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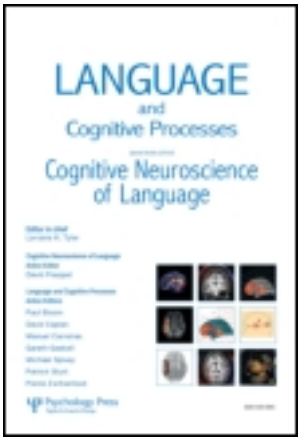

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The balance between memory and unification in semantics: A dynamic account of the N400

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At least three cognitive brain components are necessary in order for us to be able to produce and comprehend language: a Memory repository for the lexicon, a Unification buffer where lexical information is combined into novel structures, and a Control apparatus presiding over executive function in language. Here we describe the brain networks that support Memory and Unification in semantics. A dynamic account of their interactions is presented, in which a balance between the two components is sought at each word-processing step. We use the theory to provide an explanation of the N400 effect.

Keywords: Semantics; Neuroscience; N400.

1. INTRODUCTION

The human brain's ability to combine elementary representations to form complex ones is part of what gives language its seemingly boundless expressive power. There is little need to turn to evolution to see that this

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capacity entails a computational advantage vis-à-vis a special class of linguistic signals. Which one exactly? What does this advantage consist in?

One answer is that, being endowed with sophisticated combinatory machinery, the brain is able to deal with *novel* utterances (Frege, 1980; Katz & Fodor, 1963; Partee, 1984) like:

1. Last Friday the cruiser Arberia entered the port of Trieste.

A compositional algorithm that takes word meanings and the syntax to produce sentence meaning (Montague, 1970; Partee, ter Meulen, & Wall, 1990) explains the reader's ability to understand (1) despite the fact that she might not have seen this particular sentence before.

This view, however, is not without problems. Being able to process novel input signals does constitute a computational advantage for the brain. Yet why should it invest so much, providing powerful algorithms and dedicated neural resources, for what may turn out to be a small return? Language use builds upon an extensive repertoire of stereotyped, non-novel utterances, and novelty in many cases amounts to local, predictable variations that do not require a generative grammar or a compositional semantics to be accounted for (Culicover & Jackendoff, 2005). What is novel in (1) may just be the particular referential coordinates that are used, i.e., the joint occurrence of the adverbial "last Friday" and of the proper nouns "Arberia" and "Trieste", such that the partially lexically filled construction (2):

2. Last X_{NP} the cruiser Y_{NP} entered the port of Z_{NP}

may not seem as new as (1). Removing other fillers, "cruiser" and "port" for instance, would make the construction look even more familiar. In the limit, a fully stripped-down version of (2) will be stored in memory as a template specifying the syntactic-thematic environment of the verb "to enter". In this view, parsing the novel sentence (1) may amount to little more than playing a game of substitution *salva grammaticalitate*. However, syntax and semantics go well beyond that, from which follows that novelty alone is too weak a justification for linguistic combinatorics.

These considerations indicate that the class of sentences to which combinatorics applies includes, but extends beyond novel items. It is precisely the issue of storage which suggests where to draw the line. An alternative answer to the questions above is that combinatorics enable the brain to deal with *any linguistic signal that, for a variety of reasons including novelty, need not or cannot be stored in memory*. The processing advantage here is to ease the burden on storage (Baggio, van Lambalgen, & Hagoort, 2011). How should we understand this fact from the point of view of neuroscience? How are storage and computation realised in brain systems?

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1.1. Memory, unification, and control

Despite advances in neuroimaging technology and data analysis protocols, and the availability of a rapidly growing base of experimental data, detailed neurobiological models of language are only beginning to emerge. One reason for this delay is that laboratory studies postulate task-related processes (vowel discrimination, lexical decision, etc.) that cannot be readily mapped onto a cognitive architecture as proper components of the language system.

A more fruitful approach is given by the "design stance" (Dennett, 1971). Here one starts from a picture of how the brain must be organised to support language, and then derives predictions and explanations about the physiology and the overt behaviour of the system. At least three components must be in place in the brain in order for us to be able to produce and comprehend language (Hagoort, 2005): a Memory repository of phonological, syntactic, and semantic information associated with morphemes, words, and other constructions—i.e., a lexicon; a Unification buffer where stored lexical information is combined to form more complex units; and a Control apparatus that presides over executive function in language, e.g., turn taking in conversation, language switching in bilingualism, etc. Specific brain areas have been found to correspond to these three components: memory is largely localised in temporal regions (superior temporal gyrus, STG; middle temporal gyrus, MTG; and inferior temporal gyrus, ITG); Unification is subserved by the inferior frontal gyrus (IFG); and Control is exerted by anterior cingulate and dorsolateral prefrontal cortices. Here we focus on the interactions between Memory and Unification, leaving Control aside despite its potential role in linguistic combinatorics.

1.2. Unification the formal way

Nearly every psychological model of language postulates a lexicon and, therefore, a memory component, and the same *mutatis mutandis* can be said for the combinatorial or "integrative" component. The Memory–Unification–Control (MUC) model is rather unusual in that it adopts a very specific view of the latter, which is based on the notion of *unification* borrowed from computational linguistics (Joshi & Schabes, 1997; Kay, 1979). This requires some justification, which we provide below.

We suggest that stored in memory are *unification-ready structures*, examples of which are the syntactic frames of Vosse and Kempen (2000) and the scenarios that encode verb phrase meanings of van Lambalgen and Hamm (2004). Each stored construction (Goldberg, 1995) (morpheme, word, phrasal idiom, partially filled syntactic frame, etc.) is represented by sets of constraints; each set pertains to a particular level of linguistic representation (phonology, syntax, and semantics) for that construction, or to the interfaces

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between such levels (Culicover & Jackendoff, 2005; Jackendoff, 2002 2007); each constraint in a set contributes to specifying how a given construction can combine with other constructions at a particular level of linguistic representation, or how it can be filled with denoting expressions.

For example, the semantic constraints associated with the adverbial "Last Friday" in (1) may be functionally equivalent to the following (Baggio, 2008; Hamm, Kamp, & van Lambalgen, 2006; van Lambalgen & Hamm, 2004):

3. $HoldsAt(d_{Friday,}\ s) \wedge s\ <\ now \wedge |now\ -s| \leq\ 7\ \ days \rightarrow\ HoldsAt(d_{CP\ Friday},\ s)$

If a given day is a Friday (d_{Friday}) and holds at time interval *s*, *s* is earlier than the moment of speech *now*, and between *now* and *s* there are at most seven days, then the day at *s* can be defined as the closest past Friday ($d_{CPFriday}$), i.e., as last Friday. The temporal profile of the VP "entered the port of Trieste" is given by:

4. $?Happens(enter,\ t) \wedge HoldsAt(port,\ t) \wedge t\ <\ now$ succeeds

where *enter* is the culmination of the entering process and *port* denotes the consequent state of having entered the port of Trieste. The processing instruction 'succeeds' forces the system to look for a solution of the set of constraints given in (3) and (4), which is done by unifying the variables *s* in (3) and *t* in (4): $s = t$. In this way, the entering event is located within the adverbial's time frame, and the meanings of "entered" and "last Friday" are unified.

