The Proactive Comprehender: What Event-Related Potentials tell us about

the dynamics of reading comprehension.

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In: Unraveling the Behavioral, Neurobiological, and Genetic Components of Reading Comprehension. Miller,

B., Cutting, L., & McCardle, P (Eds): Baltimore: Paul Brookes Publishing\*

<sup>&</sup>lt;sup>\*</sup> This is a slightly longer version of the chapter to appear. In addition, the ideas presented in this chapter will be discussed more fully in a longer review by Gina R Kuperberg, which is in preparation.

Several years ago Danny had a scary experience when he went climbing on Mount Whitney. The scene that he witnessed made him quite afraid of venturing up there again. But his mom knew that it was important that Danny get over his fear and she wanted him to experience the mountain's beauty and wonder. She nagged Danny to join her on the climb for months. Eventually he agreed and they bought themselves some safe climbing gear. Nonetheless, about half way up the mountain, Danny got a fright as he slipped on a piece of rock. At that moment he truly regretted his mom had persuaded him to come. However, his mom gave Danny a hug and encouraged him to keep going, knowing what awaited them at the top. Finally, they rounded the last bend and were awed by the magnificent....

Imagine that, for his English homework, an 11-year old boy needs to read this passage for a comprehension test at school the next day. He knows that he has little time and he is reading quickly. It's a challenge: some of the sentences are complex and some are ambiguous. He is also becoming increasingly distracted as his mom calls him down for dinner. Fortunately, our 11-year-old has some experience with the ideas expressed in the paragraph. He has watched TV shows and read books about mountain climbing; he can understand what it's like to feel scared, and he certainly knows how persuasive moms can be!

In this chapter, I will discuss evidence suggesting that, if he can mobilize all this stored knowledge rapidly enough, he should be able to make sense of this text quickly, efficiently, deeply and flexibly. I will focus mainly on studies that have used event-related potentials (ERPs)—a direct measure of online brain activity—to track the neurocognitive mechanisms engaged as the meaning of a text unfolds, word by word. I will discuss studies suggesting that we continually draw upon our stored knowledge of events and event structures to predict<sup>1</sup> upcoming information in advance of fully accessing or combinatorially integrating the the incoming word. In Part 1, I will discuss evidence that this stored event knowledge can be used to pre-activate

<sup>&</sup>lt;sup>1</sup> Throughout this chapter, I use the term 'prediction' in the broad Bayesian sense of a prior--an assessment of the probability of accessing information, at a particular representational level, ahead of encountering all the linguistic information required to activate, retrieve or compute this representation. I do *not* assume that predictive processing is necessarily a conscious, intentional or 'active' process (although it obviously can be in some situations), and I do not assume that we always predict specific lexical items. By 'combinatorial integration', I mean a full, incremental analysis in which all available information, including the semantic and thematic structure of a verb, is used to map the conceptual features of arguments on to their semantic-thematic roles, thereby coming up with a full propositional representation of an event or state.

Gina Kuperberg. November 2012. Please cite as: Kuperberg, G.R. (2013). The Proactive Comprehender: What Event-Related Potentials tell us about the dynamics of reading comprehension. In: Unraveling the Behavioral, Neurobiological, and Genetic Components of Reading Comprehension. Miller, B., Cutting, L., & McCardle, P (Eds): Baltimore: Paul Brookes Publishing.\* conceptual features of upcoming words (or groups of words), thereby facilitating access to their meaning as they are encountered. In Part 2, I will argue that we begin to predictively map or *link* activated conceptual features on to particular semantic-thematic roles ('event predictions') and sometimes on to specific word forms ('lexical predictions'), again ahead of all the evidence that becomes available from the bottom-up linguistic input. I will discuss evidence that if the incoming word disconfirms these event or lexical predictions, the resulting prediction errors will trigger additional neural processing. In Part 3, I will discuss the advantages of this pro-active predictive system. Finally, in Part 4, I will speculate on how this system might break down, leading to impairments in comprehension.

# <u>Part 1. Activating event knowledge stored within long-term memory: facilitating access to the conceptual</u> <u>features of incoming words</u>

The idea that we draw upon our stored real-world knowledge to facilitate the processing of upcoming material is central to most memory-based models of discourse comprehension (Gerrig & McKoon, 1998; Myers & O'Brien, 1998). What ERP studies tell us is that we can access and use this knowledge extremely quickly. As we make our way through a sentence, paragraph or novel, whatever discourse-level representation we happen to have constructed at any given time will feed back to long-term memory, pre-activating relevant semantic representations that can facilitate access to the conceptual features of an incoming word within only a few hundred milliseconds of its onset. This semantic facilitation can be indexed by a reduction in the amplitude of the N400—an ERP component starting from about 300ms and peaking at approximately 400ms after word onset (Kutas & Federmeier, 2011).

Studies of the N400 show that we are able to draw upon multiple types of stored conceptual knowledge to predict or pre-activate<sup>2</sup> upcoming semantic information. Traditionally, this type of knowledge has been

<sup>&</sup>lt;sup>2</sup>These types of predictions at a single level of representation (e.g. conceptual features) can be conceptualized as 'pre-activations' that occur through a 'resonance' between the context and stored material in long-term memory (e.g. Myers & O'Brien, 1998). Stored material is pre-activated, leading to 'expectations' (Van Petten & Luka, 2012) about upcoming information at the same level of representation, facilitating access. This can be distinguished from the *predictive linking or mapping* between different levels of representation that occurs within working memory, which I will discuss in Part 2.

Gina Kuperberg. November 2012. Please cite as: Kuperberg, G.R. (2013). The Proactive Comprehender: What Event-Related Potentials tell us about the dynamics of reading comprehension. In: Unraveling the Behavioral, Neurobiological, and Genetic Components of Reading Comprehension. Miller, B., Cutting, L., & McCardle, P (Eds): Baltimore: Paul Brookes Publishing,\* conceptualized as being stored in networks that encode relationships between individual concepts along multiple semantic dimensions: associative (Collins & Loftus, 1975), categorical (Collins & Quillian, 1969) and featural (Smith, Shoben, & Rips, 1974), henceforth referred to as *semantic relatedness networks*. In this review, I will argue that we do more than simply activate semantic relationships between 'bags of words' to predict upcoming semantic information. Rather, we draw upon more structured stored representations of whole events and states that are stored at different grains of representation within long-term memory. I will refer to these types of stored representations collectively as *event knowledge*. It includes our knowledge of the conceptual features that are necessary<sup>3</sup> as well as those that are most likely (McRae, Ferretti, & Amyote, 1997) to be associated with a particular semantic-thematic role in an individual event or state. It also includes the necessary and likely temporal, spatial and causal relationships that link multiple events and states together to form sequences of events, sometimes known as scripts, frames or narrative schemas (Fillmore, 2006; Schank & Abelson, 1977; Sitnikova, Holcomb, & Kuperberg, 2008; Wood & Grafman, 2003; Zwaan & Radvansky, 1998).

