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A Neurocomputational Model of the N400 and the P600 in Language Processing

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Abstract

Ten years ago, researchers using event-related brain potentials (ERPs) to study language comprehension were puzzled by what looked like a *Semantic Illusion*: Semantically anomalous, but structurally well-formed sentences did not affect the N400 component—traditionally taken to reflect semantic integration—but instead produced a P600 effect, which is generally linked to syntactic processing. This finding led to a considerable amount of debate, and a number of complex processing models have been proposed as an explanation. What these models have in common is that they postulate two or more separate processing streams, in order to reconcile the Semantic Illusion and other semantically induced P600 effects with the traditional interpretations of the N400 and the P600. Recently, however, these multi-stream models have been called into question, and a simpler single-stream model has been proposed. According to this alternative model, the N400 component reflects the retrieval of word meaning from semantic memory, and the P600 component indexes the integration of this meaning into the unfolding utterance interpretation. In the present paper, we provide support for this “Retrieval–Integration (RI)” account by instantiating it as a neurocomputational model. This neurocomputational model is the first to successfully simulate the N400 and P600 amplitude in language comprehension, and simulations with this model provide a proof of concept of the single-stream RI account of semantically induced patterns of N400 and P600 modulations.

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1. Introduction

In electrophysiological research into language comprehension, two brain responses take center stage. The first is the N400 component, a negative deflection of the event-related brain potential (ERP) signal. It peaks around 400 ms after stimulus onset, and it is sensitive to semantic anomalies (such as “He spread his warm bread with socks,” relative to “butter”; Kutas & Hillyard, 1980). The second is the P600 component, a positive deflection that generally reaches maximum around 600 ms. This component can be found in response to syntactic violations (such as “The spoilt child throw . . .,” relative to “throws” Hagoort, Brown, & Groothusen, 1993). The dissociative sensitivity of the N400 to semantics and the P600 to syntax has led to the tenet that the N400 indexes processes of semantic integration, whereas the P600 indexes processes of a syntactic nature (see Kutas, van Petten, & Kluender, 2006, for an overview). However, this mapping, which is at the core of many neurocognitive models of language processing, has been challenged by a set of findings that started to accumulate over the last decade. A number of studies revealed that certain types of syntactically sound, but semantically anomalous sentences failed to elicit the expected N400 effect, but produced a P600 effect instead (e.g., Hoeks, Stowe, & Doedens, 2004; Kim & Osterhout, 2005; Kolk, Chwilla, van Herten, & Oor, 2003; Kuperberg, Sitnikova, Caplan, & Holcomb, 2003). For instance, Dutch sentences such as “De speer heeft de atleten geworpen” (lit: “The javelin has the athletes thrown,” meaning “the javelin threw the athletes”) produced an increase in the P600 amplitude, but not in the N400 amplitude, relative to a non-anomalous control “De speer werd door de atleten geworpen” (lit: “The javelin was by the athletes thrown,” meaning “the javelin was thrown by the athletes”; Hoeks et al., 2004). Provided the established views on the N400 and the P600, findings such as these came as a surprise. That is, as javelins cannot throw athletes, the word *thrown* should create semantic processing difficulty, and hence an increase in the N400 amplitude. Also, as there is no need for syntactic reanalysis, there should be no increase in the P600 amplitude. In search of an explanation for these “Semantic Illusion” or “Semantic P600” effects¹ that maintains the established views on the N400 and the P600, the literature has seen a shift toward the so-called multi-stream models of language processing, in which a structure-insensitive semantic analysis stream operates in parallel to (and potentially interacts with) a more structure-driven algorithmic processing stream (see Bornkessel-Schlesewsky & Schlesewsky, 2008; Brouwer, Fitz, & Hoeks, 2012; Kuperberg, 2007, for reviews).

In the present paper, we put forward an alternative, single-stream account of these “Semantic P600” effects, for which we provide explicit computational support. That is, we present a formally precise neurocomputational “neural network” model that instantiates the recent Retrieval–Integration (RI) account of the N400 and the P600 in language comprehension (Brouwer & Hoeks, 2013; Brouwer et al., 2012). We show that our

neurocomputational simulations produce relevant patterns of N400 and P600 effects reflecting semantic processing, including the “Semantic P600” effect. We argue that these results provide a proof of concept of the RI account.

2. The Retrieval–Integration account

The finding that certain types of semantically anomalous, but syntactically sound sentences, do not produce an increase in the N400 amplitude, but rather one in the P600 amplitude (relative to a non-anomalous control), has challenged the core tenet in the electrophysiology of language that the N400 indexes processes of semantic integration and the P600 indexes syntactic processing. To explain such “Semantic P600” effects, while maintaining these views on the N400 and the P600, various *multi-stream* models of language processing have been devised that incorporate multiple, potentially interacting processing streams (*Monitoring Theory*: Kolk et al., 2003; *Semantic Attraction*: Kim & Osterhout, 2005; *Continued Combinatory Analysis*: Kuperberg, 2007; the *extended Argument Dependency Model*: Bornkessel-Schlesewsky & Schlewsky, 2008; and the *Processing Competition* account: Hagoort, Baggio, & Willems, 2009). All of these models include a processing stream that is purely semantic, unconstrained by any structural information (such as word order, agreement, and case marking, etc.). In processing a sentence such as “De speer heeft de atleten *geworpen*” (lit: “The javelin has the athletes *thrown*”), this stream of independent semantic analysis does not encounter semantic processing problems on the word *thrown*, and hence does not produce an N400 effect (relative to a non-anomalous control “De speer werd door de atleten *geworpen*”; lit: “The javelin was by the athletes *thrown*”), because it can easily construct an interpretation on the basis of the words *javelin*, *athletes*, and *thrown*, which fit together rather well (i.e., the interpretation that the athletes have thrown the javelin). The output of this processing stream, however, conflicts with that from an algorithmic, structure-driven stream that does take surface structural information into account (i.e., producing the interpretation that the javelin has thrown the athletes). The effort put into resolving this problem, then, is reflected in a P600 effect, purportedly showing structural revision.

On the basis of a comprehensive review of multi-stream models and the empirical data at hand, Brouwer et al. (2012) conclude that none of the models is capable of explaining the full range of relevant findings in the literature. For one, most of the proposed models have difficulty explaining biphasic N400/P600 effects, such as those found by Hoeks et al. (2004) in response to “De speer heeft de atleten *opgesomd*” (lit: “The javelin has the athletes *summarized*,” meaning that the javelin summarized the athletes) relative to a non-anomalous control “De speer werd door de atleten *geworpen*” (lit: “The javelin was by the athletes *thrown*”). Here, the words *javelin*, *athletes*, and *summarized* do not fit together well, and hence the independent semantic analysis stream should have difficulty constructing an interpretation, which should lead to an N400 effect. Critically, the algorithmic stream should agree with the independent semantic analysis stream that the sentence is infelicitous, meaning that the streams are not in conflict, and that there should be

no P600 effect reflecting a conflict resolution process. This is inconsistent with the observed biphasic N400/P600 effect. What is more, none of the models can account for isolated P600 effects in a larger discourse. Nieuwland and van Berkum (2005), for instance, presented participants with short stories, like a story about a tourist checking into an airplane with a huge suitcase, and a woman behind the check-in counter deciding to charge the tourist extra because the suitcase is too heavy. This story was then continued with “Next, the woman told the *suitcase* [...]” At the word *suitcase*, all multi-stream models predict an N400 effect but no P600 effect (relative to the non-anomalous “*tourist*”), because the independent semantic analysis stream and the algorithmic stream should agree upon the infelicity of the sentence so far. However, the reverse was actually found: The word *suitcase* produced a P600 effect, and no N400 effect (relative to *tourist*). Hence, these multi-stream models fall short of explaining the full breadth of relevant data.

In contrast to seeking a solution for the “Semantic Illusion” phenomenon in aspects of cognitive architecture (e.g., an increase in number of processing streams), Brouwer et al. (2012) argued for a functional reinterpretation of the ERP components involved. First of all, in line with previous suggestions (Kutas & Federmeier, 2000; Lau, Phillips, & Poeppel, 2008; van Berkum, 2009), they propose that the N400 component reflects *retrieval* of lexical-semantic information, rather than semantic integration or any other kind of compositional semantic processing. Retrieving the information associated with a word is easier if that information is already (partially) activated by its prior context. This explains why the word *butter* engenders a much smaller N400 in the context of “He spread his warm bread with [...]” than the word *socks*. The lexical knowledge associated with *butter* is already activated by its prior context, as it fits well with *spread* and *warm bread*; in contrast, *socks* does not fit at all. It is important to note that this pre-activation stems from the preceding lexical items (*spread* and *bread*), as well as from the message representation that has been constructed so far (e.g., a breakfast scene). The retrieval view on the N400 also explains the absence of an N400 effect in the “Semantic Illusion” data: in both the target (“The javelin has the athletes [...]”) and the control (“The javelin was by the athletes [...]”) condition, the preceding context pre-activates the lexical features of an incoming word (e.g., *thrown*), yielding no difference in the N400 amplitude, and hence no N400 effect.

If we accept the retrieval hypothesis on the N400, the question rises where in the ERP signal the integration of the retrieved word meaning into the unfolding utterance representation shows up. Brouwer et al. (2012) argue that these integrative processes are reflected in the P600 amplitude. They hypothesize that the P600 is a family of late positive components, all of which reflect aspects of the word-by-word construction, reorganization, or updating of an utterance interpretation. This integrative processing may intensify (leading to an increase in P600 amplitude) in all kinds of processing circumstances, for instance, when new discourse entities need to be accommodated, relations between entities need to be established, thematic roles need to be assigned, information needs to be added to entities, already established relations need be revised, or when conflicts between information sources (e.g., with respect to world knowledge)

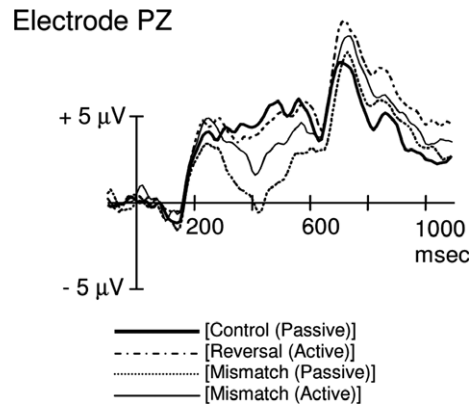


Fig. 1. Results (Pz electrode) of the ERP experiment by Hoeks et al. (2004). Positive is plotted upward. Note that this single electrode only serves as an illustration; our present simulation results are compared to the (statistically evaluated) effects found on the whole array of electrodes used in the original study.

need to be resolved. In other words, the compositional processes of integration and interpretation that were traditionally assumed to underlie N400 amplitude on the integration view, are hypothesized to be reflected in the amplitude of the P600 instead. This naturally explains the presence of a P600 effect in the “Semantic P600” sentences: Integrating the meaning of the critical word (*thrown*) with its prior context leads to an anomalous interpretation in the target condition (“The javelin has the athletes [...]”), but not in the control condition (“The javelin was by the athletes [...]”). Interestingly, this integration view on the P600 predicts that semantic anomalies, like “He spread his warm bread with *socks/butter*,” should not only produce an increase in N400 amplitude, but also an increase in the P600 amplitude (see Section 5.4 for further discussion). A close look at the data reveals that this is indeed the case (see Kutas & Hillyard, 1980, Fig. 1c, which clearly reveals a biphasic N400/P600 pattern). Not only semantic anomalies, but also syntactic complexities and anomalies can elicit a P600 effect. On the Integration view on the P600, these effects reflect difficulties in establishing a coherent utterance representation, rather than processes operating on a purely syntactic representation (Brouwer et al., 2012). We will return to this issue in the discussion.