1.3. Semantic processing as constraint satisfaction

This formal description suggests that semantic representations can be seen as including constraints, and that sets of constraints spanning several words, for instance an adverbial and a verb, can be satisfied by resorting to unification. Constraint-based analyses can be given for several phenomena in semantics, syntax and phonology, and constraint satisfaction (or its failure), possibly across levels of linguistic structure, can be investigated in language processing studies (Baggio, 2008) (Figure 1a). The ranking between (sets of) constraints is another key issue (Prince & Smolensky, 1997), which, however, has received little attention from experimentalists.

The example given above contains in a nutshell our view of the interactions between the two key units of the brain's language system: the Memory component supplies constraints across levels of description, and sets of constraints are formed as the input is incrementally given; the Unification component attempts to solve on-line those sets of constraints, again shadowing the input over time. Constraint solving is done in a dynamic fashion: Memory supplies material for Unification, which retains a context

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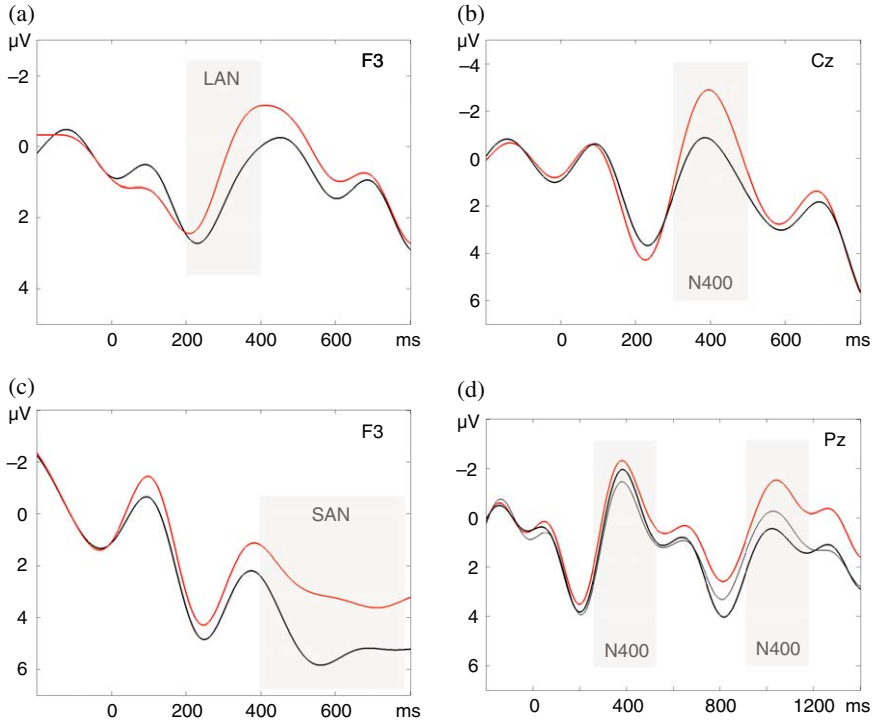

Figure 1. Event-related potential (ERP) components whose amplitudes are modulated by semantic complexity. (a) Left anterior negativity (LAN, 200–400 ms) evoked by a verb tense violation (red) *vs.* a correct verb form, e.g., "Last Friday Vincent *paints/painted* the window frames of his country house". Study details in Baggio (2008). (b) N400 (300–500 ms) evoked by a contextually unrelated word (red) compared to a related word: "The girl was writing letters when her friend spilled coffee on the *tablecloth/paper*". Reported in Baggio et al. (2008). (c) Sustained anterior negativity (SAN, 400–800 ms) evoked by a verb suppressing a previously drawn inference (red) *vs.* the same word in a neutral context: e.g., "spilled" in "The girl was writing a letter when her friend spilled coffee on the *tablecloth/paper*". In the original Dutch materials, the verb "spilled" occupied the sentence-final position. From Baggio et al. (2008). (d) Sequence of N400 effects evoked in complement coercions (red), semantic anomalies (black), and controls by the noun and the N + 1 word, e.g., "article" and "before" in "The journalist *began/astonished/read* the article before the break" (Baggio et al., 2010). [To view this figure in colour, please visit the online version of this Journal.]

for subsequent stages of memory retrieval and unification. It is precisely the neural underpinnings of this cycle that we intend to investigate in this paper.

1.4. What a theory of semantic processing should do

Formal semantic theories, whether constraint-based or not, describe how words belonging to different syntactic categories or denoting different object

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types combine to give rise to complex semantic representations. However, these theories are by design insensitive to differences between words of the same syntactic category denoting objects of the same type. For example, "port" and "hippodrome" are two such words—two nouns denoting spatially extended entities which afford entering and other actions. Now consider the sentence:

5. Last Friday the cruiser Arberia entered the hippodrome of Trieste.

It is something peculiar to do for a cruiser to enter a hippodrome, and (5) is an odd thing to say in a pragmatically well-constrained conversation setting. And yet, truth conditions can be given for (5). Moreover, the formal analysis of the VP "entered the hippodrome" would not differ from that of any other VP, regardless of what is odd to say or do. It is sufficient to replace port with hippodrome in (4) to have such a formal analysis, where (3) still holds valid:

6. ?$Happens(enter, t) \wedge HoldsAt(hippodrome, t) \wedge t < now$ succeeds.

There is an obvious perceived difference between (1) and (5), which is not reflected in their semantic analyses (4) and (6).

Here one should resist the conclusion that any phenomenon which is not relevant to or not accounted for by a formal semantics is not semantic in nature. The difference between (1) and (5) must be semantic, for it is not merely phonologic or orthographic, it is not at all syntactic, it does not just flout some conversation maxim, and has nothing to do with how the world looks like: in fact (1) is now false just as (5). The limitation of formal semantics is that its formal elegance often goes at the expense of cognitive realism. Instead of focussing on natural language as a psychological phenomenon, its main concern is "a formalization of the metaphysics of truth in natural language" (Seuren, 2009, p. 21). For example, it ignores the fact that incremental processing often recruits nonlinguistic cognitive input. Our goal is clearly different than that of model-theoretic semantics. We want to develop an account that adheres to cognitive realism, in that it explains how language users derive meaning and how the human brain instantiates the neural architecture necessary to achieve this feat. In other words, the challenge is to provide a theory of semantic processing that is both combinatoric and able to track usage-based semantic expectations of the kind that make (5) odd.

2. MEMORY AND TEMPORAL CORTEX

Language comprehension hardly ever amounts to a straightforward matching of a stimulus with a stored memory representation. As noted above, a sizeable portion of our production stock is fixed and conventionalised. Nonetheless, even the simplest of sentences like "How do you do?" or "What a lovely weather!" is interpreted in slightly different ways depending on the

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context in which the token occurs: crucially, one needs to determine the reference of the pronoun "you" in the given conversation setting, to detect irony if the weather is in fact bad, etc. Even small talk exceeds the capabilities of a simple pattern matching machine.[1]

2.1. Memory and the N400

Although Memory cannot take charge of language processing all the way to a pragmatic interpretation, it does have a prominent role to play in most cases. The N400 is arguably the most robust dependent measure of brain activity that reveals the use of semantic memory in language comprehension (Kutas & Federmeier, 2000). Kutas and Hilliyard (1980) were the first to describe this negative event-related potential (ERP) wave with an onset at about 250 ms, a peak at circa 400 ms (hence the label "N400"), and an offset around 550 ms, whose amplitude increased when the meaning of the eliciting word ("socks") mismatched with the semantics of the preceding sentence context, as in "He spread his warm bread with socks".