Evidence that we use general semantic relatedness networks during discourse comprehension comes from studies showing a smaller N400 (facilitated semantic processing) to incoming words which are semantically related in some way to the context (its individual words or its general message), despite being semantically incongruous (Ditman, Holcomb, & Kuperberg, 2007; Federmeier & Kutas, 1999; Metusalem et al., 2012; Otten & van Berkum, 2007; Paczynski & Kuperberg, 2012). For example, in two recent experiments, participants read texts similar to the mountain-climbing scenario above. Sometimes the final word was fully congruous with the context (e.g., *view*); sometimes it was incongruous but nonetheless related to its general theme (e.g., *boots*, which is related to the theme of mountain climbing), and sometimes it was both incongruous and unrelated to the general theme (e.g., *scissors*). The N400 was smaller to words like *boots* than *scissors* (Paczynski & Kuperberg, 2012; Metusalem et al., 2012). These findings suggest that the reader's general

<sup>&</sup>lt;sup>3</sup> Here, I refer to the coarse-grained conceptual features that constitute a verb's selection restriction. These selection restrictions were originally thought to encoded within the lexicon (Chomsky, 1965), but, following Jackendoff (2002), I conceptualize them as being stored as part of real-world conceptual knowledge.

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<body>

Importantly, however, a pre-activation of general relatedness networks cannot explain all the facilitatory effects of real-world knowledge. For example, Metusalem et al. (2012) found that, although the N400 was attenuated to *boots*, it was attenuated even more to the fully congruous word, *view*, even though both <boots> and <view> are equally associated with the general theme of 'mountain climbing'<sup>5</sup>. To further pre-activate (or predict) the conceptual features of <view> over those of <boots>, the reader needed to have activated a whole event representation, telling him that <a view> is the most likely thing that would cause people to experience a state of awe at the top of a mountain (McRae et al., 1997; McRae et al., 1998; Altmann & Kamide, 1999.)

Obviously, to activate an event with this degree of specificity, the context must be rich and 'event constraining'. By definition, this type of event constraining context will activate not only the conceptual *features* of the participants involved in each event, but also the semantic *roles* (Agent, Patient, Experiencer, Stimulus etc) that these participants will play in the event<sup>6</sup>. For example, in our mountain-climbing scenario, the context of the final sentence tells us to expect something that will play the particular role of Stimulus in the event, i.e. something that will *cause* Danny and his mother (who take on the role of Experiencers) to feel a state of awe, and this activation of the relevant thematic role may be what leads to more activity to the conceptual features associated with <view> than with <boots>. Moreover, most contexts that are highly event constraining contexts will also be lexically constraining (with lexical constraint or predictability usually operationalized

<sup>&</sup>lt;sup>4</sup> Throughout this chapter, I will use <> around words when I am referring to their conceptual features, and I will use italics if I am referring to its full lexical representation (a representation in which conceptual features are *linked* to a word-form).

<sup>&</sup>lt;sup>5</sup> This was quantified with Latent Semantic Analysis (LSA: Landauer & Dumais, 1997; available at <u>http://lsa.colorado.edu</u>), which captures knowledge about multiple types of semantic relationships between words and concepts, but is relatively insensitive to word order, syntax or propositional meaning.

<sup>&</sup>lt;sup>6</sup> In this chapter, I will use the term 'semantic-thematic roles', rather than 'thematic roles', to emphasize that these roles describe the configurations of participants in an event's *conceptual structure*. Semantic-thematic roles interface with syntactic structure, but they are not synonymous or reducible to 'theta roles', which, in generative grammar, particularly Government and Binding Theory (Chomsky, 1981/1993), are used to describe the number and type of noun-phrases that are *syntactically* required by a particular verb.

Gina Kuperberg. November 2012. Please cite as: Kuperberg, G.R. (2013). The Proactive Comprehender: What Event-Related Potentials tell us about the dynamics of reading comprehension. In: Unraveling the Behavioral, Neurobiological, and Genetic Components of Reading Comprehension. Miller, B., Cutting, L., & McCardle, P (Eds): Baltimore: Paul Brookes Publishing.\* through cloze probabilities), leading to predictions not only of an upcoming word's conceptual features and semantic-thematic role, but also of its lexical form, e.g. the phonological representation of *view* (DeLong, Urbach, & Kutas, 2005). As I will argue in Part 2 of this chapter, we may begin to *link* these predictions at different representational levels—conceptual features with semantic-thematic roles ('event predictions') and sometimes with form information ('lexical predictions')—ahead of accessing or combinatorially integrating the incoming word, and we will incur costs if our analysis of the subsequent input disconfirms these predicted links. Importantly, however, the amplitude of the N400 itself, between 300-500ms after the onset of the incoming word, seems to be relatively impervious to these predicted *links* between conceptual features, semantic roles and/or lexical form. It cares only about whether the *conceptual features* of an incoming word match those that have been activated by the context<sup>7</sup>.

Although many contexts that constrain for a particular event will also constrain for a specific individual word, this is not necessarily the case: as discussed further in Part 2, it is possible to use context to predict an upcoming event or event structure and its associated conceptual features, but not a specific word-form. For example, consider the context, *Every morning at breakfast the eggs would*.... Even though it is not obvious what specific word comes next, we are likely to predict the event, "people eating eggs at breakfast", and we are therefore likely to activate the conceptual features of <eat>. If the next word encountered is *eat*, the N400 will be therefore be strongly attenuated (Kuperberg et al, 2003), even we have not predicted the specific lexical form of *eat*, and even though, once *eat* is encountered, its thematic structure will lead to the assignment roles to its arguments and the output of an event representation that conflicts with our original event prediction (see also Hoeks, Stowe, & Doedens, 2004; Kim & Osterhout, 2005; Kuperberg et al, 2006). Similarly, the context, *The cat that from the mice*...(translated from the Dutch: *De kat die voor de muizen*...(Kolk, Chwilla, van Herten, &

<sup>&</sup>lt;sup>7</sup> Note, however, that in contexts that are both event and lexically constraining, the divergence of the waveform evoked by predicted (versus non-predicted) words can start before 300ms (e.g. Kim & Lai, 2012; Dikker & Pylkkanen, 2011; Federmeier, Mai, and Kutas, 2005). Indeed, in such constraining contexts, the N400 effect itself can sometimes appear to diverge before 300ms. This early divergence of the N400 might actually reflect modulation of the N250 ERP component (thought to reflect phonological access, Grainger & Holcomb, 2009), resulting from a pre-activation or prediction of that word's phonological form (Lau, Holcomb, & Kuperberg, 2013.

