texts, short sarcastic passages elicited more activation in the dmPFC, the posterior STS, and the aTL, regions overlapping with the Theory-of-Mind network. Note, however, that these regions were obtained in a comparison with a control condition, and there were no differences between the sarcastic stories and their non-sarcastic counterparts. Thus, the activations might also reflect the integration of the story content into a coherent representation. With a similar paradigm, but using simple yes/no comprehension questions, rather than an explicit sarcasm judgment, Eviatar & Just (2006) found specific activation for the irony condition in the right middle and superior temporal lobe only.

Wakusawa et al. (2007) used pictures of social situations with verbal statements of three conditions: literal, ironic, or metaphoric. For example, a man shows a friend his wallet containing only one coin, and the friend says: *You're rich!* (ironic) or *It's metal* (literal). In different blocks, the participants evaluated whether the sentence was a literally correct description or whether the comment was situationally appropriate. A full appreciation of the irony is only needed in the latter task. Once more, the dmPFC proved to be important for the integration of the non-literal sentences (both ironic and metaphoric) when the communicative appropriateness was to be evaluated. The direct comparison of ironic trials with their control trials yielded two results: activation in the right aTL, the region also found to be involved during the comprehension of inconsistent stories (Ferstl et al. 2005); and activation of the medial orbito-frontal cortex (or vmPFC), a region close to the humour appreciation region described by Goel & Dolan (2001) and Siebörger (2007).

Taken together these studies confirm that neuroimaging results can identify differential contributions of humour appreciation and of the cognitive processes necessary for correctly interpreting the humorous stimuli. While the affective reactions are reflected in limbic activations, the cognitive integration is aided by parts of the ELN, in particular the 'inference region' dmPFC and the right temporal lobe.

6. Other topics and future developments

6.1. Modality specificity

In the previous reviews, auditory and visual presentation were not differentiated under the assumption that higher level language processes are modality independent. This assumption is somewhat simplified, of course, but a number of studies using coherent text, rather than single words, have now specifically investigated modality effects (Lindenberg & Scheef 2007; Jobard et al. 2007; Spitsyna et al. 2006; Wilson et al. 2008; also Ferstl & von Cramon 2001b). An interesting study comparing production and comprehension stressed the importance of the PCC/retrosplenial cortex and the parahippocampal regions for both tasks (Awad et al. 2007). Moreover, the bilateral anterior temporal lobes emerged as crucial heteromodal integration areas.

6.2. Special populations and individual differences

The numerous replications of the most important findings have opened up the possibility to use neuroimaging to investigate individual differences and explore clinical applications. Interesting investigations of individual differences and special populations include developmental studies (Dapretto et al. 2005; Karunanayaka et al. 2007; Schmithorst et al. 2006; Vannest et al. 2009; Wilke et al. 2005), working memory ability (Virtue et al. 2006; 2008), studies of aphasia (Crinion et al. 2006), morphometric studies of patients with autism (Mason et al. 2008), or metaphor comprehension in patients with schizophrenia (Kircher et al. 2007). With the accumulation of knowledge about the neuroanatomy of text comprehension processes in healthy, adult comprehenders, we hope that neuroimaging will become a useful tool for describing and assessing text level deficits, both for educational and clinical applications.

6.3. New methodological developments

The widespread availability of neuroimaging technology and the development of measurement and analysis techniques has opened up a number of new ways to study text comprehension and pragmatics. This progress has led to more rigorous experimentation. While early imaging research often ignored basic principles of experimental design as they had been laid out in psycholinguistic research (e.g., by using blocked designs), the more recent work uses rather sophisticated manipulations, based on tested paradigms from experimental psychology.

An alternative approach is to minimize experimental manipulations in favor of more ecologically valid, natural conditions. Neuroimaging can be used to observe brain function even in the absence of an overt task. The comprehension of continuous text, either paired with psycholinguistic text analyses (e.g., Speer et al. 2007; Whitney et al. 2009), or model-free analyses (Wilson et al. 2008; see also Hasson et al. 2004) are promising first steps in this direction. Applications to dialogue and communication in natural social situations are a likely extension of this work.

The third development consists of novel analysis techniques which are starting to be applied to text comprehension research. In addition to identifying brain areas that contribute to certain tasks, and the attempt to delineate their exact function, there is now increased awareness of anatomical and functional connectivity. Consequently, methods for directly assessing the relationship and interaction between brain regions become more widely used.

Rather than using anatomical connections, functional connectivity analyses have been applied to imaging data. These analyses are based on the idea that across the entire course of an experiment, brain regions participating in the implementation of a given cognitive process should show a similar time course of activation. Starting with the time course in a seed region, other brain areas with related activation time courses are identified. The mathematical methods used are similar to correlation analyses while allowing slight temporal shifts. Using this method, Mason et al. (2008) showed weaker connectivity between the dmPFC and other Theory-of-Mind and language related regions in autistic comprehenders as compared to a control group. Siebörger et al. (2007) applied the method to aid in the interpretation of a surprisingly large network of activations when comparing closely related sentence pairs to sentence pairs that took some effort to connect via an inference. Connectivity analyses identified two subnetworks related to the language input and to the response, respectively.

Dynamic causal modeling (DCM) is another technique to describe the interplay between brain regions during task performance. Zempleni et al. (2007) used this method to further specify the specific role of the dmPFC during idiom comprehension, and Chow et al. (2008) applied DCM to data from an inference task. While these first results are promising and the methods will undoubtedly be highly useful in the future, it is important to be aware of the method's assumptions. Based on background knowledge, in particular anatomical facts and task analyses, key areas are identified and a number of candidate models are postulated. For example, Chow et al.'s (2008) connectivity assumptions were based on neuroanatomy as well as on a particular theory of language processing. Thus, the analyses were restricted to left hemisphere regions, despite the fact that functional activations were documented in the right temporal lobe, as well. Thus, the authors' conclusions about the respective roles of left hemisphere regions are informative, but the results do not shed light on the RH debate.