Since its discovery in 1980, much has been learned about the antecedent conditions of the N400 (Kutas & Federmeier, 2000; Kutas, Van Patten, & Kluender, 2006; Lau, Phillips, & Poepple, 2008; Osterhout, Kim, & Kuperberg, 2010). The N400 *component* is evoked by every content word, irrespective of the sensory modality (visual or auditory) in which it is presented. The N400 *effect*, calculated as the difference in amplitude between the N400 components evoked by two words in different experimental conditions, as Kutas and Hillyard (1984) and others have observed, does not depend on a semantic violation. Subtle differences in expectancies, as between "mouth" and "pocket" in the sentence context "Jenny put the sweet in her mouth/pocket after the lesson", can also modulate the N400 amplitude (Kutas & Federmeier, 2000; Kutas et al., 2006; Lau et al., 2008). Lexical relations are one of the factors that drive the predictability effect. A larger N400 effect is evoked by a semantically unrelated word within a sentence context, for instance "tablecloth" with respect to "paper" in "The girl was writing letters when her friend spilled coffee on the tablecloth/paper" (Baggio, van Lambalgen, & Hagoort, 2008; Kutas and Hillyard, 1984) (Figure 1b). Semantic relatedness comes in degrees, and this is

[1] Recall the early language processing programme ELIZA (Weizenbaum, 1966) which was based on pattern matching algorithms that, upon receiving an input by the user, were capable of mimicking a psychotherapist's response: e.g., User: "You are afraid of me", ELIZA: "Does it please you to believe I am afraid of you?" Obviously, the programme was not interpreting pronouns and did not know anything about the context or the world. This particular discourse genre makes pragmatic interpretation rather unnecessary, and this is the only reason why this version of pattern matching "works" here, giving the appearance of meaningful and relevant replies.

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reflected in parametric changes in the N400: as the degree of semantic match between a word and its context *de*creases, the amplitude of the N400 *in*creases. This inverse relation is independent of the type of context: it is found for a single word context (Holcomb, 1993), a sentence Kutas and Federmeier (2000), and a discourse (van Berkum, Hagoort, & Brown, 1999).

Different views exist as to what processes bring about the N400 effect. Federmeier and Kutas (1999) and Kutas and Federmeier (2000) argued that, in addition to its sensitivity to the semantics of the context, the N400 is also sensitive to the ease of accessing information in semantic memory. In this view, the N400 amplitude is modulated by the degree to which the context contains retrieval cues for selecting and accessing a stored representation for a particular word meaning. Evidence in favour of this position has recently been obtained in a study by De Long, Urbach, and Kutas (2005). These authors found an N400 effect to an indefinite article (“an” *vs.* “a”) that excluded a semantically expected continuation, as in “The day was breezy so the boy went out to fly an”, where “kite” would be the contextually expected noun. Other studies that reported modulations of the N400 component suggest that pre-activation can be remarkably specific. Contextual-semantic cues can selectively activate semantic (Federmeier & Kutas, 1999; Kutas & Hillyard, 1980, 1984), morphological (Otten, Nieuwland, & Van Berkum, 2007; Wicha, Moreno, & Kutas, 2004), phonological (De Long et al., 2005), and orthographic (Laszlo & Federmeier, 2009) information about an expected sentence completion. Preliminary evidence indicates that the N400 can also be modulated by expectations of word category: Hinojosa, Moreno, Casado, Mũnoz, and Pozo (2004) found that correct but syntactically unexpected words evoke a larger N400 than syntactically expected words.

One basic property of the N400 is that the context on the basis of which a prediction is derived is typically a *semantic* representation,[2] but the memory trace that is pre-activated can code for *any* lexically bound feature. This context-to-lexicon mapping is a key aspect of what we intend to capture in our theory, which will be presented in Sections 4 and 5.

2.2. The N400 and temporal cortex

Studies on semantic priming have demonstrated that the N400 is an inverse measure of the degree to which a prime activates some target word. The

[2] See, however, Perfetti (1999) for a review of studies suggesting that the N400 does not depend upon the presence of a semantic context, and that fit with phonological or orthographic contexts can also affect the N400 amplitude.

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N400 priming effect has been shown to have primary neuronal generators in temporal cortex, MTG in particular is the only area that, just as the N400, consistently shows effects of priming across different stimulus onset asynchronies (SOAs) and modalities (Lau et al., 2008). Increased BOLD activation particularly in left STG and MTG was found when there is a semantic mismatch between a word and the context in which it occurs (Bookheimer, 2002; Davis et al., 2007; Friederici, Ruschemeyer, Hahne, & Fiebach, 2003; Hagoort, Hald, Bastiaansen, & Petersson, 2004; Kuperberg et al., 2003; Rodd, Davis, & Johnsrude, 2005; Ruschemeyer, Fiebach, Kempe, & Friederici, 2005; Willems, Özyürek, & Hagoort, 2007, 2008). Consistent with the fMRI data, MEG source localisation shows that the N400 is produced by activity in a number of areas, in particular STG (Dale et al., 2000; Halgren et al., 2002; Helenius, Salmelin, Service, & Connolly, 1998; Van Petten & Luka, 2006). These results are in accordance with the choice of the temporal cortex as the anatomical seat for the lexicon, that is, for the Memory component in the MUC model. We will use MTG/STG as a shorthand to the set of N400 generators in temporal cortex. However, we assume that different types of lexical information might recruit different parts of the STG/MTG memory network (e.g., lexical phonology more in STG/superior temporal sulcus [STS], and lexical-syntax more in MTG). Often, given the relatively poor spatial resolution of ERP source modelling, these effects will look very similar, but in fact the dynamic reverberating circuits between LIFG and STG/MTG will vary subtly with the type of lexical information that is recruited and unified.

In terms of neural architecture, the proposed context-to-lexicon mapping translates into an X-to-MTG/STG mapping, where the to-be-determined cortical area X should fulfil two requirements: (1) being capable of encoding and maintaining active a semantic context and (2) being effectively connected to MTG/STG through white matter fibres. Not surprisingly, the most promising candidate for area X is to be found in frontal cortex.