Gina Kuperberg. November 2012. Please cite as: Kuperberg, G.R. (2013). The Proactive Comprehender: What Event-Related Potentials tell us about the dynamics of reading comprehension. In: Unraveling the Behavioral, Neurobiological, and Genetic Components of Reading Comprehension. Miller, B., Cutting, L., & McCardle, P (Eds): Baltimore: Paul Brookes Publishing.\* Oor, 2003) will strongly activate stored event representations of <mice fleeing from cats>, leading to facilitated access to the conceptual features of <flee>, even though the proposition as a whole is implausible and not what we predicted. As discussed in Part 2, in both cases, the violation of the event prediction will lead to costs that manifest on other ERP components. The important point to note here is that the N400 itself does not seem to be sensitive to these costs.

It is also important to recognize that we do not just use our stored knowledge about *specific* familiar events to generate predictions about upcoming specific events and their corresponding conceptual features. We also seem to use our knowledge about more general, canonical event structures to predict upcoming event structures, including conceptual features of whole semantic categories, such as animacy. For example, we can use the selection restrictions of verbs to predict the animacy of upcoming arguments, e.g. in the sentence, At the homestead the farmer penalized the..., the selection restrictions of penalized will constrain potential arguments to those with <animate> features, leading to a smaller N400 to the animate argument, *laborer*, than to the inanimate argument, meadow (Paczynski & Kuperberg, 2011; see also Paczynski & Kuperberg, 2012). We can also generate predictions about the animacy of arguments based simply on the order in which they are encountered in the linguistic input (Paczynski & Kuperberg, 2011). For example, in the sentence beginning, The novelist that..., our general expectation that the first argument encountered is more likely to be animate than inanimate leads to a small amount of semantic facilitation to *novelist* (a slightly smaller N400) than to *movie* in the sentence beginning, The movie that the... (Weckerly & Kutas, 1999). Similarly, our general expectation that, following an animate initial argument, we are more likely to encounter an inanimate argument than another animate argument, leads to a small amount of semantic facilitation (a smaller N400) on *meadow* in the sentence, At the homestead the farmer plowed the meadow..., relative to laborer in the sentence, At the homestead the farmer penalized the laborer... (Paczynski & Kuperberg, 2011).

Once again, note that in all these cases, our predictions about upcoming events encompass both predictions about the conceptual features of upcoming words as well as predictions about the semantic-thematic

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In sum, there is evidence that we store events and canonical event structures in memory at multiple grains of semantic representation, from coarse (Agent <animate>; Action; Patient <inanimate>) to more specific and finer-grained (Experiencer <people>; State <awe>; Stimulus <view>), and that, during word-by-word language comprehension, we activate this information to generate predictions about upcoming events, including the conceptual features and semantic-thematic roles of participants in these events. The N400, however, is primarily sensitive to whether an incoming word's *conceptual features* match these predictions. Exactly what conceptual features are pre-activated (predicted) will depend on the richness and structure of the context. So long as these features are pre-activated within long-term semantic memory ahead of the upcoming word, however, they will make it easier for us to access that word's conceptual features when it is actually encountered: the more that we have predicted ahead of time, the less work it is to retrieve a word's meaning and the smaller the N400.

## Part 2. The Costs of Prediction

The picture of language comprehension that I have painted thus far is a rosy one: we store vast amounts of knowledge about events and states in our long-term memories and, so long as the context allows, we can activate all this knowledge and use it to pre-activate the conceptual features of upcoming words, leading to facilitated semantic access, as reflected by an attenuation of the N400. In addition, I have suggested that we can also use stored event knowledge to predict the form of upcoming words, and/or the semantic roles that they will play in the upcoming event. In this way, we can predict specific lexical items and/or whole events, ahead of accessing or integrating the incoming word into its context. So long as the incoming word matches these lexical and event predictions, we will have a head start in all stages of linguistic analysis.

Of course, this scenario is somewhat ridiculous. If the input always matched our predictions, there would be no point in comprehension at all! The distinguishing feature of language is that combinations of words can be put together in infinite ways to convey events and sequences of events that are completely novel, and so we will obviously encounter information that is not already stored. And when this happens, if we have predictively mapped one representation on to another ahead of the input, and we are proved to be wrong by the subsequent input, we should incur costs.

In this section, I will present evidence from several lines of ERP research that we do indeed incur costs when we have predicted incorrectly. Specifically, I will discuss the costs that are incurred when, in highly constraining contexts, we commit to a particular event representation and/or specific lexical item, and these predictions are subsequently disconfirmed by the input. I will argue that this commitment involves more than simply pre-activating stored material within the lexicon and within long-term memory, but rather that it involves predictively *linking* activated material across levels of representation, which must occur within a distinct working memory space that is separate from long-term memory (see Jackendoff, 2002 and Lau, Holcomb & Kuperberg, 2013, for discussion). I will suggest that a violation of these types of cross-representational predictive links constitutes a *prediction error* which triggers a set of positive-going ERP components that extend past the N400 time window. I will discuss two types of prediction errors: first event prediction errors in which a particular predictive mapping between of a set of activated conceptual features on to a particular event structure is disconfirmed when full integration of the incoming word entails a different mapping between conceptual features and event structure. This event prediction error triggers a posteriorly-distributed prolonged positivity ERP effect, known as the P600. Second, lexical prediction errors, in when a particular predictive mapping between a set of activated conceptual features and a specific lexical form is disconfirmed when full lexical access to an incoming word entails a different mapping between conceptual features and lexical form.

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## 2.1 Event prediction errors: Posterior positivities (the P600)

One line of ERP studies has examined the effects of introducing *implausible* words in contexts that constrain for particular events or event structures, but not for individual words (reviewed by Kuperberg, 2007). Examples of such sentences include: *Every morning at breakfast the eggs would <u>eat</u>...(Kuperberg et al, 2003), <i>Every morning at breakfast the eggs would <u>plant</u>...(Kuperberg, Kreher, Sitnikova, Caplan, & Holcomb, 2007), <i>The cat that from the mice <u>fled</u>...*(Kolk et al., 2003), *At the homestead the farmer penalized the <u>meadow</u>... (Paczynski & Kuperberg, 2011), <i>The pianist played his music while the bass was strummed by the <u>drum</u>..., and <i>The pianist played his music while the bass was strummed by the <u>coffin</u>... (Paczynski & Kuperberg, 2012). In all these cases, the implausible word (underlined in the examples above) produced a positivity effect, sometimes with and sometimes without an N400 effect. This positivity effect has a posterior scalp distribution and is known as the 'semantic P600'<sup>9</sup>.* 

The semantic P600 effect peaks at parietal electrode sites. It starts at around 500ms after word onset, although it can begin earlier within the N400 time window, or later than 500ms, and it often continues for several hundred milliseconds. Unlike the N400, which is large to unpredicted (zero cloze) words in the absence of a constraining context, the semantic P600 is not always seen to unpredicted words in non-constraining

