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Plausibility, Probability, Prediction and the P600

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1 Introduction

The two most salient event-related potential (ERP) components in language comprehension, measured through electroencephalography (EEG) techniques, are the N400 and P600. Neural responses to particular events or stimuli can be extracted as ERPs from EEG data, which records electrical activity in the brain. The N400 is a negative deflection with a central-parietal distribution that peaks around 300-500ms post-stimulus onset, reliably modulated by a word's predictability depending on the preceding context. More predictable words elicit a smaller effect than unpredictable words (DeLong, Urbach & Kutas 2005, Wlotko & Federmeier 2012) and can be observed in the processing of visual and auditory linguistic stimuli as well as non-linguistic stimuli (Federmeier, Kutas & Dickson 2016). In contrast, the P600 component is a later positive deflection beginning around 500ms post-onset-stimulus with either a centro-parietal (posterior P600) or frontal (frontal P600) scalp distribution (Figure 1). Broadly, unexpected stimuli elicit a frontal P600 response and implausible stimuli elicit a posterior P600 response (Table 1)[1]. Research has primarily investigated either the posterior P600 effect or the frontal P600 effect; only recent research has elicited both within the same study, distinguishing the components as independent processors with distinct roles in language comprehension. Four recent studies, differentiating frontal and posterior P600 responses with the same experimental design, provide the focus of this review, which aims to understand the results within the broader literature on predictive processing in language. This paper will first outline the current literature on the frontal and posterior P600 components in psycholinguistic research, as well as their connections to predictive processing, before presenting the four studies. After critically examining the results within predictive coding accounts, this review will identify limitations and suggest directions for future research.

2 Reviewing the P600: Frontal and Posterior Scalp Distributions

2.1 Posterior P600

A posterior P600 amplitude was originally observed in psycholinguistic experiments by Osterhout & Holcomb (1992) in response to garden path sentences containing

[1] The literature uses both expectancy/probability and implausible/anomalous interchangeably. For consistency this paper only uses expected and plausible.

Condition	Example
Expected	Like many foreigners he spoke with an *accent.*
Unexpected	Like many foreigners he spoke with a *lisp.*
Implausible	Like many foreigners he spoke with an *apron.*

Table 1 Expected, unexpected and implausible sentence continuations (DeLong et al. 2014).

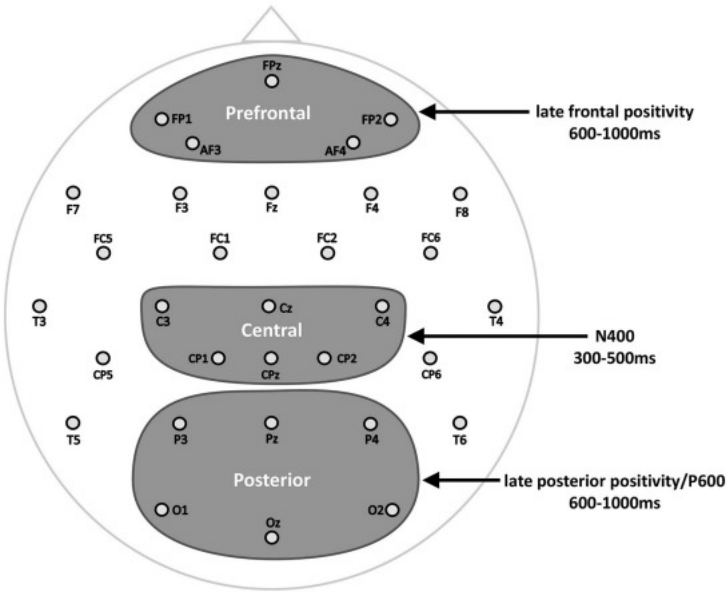

Figure 1 Neuroanatomical distinction of frontal and posterior P600 effects (Kuperberg et al. 2020).

a syntactic ambiguity: "The broker persuaded to sell the stock was sent to jail". Similar studies have also found that complex sentences without actual syntactic violations elicit a posterior P600 response (Osterhout, Holcomb & Swinney 1994, Kaan & Swaab 2003). Additionally, parallel effects have been found in response to morphosyntactic, syntactic and phrase structure violations, including word category and agreement violations, in both spoken and written stimuli (Coulson, King & Kutas 1998, Hagoort, Brown & Groothusen 1993, Osterhout & Mobley 1995). For example, Hagoort & Brown (2000) observed a larger posterior P600 in response to (1a) in comparison to (1b):

(1) a. *The spoiled child throw the toys on the floor.*

b. *The spoiled child throws the toys on the floor.*

Therefore, the posterior P600 was linked to both syntactic anomalies and violations. In combination with research connecting the N400 to semantic violations, these results suggested that the N400 indexed semantic processing and the P600 indexed syntactic processing (Osterhout & Nicol 1999).