3. UNIFICATION AND FRONTAL CORTEX

As we have just seen, research has found the involvement of MTG/STG and modulations of the N400 as a function of the degree with which lexical properties of the incoming word are pre-activated by the semantics of the context. Generative grammar and compositional semantics regard language as a system where complexity is built into structure assembly rules (see Culicover & Jackendoff, 2005 for a discussion). Neuroscience, on the contrary, shows that the brain tries to do as much processing mileage as possible with what is stored in memory. Pre-activation phenomena across levels of linguistic representation suggest that the system may be seeking the nearest attractor state at each

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word-processing step.[3] While this is best seen as a mandatory and input-driven set of processes, it is unlikely that the temporal cortex can carry them out in isolation from other brain regions. Interestingly, feed-back connections from areas higher in the cortical hierarchy seem necessary to explain the generation of endogenous ERP components whose amplitude depends on expectancy (Garrido, Kilner, Kiebel, & Friston, 2007), among which is the N400. In the limit, top-down influences may be relatively inconspicuous, as when an input signal can be processed largely based on stored memories: a rigid phrasal idiom such as "kick the bucket" may be a case in point.[4] In other situations, however, feed-back from frontal cortex becomes more prominent: novel items, as perhaps (1), are an example, and so may be nonstored items that require combinatorics or noncombinatorial processes over longer time intervals (Gold et al., 2006).

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3.1. Unification and integration

How does unification relate to the more standard notion of integration? In current models of language processing (Cutler & Clifton, 1999; Perfetti, 1999), and as a result in the debate on the nature of the N400 too, "integration" is used in a variety of senses, often equivalent to "unification". However, we can enrich our conceptual repertoire and avoid confusion if we employ the two terms to refer to different operations. Integration is at stake if different sources of information converge on a common memory representation (see Mesulam, 2008, for a theoretical framework). Consider the sound and sight of a barking dog. The sight of the dog, the barking sound, and their joint occurrence presumably activate a memory representation that has multi-modal characteristics. On the other hand, semantic unification is a constructive process which results in a representation that is not already available in memory.

Integration and unification license opposite predictions for BOLD responses. Unification is expected to be always harder for semantic incongruities, which should lead to stronger responses in the BOLD signal

[3] There are at least two ways to account for this fact (Laszlo & Federmeier, 2009): one based on attractor networks (Hopfield, 1982), the other on Bayesian predictive coding (Friston, 2005). The theory presented in Sections 4 and 5 is more consistent with the former framework, which is also a more standard approach to language in the brain than Bayes.

[4] The rigidity of phrasal idioms may be of lesser importance in language comprehension, where incrementality implies that processing idiom fragments, e.g., "John kicked the", relies on unification too. This may be one reason why fMRI studies on idioms find increased activation in temporal *and* frontal cortices (Lauro, Tettamanti, Cappa, & Papagno, 2008; Zempleni, Haverkort, Renken, & Stowe, 2007), and similar evidence has been provided by TMS (Oliveri, Romero, & Papagno, 2004; Rizzo, Romero, & Papagno, 2007) and neuropsychological investigations (Papagno, Curti, Rizzo, Crippa, & Colombo, 2006; Papagno, Tabossi, Colombo, & Zampetti, 2004).

than semantically congruent items. In contrast, semantically congruent input results in converging support for a stored representation, which may thus be more strongly activated compared to a case with incongruent input. During integration, the congruent condition is therefore expected to elicit a stronger BOLD response than the incongruent condition. Studies on multi-modal integration have indeed reported activation increases to matching stimulus combinations: van Atteveldt, Formisano, Goebel, and Blomert (2004) observed a higher activation level in the left superior temporal cortex in response to matching phoneme–letter combinations (e.g., letter "p" with phoneme [p]) as compared to mismatching combinations (e.g., letter "k" with phoneme [p]) (see Calvert, Campbell, & Brammer, 2000, for a study with lip movements and speech sounds). The same pattern of BOLD responses was found by Beauchamp, Lee, Argall, and Martin (2004): increased activation in left posterior temporal cortex to the matching picture–sound combination as compared to the mismatching combination.

The study by Hein et al. (2007) provides evidence for a functional dissociation between frontal and temporal cortex that is of great relevance for our purposes. IFG showed stronger BOLD responses to incongruent familiar animal sounds and images (e.g., a meowing dog) than to congruent combinations (e.g., a barking dog). This effect was, however, not observed in STG or STS. STS was more strongly active in highly familiar combinations of objects and sounds compared to artificial object–sound combinations. That is, audio-visual integration in IFG was sensitive to semantic congruency, but did not depend on familiarity. In contrast, STS combined audio-visual features of objects independently of semantic congruency, but was sensitive to stimulus familiarity. These results point towards a possible division of labour between frontal and temporal areas, with a stronger contribution to integration for STG and a more prominent role for IFG in unification.

Hereafter, we will focus on left IFG and MTG/STG. The neural architecture of language presented in Section 4 does include other areas, such as the angular gyrus and the temporal pole (Binder, 2009; Lau et al., 2008; Visser, Jefferies, & Lambon Ralph, 2010), that play a role in semantic processing. However, we will not comment on the function of these regions here, and the same applies to the right hemisphere (Ferstl, Neumann, Bogler, & con Cramon, 2008; Vigneau et al., 2010).

3.2. Unification and the N400

In earlier sections, we reviewed several studies suggesting that the N400 is a signature of pre-activation: the more the semantics of the context activates lexical features of an incoming word, the smaller the amplitude of the N400 evoked by that word. A convincing case can be made in support of this

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particular notion of the N400 (Lau et al., 2008). However, there is a seemingly irreconcilable body of work which suggests that words that require additional effort to be combined within the current contextual meaning also modulate the amplitude of the N400. The contrast between these two views of the N400—pre-activation *vs.* unification[5]—can be characterised as follows: in the pre-activation view, combinatorics are only recruited when constructing a meaning for the context, whereas the process indexed by the N400 (activation of a memory representation) is noncombinatorial in nature; in the unification account, the process underlying the N400 is itself combinatorial. Therefore, one of the key questions which research on the neural basis of meaning should address is: *does the N400 reflect a combinatorial or a noncombinatorial kind of process?*

A yes/no answer to this question would seem rather premature, for two reasons: first, it is still unclear what counts as a combinatorial operation from a brain systems perspective; second, experimental designs that are able to produce combinatorial and noncombinatorial semantic processes in a controlled manner (i.e., such that the two can be disentangled during data analysis) are hard to devise, and as a result decisive data are still missing.

Even so, a few recent studies lend some plausibility to the unification view of the N400. For example, a distinction can be made between two levels of meaning: conceptual content and information structure. The latter refers to the subdivision of a sentence's content into information that is in the foreground or in the background (topic *vs.* focus; given *vs.* new). In many languages, new information is accented, whereas old information is de-accented. Li, Hagoort, and Yang (2008) found that, in Chinese, the N400 to new accented information was larger than the N400 to new de-accented information, despite the fact that the accentuation was contextually appropriate, whereas the absence of an accent was not. The authors suggest that these findings are best explained by the recruitment of additional unification resources for information that is marked as more salient by means of accentuation. It is unclear how the pre-activation view would fare with respect to these data.

Besides, sentences that are hypothesised to require additional combinatorial operations, such as complement coercions ("The journalist began the article", where the writing activity must be inferred) evoke a larger N400 at the coercing noun ("article") compared to controls ("The journalist wrote the article") (Figure 1d) (Baggio, Choma, van Lambalgen, & Hagoort, 2010;

[5] In the literature, this is discussed as the "integration view" of the N400 effect (Lau et al., 2008).