<sup>&</sup>lt;sup>8</sup> In both these situations, predictive mappings across levels of representation are generated with a high degree of certainty. Indeed, it may be this certainty that allows us to *commit* to a such mappings within working memory, and that also increases the likelihood that we will *detect* a prediction error at the point of the incoming word. In other situations, however, the context may not constrain for a particular event or a particular lexical item, and we will be more reliant on bottom-up information associated with the incoming word. Finally, in other situations, the context may constrain towards more than one event structure and/or towards more than one possible lexical item. In these cases, we may prioritize some candidates over others but we may not actually *commit* to a particular mapping, ahead of information from the upcoming word. Upon encountering the incoming word, however, we may still incur costs as we select one event and/or lexical candidate over another. These additional selection demands may be associated with a set of prolonged negativities, also extending past the N400 time window, with a widespread and sometimes anterior scalp distribution (see Wittenberg, Paczynski, Wiese, Jackendoff & Kuperberg, and Paczynski, Jackendoff & Kuperberg, under review for discussion; see also Baggio, van Lambalgen, and Hagoort, 2008; Wlotko & Federmeier, 2012, and Coulson, 2001 for additional examples).

<sup>&</sup>lt;sup>9</sup> This is a descriptive term used to distinguish it from the P600 that has been traditionally associated with *syntactic* anomalies and ambiguities. However, as pointed out by Van Petten and Luka (2012), evidence for posteriorly distributed positivity effects to semantically implausible (versus plausible) words in semantically constraining contexts has existed for many years.

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I suggest that the semantic P600 reflects costs that are incurred when full combinatorial integration of the incoming word disconfirms our predictions of specific *links* between a particular set of conceptual features and a particular semantic-thematic role, i.e. when full incremental analysis disconfirms our prediction of a particular event or event structure, and this event prediction error is detected by the comprehender. For example, when we read the context, *Every morning at breakfast the eggs would...*, our anticipation of an eating event leads us to predictively link the conceptual features of <eggs> with the semantic-thematic role of Theme. When we read the context, *The cat that from the mice...*, we predict a link between <cats> and Agent, and between <mice> and Patient. Similarly, the context, *At the homestead the farmer penalized the...*, leads us to predict an Experiencer that is <animate>. In all these cases, full combinatorial analysis of the input (full assignment of thematic roles using semantic and syntactic constraints) disconfirms our predicted links between these conceptual features and these semantic-thematic roles, i.e. it disconfirms the events or event structures we have predicted. The semantic P600 appears to reflect costs incurred as a result of detecting this event prediction error.

<sup>&</sup>lt;sup>10</sup> Kim and Osterhout (2005, Experiment 2) reported no P600 effect to verbs whose semantic features were unrelated to nonconstraining single Agent contexts (e.g. *The dusty tabletops were \*devouring*), although another study using the same stimuli did show a P600 effect on critical words (Stroud, 2008). As discussed in Part 1, the N400 produced by words whose features match those of their context will be small, regardless of whether their semantic-thematic role has been correctly predicted. This can lead to seemingly paradoxical pattern of a large P600 effect and no N400 effect to clear semantic violations (Kuperberg et al., 2003; Kolk et al., 2003, reviewed by Kuperberg, 2007).

This account can, in part, explain why a P600 effect is produced by words that are *syntactically* illformed (Hagoort, Brown, & Groothusen, 1993) or dispreferred in syntactically ambiguous structures (Osterhout & Holcomb, 1992)—the situations where the P600 of course was first described. Here too the comprehender is likely to detect conflict between the event structure that he predicted and the anomalous event structure that is produced as he attempts to combinatorially integrate the incoming word into its context. Consistent with this idea is the finding that the syntactic P600 is larger when its preceding context constrains strongly for a particular event than when it does not constrain for an event (Gunter, Friederici, & Schriefers, 2000, discussed by Kuperberg, 2007).

If the P600 reflects the response to the detection of an event prediction error, this raises important questions about its functional significance: what purpose does the additional analysis reflected by this component serve? At a broad level, one can conceive of the additional analysis reflected by this component as indexing the costs of abandoning the predicted event representation, and updating working memory with the event representation that is determined by full integration of the incoming word. This may entail fully reanalyzing the input in relation to the immediate context; it may also entail further attempt to integrate the input into the wider discourse level context, and it may entail learning. I will return to these ideas in Part 3.

## 2.2. Lexical prediction errors: Anterior positivities

A second line of ERP research has focused on the effects of introducing unexpected, but fully plausible words in contexts that constrain strongly for both events and specific words, e.g. following our event constraining mountain climbing scenario, encountering the sentence, *Finally, they rounded the last bend and were awed by the magnificent tree*. As discussed in Part 1, unpredicted words like *tree* will produce a larger N400 than predicted words like *view*, reflecting the mismatch between the conceptual features predicted by the context and the conceptual features associated with the incoming word. An N400, however, is not the only effect produced by *view*. It also evokes a larger positive-going waveform than predicted words (Federmeier, Wlotko, De Ochoa-Dewald, & Kutas, 2007), which can begin within the N400 time window (Delong, Urbach,

Potentials tell us about the dynamics of reading comprehension. In: Unraveling the Behavioral, Neurobiological, and Genetic Components of Reading Comprehension. Miller, B., Cutting, L., & McCardle, P (Eds): Baltimore: Paul Brookes Publishing.\* Groppe, & Kutas, 2011)<sup>11</sup>, although it often continues past this window (e.g. Federmeier, Wlotko, De Ochoa-Dewald, & Kutas, 2007; see Van Petten & Luka, 2012 for a review). This positivity effect has a more anterior or anterior-central scalp distribution than the P600 discussed above. However, analogous to the P600, and unlike the N400, the anterior positivity is *not* seen to unpredicted words in non-lexically-constraining contexts (Federmeier, Wlotko, De Ochoa-Dewald, & Kutas, 2007). Moreover, also in contrast to the N400, but like the P600, the anterior positivity effect is not necessarily modulated by the match between the conceptual features of the incoming word and the conceptual features activated by the context: it is produced both by words whose features are semantically related and unrelated to the context (Thornhill & Van Petten, 2012). Together, these findings suggest that the anterior positivity effect does not simply reflect a mismatch between the conceptual features of an incoming word and the conceptual features activated by the context. Rather, it is triggered when the input disconfirms a predicted *link* between a set of conceptual features and a particular word-form, i.e. it reflects the costs of a lexical prediction error. Consistent with this idea, a positivity effect with a widespread distribution is also seen to pseudohomophones versus correctly-spelled words of semantically expected words in lexically constraining contexts (Vissers, Chwilla & Kolk, 2006). In this situation too the input disconfirms a predicted *link* between form and meaning, which may trigger a late prolonged positivity effect.