Given the Retrieval view on the N400 component and the Integration view on the P600 component, Brouwer et al. (2012) suggested that language is processed in biphasic N400/P600—RI—cycles: Every incoming word modulates the N400 component, reflecting the processes involved in activating its associated conceptual knowledge. Every word also modulates the P600 component, reflecting the processes involved in integrating this activated knowledge into an updated utterance representation. Although they have argued that the resultant single-stream RI account has the broadest empirical coverage of extant models (Brouwer et al., 2012; Hoeks & Brouwer, 2014), this account is still a conceptual one. In what follows, we will offer a formally precise neurocomputational instantiation of the RI account and present a simulation of the results of an ERP experiment by Hoeks et al. (2004), thereby providing the RI account with a proof of concept.

3. The neurocomputational model

Our aim is to derive a neurocomputational model of language processing that indexes the N400 and the P600 components of the ERP signal in language processing. In deriving such a model, we want to minimally adhere to the following design principles. First, we should model the N400 and the P600 in a single comprehension architecture, rather than in two separate models. Second, we should model the right level of granularity: We aim to index scalp-recorded summations of post-synaptic potentials in large neural populations, and we should therefore model the processes underlying the N400 and the P600 at that level. Third, estimates of N400 and the P600 amplitude should emerge from the processing behavior of the model; that is, the model should not be explicitly trained to produce these estimates. Fourth, the model should account for the relevant patterns of ERP effects induced by semantic processing. We take the model to be successful if for a given contrast it produces the correct N400 effect and/or P600 effect (or the absence thereof). Finally, to assure the generalizability of the model, we want to obtain these effects in at least two separate, independent simulations.

In what follows, we will show how we derived a neurocomputational model of language processing that adheres to these design principles. To satisfy the first three principles, we employ a single artificial neural network architecture, which offers the right level of granularity and allows for modeling the N400 and the P600 as emergent phenomena of processing. To satisfy principle four, we want to capture “Semantic P600” effects, as well as traditional semantically induced biphasic N400/P600 effects (cf. Kutas & Hillyard, 1980). To this end, we will model an experiment by Hoeks et al. (2004). This study compared semantically anomalous Dutch sentences like “De speer *heeft* de atleten geworpen” (lit: “The javelin *has* the athletes thrown”) to normal controls like “De speer *werd door* de atleten geworpen” (lit: “The javelin *was by* the athletes thrown”). This comparison revealed a P600 effect on the final verb *thrown*, but no N400 effect (see Table 1 and Fig. 1). Two other semantically anomalous conditions were also compared to the same control, and both showed a biphasic N400/P600 effect on the final word: “De

Table 1
Materials and effects of the Hoeks et al. (2004) study

Item	Condition	Effect
De speer werd door de atleten <u>geworpen</u> <i>The javelin was by the athletes thrown</i>	Control (Passive)	—
De speer heeft de atleten <u>geworpen</u> <i>The javelin has the athletes thrown</i>	Reversal (Active)	P600
De speer werd door de atleten <u>opgesomd</u> <i>The javelin was by the athletes summarized</i>	Mismatch (Passive)	N400/P600
De speer heeft de atleten <u>opgesomd</u> <i>The javelin has the athletes summarized</i>	Mismatch (Active)	N400/P600

Notes. Materials used in the event-related brain potential experiment by Hoeks et al. (2004), as well as the effects that were observed for each condition (relative to control).

speer *heeft* de atleten *opgesomd*” (lit: “The javelin *has* the athletes *summarized*”) and “De speer *werd door* de atleten *opgesomd*” (lit: “The javelin *was by* the athletes *summarized*”) (see Table 1 and Fig. 1). Finally, to satisfy principle five, we will conduct two independent simulations of this experiment. Below, we will first introduce the overall architecture of the model, which we will subsequently break down in detail. Next, we will introduce the results of our simulations of the Hoeks *et al.* experiment.

3.1. Model architecture

The RI account postulates that incremental, word-by-word language processing proceeds in RI cycles. Mechanistically, each cycle can be conceptualized as a function *process*: (*word form, utterance context*) → *utterance representation*, mapping a perceived word w_t (word form), and the context established after processing words w_1, \dots, w_{t-1} that precede w_t (utterance context), into an updated utterance interpretation spanning words w_1, \dots, w_t (utterance representation). Critically, this mapping is not direct. The RI account breaks it down into a Retrieval and an Integration subprocess by introducing an intermediate representation encoding the meaning of word w_t . This intermediate representation is the output of the Retrieval process, which can be conceptualized as a function *retrieve*: (*word form, utterance context*) → *word meaning*, mapping a word w_t (word form) into a representation of its meaning (word meaning), while taking into account the context in which it occurs (utterance context). The output of this Retrieval process, a representation of the meaning of word w_t , serves as input to the Integration process. During Integration, it is combined with the context established after processing words w_1, \dots, w_{t-1} to produce an updated utterance representation spanning the entire utterance w_1, \dots, w_t . Hence, the Integration process can be conceptualized as a function *integrate*: (*word meaning, utterance context*) → *utterance representation*, mapping the meaning of a word w_t (word meaning) and its prior context (utterance context) into an updated utterance interpretation (utterance representation).

Our neurocomputational model is effectively an “extended” Simple Recurrent Network (SRN; Elman, 1990) that instantiates the *process* function, broken down into its *retrieve* and *integrate* subprocesses. Fig. 2 provides a schematic overview of our model. The model consists of five layers of artificial neurons, implementing the input to the model (INPUT), a Retrieval module (RETRIEVAL and RETRIEVAL_OUTPUT), and an Integration module (INTEGRATION and INTEGRATION_OUTPUT). All artificial neurons in the model are logistic dot-product units, meaning that the activation level y_j of a unit j is defined as:

$$y_j = \frac{1}{1 + e^{-x_j}}, \quad (1)$$

where x_j is the net input to unit j :

$$x_j = \sum_i y_i w_{ij}, \quad (2)$$

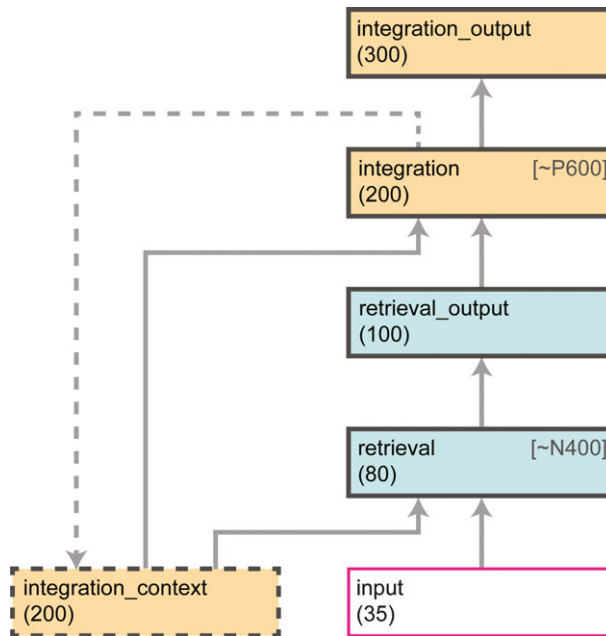


Fig. 2. Schematic illustration of the neurocomputational model instantiating the Retrieval–Integration account of the N400 and the P600. Each rectangle represents a vector of artificial (logistic dot-product) neurons, and each solid arrow represents a matrix of connection weights that connect each neuron in a projecting layer to each neuron in a receiving layer. The network receives its input at the INPUT layer and produces its output at the INTEGRATION_OUTPUT layer. The rectangle with a dashed border is a context layer (cf. Elman, 1990), and the dashed arrow represents a copy projection; prior to feedforward propagation of activation from the INPUT to the INTEGRATION_OUTPUT layer, the INTEGRATION_CONTEXT layer receives a copy of the INTEGRATION layer. At time step $t = 0$, the activation value of each unit in the INTEGRATION_CONTEXT layer is set to 0.5. All layers except the INPUT and INTEGRATION_CONTEXT layer also receive input from a bias unit (not shown), the activation value of which is always 1.

which is determined by the activation level y_i of each unit i that propagates to unit j , and the weight w_{ij} on the connection from i to j . Time in the model is discrete, and at each processing timestep t , activation flows from the INPUT layer, through the RETRIEVAL layer to the RETRIEVAL_OUTPUT layer, and from RETRIEVAL_OUTPUT layer through the INTEGRATION layer to the INTEGRATION_OUTPUT layer. To allow for context-sensitive retrieval and integration (see below), the RETRIEVAL and the INTEGRATION layer both also receive input from the activation pattern in the INTEGRATION layer as established at the previous timestep $t - 1$, effectuated through an additional context layer (INTEGRATION_CONTEXT; cf. Elman, 1990). Prior to feedforward propagation of activation from the INPUT to the INTEGRATION_OUTPUT layer, this INTEGRATION_CONTEXT layer receives a copy of the INTEGRATION layer (at timestep $t = 0$, the activation value of each unit in the INTEGRATION_CONTEXT layer is set to 0.5). Finally, all layers except the INPUT and INTEGRATION_CONTEXT layer also receive input from a bias unit, the activation value of which is always 1.

Overall, the model is trained to map sequences of word forms, clamped onto the INPUT layer, into an utterance representation encoding sentence meaning in the INTEGRATION_OUTPUT layer. It does so on an incremental, word-by-word basis, thereby instantiating the *process* function (the processing of a word takes a single time tick; cf. Elman, 1990). In the model, word forms are localist word representations, and the utterance representations are thematic-role assignment representations (i.e., *who-does-what-to-whom/what*; cf. Crocker, Knoeferle, & Mayberry, 2010; Mayberry, Crocker, & Knoeferle, 2009). We will further elaborate upon these representations below. Importantly, the mapping from word forms into an utterance representation is not direct, as it is broken down into the *retrieve* and *integrate* subprocesses, which can be directly linked to the N400 and the P600 component, respectively. Provided an incoming word w_t (INPUT), and the unfolding context (INTEGRATION_CONTEXT), the RETRIEVAL layer serves to activate a word meaning representation of w_t in the RETRIEVAL_OUTPUT layer. Hence, the function of the RETRIEVAL layer is to *retrieve* word meaning. In the model, word meaning representations take the form of distributed semantic feature vectors, which we will elaborate below. The INTEGRATION layer, in turn, combines the activated word meaning representation (RETRIEVAL_OUTPUT) with the unfolding context (INTEGRATION_CONTEXT), into an updated utterance representation (INTEGRATION_OUTPUT). The INTEGRATION layer thus serves to *integrate* word meaning into the unfolding interpretation.

In what follows, we will provide a detailed derivation of the overall model, broken down into a Retrieval and an Integration module. We will describe how each of these modules was trained, and we will give a formal description of the representations involved. Next, we will provide a word-by-word walk-through of the processing dynamics of the model, as well as a derivation of the linking hypotheses to the N400 and the P600 component.

3.2. (De)constructing the Integration module

In the model, the processing of a single word entails two context-sensitive mappings: one from a word form representation into a word meaning representation (*retrieve*), and one from a word meaning representation into an utterance representation (*integrate*). In order to get the model to produce the intermediate word meaning representations, we employ a two-stage training procedure in which we first construct the Integration module, and subsequently add the Retrieval module (the reason for this will be explained in section 3.3.2).