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Kuperberg, Choi, Cohn, Paczynski, & Jackendoff, 2010).[6] This effect was very similar to the N400 evoked by semantic anomalies. In this study, coercions but not anomalies elicit an N400 effect also at the word downstream of the coercing noun (Figure 1d) (Baggio et al., 2010). None of these words seems to tax access or retrieval processes, which makes it hard to see how a noncombinatorial account could explain these data.

fMRI research on meaning processing either compared sentences that contain semantic or pragmatic anomalies with their correct counterparts (Friederici et al., 2003; Hagoort et al., 2004; Kuperberg et al., 2000; Newman, Pancheva, Ozawa, Neville, & Ullman, 2001; Ni et al., 2000; Ruschemeyer, Zysset, & Friederici, 2006) or compared sentences with and without semantic ambiguities (Davis et al., 2007; Hoenig & Scheef, 2005; Rodd et al., 2005; Zempleni et al., 2007). The most consistent finding across these studies is the activation of the left inferior frontal cortex (LIFC), in particular Brodmann's areas 45 and 47, that is, respectively, *pars triangularis* and *pars orbitalis* of the third frontal convolution (IFG). As we noted above, the posterior middle and superior temporal gyri are also found to be activated in most semantic processing studies. For instance, Rodd et al. (2005) had participants listen to sentences in English like "There were dates and pears in the fruit bowl" and compared the hemodynamic BOLD response of these sentences to that of stimuli like "There was beer and cider on the kitchen shelf". The crucial difference between these sentences is that the former contains two homophones, i.e., "dates" and "pears", which, when presented auditorily, have more than one meaning. This is not the case for the words in the second sentence. Sentences containing lexical ambiguities led to increased activation in IFG and in the left posterior middle and inferior temporal cortex.

Another strand of evidence suggesting the involvement of IFG in semantic unification comes from research on multi-modal language comprehension. Using fMRI, Willems et al. (2007) assessed the neural interplay of semantic information from spoken words and from iconic co-speech gestures in a given sentence context. Sentences were presented in which a critical word was accompanied by an iconic gesture. Either the critical word or the gesture, or both, could be semantically incongruous with respect to the preceding sentence context. Both an incongruous word and an incongruous gesture led to increased BOLD responses in IFG as compared to congruous words and gestures (see Willems et al., 2008 for similar results with words accompanied by pictures of objects). Interestingly,

[6] Complement coercions are seen as requiring additional combinatorial operations in different formal semantic frameworks, by both type-based (Pustejovsky, 1995) and type-free theories (van Lambalgen & Hamm, 2004), but the precise characterisation of these operations is not the same across frameworks.

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the activation of left posterior STS was increased by an incongruous spoken word, but not by an incongruous hand gesture. The latter resulted in an increased BOLD response in dorsal pre-motor cortex. This suggests that neural activity in left posterior temporal cortex is triggered most strongly by processes involving the activation of lexical–semantic information, while the role of IFG is to unify semantic information, in this case from different modalities.

3.3. Unification and selection

Though IFG, including Broca's area, has traditionally been regarded as a language region, there is a wealth of recent neuroimaging research suggesting that its role extends beyond language. Several authors have argued that the function of IFG can be best characterised as "controlled retrieval" or "(semantic) selection" (Badre, Poldrack, Pare-Blagoev, Insler, & Wagner, 2005; Gold, Balota, Kirchhoff, & Buckner, 2005; Moss et al., 2005; Thompson-Schill, Bedny, & Goldberg, 2005; Thompson-Schill et al., 1997; Wagner, Pare-Blagoev, Clark, & Poldrack, 2001). Thompson-Schill, D'Esposito, Aguirre, and Farah (1997) showed that the left IFG was more strongly activated in a verb generation task when the noun serving as the cue allowed for several different verb responses, as opposed to nouns which could be related to only one or a few verbs. For example, in response to "scissors" participants tend to generate the verb "to cut", whereas "wheel" triggers a more diverse set of responses. On the basis of these and other findings, it was argued that IFG guides semantic selection among competing alternatives, with higher activation when there are more competitors.

How does the selection account of IFG function relate to the unification account? As one of us discussed in more detail elsewhere (Hagoort, 2005), unification often implies selection. For instance, in the study by Rodd et al. (2005), increased activation in IFG is most likely due to increased selection demands in response to sentences containing ambiguous words. Selection is often, but not always, a prerequisite for unification. Unification with or without selection is a core feature of language processing. Some information sources that are unified with linguistic signals do not have a stable semantic representation in long-term memory, such that they can undergo selection processes in a strict sense. For example, van Berkum, van den Brink, Tesink, Kos, and Hagoort (2008) and Tesink et al. (2009) had participants listen to sentences spoken by a number of different individuals. In some cases, the sentence contained a word that did not match semantically with the hearer's expectations about what a particular speaker would say: for example, "Every evening I drink some wine before I go to sleep" spoken by a young child's voice. They observe that these kind of semantic–pragmatic mismatches

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(which the authors call "speaker inconsistencies") elicit an N400 which is entirely similar, albeit scaled down in size by a Factor 4, to the N400 effect evoked by standard semantic anomalies (van Berkum et al., 2008). Increased activation levels were also observed in IFG for the same mismatch (Tesink et al., 2009). It seems unlikely that integration of information about characteristics of the speaker (gender or age) as indicated by the acoustics of the voice relies on selection. Analogously, there seems to be no fixed or conventionalised meaning of iconic co-speech gestures, which are often ambiguous outside a communicative context. However, increased activation is observed in IFG, for instance when the unification load of information from co-speech gestures is relatively high (Willems et al., 2007). Therefore, unification is a more general account of IFG function than selection, in the sense that it does imply selection, but covers additional combinatorial processes as well.

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4. THE BALANCE BETWEEN MEMORY AND UNIFICATION

In earlier sections, we have characterised the function and structure of the brain networks that support memory and unification in semantics. We have ascribed the memory storage of lexical information, integration (defined as convergence on a memory representation) and to some extent prediction-based processing to temporal cortex (MTG/STG), and unification to frontal cortex (IFG). However, while this picture is probably approximately correct, it is rather too static to capture experimental data in their full complexity. For instance, several studies on sentence processing have reported increased activation in especially left STG and MTG when the semantic unification load of a word increases given the preceding sentence context (Bookheimer, 2002; Davis et al., 2007; Friederici et al., 2003; Willems et al., 2007, 2008). Hagoort, Baggio, and Willems (2009) suggested that this may be the result of top-down signals from IFG indicating that, in the service of unification, lexical–semantic information needs to be maintained active longer, or needs to be re-accessed when unification load is increased (Humphries, Binder, Medler, & Liebenthal, 2007). Therefore, it is the dynamic interplay between IFG and MTG/STG that gives rise to successful semantic unification.