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Once again, this raises the question of what level of analysis is reflected by the prolonged anteriorlydistributed positivity effect. One possibility is that, having predictively committed to link between a particular set of conceptual features and a particular word-form ahead of bottom-up input, the comprehender begins to map this lexico-semantic prediction on to the emerging syntactic tree structure. When he encounters the unpredicted word, he needs to abandon his initial analysis and update working memory in order to syntactically integrate the actual word into its context. The incoming word will be successfully integrated: it is, after all, fully plausible—the semantic-thematic role it plays in the event was successfully predicted. However, more

<sup>&</sup>lt;sup>11</sup>Because of this temporal and spatial overlap with the N400, this positivity is sometimes quite difficult to detect at the scalp surface. For example, a large N400 at central sites can obscure a small positivity at central sites. Similarly a large positivity at central sites can obscure a small N400 at central sites.

Gina Kuperberg. November 2012. Please cite as: Kuperberg, G.R. (2013). The Proactive Comprehender: What Event-Related Potentials tell us about the dynamics of reading comprehension. In: Unraveling the Behavioral, Neurobiological, and Genetic Components of Reading Comprehension. Miller, B., Cutting, L., & McCardle, P (Eds): Baltimore: Paul Brookes Publishing.\* processing resources are required to combinatorially syntactically integrate it into its context. On this account, the anterior positivity effect reflects the costs of revising the contents of working memory in order to combinatorially integrate the incoming word into its context using all available bottom-up information.

#### 3. A Predictive Comprehension system

In sum, ERP studies tell us that we are pro-active comprehenders. We use our stored knowledge about events and states to generate predictions at multiple levels of representation, and, moreover, in some circumstances,, we begin to map or link these predicted representations on to one another, ahead of the actual input. If our predictions about the conceptual features of upcoming words are correct, semantic access to these words is facilitated, as reflected by an attenuation of the N400. If, however, the input disconfirms these predictions of *links* between conceptual features and specific semantic-thematic roles (event prediction errors) and/or predictions of links between these conceptual features and specific word-forms (lexical prediction errors), we will incur costs, which manifest on a set of later positive-going ERP components.

As already noted, the most obvious benefit of a predictive language processing architecture is comprehension efficiency. If we have predicted correctly, then every step of accessing and integrating an incoming word into its context should be easier than if we hadn't predicted at all. But what about when we predict incorrectly? Are the risks of incurring additional costs in processing—the prediction errors discussed in Part 2—worth the benefits?

Here, I will suggest that, not only are our prediction errors worth the benefits of more efficient comprehension, but that they themselves are a crucial component of our comprehension system. I will argue that they may function to save us from interpretation errors in noisy environments, and that the P600, in particular, may allow us to recover meaning from sentences conveying novel events that at first seem to make no sense. Finally, I will suggest that prediction errors, and their associated costs, may also offer a mechanism by which we can *learn* and flexibly adjust our comprehension strategies in rapid response to an ever-changing linguistic

Gina Kuperberg. November 2012. Please cite as: Kuperberg, G.R. (2013). The Proactive Comprehender: What Event-Related Potentials tell us about the dynamics of reading comprehension. In: Unraveling the Behavioral, Neurobiological, and Genetic Components of Reading Comprehension. Miller, B., Cutting, L., & McCardle, P (Eds): Baltimore: Paul Brookes Publishing.\* and non-linguistic environment. To illustrate each of these points, let us return to our 11-year-old boy, hurrying to read his homework passage before dinner.

#### 3.1 Avoiding interpretation errors in noisy environments

Envisage our reader at the final sentence of the text, right at the instant before he sees the final word, *view*. His increasingly irate Mom calls him one last time for dinner and, just as he encounters the word, *view*, he is distracted by her voice. As a result, he mistakenly interprets *view* as *vow* and ends up processing the final sentence as, *They looked around them and were awed by the magnificent vow*.... There is nothing inherently ill-formed about being awed by a vow. It is certainly implausible in relation to its discourse context, but it is not a syntactic violation. Fortunately, however, even before he has seen the word *view*, our reader has used his event knowledge to predict its conceptual features, its word-form, and its semantic-thematic role in the event, and he has begun to map these representations on to one another within working memory. When he mistakenly interprets the final word of the sentence as *vow*, therefore, the resulting lexical and event prediction errors, and all the additional analysis that these trigger, ensures that he devotes the necessary resources to interpret the input accurately.

In another situation, the error may be in the input itself. For example, if there was a typo and the text did actually say *vow* instead of *view*, additional analysis would confirm that the input was, in fact, highly implausible. Here, however, the similarity in orthography between the predicted and encountered word may lead our reader to suspect a typo, and to interpret the input according to his initial prediction.

What both these situations illustrate is that, when inputs are noisy, our predictions can serve us well by triggering us to look more carefully at what we have just read, rather than simply move on (Levy, 2011; van de Meerendonk, Kolk, Chwilla, & Vissers, 2009). This is necessary in the real world when what we hear and read is often incomplete, impoverished or inaccurate. It would be hugely inefficient to devote additional processing resources to analyzing and reanalyzing every word we encounter. It therefore makes most sense to conserve these resources for when we are most likely to be wrong, i.e., when we have predicted an alternative analysis in

Gina Kuperberg. November 2012. Please cite as: Kuperberg, G.R. (2013). The Proactive Comprehender: What Event-Related Potentials tell us about the dynamics of reading comprehension. In: Unraveling the Behavioral, Neurobiological, and Genetic Components of Reading Comprehension. Miller, B., Cutting, L., & McCardle, P (Eds): Baltimore: Paul Brookes Publishing.\* a constraining context. Our prediction errors, and the additional analysis they trigger, may therefore serve a vital function in protecting us from interpretative errors.

#### 3.2 Updating the situation model through additional discourse-level analysis

Now imagine that, instead of ending with the expected word, *view*, the mountain-climbing passage ends unexpectedly, and that the final sentence reads, Finally, they rounded the last bend and were awed by the magnificent dragon. Just as described above, our reader will compute an implausible event (encountering a magnificent dragon) when he had predicted a much more likely alternative (encountering a magnificent view). And once again, because he had generated specific event and lexical predictions for something quite different in the highly constraining discourse context, he will invest additional resources to further analyze the input, manifest as positivity effects. This time, however, the additional analysis will confirm that he was correct on his first reading—that there was no error in the input, and that Danny and his Mom were, indeed, awed by a dragon upon reaching the top of the mountain. This additional analysis, however, has not been in vain. It may play an important role in triggering our reader to look beyond the specific event described (being awed by a dragon) and to re-evaluate it in relation to the wider situation model: he now knows that Danny's world is not quite what he had assumed. This type of situation-level updating may play an important role in helping us to come up with novel interpretations of the roles a particular entity may play in a predicted action (Sitnikova, Holcomb, Kiyonaga, & Kuperberg, 2008) or to go beyond a literal interpretation to make sense of metaphorical language (e.g. De Grauwe, Swain, Holcomb, Ditman, & Kuperberg, 2010). All these situations are quite different from one another, but notably, they are all associated with robust P600 effects (see Brouwer, Fitz, & Hoeks, 2012, for discussion).