The Integration module is a subnetwork of the overall model: An SRN consisting of the RETRIEVAL_OUTPUT (input to the SRN), INTEGRATION (hidden), INTEGRATION_OUTPUT (output), and INTEGRATION_CONTEXT (context) layers (hence, it is the overall model minus the INPUT and RETRIEVAL layers). Recall that we want the Integration module to implement the function *integrate*: $(\text{word meaning}, \text{utterance context}) \rightarrow \text{utterance representation}$, mapping the meaning of a word w_t (word meaning) and its prior context (utterance context) into an updated utterance interpretation (utterance representation). To this end, we train the Integration module to map sequences of word meaning representations, clamped onto the RETRIEVAL_OUTPUT layer, into an utterance representation in the INTEGRATION_OUTPUT layer.

3.2.1. Word meaning representations

Following the intuition behind many influential theories of word meaning, our model employs feature-based semantic representations as word meaning representations (see McRae, Cree, Seidenberg, & McNorgan, 2005, for an overview on semantic features). More specifically, it employs 100-dimensional binary representations, which were derived from a large corpus of Dutch newspaper texts (the TwNC corpus; Ordelman, Jong, Hessen, & Hondorp, 2007), using the correlated occurrence analogue to lexical semantics (COALS; Rohde, Gonnerman, & Plaut, unpublished data). We derived these representations both for words belonging to the open word class as well as for words belonging to the closed word class. Appendix S2 provides a detailed description of this derivation procedure.

3.2.2. Utterance representations

The utterance representations produced by our model are thematic-role assignment representations (i.e., *who-does-what-to-whom/what*; cf. Crocker et al., 2010; Mayberry et al., 2009). These thematic-role assignment representations are 300-dimensional vectors, which are divided into three 100-dimensional slots. These three slots respectively identify the word meaning representations of the elements that will be *agent*, *action*, and *patient* (cf. Mayberry et al., 2009).

3.2.3. Training data

Our aim is to model the study by Hoeks et al. (2004), which includes active and passive constructions (see Table 1). To this end, we want the model to “understand” sentences with the following template structure:

Active sentences:

de	[AGENT]	heeft	het/de	[PATIENT]	[ACTION]
the	[AGENT]	has	the _(+/-NEUTER)	[PATIENT]	[ACTION]

Passive sentences:

het/de	[PATIENT]	werd	door	de	[AGENT]	[ACTION]
the _(+/-NEUTER)	[PATIENT]	was	by	the	[AGENT]	[ACTION]

Importantly, we want the model to “know” (like human language users) that (a) any noun can theoretically be an *agent* or a *patient* (productivity), but (b) there are certain combinations of *agents*, *actions*, and *patients* that are more plausible (stereotypicality; ~ minimal world knowledge, cf. Mayberry et al., 2009). For each simulation, we generated a separate set of training sentences from the above templates, by filling in the *agent*, *patient*, and *action* slots, using the nouns (agent and patient) and verbs (action) listed in Appendix S1 (note that each of the two simulations uses a completely different set of nouns and verbs, corresponding to different word meaning representations, and therefore different utterance representations). Agent nouns were always preceded by the determiner “de” (the_{-NEUTER}), and patient nouns by either “de” (the_{-NEUTER}) or “het” (the_{+NEUTER}), depending on the gender of the noun (note that “het” unambiguously signals a neuter

noun in Dutch; see Table A1 in Appendix S1). The items in each set can be divided into two halves. The first half of each set is intended to teach the model principle (1) and consists of sentences constructed by permuting each of the 20 nouns (agents plus patients) with each verb, yielding $20 \times 20 \times 10 = 4,000$ active sentences, and $20 \times 20 \times 10 = 4,000$ passive sentences (i.e., 8,000 items in total). The second half of training set is intended to induce principle (2) and consists only of sentences with stereotypical agent–action–patient combinations (rows of Table A1). This means that each stereotypical triplet occurs $8,000/10 = 800$ times in this half of the training data. Again, half of these items are actives, and half of them are passives. As a result, each full set contains 16,000 training items (50% actives and 50% passives), in which each verb appears 1,600 times, 802 times ($\approx 1:1$) of which in a stereotypical agent–action–patient construction, and two times ($\approx 0.001\%$) of which in *each* of the non-stereotypical constructions. Hence, each stereotypical agent-action-patient construction occurs 401 times more frequently than any non-stereotypical agent-action-patient triplet. Overall, this yields a stereotypicality/non-stereotypicality ratio of $0.50125/0.49875 \approx 50\%$, which we take to reflect no a priori bias toward either productivity (principle 1) or stereotypicality (principle 2) (cf. Mayberry et al., 2009).

As the Integration module must learn to process sentences word-by-word, each training item consists of a sequence of either 6 (active sentences) or 7 (passive sentences) *pairs* of input and target patterns. The input patterns consist of word meaning representations, and the target is always the desired utterance representation. Note that for anomalous agent–action–patient combinations, these targets also reflect the corresponding anomalous utterance representations.

3.2.4. Training procedure

We trained the Integration module using bounded gradient descent (Rohde, 2002), a modification of the standard backpropagation algorithm (Rumelhart, Hinton, & Williams, 1986). Each model (i.e., one for each simulation) was trained for 7,000 epochs, minimizing mean-squared error (*MSE*). In each epoch, gradients were accumulated over 100 items before updating the weights (within each item, error was backpropagated after each word). Training items were presented in a permuted order, such that by the end of training, the model has seen each item at least 43 times ($7,000/(16,000/100) = 43.75$). After all of the 16,000 items were presented once, the training order was permuted again. Weights were initially randomized within a range of $(-0.25, +0.25)$ and were updated using a learning rate of 0.2, which was scaled down to 0.11 with a factor of 0.95 after each 700 epochs (that is, after each 10% interval of the total epochs; $0.2 \times 0.95^{10} \approx 0.11$). The momentum coefficient was set to a constant of 0.9. Finally, we used a zero error radius of 0.1, such that no error was backpropagated when the difference between the produced activity level y_j of a unit j and the desired activity level d_j of this unit was smaller than 0.1, that is, when $|y_j - d_j| < 0.1$. Appendix S3 provides a detailed, mathematical description of the training procedure.

After training, we evaluated the comprehension performance of the model, using an output-target similarity matrix. For each item, we computed the cosine similarity between

the output vector for that item, and each of the 16,000 different target vectors (see Appendix S3). The output vector for an item was considered correct if it was more similar to its corresponding target vector than to the target vector of any other item. Comprehension performance was perfect (100% correct) for each of the two models ($MSE_{\text{model}_1} = 0.212$; $MSE_{\text{model}_2} = 0.206$).

3.3. (De)constructing the Retrieval module

With the Integration module in place, we can now add in the Retrieval module to arrive at the overall model as outlined above (and depicted in Fig. 2). Like the Integration module, the Retrieval module can be seen as a subnetwork of the overall model: An SRN consisting of the INPUT (input to the SRN), RETRIEVAL (hidden), RETRIEVAL_OUTPUT (output), and INTEGRATION_CONTEXT (context) layers. Recall that we want the Retrieval module to implement the function *retrieve*: (*wordform*, *utterance context*) \rightarrow *word meaning*, mapping a word w_t (word form) into a representation of its meaning (word meaning), while taking into account the context in which it occurs (utterance context). To this end, we train the Retrieval module to map word form representations, clamped onto the INPUT layer, into word meaning representations in the RETRIEVAL_OUTPUT layer, while taking into account the unfolding context in the INTEGRATION_CONTEXT layer.

3.3.1. Word form representations

The word form representations that serve as input to the Retrieval module, and hence to the overall model, are localist word representations encoding word identity. That is, the model employs 35-dimensional localist word representations, in which each unit corresponds to a single word (20 nouns + 10 verbs + 2 auxiliary verbs + 2 determiners + 1 preposition = 35 words).

3.3.2. Training data and procedure

If one ignores context (INTEGRATION_CONTEXT), the mapping from word form representations (INPUT) into word meaning representations (RETRIEVAL_OUTPUT), the *retrieve* function, is a straightforward recoding problem; the RETRIEVAL layer must simply map each of the 35 unique word form representations into its corresponding, unique word meaning representation. However, on the RI account, the retrieval of word meaning is assumed to be strongly context-driven, and therefore we want the RETRIEVAL layer to take into account the utterance context in the INTEGRATION_CONTEXT layer. For reasons laid out below, getting the model to produce this behavior is not straightforward, and in order to obtain the intended behavior, we derive a rather non-standard training procedure, which involves training the Retrieval module as part of the overall model. Note, however, that we do not posit our model as a model of language acquisition, and hence do not attribute any psychological or biological reality to our training procedure; our only interest is the resultant comprehension model.

An intuitively attractive, but incorrect approach would be to train the Retrieval module as a standalone SRN, before combining it with the Integration module to arrive at

the overall model. That is, one could present the Retrieval module with sequences of input-target patterns, of which the inputs are word form representations and the targets are word meaning representations. This approach requires the utterance contexts as constructed by the Integration module (*INTEGRATION_CONTEXT*), which could in principle be recorded, and presented to the Retrieval module as inputs along with the word form representations. However, this approach boils down to the same straightforward recoding outlined above (i.e., mapping from 35 unique word form representations into their corresponding, unique word meaning representations), but now with an additional source of information: the utterance contexts. Because these contexts vary substantially across sentences, they will be nothing but noise to the model, and hence the model is better off ignoring them. Crucially, this is true for all approaches in which the Retrieval module is explicitly trained to produce the correct word meaning representations (see Appendix S4 for empirical support). Hence, we need an approach to training that pressures the model to take utterance context into account. To achieve this, we trained the Retrieval module as part of the overall network. After training the Integration module, we added in the *INPUT* and *RETRIEVAL* layers, to arrive at the overall model as depicted in Fig. 2. In this model, we froze all the weights in the Integration module, that is, all weights on the projections: *RETRIEVAL_OUTPUT* \rightarrow *INTEGRATION*, *INTEGRATION* \rightarrow *INTEGRATION_OUTPUT*, and *INTEGRATION_CONTEXT* \rightarrow *INTEGRATION* (as well as those on the relevant biases). We then trained the overall model, using the same procedure and the same patterns as we used for training the Integration module, with the exception that the inputs to the model were now word form representations, clamped onto the *INPUT* layer. Thus, the overall model has to learn to map sequences of word form representations into an utterance representation. This approach has two important consequences for our desired behavior.

First, due to the fact that the Integration module is no longer malleable (its weights are frozen), it becomes fully deterministic. This means that in order to map a sequence of word form representations (*INPUT*) into an utterance representation (*INTEGRATION_OUTPUT*), the model has to find a way to activate the right inputs to the Integration module (*RETRIEVAL_OUTPUT*). As the Integration module was trained to high accuracy, this means that for a given word form representation, the output of the Retrieval module (*RETRIEVAL_OUTPUT*) is forced to be close to the corresponding word meaning representation (or a subset of its relevant semantic features, depending on the solution found during the training of the Integration module).

Second, the error signal is now driven by the desired utterance representations, rather than by the word meaning representations. This means that in order for the model to incrementally construct such an utterance representation, it must take into account the utterance context. That is, without context, it would simply try to map each individual word form (in isolation) into an utterance representation. Hence, this approach pressures the Retrieval module of the model to take the utterance context (*INTEGRATION_CONTEXT*) into account when trying to map a word form (*INPUT*) into the utterance representation (*INTEGRATION_OUTPUT*). As described above, this in itself requires the model to activate the

right inputs (RETRIEVAL_OUTPUT)—the right word meaning representations (or relevant semantic features thereof)—for the Integration module.