4.1. Connectivity matters

How are IFG and MTG/STG wired together? The view that has prevailed over the past century is that Broca's region (*pars opercularis* and *pars triangularis* of the IFG, BA 44 and BA 45) and Wernicke's area (posterior STG, BA 22) are connected by a dorsal bundle of white matter fibres: the arcuate fasciculus. Recent DTI studies of white matter connectivity within

the perisylvian language network indicate that there is a greater structural complexity of the *fasciculus arcuatus* than was previously thought: there are *three* separate white matter tracts connecting reciprocally temporal, parietal, and prefrontal areas. Still, the route from posterior superior and middle temporal gyri to inferior frontal cortex, and back, appears to pass through the classic dorsal pathway: the long, direct segment of the arcuate fasciculus (Catani, Jones, & Ffytche, 2004; Catani & Mesulam, 2008) (Figure 2).

This now-traditional notion was first proposed by Costantin von Monakow, and became later accepted by Carl Wernicke, who had, however, entertained a different view until then (Catani & Mesulam, 2008; Geschwind, 1967, 1970; Wernicke, 1874). Wernicke (1874) thought that temporal and frontal language areas were connected through a *ventral* pathway: the *fibrae propriae*, approximately corresponding to what modern neuroanatomy identifies as the extreme capsule (Makris & Pandya, 2009). There is some DTI evidence for the existence of a ventral language pathway, going against the classical view as supported by the first reconstruction of Catani et al. (2004). For instance, Saur et al. (2008) found that the dorsal pathway (the arcuate fasciculus) only connects temporal to pre-motor cortex (BA 6;

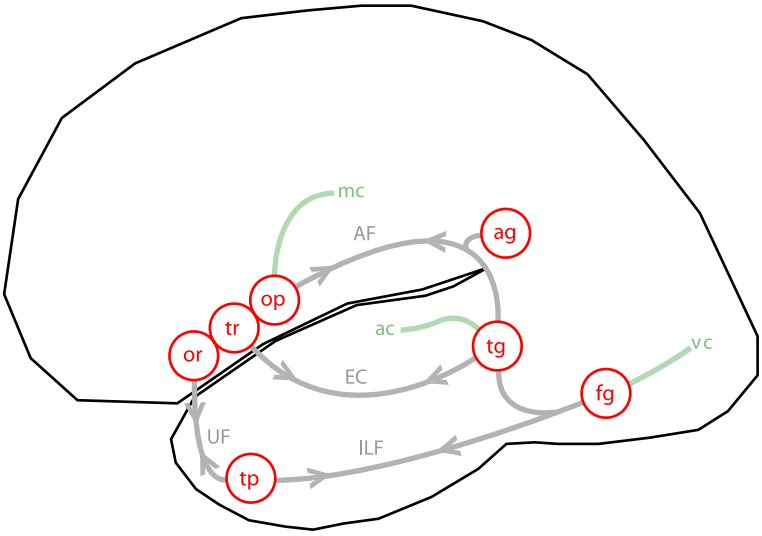

Figure 2. Simplified illustration of the anatomy and connectivity of the left hemisphere language network. Cortical areas are represented as red circles: pars orbitalis (or), pars triangularis (tr) and pars opercularis (op) of the LIFG; angular gyrus (ag), superior and middle temporal gyri (tg), fusiform gyrus (fg) and temporal pole (tp). White matter fibres are shown in grey, arrows emphasise bi-directional connectivity: arcuate fasciculus (AF), extreme capsule (EC), inferior longitudinal fasciculus (ILF), and uncinate fasciculus (UC). Interfaces with sensory-motor systems are shown in green: visual cortex (vc), auditory cortex (ac), and motor cortex (mc). [To view this figure in colour, please visit the online version of this Journal.]

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Figure 2); based on a pseudo-word repetition task, the authors argued that this network is involved in phonological processing and articulation. By contrast, temporal cortex projects onto frontal cortex (BA 45) through a ventral pathway, probably the extreme capsule (Figure 2); this network was found to be more active during a sentence comprehension task. These data have been taken to support a dual-route view of language (Hickok & Poeppel, 2004). Further evidence for a ventral bi-directional pathway has come from DTI (Frey, Campbell, Pike, & Petrides, 2008; Makris & Pandya, 2009) and cortical stimulation studies (Duffau et al., 2005; Mandonnet, Nouet, Gatignol, Capelle, & Duffau, 2007; Matsumoto et al., 2004).

Why should anatomical connectivity matter? One obvious answer is that neural models of language comprehension are bound to look rather different depending on whether there are direct or indirect pathways connecting the crucial nodes within a network supporting a particular set of linguistic operations. Suppose the direct connection through the extreme capsule did not exist. In that case, the posterior middle and superior temporal cortex would have to be wired up to the *pars triangularis* (BA 45) and *pars orbitalis* (BA 47) of IFG indirectly, first via a long-distance route connecting the arcuate fasciculus to pre-motor cortex (BA 6), and then via local connectivity within Broca's complex (IFG), which appears to be organised following a posterior-dorsal to anterior-ventral gradient: phonology (BA 6/44), syntax (BA 44/45), and semantics (BA 45/47) (Hagoort, 2005) (see Figure 2). This indirect dorsal route seems to be more consistent with a serial architecture (phonology-first, syntax-next, semantics-last, and possibly including feed-back) than with a fully parallel one (Jackendoff, 2007). The existence of a ventral pathway running through the extreme capsule suggests that, possibly alongside a serial processing stream (Sahin et al., there is also a parallel route which might play a role in language comprehension (Catani & Mesulam, 2008; Catani & Thiebaut de Schotten, 2008; Friederici, 2009; Makris & Pandya, 2009; Saur et al., 2008).

4.2. Neurotransmitter dynamics

With a rough sketch of the neuroanatomy of language in place, the remaining ingredients of our theory should be found in neurophysiology. This part is still very speculative, given the many unknowns about the neurotransmitter dynamics in the language relevant areas of the brain. Nevertheless, we will provide some tentative suggestions as an illustration of the direction we want to go. Friston (2005) assigns different roles to different neurotransmitters, depending on their decay times. Feed-forward connections appear to mediate their post-synaptic effects through fast AMPA (decay time: $\approx$2 ms) and GABAa receptors (decay time: $\approx$6 ms), and feed-back connections are most probably mediated by much slower NMDA receptors (decay time: $\approx$50 ms).

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These seem to be relatively frequent in supra-granular layers, where backward connections terminate (Sherman and Guillery 1998; Sherman 2007; Kiebel et al., 2008 NMDA-mediated channels may have a role in relaying modulatory effects that are more extended in time (Brunel, 2001; Wong & Wang, 2006). Lisman, Fellous, and Wang (1998) have shown that NMDA-receptor mediated EPSPs might be critical for the maintenance of information in working memory. They allow a network to maintain its active state without the need for synaptic modification. There is increasing evidence that cortical reverberation by re-entry is important for working memory (Fuster, 2009; Wang, 1999). We hypothesise that the same is true for language. The feed-forward MTG/STG-to-IFG pathway may be a rapid-decay route requiring NMDA mediated re-entry from IFG to MTG/STG to maintain lexical information active over time, as is essential for multi-word unification.