## 3.5. Error-based learning and adaptation

Above, I have argued that the additional analysis associated with prediction errors can help us avoid misinterpretations and that it can also lead us to update our situation model when we encounter implausible, unexpected events. All this additional analysis, however, would be somewhat counterproductive if we failed to

Gina Kuperberg. November 2012. Please cite as: Kuperberg, G.R. (2013). The Proactive Comprehender: What Event-Related Potentials tell us about the dynamics of reading comprehension. In: Unraveling the Behavioral, Neurobiological, and Genetic Components of Reading Comprehension. Miller, B., Cutting, L., & McCardle, P (Eds): Baltimore: Paul Brookes Publishing.\* learn from our mistakes and continued to predict wrongly. Suppose, for example, our 11-year old repeatedly encountered typos in his assigned text. We would hope that, by the fifth typo, he would not be investing processing resources to re-evaluate the input. We would also hope that, having understood that, in Danny's world it is plausible to encounter a *dragon*, our reader will update his situation model and will not invest as many processing resources when, the next day at school, he learns about Danny's encounter with a *goblin*. What we want him to do is to use his prediction errors to *learn* from the input so that he eventually comes to 'expect the unexpected'.

We have actually known that the P600 is closely linked to our ability to 'expect the unexpected' since the late 1990s, when Coulson, King, & Kutas (1998) showed that its amplitude was sensitive to the proportion of syntactic anomalies in the experimental environment. At the time, this was interpreted as evidence against the P600 being particularly relevant to syntactic (or indeed language) processing. It is only quite recently that predictive error-based learning has been recognized as playing an important role in adult comprehension (e.g. Jaeger & Snider, 2013; Fine & Jaeger, 2011), although it has been discussed for some time in the developmental literature (e.g. Chang, Dell, & Bock, 2006; Ramscar & Dye, 2012), Here, I would like to suggest that such error-based learning may be closely linked to the anterior and P600 positivity effects discussed in this chapter, and that it is plays an important role in allowing us to adapt our processing strategies in response to changing environmental demands, as well as to continually update our real-world and linguistic knowledge on the basis of what we hear and read.

Some evidence for this idea comes from a recent study in which people listened to language spoken with a foreign accent. They failed to produce a P600 effect at all in response to clear syntactic violations. This suggests that we are quickly able to adjust our expectations about the likelihood of encountering a syntactic anomaly, based on speaker identity (Hanulikova, van Alphen, van Goch, & Weber, 2012). We have also shown that the amplitude of the P600 produced by syntactic violations is smaller whether readers had just encountered another syntactic violation in the preceding sentence (Kuperberg, Lau, & Clegg, 2011), suggesting that

Gina Kuperberg. November 2012. Please cite as: Kuperberg, G.R. (2013). The Proactive Comprehender: What Event-Related Potentials tell us about the dynamics of reading comprehension. In: Unraveling the Behavioral, Neurobiological, and Genetic Components of Reading Comprehension. Miller, B., Cutting, L., & McCardle, P (Eds): Baltimore: Paul Brookes Publishing.\* predictive error-based learning may be extremely rapid and can be used to adjust processing in a highly dynamic fashion (cf. Botvinick, Braver, Barch, Carter, & Cohen, 2001).

#### 4. Implications for poor comprehension

It should be clear from this review that a reader who can quickly mobilize his real-world knowledge to predict upcoming information—words and events—will be a good comprehender. If he is correct in his predictions, he will have a head start in all phases of accessing and combinatorially integrating incoming words into their context, and in interpreting the resulting propositions. If the input is ambiguous or complex, his predictions may allow him to avoid costly garden paths and flexibly restructure events to make sense of the input. If he incorrectly decodes the input, encounters a typo, or comes across a genuine surprise, any predictions he made ahead of time still serve him well: by triggering additional analysis to the incoming word, they protect him from misinterpretation, help him interpret novel events, and lead him to adjust his processing strategy in preparation for what lies ahead.

All of this, however, hinges on being able to pre-activate relevant event knowledge very quickly, prior to encountering the next word. This is not always so simple as it relies on a tight interaction between long-term memory and combinatorial mechanisms of language processing. There are therefore many reasons why, by failing to access this information, comprehension may break down. For example, we may not store relevant event/state knowledge in the first place; combinatorial processing may be too slow to build a partial propositional representation of the linguistic input in time to feed back to semantic memory and activate relevant event knowledge before the next word appears; or the connections between the combinatorial processing and memory may themselves be slow or inefficient.

Regardless of the underlying cause, the consequences of a reader failing to mobilize event knowledge to predict in this fashion will be the same. Semantic access will be slower and less efficient. He will be led down garden paths in ambiguous or complex sentences. He will be more prone to error in noisy environments. He Gina Kuperberg. November 2012. Please cite as: Kuperberg, G.R. (2013). The Proactive Comprehender: What Event-Related Potentials tell us about the dynamics of reading comprehension. In: Unraveling the Behavioral, Neurobiological, and Genetic Components of Reading Comprehension. Miller, B., Cutting, L., & McCardle, P (Eds): Baltimore: Paul Brookes Publishing.\* may fail to make sense of and encode novel, unexpected information. And, finally, he will fail to adjust his processing strategy flexibly in response to the demands of his environment.

On a more optimistic note, the very flexibility of the language processing system provides several points of entry to intervene and improve comprehension, regardless of the underlying causes. The trick is to activate specific event/state knowledge in time to guide parsing. This may entail slowing down the pace of reading. It may require triggering the activation of event/state knowledge through other modalities. And/or it may involve explicit tasks and instructions that encourage predictive strategies. The final approach may be particularly fruitful given experimental evidence that task instructions can shift the threshold at which additional analysis is initiated, as reflected by the P600 (see Kuperberg, 2007, for discussion).

## 5. Conclusions

In conclusion, ERP studies tell us that we can mobilize our stored real-world event knowledge amazingly quickly to facilitate access to the meaning of incoming words. I have also suggested that we go still further by mapping our predictions at multiple levels of representation, on to one another, ahead of integrating the input. This helps us parse ambiguous and complex sentences, allows us to allocate our processing resources rationally in noisy environments, helps us make sense of novel information, and ensures that we flexibly adjust our comprehension strategies in response to ever-changing task and environmental demands. Finally, I hope to have shown how a detailed understanding of the neurocognitive mechanisms engaged in word-by-word language processing can potentially directly translate to inform the development of targeted strategies to improve reading comprehension.