After training, we again computed an output-target similarity matrix, but this time on the overall model. Comprehension performance was perfect (100% correct) for each of the two models ($MSE_{\text{model}_1} = 0.273$; $MSE_{\text{model}_2} = 0.248$). Moreover, we also computed the cosine similarity between the produced word-meaning representations at RETRIEVAL_OUTPUT and their desired targets, for each word in each possible sentence. As expected, the Retrieval module outputs word meaning representations that are highly similar to the word meaning representations used in training the Integration module ($\text{cos}_{\text{model}_1} = .951$ [$SD = .023$]; $\text{cos}_{\text{model}_2} = .961$ [.021]).

3.4. Processing in the model

Now that we have arrived at the full model, we can walk through its processing dynamics on a word-by-word basis. As our aim is to model the ERP experiment by Hoeks et al. (2004), we will show how the model processes each of the four conditions contrasted in this study (see Table 1). To this end, we constructed an example sentence for each condition, using materials from simulation 1: a control sentence “De maaltijd werd door de kok bereid” (lit: “The meal was by the cook prepared”; [Control (Passive)]), a role-reversed sentence “De maaltijd heeft de kok bereid” (lit: “The meal has the cook prepared”; [Reversal (Active)]), a passive mismatch sentence “De maaltijd werd door de kok gezongen” (lit: “The meal was by the cook sung”; [Mismatch (Passive)]), and an active mismatch sentence “De maaltijd heeft de kok gezongen” (lit: “The meal has the cook sung”; [Mismatch (Active)])—see Section 4.1 for more details on how we derived these sentences. To gain insight into what the model anticipates at different points in processing, Fig. 3 shows how close (in terms of cosine similarity) the word meaning representation in each thematic-role slot (in the INTEGRATION_OUTPUT layer) is to either the representation of each of the nouns (“kok”/“cook” and “maaltijd”/“meal”) for the *agent* and *patient* slots, or to that of each of the verbs (“bereid”/“prepared” and “gezongen”/“sung”) for the *action* slot.

A first thing to note about the processing dynamics of the model is that once it encounters the first noun “maaltijd”/“meal,” it moves from a state of relative indecision about the sentence interpretation (at “de”/“the”),² to a state in which it strongly anticipates the interpretation that the “meal was prepared by a cook”; hence, not only does it anticipate “meal” to obtain a *patient* role, it also anticipates (albeit to a somewhat lesser extent) “cook” to be the *agent* and “prepared” to be the *action*. If the sentence unfolds as a passive construction ([Control (Passive)] and [Mismatch (Passive)] conditions in Fig. 3), signaled by the auxiliary verb “werd”/“was,” these predictions are gradually confirmed by the consecutive words. The sentence-final verb, then, either completely confirms the anticipated interpretation (“bereid”/“prepared”) or disconfirms it by signaling that the anticipated *action* should be revised (“gezongen”/“sung”). On the other hand, if the noun “maaltijd”/“meal” turns out to be part of an active construction ([Reversal (Active)] and [Mismatch (Active)] conditions in Fig. 3), as signaled by the auxiliary

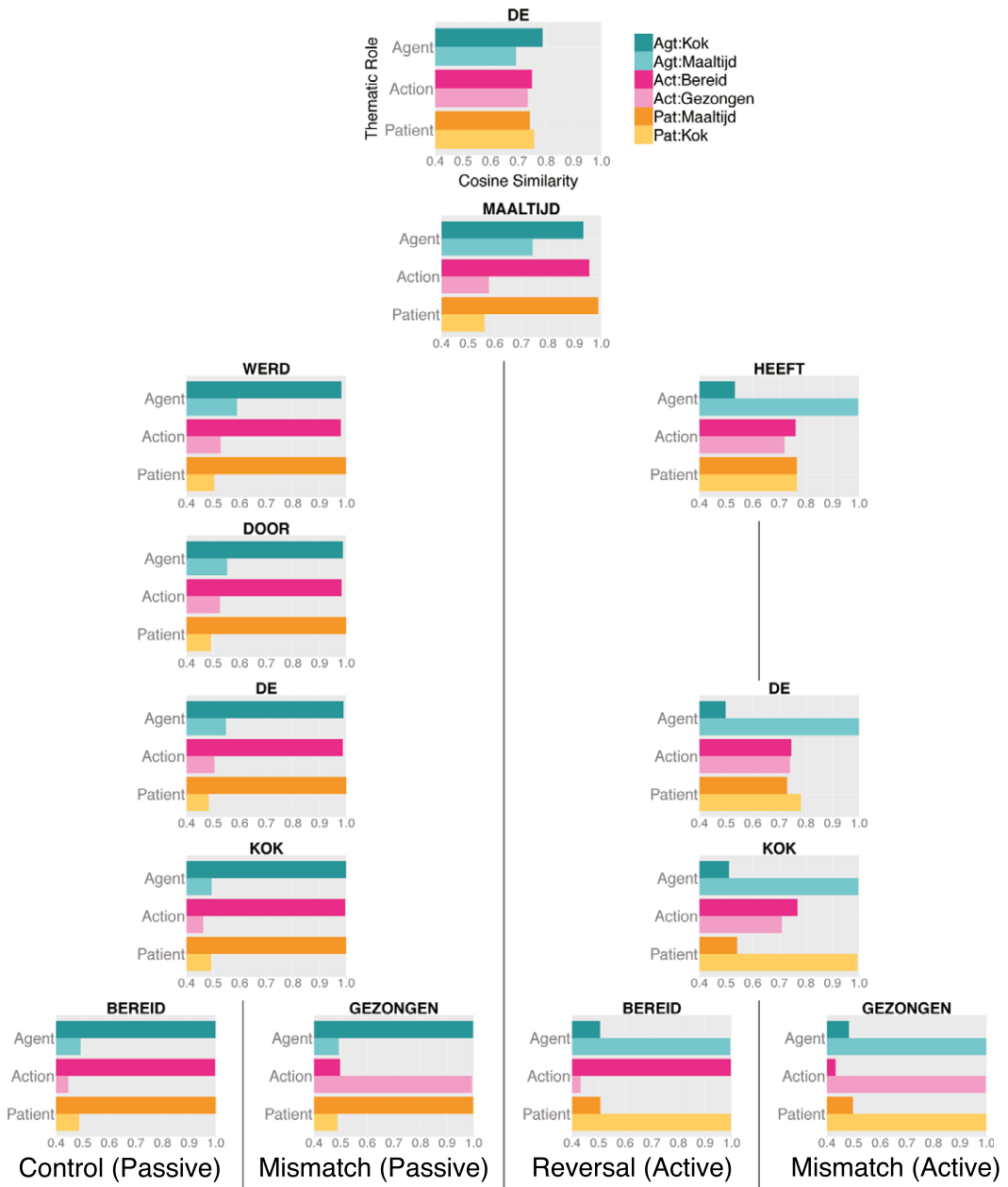


Fig. 3. Illustration of the word-by-word processing of an example sentence (from simulation 1) for each condition of the Hoeks et al. (2004) experiment (see text). The bar plots show the cosine similarity of the word meaning representation in each thematic-role slot (in the INTEGRATION_OUTPUT layer) relative to either the representation of each of the nouns (“kok”/“cook” and “maaltijd”/“meal”) for the *agent* and *patient* slots, or to that of each of the verbs (“bereid”/“prepared” and “gezongen”/“sung”).

“heeft”/“has,” the model immediately revises its anticipated interpretation to one in which the “maaltijd”/“meal” is assigned the role of *agent*, and in which the *patient* and *action* have yet to be determined. The model updates the former upon encountering the second noun “kok”/“cook,” and the latter upon encountering the sentence-final verb (“bereid”/“prepared” or “gezongen”/“sung”).

Crucially, the model thus differentially anticipates the interpretations of active and passive sentences, as well as the sentence-final verbs across these constructions (i.e., see the interpretation constructed at the pre-final word “kok”/“cook”). This means that the internal representation at the INTEGRATION layer of the model contains different information across these constructions. Consequently, the contextual inputs to the RETRIEVAL layer (from the INTEGRATION_CONTEXT → RETRIEVAL projection) and the INTEGRATION layer of the model (from the INTEGRATION_CONTEXT → INTEGRATION projection) also differ across these constructions. If we compare the activation pattern in the INTEGRATION layer after processing the noun “kok”/“cook” in either an active or a passive construction, using cosine similarity, these patterns are clearly different ($\cos = .569$). Moreover, if we look at the activation patterns in the RETRIEVAL layer and the INTEGRATION layer after processing the sentence-final verb “bereid”/“prepared,” we see an effect of these different contexts. That is, although the sentence final words (and therefore their word form and word meaning representations) are the same, the activation patterns are different at the RETRIEVAL layer (.847) and the INTEGRATION layer (.567) across actives and passives. Hence, the activity patterns at both the RETRIEVAL and the INTEGRATION layer are modulated by context. Interestingly, the effect of context is not reflected in the output of Retrieval module at the RETRIEVAL_OUTPUT layer (.952); the same word forms obtain highly similar word meaning representations in different contexts (as is evidenced by the mean similarity scores reported at the end of Section 3.3.2). If, on the other hand, different sentence final-words (e.g., “bereid”/“prepared” vs. “gezongen”/“sung”) occur in the same context, this also modulates the activation patterns at the RETRIEVAL (active: .359; passive: .268) and INTEGRATION layer (active: .735; passive: .771). In summary, then, the RETRIEVAL and INTEGRATION layers appear to successfully implement the *retrieve* and *integrate* functions, respectively.

3.5. Linking hypotheses

Provided the observed processing behavior of the model, we can now formulate a linking hypothesis between N400 amplitude and activity in the RETRIEVAL layer, and a linking hypothesis between the P600 amplitude and activity in the INTEGRATION layer.

3.5.1. Linking hypothesis to the N400

On the RI account, N400 amplitude is an index of the amount of processing involved in activating the conceptual knowledge associated with an incoming word in memory. More specifically, at any given point in processing, we assume the semantic memory system to be in a particular state, reflecting the preceding word and prior context. Upon encountering a next word in the current context, activation of the conceptual knowledge

associated with this word involves an alteration of this state. The process of altering the state of semantic memory from one word to the next is what we assume to be reflected in the N400 component; if the previous and new state are relatively similar (because the new state was anticipated by the previous state; i.e., context pre-activated the conceptual knowledge associated with the incoming word), state transition requires little work, and N400 amplitude will be reduced. If, on the other hand, the previous and new state are highly dissimilar (context did non pre-activate the conceptual knowledge associated with the incoming word), state transition requires more effort, and N400 amplitude is increased. Hence, we take the N400 amplitude to be a measure of the *processing* induced by a mismatch between the predicted conceptual knowledge and the conceptual knowledge associated with the observed word; that is, we do not take N400 amplitude to be a direct measure of the mismatch itself.