4.3. A typical processing cycle

Figure 2 provides a simplified scheme of the main nodes and connections supporting the Memory and Unification components. Figure 3 represents a processing cycle within the semantic unification network, including

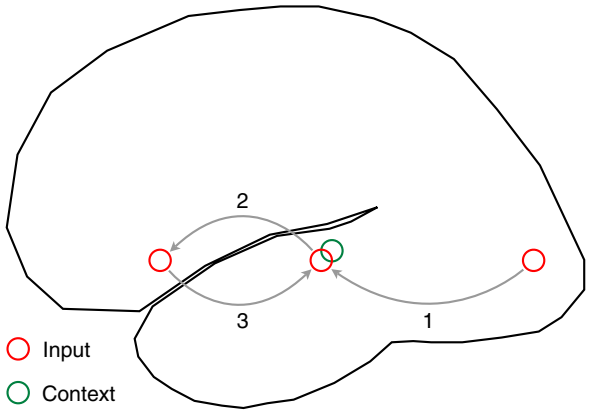

Figure 3. Processing cycle subserving word meaning comprehension in the left hemisphere language network. Inputs are conveyed from sensory regions (here visual cortex) to the inferior, middle and superior temporal gyri (1), where lexical information is activated. Signals are hence relayed to the inferior frontal gyrus (2), where neurons respond with a sustained firing pattern. Signals are then fed back into the same areas in temporal cortex from where they were received (3). A recurrent network is thus setup, which allows information to be maintained on-line, a context (green circle) to be formed during subsequent processing cycles, and incoming words to be unified within the context. At each processing cycle a balance is achieved by letting input-driven activity find attractor states, i.e., the maximum possible overlap with active populations in temporal cortex. [To view this figure in colour, please visit the online version of this Journal.]

MTG/STG and IFG (BA 45), connected by the extreme capsule. Let us for a moment ignore the context, shown as a green circle in Figure 3. Furthermore, we will assume that linguistic input, such as a word, is delivered visually.[7] We shall not comment on the purely visual aspects of word recognition or on visual-to-lexical transcoding (Perfetti, 1999). Here we only assume that structures in the inferior temporal lobe can act as interfaces between the visual system and the lexicon (Binder et al., 2003; Binder, Medler, Westbury, Liebenthal, & Buchanan, 2006; Cohen et al., 2000; Devlin, Jamison, Gonnerman, & Matthews, 2006; Nobre, Allison, & McCarthy, 1994), perhaps in cooperation with other brain areas (Mechelli, Gorno-Tempini, & Price, 2003; Price & Devlin, 2003). The mapping from visual input to lexical structures stored in the Memory component is represented by arrow 1 in Figure 3. This process exploits to some extent a direct ventral white matter route—the inferior longitudinal fasciculus (ILF, Figure 2) (Catani & Mesulam, 2008; Catani & Thiebaut de Schotten, 2008)—and is carried out during the first 200 ms after word onset (Hauk, Davis, Ford, Pulvermuller, & Marslen-Wilson, 2006). For simplicity, here we ignore processing of ILF-conveyed signals in the anterior temporal lobe, despite their possible role in semantic combinatorics (Lau et al., 2008; Visser et al., 2010).

In posterior temporal regions, neuronal populations are activated that represent lexical information associated with the incoming word, including semantic constraints that can in some respects be captured using logical formalisms as described earlier on. At this stage, input from other information streams (e.g., other sensory modalities) delivering stimuli that are associated with the given word (e.g., a barking sound or the sight of a dog co-occurring with the word "dog") are integrated in temporal cortex. From here, neural signals can only follow two routes. The first exploits local connectivity within temporal areas, through links that have the strongest connection weights, resulting in a graded activation of neighbouring neuronal populations, coding for related lexical structures. Such local spread of activation contributes to setting up a semantic context in temporal cortex (Figure 3, green circle), and may underlie priming and pre-activation at short SOAs (Lau et al., 2008). The second route is based on long-distance connections to IFG, through direct white matter fibres (extreme capsule) resulting in the selective activation of populations of frontal cortex neurons. These will respond with a self-sustaining firing pattern (see Durstewitz, Seamans, & Sejnowski, 2000 for a review). Efferent signals in this case can only take the long-range route back: in contrast with what happens in temporal cortex, we assume there are no memory patterns that are permanently stored in frontal cortex, which also means that

[7] This is for consistency with the ERP data shown in Figure 1, taken from experiments in which stimulus sentences were presented visually word-by-word (Baggio, 2008; Baggio, et al., 2008, 2010).

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there will be little or no spread of activation to neighbouring IFG populations through local connectivity. The most parsimonious account here is that frontal neurons will send efferent signals back to the *same* regions in temporal cortex from where afferent signals were received. This produces another spread of activation to neighbouring temporal areas, which implies that connections representing a given semantic context will be strengthened. This may subserve priming at longer SOAs, when the contribution of IFG is also more prominent (Lau et al., 2008). During each word processing cycle the system seeks a balance between the Memory (posterior temporal) and the Unification (inferior frontal) components, by letting activation reverberate through the circuit in Figure 3. Achieving such a balance may be more or less demanding, depending on how close the relation is between input and context, as we shall see below.

This description of a typical word processing cycle appears to be the simplest possible solution given constraints from brain imaging (the involvement of posterior temporal and inferior frontal areas), neuroanatomy (the existence of a direct white matter pathway, the extreme capsule, and connecting MTG/STG and IFG), and neurophysiology (persistent firing of IFG neurons). However, the proposed theory is rather a sketch that requires further elaboration, and crucially a computational implementation that would confer a precise meaning to the envisaged processing steps.

The distinction between the functions realised by Memory and Unification seems to be necessary to accommodate the linguistic distinction between type and token. Consider the "problem of 2" (Jackendoff, (2002), which is the problem of representing *different* occurrences of the *same* symbol. For example, the sentence "The little star is besides the big star" recruits twice during processing a lexico-semantic representation for the word "star". It cannot be the case that two (or arbitrarily many) copies of the meaning of "star" are stored in Memory, or that the same lexical type is copied in a working memory buffer where it gets interpreted and manipulated. In our theory, *different* neuronal populations in IFG can establish dynamic links to the *same* region in temporal cortex, acting as tokens of the same stored lexical type. This is not original: see Ballard, Hayhoe, Pook, and Rao (1997) for an earlier proposal. What may be new here is the account of the N400 that is suggested by our theory, to which we now turn.

5. A DYNAMIC ACCOUNT OF THE N400

The MUC model assigns the storage of lexical items to temporal cortex and the unification of retrieved structures to frontal cortex. Putting MUC in a more dynamic perspective, our theory of the interactions between Memory and Unification views retrieval as taking place during the feed-forward sweep

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through lexical types stored in MTG/STG, terminating in the activation of IFG populations representing lexical tokens; and unification as essentially the result of the co-activation of different tokens in IFG, dynamically linked to their lexical types in MTG/STG via persistent neuronal firing and feed-back connections. We propose that this cycle from temporal to frontal regions and back is manifested in the ERPs by the N400 component.