## References

- Altmann, G. T. M., Kamide, Y. (1999). Incremental interpretation at verbs: restricting the domain of subsequent reference. *Cognition*, 73(3), 247-264.
- Baggio, G., van Lambalgen, M., Hagoort, P. (2008). Computing and recomputing discourse models: An ERP study. *Journal of Memory and Language*, 59(1), 36-53.
- Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Review*, *108*(3), 624-652.
- Bornkessel-Schlesewsky, I. & Schlesewsky, M. (2009). The role of prominence information in the real-time comprehension of transitive constructions: A cross-linguistic approach. *Language and Linguistics Compass 3(1)*. 19–58.
- Brouwer, H., Fitz, H., & Hoeks, J. (2012). Getting real about semantic illusions: rethinking the functional role of the P600 in language comprehension. *Brain Research*, 1446, 127-143.
- Chang, F., Dell, G. S., & Bock, K. (2006). Becoming syntactic. Psychology Reviews, 113(2), 234-272.
- Chomsky, N. (1965). Aspects of the theory of syntax. MIT Press.
- Chomsky, N. (1981/1993). Lectures on Government and Binding: The Pisa Lectures. Mouton de Gruyter.
- Collins, A. M., & Loftus, E. F. (1975). A spreading activation theory of semantic processing. *Psychological Review*, 82, 407-428.
- Collins, A. M., & Quillian, M. R. (1969). Retrieval time from semantic memory. *Journal of Verbal Learning* and Verbal Behavior, 8, 240-247.
- Coulson, S. (2001). Semantic Leaps: Frame Shifting and Conceptual Blending in Meaning Construction. New York: Cambridge University Press.
- Coulson, S., King, J., & Kutas, M. (1998). Expect the unexpected: Event-related brain responses to morphosyntactic violations. *Language and Cognitive Processes*, 13, 21-58.
- De Grauwe, S., Swain, A., Holcomb, P. J., Ditman, T., Kuperberg, G. R. (2010). Electrophysiological insights into the processing of nominal metaphors. *Neuropsychologia*, 48(7), 1965-1984.
- Delong, K. A., Urbach, T. P., Groppe, D. M., & Kutas, M. (2011). Overlapping dual ERP responses to low cloze probability sentence continuations. *Psychophysiology*, 48(9), 1203-1207.
- DeLong, K. A., Urbach, T. P., & Kutas, M. (2005). Probabilistic word pre-activation during language comprehension inferred from electrical brain activity. *Nature Neuroscience*, 8(8), 1117-1121.
- Dikker, S., & Pylkkanen, L. (2011). Before the N400: effects of lexical-semantic violations in visual cortex. *Brain and Language*, 118(1-2), 23-28.
- Ditman, T., Holcomb, P. J., & Kuperberg, G. R. (2007). The contributions of lexico-semantic and discourse information to the resolution of ambiguous categorical anaphors. *Language and Cognitive Processes*, 22, 793-827.

Federmeier, K. D., & Kutas, M. (1999). A rose by any other name: Long-term memory structure and sentence processing. *Journal of Memory and Language*, *41*, 469-495.

- Federmeier, K.D., Mai, H., & Kutas, M. (2005). Both sides get the point: Hemispheric sensitivities to sentential constraint. *Memory and Cognition*, 33(5), 871-886.
- Federmeier, K. D., Wlotko, E. W., De Ochoa-Dewald, E., & Kutas, M. (2007). Multiple effects of sentential constraint on word processing. *Brain Research*, 1146, 75-84.
- Fillmore, C. J. (2006). Frame semantics. Cognitive Linguistics: Basic Readings, 34, 373-400.
- Fine, F. B., & Jaeger, T. F. (2011). Language comprehension is sensitive to changes in the reliability of lexical cues. The 33<sup>rd</sup> Annual Meeting of the Cognitive Science Society. Boston, MA. July, 2011, 925-930.
- Garnsey, S. M., Pearlmutter, N. J., Myers, E., & Lotocky, M. A. (1997). The contributions of verb bias and plausibility to the comprehension of temporarily ambiguous sentences. *Journal of Memory and Language*, *37*(1), 58-93.

- Gerrig, R. J., & McKoon, G. (1998). The readiness is all: The functionality of memory-based text processing. *Discourse Processes*, 26(2-3), 67-86.
- Grainger, J., & Holcomb, P. J. (2009). Watching the word go by: On the time-course of component processes in visual word recognition. *Language and Linguistic Compass*, *3*, 128-156.
- Gunter, T. C., Friederici, A. D., Schriefers, H. (2000). Syntactic gender and semantic expectancy: ERPs reveal early autonomy and late interaction. *Journal of Cognitive Neuroscience*, *12*, 556-558.
- Hagoort, P., Brown, C., & Groothusen, J. (1993). The syntactic positive shift (SPS) as an ERP measure of syntactic processing. In S. M. Garnsey (Ed.), *Language and cognitive processes*. Special Issue: Eventrelated brain potentials in the study of language (Vol. 8(4), pp. 439-483). Hove: Lawrence Erlbaum Associates.
- Hagoort, P., Hald, L., Bastiaansen, M., & Petersson, K. M. (2004). Integration of word meaning and world knowledge in language comprehension. *Science*, *304*(5669), 438-441.
- Hanulikova, A., van Alphen, P. M., van Goch, M. M., & Weber, A. (2012). When one person's mistake is another's standard usage: the effect of foreign accent on syntactic processing. *Journal Cognitive Neuroscience*, 24(4), 878-887.
- Hoeks, J. C. J., Stowe, L. A., Doedens, G. (2004). Seeing words in context: The interaction of lexical and sentence level information during reading. *Cognitive Brain Research*, 19, 59-73.
- Jaeger, T. F., & Snider, N. (2013). Alignment as a consequence of expectation adaptation: syntactic priming is affected by the prime's prediction error given both prior and recent experience. *Cognition*. 127(1), 57-83.
- Kaan, E., Harris, A., Gibson, E., & Holcomb, P. J. (2000). The P600 as an index of syntactic integration difficulty. *Language and Cognitive Processes*, 15(2), 159-201.
- Kim, A. & Lai, V. (2012). Rapid interactions between lexical-semantic and word-form analysis during word recognition in context: evidence from ERPs. *Journal of Cognitive Neuroscience*, 24(5), 1104-1112
- Kim, A., & Osterhout, L. (2005). The independence of combinatory semantic processing: Evidence from eventrelated potentials. *Journal of Memory and Language*, 52, 205-225.
- Kolk, H. H. J., Chwilla, D. J., van Herten, M., & Oor, P. J. (2003). Structure and limited capacity in verbal working memory: A study with event-related potentials. *Brain and Language*, 85(1), 1-36.
- Kuperberg, G. R. (2007). Neural mechanisms of language comprehension: Challenges to syntax. *Brain Research, Special Issue: Mysteries of Meaning, 1146*, 23-49.
- Kuperberg, G. R., Caplan, D., Sitnikova, T., Eddy, M., Holcomb, P. J. (2006). Neural correlates of processing syntactic, semantic and thematic relationships in sentences. *Language and Cognitive Processes*, 21(5), 489-530.
- Kuperberg, G. R., Kreher, D. A., Sitnikova, T., Caplan, D. N., & Holcomb, P. J. (2007). The role of animacy and thematic relationships in processing active English sentences: evidence from event-related potentials. *Brain and Language*, 100(3), 223-237.
- Kuperberg, G. R., Lau, E. F., & Clegg, L. (2011). A Gratton effect on the syntactic P600: Evidence that syntactic processing is subject to a dynamic adjustment of executive control. *Annual Meeting of the Cognitive Neuroscience Society*.
- Kuperberg, G. R., Sitnikova, T., Caplan, D., & Holcomb, P. J. (2003). Electrophysiological distinctions in processing conceptual relationships within simple sentences. *Cognitive Brain Research*, 17(1), 117-129.
- Kutas, M., & Federmeier, K. D. (2011). Thirty years and counting: Finding meaning in the N400 component of the event-related brain potential (ERP). *Annual Review of Psychology*, 62, 621-647.
- Landauer, T. K., & Dumais, S. T. (1997). A solution to plato's problem: The latent semantic analysis theory of acquisition, induction, and representation of knowledge. *Psychological Review*, 104, 211-240.
- Lau, E. F., Holcomb, P. J., & Kuperberg, G. R. (2013). Dissociating N400 effects of prediction from association in single word contexts. *Journal of Cognitive Neuroscience*.
- Levy, R. (2011). Probabilistic linguistic expectations, uncertain input, and implications for eye movements in reading. *Studies of Psychology and Behavior*, 9(1), 52–63.