In the model, retrieval processes take place in the RETRIEVAL layer, which implements the function *retrieve*: (*word form, utterance context*) \rightarrow *word meaning*. Given the identity (word form) of a given word w_t , and the utterance context as established after processing words w_1, \dots, w_{t-1} that precede w_t (INTEGRATION_CONTEXT), the Retrieval module will draw upon its input history to activate the meaning representation (or the relevant semantic features thereof) corresponding to word w_t . Crucially, the training of the Retrieval module was driven by the utterance representation, which forced the model into a context-dependent solution for this word form to word meaning mapping. As a result, the internal representations constructed at the RETRIEVAL (hidden) layer of the module are high-dimensional abstractions over the word form representations and utterance contexts (its inputs) and word meaning representations (its outputs), rather than intermediate word meaning representations. Hence, any changes in the activation pattern of the RETRIEVAL layer can be taken to reflect changes in the semantic memory state of the model, and therefore as processing required for activating and/or deactivating semantic features. As such, we estimate N400 amplitude for a given word w_t as the degree of change that this word induces in the activity pattern of the RETRIEVAL layer, provided the activity pattern as established after processing the previous word w_{t-1} , using cosine dissimilarity:

$$\text{N400} = 1 - \cos(\text{RETRIEVAL}_t, \text{RETRIEVAL}_{t-1}) \quad (3)$$

3.5.2. Linking hypothesis to the P600

On the RI account, the P600 amplitude reflects the amount of processing involved in the word-by-word construction, reorganization, or updating of an utterance interpretation. In the model, this processing takes place in the INTEGRATION layer, which implements the *integrate* function. Given the meaning of a word w_t (RETRIEVAL_OUTPUT), and the utterance context as established after processing words w_1, \dots, w_{t-1} that precede w_t (INTEGRATION_CONTEXT), the Integration module will draw upon its input history to predict the most likely utterance representation for the sentence so far (see Section 3.4). Crucially, the anticipatory state of the Integration module (an SRN) is contained within its internal representation at the INTEGRATION (hidden) layer, which constitutes a high-dimensional

abstraction over the inputs to the module (word meaning representations and utterance contexts), and its outputs (utterance representations). Hence, any changes in the activation pattern of the INTEGRATION layer can be taken to reflect processing involved in (re)composing the utterance representation. As such, we estimate the P600 amplitude for a given word w_t as the degree of change that its meaning induces in the activity pattern of the INTEGRATION layer, provided the activity pattern as established after processing the previous word w_{t-1} , using cosine dissimilarity (cf. Crocker et al., 2010):

$$\text{P600} = 1 - \cos(\text{INTEGRATION}_t, \text{INTEGRATION}_{t-1}) \quad (4)$$

4. Simulations

With the model in place, we can now turn to the simulation of the actual data from an ERP experiment. Recall that we want our model to capture “Semantic P600” effects, as well as traditional semantically induced biphasic N400/P600 effects (cf. Kutas & Hillyard, 1980). To this end, we set out to model the study by Hoeks et al. (2004). Table 1 lists the materials of this study and their associated effects, and Fig. 1 shows their ERP modulations at the Pz electrode.

4.1. Testing procedure

To test the contrasts from the Hoeks et al. (2004) study in the model, we generated two sets of 40 test sentences, one set for each simulation. Each set contains 10 passive stereotypical agent-action-patient sentences [Control (Passive)], 10 active role-reversed sentences [Reversal (Active)], 10 passive semantic mismatch sentences [Mismatch (Passive)], and 10 active semantic mismatch sentences [Mismatch (Active)]. The role-reversed sentences were constructed by swapping the stereotypical agents and patients. The passive mismatch sentences were constructed in the same way as the control sentences, except that the stereotypical action verb was replaced by a mismatch verb (listed in Table A1 in Appendix S1). The active mismatch sentences, finally, were constructed like the role-reversed sentences, but also had the stereotypical action verb replaced by a mismatch verb.

We presented these materials to the model³ and recorded its N400 and P600 estimates at the critical words. The model produces estimates in the range [0, 1] (cosine dissimilarities), whereas the original ERP modulations are voltage fluctuations on an “unbounded” microvolts scale [$-\mu\text{V}$, $+\mu\text{V}$]. In order to visually compare the model estimates to the ERP data, we therefore transformed the ERP amplitudes to a zero-to-one scale, using the transformation $(\mu\text{V} - \min(\mu\text{V})) / (\max(\mu\text{V}) - \min(\mu\text{V}))$. Fig. 4 compares the N400 estimates as produced by the models (one for each simulation) to the N400 modulations in the ERP experiment (at the Pz electrode), and Fig. 5 shows the comparison between the P600 estimates produced by the models, and the P600 modulations in the ERP experiments (also at the Pz electrode). Note that this visual comparison of the model estimates to the ERP modulations at the Pz electrode only serves as an illustration. Below, we will

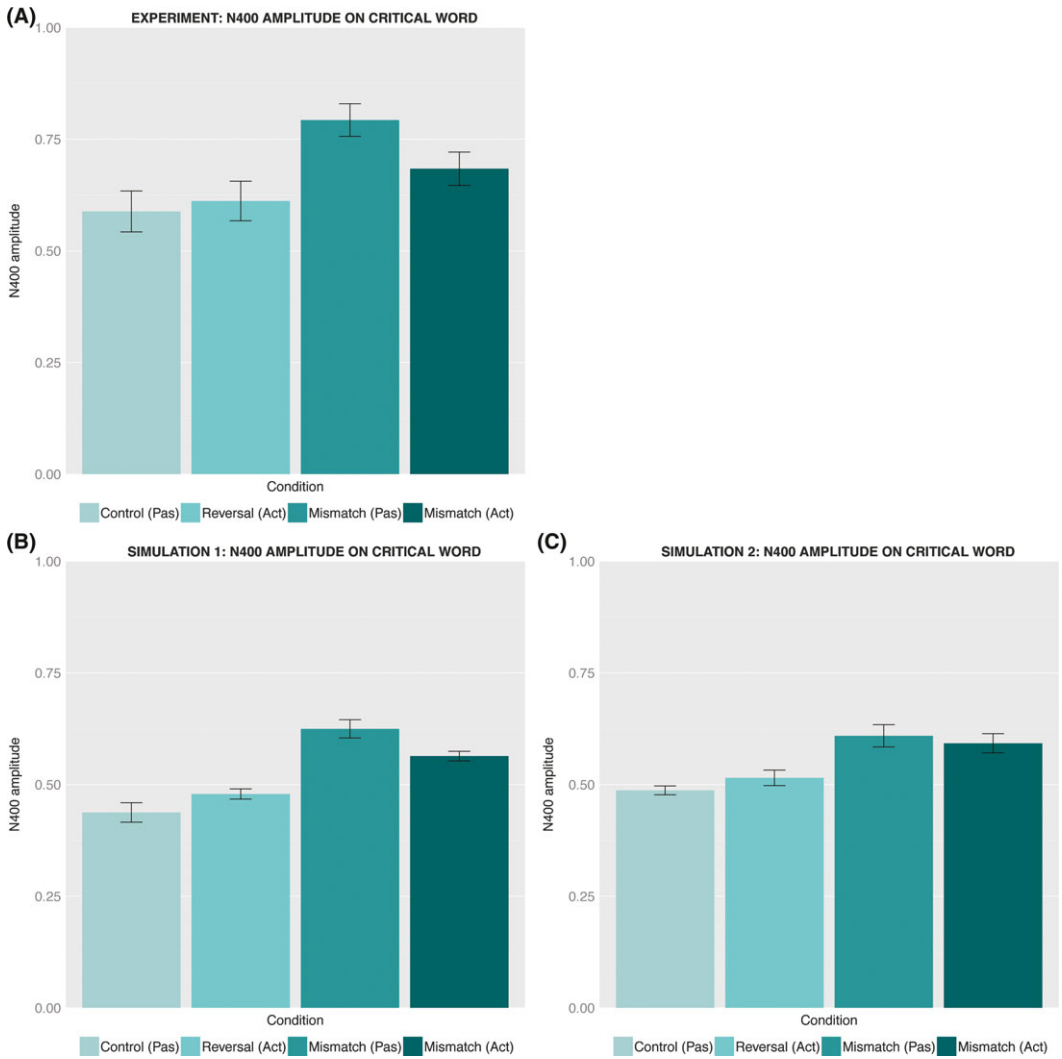


Fig. 4. N400 results of the simulations in comparison to the results of the original experiment by Hoeks et al. (2004). Panel (A) shows the N400 amplitudes as measured in the original experiment (at the Pz electrode), transformed to a zero-to-one scale (see text). Panel (B) shows the N400 estimates measured in simulation 1, and panel (C) those measured in simulation 2. Error bars show standard errors.

compare our simulation results to the (statistically evaluated) effects found on the whole array of electrodes used in the original study.

4.2. N400 results

Recall that we take the model to be successful if for a given contrast it produces the same N400 effect and P600 effect (or the absence thereof) as found in the Hoeks et al.

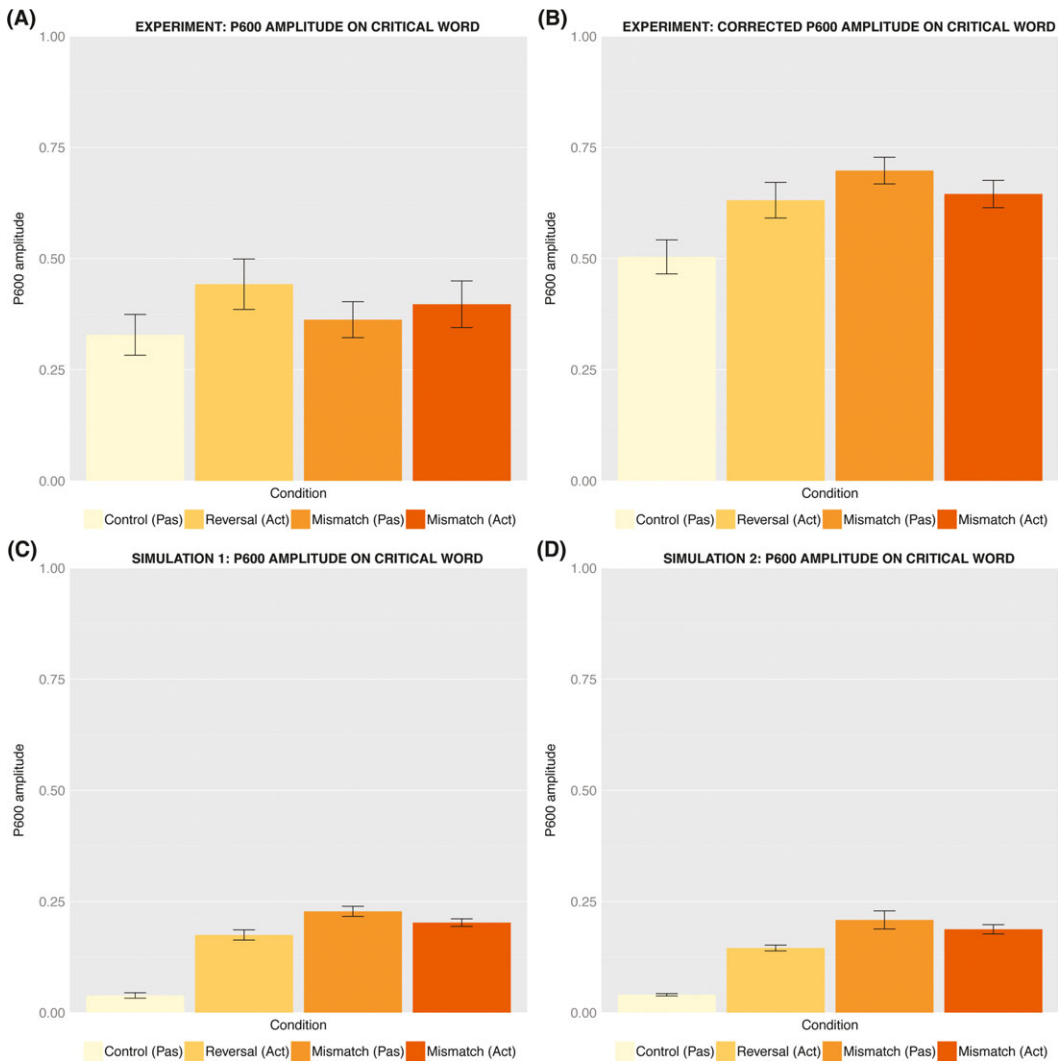


Fig. 5. P600 results of the simulations in comparison to the results of the original experiment by Hoeks et al. (2004). Panel (A) shows the P600 amplitudes as measured in the original experiment (at the Pz electrode), transformed to a zero-to-one scale (see text). Panel (B) shows these P600 amplitudes corrected for overlap with the N400 component (also at Pz and on a zero-to-one scale). Panel (C) shows the P600 estimates measured in simulation 1, and panel (D) those measured in simulation 2. Error bars show standard errors.