5.1. The N400 component

The fronto-temporal circuitry described above was suggested by the data reviewed in Sections 2 and 3, that include source modelling of the N400 effect as well as fMRI activity patterns evoked by similar antecedent conditions to those that give rise to the N400. Therefore, our theory of fronto-temporal interactions in semantics could serve as a basis for a neurocomputational model of the N400. Here we argue that the N400 component reflects reverberating activity within the MTG/STG–IFG network during one or perhaps several cycles, as shown in Figure 3. Activity starts building up around 250 ms from word onset, reflecting the summation of post-synaptic currents injected in MTG/STG by inferior temporal areas and by neighbouring populations in MTG/STG. The direct white matter route allows for a rapid spread of activation to IFG. The peak of the N400 coincides with the completion of the cycle that is with the re-injection of currents into MTG/STG.

5.2. The N400 effect

Across several word-processing cycles, a pattern of neuronal activity is set up in MTG/STG, encoding a context. This is the result of activation spreading to areas neighbouring to those activated by the input during the feed-forward sweep, and of a similar process taking place during the feed-back from IFG to MTG/STG. This process strengthens learned associations between semantic features, and is one aspect of acquiring a lexicon.

Consider now the case in which semantic relatedness is manipulated, for instance in "The girl was writing letters when her friend spilled coffee on the tablecloth/paper" (Baggio et al., 2008) (Figure 1b). Processing the fragment "The girl was writing letters when her friend spilled coffee on the" sets up a context in MTG/STG, maintained over time by feed-back currents from IFG. Semantic features associated with the words "writing" and "letters" are activated (Brunel & Lavigne, 2009; Cree & McRae, 2003; Cree, McRae, & McNorgan, 1999; Masson, 1991, 1995; McRae, 2004; Moss, Hare, Day, & Tyler, 1994). If these include features that contribute to the concept of paper, then there will be some overlap between the populations in MTG/STG representing the context and those that selectively respond to the given input

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that is to the incoming word "paper". Such overlap will be smaller for "tablecloth". The larger the overlap between context and input, the smaller the amplitude of the scalp ERP. In particular, the incoming word that benefits from a larger overlap with the context ("paper") results in a smaller N400 compared to the word that leads to a smaller overlap ("tablecloth"). *The inverse relation between semantic relatedness and N400 amplitude follows from an inverse relation between the degree of overlap of neuronal sources and the amplitude of scalp-recorded ERPs.* The amplitude of any given neural generator, in this case the superior temporal N400 generator, scales with the size of the neuronal population that is concurrently activated and for which this generator can be modelled as a single dipole. Hence, the sparser the neuronal population overlap, the smaller the amplitude.

A similar logic can be used to explain the "N400 priming effect". Under the assumption that there is something like an "N400 unification effect", the increase in the N400 amplitude as a function of unification load can be explained as follows. One possible neural account of unification is that two populations in IFG (coding for two different semantic tokens), upon receiving input from temporal cortex, start firing in a sustained manner, and inject currents back into the same temporal regions (coding for the two respective semantic types) from where signals were received, such that transient links are dynamically established between semantic types stored in temporal cortex. In all these cases, regardless of whether the N400 effect is driven by pre-activation or by unification, the theory is consistent with the finding that some of the strongest neuronal generators of N400 are localised in the left middle and superior temporal cortex. The post-synaptic currents that are responsible for the N400 are localised in MTG/STG because there is where most afferent signals are relayed: (1) from peripheral areas via inferior temporal cortex during early processing stages ($\approx$ 200 ms); (2) through local connectivity in MTG/STG due to spreading activation from input-selective populations to neighbouring temporal areas; and (3) from IFG during the feed-back that supports unification and the on-line maintenance of context. IFG may show a comparatively smaller net effect of post-synaptic currents over shorter time intervals, possibly due to fewer signals re-injected through local connectivity in IFG itself, but a stronger activation (as revealed by metabolic measures, and not by recording post-synaptic voltages) over longer times, due to the persistent firing patterns produced by IFG neurons. This could explain why MEG/EEG source analyses may fail to reveal significant contributions of IFG, whereas fMRI does show a strong or even the strongest response in IFG. Also, the time-locking of neural responses appears to be sharper in posterior temporal cortex than in inferior frontal areas (Liljeström, Hultén, Parkkonen, & Salmelin, 2009). This could be due to the fact that activity in IFG is less sensitive to the onset and offset times of

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the stimuli, and is rather a self-sustaining state which is relatively unaffected by trial-to-trial variation. In contrast, bottom-up activation in MTG/STG may have tighter deadlines, partly due to the proximity to sensory areas.

5.3. Testability and falsifiability

The theory predicts that IFG and MTG/STG are always jointly involved in word processing, albeit giving different contributions depending on the actual utterance to be processed and on the context in which that utterance occurs. One key consequence of this is that the theory would be refuted if it were shown that IFG (BA 45/47) is not among the neuronal generators of the N400. While this particular aspect of the theory appears to be *strongly falsifiable* in principle—i.e., falsifiable based on observation alone—in practice here one is looking for a null effect (i.e., the absence, relative to some threshold, of a response in IFG), with all the ensuing methodological problems. Nonetheless, clinical data could make the hypothesis testable also in practice: patients with focal lesions in BA 45 or BA 47 are expected to show at most the onset of an N400 response corresponding, in the theory, to the feed-forward spread of activation from sensory areas and inferior temporal cortex to MTG/STG (see Friederici, von Cramon, & Kotz, 1999; Hagoort, Brown, & Swaab, 1996; Kojima & Kaga, 2003 for some relevant data); for example, dynamic aphasia patients with focal atrophy affecting BA 45 may be especially suitable for testing this aspect of the theory (Luria, 1973, Robinson, Blair, & Cipolotti, 1998, Robinson, Shallice, & Cipolotti, 2005). A similar prediction applies to patients with a lesioned or atrophied extreme capsule. Fronto-temporal or semantic dementia patients too (Neary, Snowden, & Mann, 2005; Patterson, Nestor, & Rogers, 2007; Snowden, Neary, & Mann, 2002; Warrington 1975) may show reduced or degraded N400 components.

Testing the directionality of IFG–MTG/STG interactions during the two main stages of the generation of the N400 requires assessing the degree of fit of imaging data with models of neuronal source dynamics with or without backward connections (Garrido, Kilner, Kiebel, & Friston, 2007). This aspect of the theory is *weakly falsifiable*—i.e., falsifiable based on observation combined with modelling—in view of the possible finding that a purely feed-forward model explains best the source data.

6. CONCLUSIONS

In this paper, we presented an explicit account of processing word meaning in context based on insights from theoretical linguistics and findings from cognitive neuroscience. We take this to be the simplest possible theory that is

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consistent with the available anatomical and functional data, and that moreover is based on a falsifiable core hypothesis (the cycle shown in Figure 3). The theory explains the N400 as the result of the summation of currents injected by frontal into temporal areas (unification) with currents that are already circulating within temporal cortex due to the local spread of activation to neighbouring neuronal populations (pre-activation). In our theory, pre-activation and unification are not independent step-like processes, suggesting mutually exclusive accounts of the N400. Indeed, the two operations are theoretically distinct, and can to some extent be manipulated as independent variables. However, in realistic processing situations, access, retrieval, pre-activation and unification are all part of a word processing *cycle*—a continuous pattern of neuronal activity unfolding over time within a distributed cortical network.

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