- MacDonald, M. C., Pearlmutter, N. J., & Seidenberg, M. S. (1994). The lexical nature of syntactic ambiguity resolution. *Psychological Review*, *101*, 676-703.
- McRae, K., Spivey-Knowlton, M. J., & Tanenhaus, M. K., (1998). Modeling the influence of thematic fit (and other constraints) in on-line sentence comprehension. *Journal of Memory and Language*, *38*, 283-312.
- McRae, K., Ferretti, T. R., & Amyote, L. (1997). Thematic roles as verb-specific concepts. *Language and Cognitive Processes*, *12*, 137-176.
- Metusalem, R., Kutas, M., Urbach, T. P., Hare, M., McRae, K., & Elman, J. L. (2012). Generalized event knowledge activation during online sentence comprehension. *Journal of Memory and Language*, 66(4), 545-567.
- Myers, J. L., & O'Brien, E. J. (1998). Accessing the discourse representation during reading. *Discourse Processes*, 26(2-3), 131-157.
- Osterhout, L., & Holcomb, P. J. (1992). Event-related potentials elicited by syntactic anomaly. *Journal of Memory and Language*, 31, 785-806.
- Otten, M., & van Berkum, J. J. (2007). What makes a discourse constraining? Comparing the effects of discourse message and scenario fit on the discourse-dependent N400 effect. *Brain Research*, 1146, 158-171.
- Otten, M., & van Berkum, J. J. (2008). Discourse-based lexical anticipation: Prediction or priming? *Discourse Processes*, 45(6), 464-496.
- Paczynski, M., Jackendoff, R., & Kuperberg, G. R. (Under review). When events change their nature.
- Paczynski, M., & Kuperberg, G. R. (2011). Electrophysiological evidence for use of the animacy hierarchy, but not thematic role assignment, during verb argument processing. *Language and Cognitive Processes*, 26(9), 1402-1456.
- Paczynski, M., & Kuperberg, G. R. (2012). Multiple influences of semantic memory on sentence processing: Distinct effects of semantic relatedness on violations of real-world event/state knowledge and animacy selection restrictions. *Journal of Memory and Language*, 67(4), 426-448.
- Ramscar, M., & Dye, M. (2012). Error and expectation in language learning: The curious absence of "mouses" in adult speech. *Language*.
- Schank, R. C., & Abelson, R. P. (1977). Scripts, plans, goals, and understanding : An inquiry into human knowledge structures. Hillsdale, N.J.: L. Erlbaum Associates.
- Sitnikova, T., Holcomb, P. J., Kiyonaga, K. A., & Kuperberg, G. R. (2008). Two neurocognitive mechanisms of semantic integration during the comprehension of visual real-world events. J Cogn Neurosci, 20(11), 2037-2057.
- Sitnikova, T., Holcomb, P., & Kuperberg, G. R. (2008). Neurocognitive mechanisms of human comprehension. In T. F. Shipley & J. M. Zacks (Eds.), Understanding Events: How Humans See, Represent, and Act on Events (pp. 639-683): Oxford University Press.
- Smith, E. E., Shoben, E. J., & Rips, L. J. (1974). Structure and process in semantic memory: A featural model for semantic decisions. *Psychological Review*, 81, 214-241.
- Stroud, C. (2008). Structural and semantic selectivity in the electrophysiology of sentence comprehension. PhD dissertation. University of Maryland.
- Thornhill, D. E., & Van Petten, C. (2012). Lexical versus conceptual anticipation during sentence processing: Frontal positivity and N400 ERP components. *International Journal of Psychophysiology*, 83(3), 382-392.
- Traxler, M. J., Williams, R. S., Blozis, S. A., & Morris, R. K. (2005). Working memory, animacy, and verb class in the processing of relative clauses. *Journal of Memory & Language*, 53, 204-224.
- van de Meerendonk, N., Kolk, H. H. J., Chwilla, D. J., & Vissers, C. T. W. M. (2009). Monitoring in language perception. *Language and Linguistics Compass*, *3*(5), 1211-1224.
- Van Petten, C., & Luka, B. (2012). Prediction during language comprehension: Benefits, costs, and ERP components. *International Journal of Psychophysiology*, 83(2), 176-190.

- Vissers, C. T., Chwilla, D. J., Kolk, H. H. (2006). Monitoring in language perception: The effect of misspellings of words in highly constrained sentences. *Brain Research*, *1106*(1), 150-163.
- Weckerly, J., & Kutas, M. (1999). An electrophysiological analysis of animacy effects in the processing of object relative sentences. *Psychophysiology*, 36(5), 559-570.
- Wittenberg, E., Paczynski, M., Wiese, H., Jackendoff, R., Kuperberg, G. R. (Under Review). Light verbs make heavy work: An ERP study of processing an argument structure mismatch.
- Wlotko, E. W., & Federmeier, K. D. (2012). So that's what you meant! Event-related potentials reveal multiple aspects of context use during construction of message-level meaning. *Neuroimage*, 62(1), 356-366.
- Wood, J. N., & Grafman, J. (2003). Human prefrontal cortex: Processing and representational perspectives. *Nature Reviews Neuroscience*, 4(2), 139-147.
- Zwaan, R. A., & Radvansky, G. A. (1998). Situation models in language comprehension and memory. *Psychological Bulletin*, 123(2), 162-185.

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