(2004) study (see Table 1). For the N400, statistical evaluation, using repeated-measures ANOVA (with Condition as four-level within-items factor and Huynh-Feldt correction where necessary) showed a successful simulation of the original findings. The main effect of Condition was significant in each of the simulation experiments (Exp 1: $F(3, 27) = 45.1; p < .001$; Exp 2: $F(3, 27) = 12.3; p < .001$), and subsequent pairwise comparisons showed that (a) the N400 effect was absent in role-reversed “Semantic

Illusion” sentences (Exp 1: $p = .47$ [Bonf.]/ $p = .08$ [Uncorr.]; Exp 2: $p = .91$ [Bonf.]/ $p = .15$ [Uncorr.]), and (b) there was a significant N400 effect for the two other anomalous conditions (Exp 1: $p < .005$; Exp 2: $p < .01$).

4.3. P600 results

For the P600 component, we also successfully simulated the original findings. In both simulations, the P600 amplitude was significantly higher for all anomalous sentences (including the role reversed “Semantic Illusion” sentences) compared to controls (Main effect of Condition: Exp 1: $F(3, 27) = 136.5$; $p < .001$; Exp 2: $F(3, 27) = 70.1$; $p < .001$); pairwise comparisons showed that there was a significant P600 effect for all three anomalous conditions compared to control (Exp 1: all three p -values $< .001$; Exp 2: all three p -values $< .001$).

4.4. On the ordering of effect sizes

The model successfully simulated the desired effects on all planned contrasts. An additional question is if the model also produces the same relative ordering of effects as revealed in the ERP data. For the N400, the model estimates do indeed numerically follow the ordering of the empirical data. However, for the P600, the model predicts the P600 amplitude to be largest for the [Mismatch (Passive)] and [Mismatch (Active)] conditions, whereas in the empirical data, it is the largest for the [Reversal (Active)] condition. A possible reason for this difference is that in the ERP experiment the amplitude of the P600 may be affected by the amplitude of the preceding N400 (see Brouwer & Hoeks, 2013; Hagoort, 2003). If we correct for this, by pointwise subtraction of the N400 amplitude from the P600 amplitude in each condition, the pattern of results as far as the relative order within the three anomalous conditions is concerned comes in line with the results of the simulations (mismatch conditions larger than the role-reversed sentences; Fig. 5, Panel (B)). We take this to be an interesting observation for further study, and we return to it in the discussion.

5. Discussion

We have presented a neurocomputational model that instantiates the recent RI account of the N400 and the P600 in language processing (Brouwer & Hoeks, 2013; Brouwer et al., 2012). We have provided explicit and scalable (i.e., to larger groups of neurons mimicking true cortical areas, as well as to models with larger empirical coverage) linking hypotheses between processing behavior in the model and estimates of the N400 and the P600, and we have shown that the model is able to capture traditional biphasic N400/P600 effects, as well as “Semantic P600” effects. Overall, we take our results to provide a “proof of concept” of the RI account of the electrophysiology of language processing. Moreover, as our model instantiates a single-stream architecture, we take it to support the

claim that there is no need for multiple processing streams (such as an independent semantic analysis stream) to explain “Semantic P600” effects. Below, we will discuss the implications of our model and sketch directions for future research.

5.1. On the N400 and the role of context

On the RI account, the retrieval of word meaning, reflected in N400 amplitude, is assumed to be contextually driven. This poses an architectural constraint on the model, as we want its Retrieval module to instantiate this context-sensitivity. To this end, we trained the Retrieval module as part of the overall model, rather than as a separate module (see Section 3.3.2). Our model successfully predicted the desired N400 effects for the contrasts tested in the Hoeks et al. (2004) study: No N400 effect for the role-reversed condition [Reversal (Active)] relative to control [Control (Passive)], and an N400 effect for both the passive mismatch [Mismatch (Passive)] condition and the active mismatch condition [Mismatch (Active)] relative to control. In Appendix S4, we show empirically that other approaches toward training the Retrieval module do not induce such context-sensitivity and hence do not yield the desired results.

The reliance of the retrieval of word meaning on context supports the theoretical idea that the absence of an N400 effect for the role-reversed sentences “De maaltijd heeft de kok bereid” (lit: “The meal has the cook prepared”) relative to controls “De maaltijd werd door de kok bereid” (lit: “The meal was by the cook prepared”) is explained through contextual priming, stemming from both the preceding lexical items (e.g., “meal” and “cook”), as well as from the message representation that has been constructed so far (a scene involving a meal and a cook). Yet a better understanding of where this and the other observed N400 patterns stem from in our model requires further scrutiny of the factors driving them. Each individual N400 estimate depends on two factors: the state of the RETRIEVAL layer after processing the pre-critical word (RETRIEVAL_{t-1}), and the state of the RETRIEVAL layer after processing the critical word (RETRIEVAL_t). Consequently, an N400 *effect* is governed by four factors: the two states of the RETRIEVAL layer in a target sentence (T:RETRIEVAL_{t-1} and T:RETRIEVAL_t), and the two states of the RETRIEVAL layer in the control sentence (C:RETRIEVAL_{t-1} and C:RETRIEVAL_t). More precisely, an N400 effect for a contrast may stem from differences between conditions at the pre-critical word ($\text{T:RETRIEVAL}_{t-1} \neq \text{C:RETRIEVAL}_{t-1}$), differences at the critical word ($\text{T:RETRIEVAL}_t \neq \text{C:RETRIEVAL}_t$), or both. To identify which of these factors govern our results, we numerically dissect the tested contrasts, using the sentences shown in Fig. 3 (from simulation 1): “De maaltijd [werd door]/[heeft] de kok bereid/gezongen” (lit: “The meal [was by]/[has] the cook prepared/sung”).

In the [Mismatch (Passive)] versus [Control (Passive)] contrast, the sentences are identical up to the critical word (“De maaltijd werd door de kok”); that is, after processing the pre-critical word, there is no difference in the state of the RETRIEVAL layer between conditions ($\text{COS}(\text{T:RETRIEVAL}_{t-1}, \text{C:RETRIEVAL}_{t-1}) = 1$). Hence, for this contrast the observed N400 effect is driven by the differences in the state of the RETRIEVAL layer induced by the critical word ($\text{COS}(\text{T:RETRIEVAL}_t, \text{C:RETRIEVAL}_t) = .268$). In the [Mismatch (Active)] versus [Control (Passive)] contrast, however, the sentences differ prior to the

critical word, which is reflected in the differential state of the RETRIEVAL layer ($\cos(T:\text{RETRIEVAL}_{t-1}, C:\text{RETRIEVAL}_{t-1}) = .879$). At the critical word, however, the difference in the state of the RETRIEVAL layer is much more pronounced ($\cos(T:\text{RETRIEVAL}_t, C:\text{RETRIEVAL}_t) = .235$). Hence, the N400 effect for this contrast is again predominantly induced by the processing of the critical word. Indeed, the absence of an N400 effect for the [Reversal (Active)] versus [Control (Passive)] contrast lends further support for this view. Here, the difference at the pre-critical word is the same as in the [Mismatch (Active)] versus [Control (Passive)] contrast ($\cos(T:\text{RETRIEVAL}_{t-1}, C:\text{RETRIEVAL}_{t-1}) = .879$). Yet, at the critical word, the state of the RETRIEVAL layer is also highly similar across conditions ($\cos(T:\text{RETRIEVAL}_t, C:\text{RETRIEVAL}_t) = .847$). This tells us that, all things equal, a difference in voice (active/passive) only minimally affects the state of the RETRIEVAL layer. Hence, the N400 effects obtained in our simulations are primarily driven by the processing of the critical word. Of course, other manipulations of the pre-critical material, for instance, replacing one of the nouns, may have a stronger effect on the state of the RETRIEVAL layer at the pre-critical word, and hence on the N400 estimate at the critical word. In extending the model, this behavior may prove crucial for capturing N400 effects in context manipulation designs.

Given that we estimate the N400 amplitude as the dissimilarity of the RETRIEVAL layer at two consecutive timesteps, the model predicts an additional potential influence on the N400 amplitude: featural overlap between consecutive words. More specifically, our linking hypothesis predicts that N400 amplitude may be affected by the degree to which two consecutive words share semantic features in their meaning representations. This raises the question if such featural overlap is at play in our simulations, and if so, how they affect our N400 effects; that is, it could be that part of our N400 effects are driven by a larger similarity of the second noun (e.g., "cook") to the congruent sentence-final verbs (e.g., "prepared" in the [Control (Passive)] and [Reversal (Active)] conditions) compared to the incongruent sentence-final verbs (e.g., "sung" in the [Mismatch (Passive)] and [Mismatch (Active)] conditions). The cosine similarities between the nouns and verbs, however, reveal that this was not the case. In simulation 1, there was only a small bias toward congruent continuations (congruence: .531 [$SE = .014$]; incongruence: .490 [.018]), whereas congruent and incongruent continuations were balanced in simulation 2 (congruence: .496 [.023]; incongruence: .495 [.020]). If any at all, featural overlap between consecutive words should thus have only a very minimal effect on our N400 effects. Hence, our effects are being driven by context. However, this does not mean that featural overlap between consecutive words should generally not affect N400 amplitude; N400 effects in word pairs, for instance, in which a semantically unrelated second word of a pair produces a larger N400 than a semantically related one (Bentin, McCarthy, & Wood, 1985; Boddy, 1981), might be largely driven by featural overlap, rather than contextual priming.

A further illustration of contextual modulation of our N400 estimates is the fact that the model correctly predicted the relative ordering of the N400 effects ([Control (Passive)] < [Reversal (Active)] < [Mismatch (Active)] < [Mismatch (Passive)]). Crucially, these relative differences can only be attributed to context, as the second nouns and final

verbs are the same for the [Control (Passive)] and [Reversal (Active)] conditions (“kok/“cook” and “bereid”/“prepared”), and for the [Mismatch (Passive)] and [Mismatch (Active)] conditions (“kok/“cook” and “gezongen”/“sung”).

5.2. Relation to other neurocomputational models

The simulations presented in the current paper focused on modeling the amplitudes of the N400 and the P600 component in sentence processing. Whereas our model is the first to capture the amplitude of both the N400 and the P600 component in a single neurocomputational model, our work is not the first attempt to model the processes underlying language-related ERP components. Recently, at least three other neurocomputational models have been put forward to explain certain aspects of the electrophysiology of language processing (all of which build on a rich history of neurocomputational—*connectionist*—models; see Christiansen & Chater, 2001, for an overview). These models differ in the type of linguistic processing that they aim to explain, as well as in the granularity of neurophysiological detail that they incorporate.