Beyond the scope of this article, but crucially important, are other neuroscientific techniques besides fMRI. Most widely used, and often applied to the topic of pragmatics, are event-related brain potentials (ERPs; see Van Berkum 2004, for review), and to a lesser extent, magneto-encephalography (MEG). A more recent development is the application of transcranial magnetic stimulation (TMS), a method that simulates the effects of small transient lesions. A weak magnetic pulse applied to the surface of the scalp briefly impairs the function of the underlying cortex. If the pulse is appropriately time-locked to a cognitive task, effects on reaction times or error rates can be observed. In contrast to investigations on word-level processes and syntactic parsing (see Devlin & Watkins 2007, for review), the method has only rarely been utilized in to study text comprehension or pragmatics (e.g., metaphor comprehension: Pobric et al. 2008). In our own lab, preliminary TMS results confirm the contribution of the posterior temporal lobes to contextual sentence integration (Franzmeier et al. *in preparation*). LH stimulation impaired the comprehension of highly predictable sentence continuations (e.g., *The pilot flies the plane*), whereas RH stimulation increased reaction times specifically for possible, but unpredictable sentence continuations (e.g., *The pilot flies the kite*).

7. Conclusions

The progress made in the area is impressive. Starting with a small number of studies just a few years ago, we are now in a position to compare and contrast the methods and results of studies based on sound psycholinguistic theory. As is often the case in neuroscience, these comparisons do not always converge as clearly as we would wish. Some results can only be understood by drawing on post-hoc explanations based on findings from very disparate research areas (e.g., Theory-of-Mind explanations of communication). Some results involve the predicted areas, but are in unpredicted directions. Some results seem to teach us about an aspect of the experimental task that had not been properly acknowledged before (e.g., differences in memory demands or difficulty, Ferstl et al. 2005). From a psycholinguistic point of view this might be an unsatisfying state of affairs. However, with time and more empirical research, cognitive neuroscience will greatly aid in the formulation of more comprehensive theories of language interpretation, which will incorporate previously neglected social and emotional factors (e.g., emotion and motivation, Theory-of-Mind).

Interestingly, many of the conclusions from the very first imaging studies still hold. The ELN, for instance, was first described by Mazoyer et al. (1993), including the important roles of the dmPFC and the anterior temporal lobes, as well as the often replicated left-sided dominance. This result has since been replicated numerous times. We can be confident that language interpretation proceeds in a similar fashion, independent of the input modality. Although reading and listening impose different strategies, the processes of inference and situation model building manifest themselves whenever language interpretation is attempted.

A second convergence is the separability of qualitatively distinct processes using neuro-imaging. The most striking example is the more specific delineation of the role of the parieto-medial areas. In the early works, the posterior cingulate cortex had been implicated (e.g., Fletcher et al. 1995; Maguire et al. 1999; Ferstl & von Cramon 2001), but not been considered central (see Mar 2004; Mason & Just 2006). Recent experiments have now accumulated overwhelming evidence for this cortical area to be crucial for situation model updating.

Similarly, the role of the dorso-medial prefrontal cortex (dmPFC) for inference processes is by now without dispute. The exact functional attribution of this area is still under debate (e.g., Theory-of-Mind, self-relevant processing, default network, evaluation), but it seems safe to conclude from a number of recent studies that the dmPFC is involved in strategic, non-automatic coherence building processes (cf. Ferstl & von Cramon 2002). While the formulation of concrete predictions is sometimes difficult (e.g., which condition is predicted to induce ‘more inferencing’?), activation in this area always necessitates an evaluation of the inference requirements of the materials used in the study.

Other regions, such as the anterior temporal lobes, the inferior parietal cortex, and the left lateral prefrontal areas are also consistently activated in imaging studies on text comprehension. However, their functional attribution leans rather strongly on findings from other research areas, rather than from a convergence of text comprehension studies investigating one particular subprocess. For instance, there is extensive knowledge about the functions of specific subregions of the lateral PFC (or dorso-lateral PFC), but in many text comprehension studies there is less activation in this area than would be expected.

The crucial issue of the involvement of the RH in discourse comprehension has not been resolved, however. And it would be surprising if this was the case. It will be necessary to specify in more detail exactly which subprocesses of text comprehension correspond to which function of the RH, and in particular which region within the RH. In addition to the coarse coding hypothesis (Jung-Beeman 2005), which makes predictions on right temporal contributions to semantic processing, other theories, such as visuo-spatial processing or resource theories need to be considered (see Ferstl 2007). Furthermore, experimental results will be useful for specifying more detailed hypothesis about the conditions under which RH involvement is likely. An example for such a refined, differentiated view is Schmidt & Seger's (2009) proposal for metaphor comprehension.

Finally, many issues that have been studied in linguistics and psycholinguistics have not yet been investigated using neuroimaging methods, or are just starting to be studied more extensively. Examples are verbal humour, embodied cognition, or the social facets of pragmatics, such as turn-taking in dialogue, politeness, the choice of a language level, and many more.

The neuroanatomy of text comprehension is a vital research area with promising new developments. A combination of classical paradigms developed in psycholinguistics, paired with novel methods and technical developments will shed light on theories of text and discourse comprehension. Furthermore, branching into social cognitive neuroscience, and introducing concepts such as Theory-of-Mind into the experimental study of language and communication will greatly extend the range of research topics.

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Notes

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