Crocker et al. (2010), for instance, propose a model of situated sentence processing that learns to mediate utterance and visual scene information, in order to construct a sentence interpretation in the form of a thematic role assignment representation (see also McClelland, St. John, & Taraban, 1989). This model produces P600 correlates for each word in a sentence, in a similar fashion as our model. However, the Crocker et al. model does not incorporate the N400, as we do in our model. The two other models focus on word recognition rather than sentence processing. Laszlo and Plaut (2012) propose a neurally plausible model of visual word recognition, which they show is able to successfully simulate N400 amplitude modulations during the reading of words, pseudowords, acronyms, and illegal strings, as well as to perform lexical decision. One aspect that is particularly noteworthy about this model is that it also successfully captures the temporal dynamics of the N400 component; that is, the development of the N400 amplitude over time. In the Laszlo and Plaut model, N400 amplitude is estimated as the mean semantic activation in the semantics layer of a connectionist architecture. Rabovsky and McRae (2014), however, challenge this relation between N400 amplitude and mean semantic activation. Using a set of simulations with a feature-based connectionist attractor network, they show that implicit prediction error—the difference between the semantic features that the model expected to encounter, and those actually encountered—provides a better account for N400 amplitude over a wide range of word processing phenomena, such as effects of semantic priming, semantic richness, frequency, and repetition. Interestingly, the idea of modeling the N400 amplitude as implicit prediction error seems to be highly compatible with our approach toward modeling the N400 amplitude as a measure of how much the pattern of activation changes in memory due to the processing of an incoming word; changes are large when pre-activated (implicitly predicted) features mismatch with the actual features of an incoming word. Although both the model by Laszlo and Plaut and the model by Rabovsky and McRae contribute to fine-grained insight into N400 modulations during word recognition, neither of the models captures N400 effects due to

priming from the larger sentential context. Here, our model makes a novel contribution, as it is able to simulate contextually induced N400 modulations. What is more, our model also produces estimates of sentence-level P600 modulations, which may prove difficult to incorporate in models of visual word recognition.

5.3. Toward covering a broader spectrum of the ERP phenomena

In the present simulations, we focused on showing that our model can account for important patterns of ERP modulations in semantic processing. An important next step is to see if the model can also account for processing phenomena beyond semantically induced effects, especially for the class of syntactically induced ERP modulations, such as P600 effects to agreement violations (Hagoort et al., 1993) and garden paths (Osterhout, Holcomb, & Swinney, 1994). On the RI account, these syntactically induced P600 effects are taken to index difficulty in integrative processing, operating on the level of the utterance representation, rather than on the level of syntactic structure (see Brouwer et al., 2012, for further discussion). It is rather straightforward to see how this could explain the processing of garden-paths, as they entail a revision of the unfolding utterance interpretation. Indeed, here a “syntactic structure”-based and an “utterance representation”-based explanation are quite similar (i.e., revision of the analysis constructed thus far). The difference between these views, however, will become apparent if we turn to agreement violations, for which the RI account might at first glance seem less intuitive. A verb inducing an agreement violation, such as *throw* in “The spoilt child throw [...]” has been shown to produce a P600 effect relative to a felicitous control “The spoilt child throws [...]” (Hagoort et al., 1993). On a syntactic account of the P600, this reflects some kind of repair of the infelicitous inflection on the verb (*throw* → *throws*). On the RI account, however, we take this P600 effect to reflect difficulty in establishing a coherent utterance representation; the mismatch between *the spoilt child* and *throw* induces uncertainty about the input (cf. Levy, 2008), for instance, about whether the speaker was talking about a single child or perhaps about multiple children (in which case not the inflection of the verb is incorrect, but the inflection of the noun).

To model the RI view on syntactically induced ERP modulations, we need a richer representational scheme for utterance representations than thematic-role assignments. That is, we require a scheme that allows us, for instance, to differentiate between the different interpretations involved in the incremental processing of garden-path constructions, as well as to represent uncertainty about the singularity/plurality of agents and patients in agreement violations. In future work, we aim to replace the thematic-role assignment representations that serve as utterance representations in the current model, with richer utterance representations in terms of distributed situation space vectors (Frank, Koppen, Noordman, & Vonk, 2003; Frank, Haselager, & van Rooij, 2009).⁴ Beyond capturing syntactically induced P600 modulations, this approach will allow us to extend the model toward pragmatically induced P600 effects (e.g., Hoeks, Stowe, Hendriks, & Brouwer, 2013; see Hoeks & Brouwer, 2014, for an overview).

5.4. Toward understanding processing in time

A general assumption in the literature is that the P600 component follows the N400 component in time. This entails that the processes generating the N400 component must be finished before those generating the P600 initiate. When applied to the RI account, this means that the retrieval of word meaning must be fully completed, before integrative processing can commence. Our neurocomputational model of the RI account does indeed implement such a *serial* perspective: Retrieval of word meaning precedes Integrative processing. However, given the highly *parallel* nature of processing in the brain, this is almost certainly wrong. That is, the processes underlying the N400 and the P600 may actually overlap in time, and as ERPs are additive, such overlap between components means that the P600 amplitude will be affected by the N400 amplitude, and vice versa (see Brouwer & Hoeks, 2013; Hagoort, 2003; Kutas et al., 2006). This has important implications for the interpretation of ERP data (recall the discussion in Section 4.4), which can be exemplified by means of a recent discussion on ERP effects in response to semantic anomalies.

Van Petten and Luka (2012) provide a review of 45 ERP studies in which semantically anomalous and non-anomalous sentence-final words are contrasted in sentences that are otherwise (syntactically) correct. Out of a total of 64 comparisons, only 20 contrasts are reported to yield a significant Post-N400 Positivity (PNP). Upon careful examination of the critical waveforms of the reviewed studies (through digitization), however, we found that in only a small fraction of the comparisons the anomalous condition is numerically less positive than the non-anomalous condition. Hence, in the majority of contrasts, there is a numerical positivity for anomalous relative to the non-anomalous sentence-final words. This outcome is at odds with views that take the N400 to be a standalone deflection in the ERP signal. If pure semantic anomaly only affects N400 amplitude, without any influence on the P600, we should expect an approximately equal number of numerical post-N400 *positivities* and *negativities* (assuming the signal returns to pre-stimulus baseline). The prevalence of numerical positivities in the post-N400 time-window, then, suggests that the N400 effect for semantic anomaly is followed by a late positivity. A potential explanation for why these positivities fail to reach significance in the reviewed contrasts, is that P600 amplitude is reduced due to spatiotemporal overlap with the N400.⁵ Indeed, in the majority of cases in which absence of a significant P600 effect is reported, the N400 effect is “followed” by a numerical positivity, and in the few cases where this numerical positivity is not present, the N400 effect appears to be particularly large. If this kind of overlap is indeed at play, it not only applies to the review by van Petten and Luka (2012)—component overlap likely affects the majority of relevant ERP studies. This problem has been noted in the literature (Brouwer & Hoeks, 2013; Hagoort, 2003; Kutas et al., 2006), but it has remained unclear how to deal with it both theoretically and in terms of (statistical) analysis of ERPs.

One approach toward getting to grips with component overlap, is to use explicit computational modeling to obtain a better understanding of the temporal dynamics of the processes indexed by the N400 and the P600. More specifically, instead of only estimating

the word-elicited mean amplitude of these components, we propose to modify the neurocomputational model to estimate how the N400 and the P600 develop over time. To this end, a potential modification to the model will be to extend it with a more elaborate notion of time. That is, in the current model, word processing takes a single discrete time *tick*. Within this time tick, we take the retrieval of word meaning to precede its integration; that is, we take the feedforward propagation of activation from the INPUT to the INTEGRATION_OUTPUT layer to be itself a temporally extended process (activation first arrives at the RETRIEVAL layer, before it arrives at the RETRIEVAL_OUTPUT layer, and so forth). Consequently, N400 estimates temporally precede the P600 estimates in the model and hence do not overlap in time. In an extended model, word processing could be distributed over multiple time ticks (cf. Laszlo & Plaut, 2012), such that we obtain amplitude estimates of the N400 and the P600 at each of these. Component overlap can then be modeled, for instance, by combining the P600 estimate at timestep t with the N400 estimate at timestep $t + 1$. A first test-case for this extended model would be to see if it would get the ordering of the P600 effects in the Hoeks et al. (2004) study right, by assuming temporal overlap between the N400 and the P600.

5.5. Toward a cortical implementation of the model

At the core of our neurocomputational model are two relatively independent, but interacting subsystems: a *retrieval* module and an *integration* module. Taken together, these subsystems implement a high-level language processing circuit. An important question is whether we can find out how this processing circuit might be neurally implemented in the brain. Brouwer and Hoeks (2013) provide a speculative answer to this question (see also Brouwer & Crocker, 2016). By focusing on computational *epicenters* (Mesulam, 1990, 1998) or *hubs* (Buckner et al., 2009), they propose a mapping of the RI account onto a minimal processing circuit. On this mapping, retrieval of word meaning is assumed to be mediated by the left posterior middle temporal gyrus (lpMTG; BA 21), and this region is the presumed main generator underlying the N400 component. Integrative processing, on the other hand, is mediated by the left inferior frontal gyrus (IIFG; BA 44/45/47), the presumed main generator of the P600 component. Brouwer and Hoeks (2013) provide a detailed derivation of this functional-anatomic mapping, which we will briefly summarize below.

On the basis of extensive evidence from neuroimaging and lesion studies (Binder, Desai, Graves, & Conant, 2009; Bookheimer, 2002; Cabeza & Nyberg, 2000; Dronkers, Wilkins, van Valin, Redfern, & Jaeger, 2004; Lau et al., 2008; Price, 2010; Turken & Dronkers, 2011), Brouwer and Hoeks (2013) proposed the lpMTG (BA 21) as the epicenter mediating lexical retrieval (see Fig. 6, top). The recognition of spoken and written words, for instance, both in isolation and in sentences, consistently activates the lpMTG (Cabeza & Nyberg, 2000), and lesions in this region have been found to lead to difficulties in word-level comprehension (Dronkers et al., 2004). This suggests that the lpMTG is involved in wordform to meaning mapping (=lexical retrieval). What is more, the lpMTG is the only region that is active at both short and long stimulus onset asynchronies in

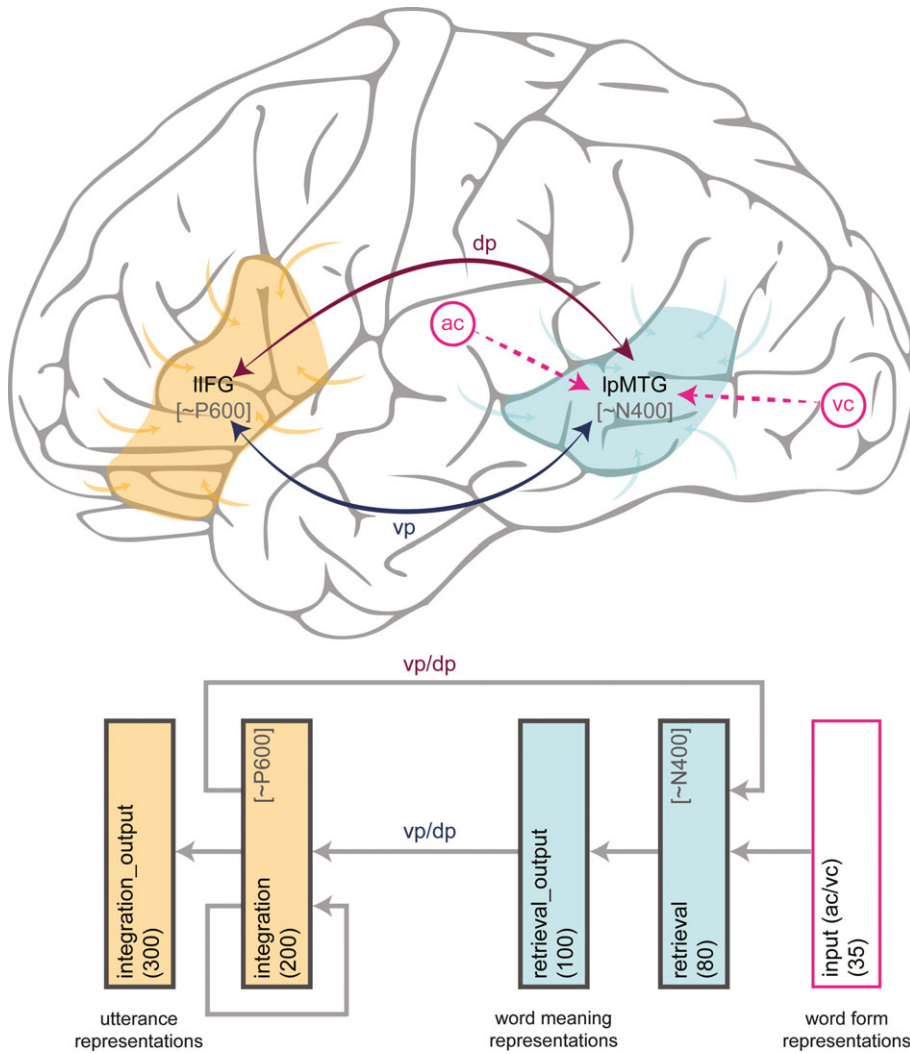


Fig. 6. Schematic illustration of the functional-anatomic mapping of the Retrieval-Integration account onto the core language network (top), and its relation to the neurocomputational model (bottom). Note that the schematic of the model uses a shorthand notation for the contextual input to the RETRIEVAL and INTEGRATION layers (by omitting the INTEGRATION_CONTEXT layer). An incoming word reaches the lpMTG via either the auditory cortex (ac) or visual cortex (vc) (corresponding to the INPUT layer in the model). The lpMTG then retrieves the conceptual knowledge associated with this word from the association cortices (RETRIEVAL → RETRIEVAL_OUTPUT), thereby generating the N400. Next, this retrieved meaning is sent to the IIFG (RETRIEVAL_OUTPUT → INTEGRATION), where it is integrated with its prior context (INTEGRATION → INTEGRATION) into an updated utterance representation (INTEGRATION → INTEGRATION_OUTPUT). This integration process is reflected in the P600 component. The updated utterance representation in the IIFG subsequently provides a context for the retrieval of the conceptual knowledge associated with the next word (INTEGRATION → RETRIEVAL).

lexical semantic priming studies (see Lau et al., 2008, for a large-scale review), supporting the idea that it plays a crucial role in the generation of the N400 component. This is consistent with source localization of the N400m, the magnetic field equivalent of the N400, which also points to the lpMTG as its main generator (Halgren et al., 2002). Finally, the lpMTG shows a particularly rich pattern of connectivity, both structurally and functionally, to frontal, parietal, and temporal regions of both hemispheres (Turken & Dronkers, 2011; see also Binder et al., 2009; Buckner et al., 2009; Koyama et al., 2010), supporting its role as a memory epicenter that retrieves and binds together conceptual knowledge from the association cortices, across which it is stored in a distributed manner.

Brouwer and Hoeks (2013) identified the IIFG (BA 44/45/47) as the epicenter mediating utterance (re)composition, and as such as the main generator of the P600 component (see Fig. 6, top). It has proven difficult to localize the neural generators underlying the P600 (Friederici, 2011). For one thing, consistent with the above hypothesis, a number of studies using fMRI have linked the P600 to the IIFG (see van de Meerendonk, Indefrey, Chwilla, & Kolk, 2011, for a discussion). However, attempts at reconstructing its generators using source localization have also identified the middle temporal gyrus and the posterior part of the temporal lobe as generator sites for the P600 (Kwon et al., 2005; Service, Helenius, Maury, & Salmelin, 2007). Brouwer and Hoeks (2013) tried to overcome these inconsistencies by looking for the generators of the P600 using a “process alignment” strategy, where they attempt to align data regarding the nature and time course of cognitive processing (from ERPs) with data on the cortical organization underlying it (from fMRI). This approach pointed them to the IIFG as the generator of the P600. The involvement of the IIFG in language processing is well-established, but the precise functional role of this region is a matter of ongoing debate (see Grodzinsky & Santi, 2008; Rogalsky & Hickok, 2011, for overviews). Rogalsky and Hickok (2011), for instance, point out that Broca’s area (BA 44/45)—which is subsumed by the IIFG—has been hypothesized to be responsible for syntactic movement (Grodzinsky & Santi, 2008), hierarchical processing and phrase structure building (Friederici, 2009), order-related linearization processes (Bornkessel-Schlesewsky, Schlewsky & von Cramon, 2009), working memory (Buchsbaum & D’Esposito, 2008; Buchsbaum, Olsen, Koch, & Berman, 2005), cognitive control (Novick, Trueswell, & Thompson-Schill, 2005), semantic unification (Hagoort, 2005), and thematic role checking and reanalysis (Caplan, Chen, & Waters, 2008; Caplan, Stanczak & Waters, 2008). Others have stressed the role of the IIFG in the control of memory (Badre & Wagner, 2007). Rather than choosing between these different hypotheses, Brouwer and Hoeks (2013) proposed to unify them. That is, they proposed that the IIFG as a whole is host to a variety of processes involved in the (re)composition of an utterance representation, including syntax-based processes, semantic processes, (working) memory-related processes, and control processes, thereby subsuming the aforementioned hypotheses. Critically, recent anatomical investigations have identified a complex neuroarchitectural parcellation of the IIFG (Amunts & Zilles, 2012; Amunts et al., 2010), and Brouwer and Hoeks suggest that this parcellation may form the neuroanatomical basis for a fine-grained functional topology, in which different subprocesses of utterance representation (re)composition may be subserved by different, but potentially

overlapping subparts of the IIFG (see Friederici, 2011; Hagoort, 2005; and Friederici & Singer, 2015 for similar ideas, also see Goucha & Friederici, 2015, for recent evidence supporting such a division of labor).

The word-associated conceptual knowledge retrieved by the lpMTG needs to be connected to the IIFG, where it will be integrated into the current utterance representation, producing an updated utterance representation. Subsequently, this updated interpretation needs to be connected back to the lpMTG, such that contextual cues can pre-activate the conceptual knowledge that may be associated with possibly upcoming words. This information sharing requires bi-directional connectivity between the lpMTG and the IIFG. White matter fiber tractography, using diffusion tensor imaging (DTI), has led to the identification of a rather rich pattern of structural connectivity between the temporal and the frontal lobe (e.g., Catani, Jones, & ffytche, 2005; Makris & Pandya, 2009; Saur et al., 2008; Turken & Dronkers, 2011). This pattern consists of a dorsal pathway (dp) and a ventral pathway (vp) (see Fig. 6, top). The functional role of these pathways is, however, subject to an ongoing debate (Baggio & Hagoort, 2011; Bornkessel-Schlesewsky & Schlesewsky, 2013; Friederici, 2009, 2011, 2012; Hickok & Poeppel, 2004, 2007; Saur et al., 2008; Tyler et al., 2011; Weiller, Musso, Rijntjes, & Saur, 2009), which turns out to be difficult to settle as DTI does not allow for the determination of pathway directionality (Friederici, 2011). Nonetheless, the existence of these pathways clearly shows that there is white matter connectivity that supports the bi-directional information sharing between the lpMTG and IIFG required for RI processing cycles (see Brouwer & Hoeks, 2013, for further discussion).

Given the mapping of retrieval/N400 and integration/P600 onto, respectively, the lpMTG and the IIFG, and the existence of connectivity between these epicenters, Brouwer and Hoeks (2013) outlined a typical RI processing cycle. Depending on whether linguistic input is spoken or written, words reach the lpMTG via, respectively, the auditory cortex (ac) or the visual cortex (vc). The lpMTG then retrieves the conceptual knowledge associated with an incoming word from the association cortices. These retrieval processes generate the N400 component. The retrieved word meaning is then sent to the IIFG, via either the dorsal pathway (dp) or the ventral pathway (vp), where it is integrated with the current utterance representation, into an updated utterance representation. This integrative processing generates the P600 component. Finally, the updated utterance representation is connected back via one of the pathways (dp or vp) to the lpMTG, where it serves to pre-activate the conceptual knowledge associated with possible upcoming words. Fig. 6 (top) provides a schematic overview of the outlined cortical RI processing circuit. This circuit aligns well with the architecture of the neurocomputational model implementing the RI account (see Fig. 6, bottom), and hence provides a starting point for a more integrated functional-neuroanatomic model.

6. Conclusion

We have presented a neurocomputational model that instantiates the recent RI account of the N400 and the P600 in language processing (Brouwer & Hoeks, 2013; Brouwer

et al., 2012). We have provided explicit and scalable linking hypotheses of processing behavior in the model to estimates of the N400 and the P600, and we have shown that the model is able to capture both traditional biphasic N400/P600 effects and “Semantic P600” effects. Moreover, as our model instantiates a single-stream architecture, we take it to support the claim that there is no need for an independent semantic analysis stream to explain “Semantic P600” effects, and as such as evidence against multi-stream architectures. We also outlined how our model can be extended to expand the spectrum of processing phenomena that it accounts for and how it can be adapted to provide insights into the temporal dynamics of the processes underlying the N400 and the P600. Finally, we have speculated about a potential cortical instantiation of our model. We believe that by offering a formally precise neurocomputational implementation of the RI account, we have not only elevated the debate on the functional interpretations of the N400 and the P600, but also raised the bar for competing models to move from conceptual to formally precise descriptions of their assumed architecture, computational principles, and representations.

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Notes

1. Henceforth, we will use the terms “Semantic Illusion” effect and “Semantic P600” effect interchangeably.
2. The difference in anticipation about the *agent* role after processing the determiner “de”/“the_{-NEUTER}” is due to the fact that this determiner occurs less frequently with inanimate nouns than the neutral determiner “het”/“the_{+NEUTER},” whereas all animate nouns occur with “de”/“the_{-NEUTER}” (see Appendix S1). Since animate nouns typically occur in the *agent* role in the training data, encountering a sentence-initial “de”/“the_{-NEUTER}” results in a slightly biased anticipation toward “kok”/“cook” relative to “maaltijd”/“meal” as *agent*.
3. Note that the test items are a subset of the training items, and that comprehension performance is therefore perfect (100% correct) on both test sets.
4. For preliminary (unpublished) results using this approach, see Brouwer, Hoeks, and Crocker (2015).
5. There is another factor that affects P600 amplitude: The processes underlying the P600 component are strongly task dependent. That is, if an experiment does not involve any acceptability or plausibility judgment on a per-item basis, this typically leads to

attenuated P600 amplitudes (Brouwer et al., 2012; see also Kolk et al., 2003). Critically, the studies reviewed by van Petten and Luka (2012) were explicitly selected to not involve any overt task, thereby biasing their results toward absence of P600 effects.

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Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix S1. Simulation materials.

Appendix S2. Derivation of word meaning representations.

Appendix S3. Details of the training procedure.

Appendix S4. Training on perfect word meaning representations.