However, this "pleasing dichotomy of semantic N400 and syntactic P600" (Van Petten & Luka 2012: 183), was later challenged by studies observing a P600 effect in response to non-syntactic manipulations where semantic conflicts elicited a posterior P600 effect. Thematic role violations, such as 'the hearty meal was devouring…', elicited robust posterior P600 effects, as did animacy violations and semantically anomalous sentences (Kim & Osterhout 2005, van Herten, Kolk & Chwilla 2005, van Herten, Chwilla & Kolk 2006, Kuperberg, Caplan, Sitnikova, Eddy & Holcomb 2006, Kuperberg, Sitnikova, Caplan & Holcomb 2003, Chow & Phillips 2013). Additionally, the posterior P600 has been linked to plausibility: implausible sentence continuations, in comparison to plausible continuations, elicit larger posterior P600 amplitudes (Hoeks, Stowe & Doedens 2004, Kim & Osterhout 2005, Nieuwland & Van Berkum 2005). To reconcile the semantic and syntactic posterior P600, Kim & Osterhout (2005) posited one single posterior P600 response, triggered by either difficulty in processing syntax (syntactic P600) or interpretations of syntax errors arising from competing semantic interpretations (semantic P600).

2.2 Frontal P600

Moreover, a separate stream of research has focused on interpreting P600 amplitudes with frontal scalp distributions (see Figure 1); understanding what conditions elicit a frontal P600 has followed a simpler trajectory. Early literature found that in highly constrained sentences, unexpected endings elicited a frontal P600, in comparison to high cloze[2] endings (Kutas 1993). For example, (2a) elicited a larger frontal P600 response than (2b).

(2) a. *William went to the bank to borrow some cash.*

b. *William went to the bank to borrow some money.*

This effect has been robustly replicated (DeLong, Urbach, Groppe & Kutas 2011, Coulson & Van Petten 2007, Brothers, Swaab & Traxler 2015) and also observed in bilinguals (Moreno, Federmeier & Kutas 2002). Therefore, contrasting the posterior P600, the frontal P600 is elicited by unexpected stimuli rather than syntactic, semantic or pragmatic violations.

Despite a wealth of evidence eliciting frontal and posterior P600 amplitudes, there has been little research investigating both responses within the same experimental design; this has led to a deficit of research that directly disassociates them as independent processes with different functions.

[2] Cloze probability refers to how expected a word is within a given context.

2.3 Prediction and the P600

EEG studies are often linked to prediction in language processing which assumes that context is used to anticipate upcoming input before the input is received, thereby facilitating the processing of input when it is encountered. The psychological reality of predictive processing in language is well-established (Ryskin & Nieuwland 2023) and research often links the N400 and P600 components as neural signals evidencing prediction in the brain. Predictive coding accounts suggest the brain generates top-down predictions and learns from any prediction errors by updating its beliefs (Bayesian inferencing); within a hierarchically structured system, top-down predictions are fed forward from higher to lower levels of representation and bottom-up prediction errors are fed back to higher levels (Clark 2013). To exemplify, the accounts suggest that after hearing '*the genie granted his third and final…*' (Laszlo & Federmeier 2009), the brain has generated a conceptual representation of the event using multiple levels of representation; a top-down prediction is generated ('*genie*') and flows down the hierarchy to pre-activate lower levels. If bottom-up input ('*dish*') conflicts with the prediction, an error is generated which flows up the hierarchy to update the model and minimise future prediction errors.

Some predictive coding accounts suggest ERP components index predictive processes in language comprehension. One account suggests the N400 reflects the retrieval of a word's lexical meaning from long-term memory and the posterior P600 indexes its subsequent integration into the preceding context (Brouwer, Crocker, Venhuizen & Hoeks 2017, Brouwer, Fitz & Hoeks 2012). This hypothesis is supported by psycholinguistic experiments: when ease of retrieval was controlled, posterior P600 amplitudes were larger when integration was more difficult (Delogu, Brouwer & Crocker 2021, Aurnhammer, Delogu, Brouwer & Crocker 2023). Although some predictive coding accounts have successfully simulated and thereby accounted for, a range of N400 findings and posterior P600 findings, their frameworks are limited as they neither distinguish between frontal and posterior P600 responses, nor account for the effect of contextual constraint (Nour Eddine, Brothers, Wang, Spratling & Kuperberg 2024).

3 Distinguishing the Frontal and Posterior P600: a Review of Four Studies

This paper will now focus on four studies that have distinguished frontal and posterior late positivities using similar experimental designs. The studies included in this review were found through the University of Cambridge's *iDiscover* search engine (keyword search: 'ERP', 'P600', 'plausibility') and then through reference lists of relevant studies. The studies required the following inclusion criteria: healthy adult participants; ERP measurements across both frontal and posterior sites; direct comparison of unexpected/expected and plausible/implausible stimuli; written or auditory presentation of stimuli; published in English and peer-reviewed.

DeLong et al. (2014) were the first to use an experimental design specifically dissociating frontal and posterior P600 responses, manipulating expectancy and plausibility based on previously established links. Using native English speakers, the design combined sentence pairs with three possible sentence continuations (see Table 2 for example conditions):

i. Expected

ii. Unexpected

iii. Unexpected, implausible

Condition	Example	P600 topography
Expected	For the snowman's eyes the kids used two pieces of coal. For his nose they used a carrot from the fridge.	**None**
Unexpected	For the snowman's eyes the kids used two pieces of coal. For his nose they used a banana from the fridge.	**Frontal**
Implausible	For the snowman's eyes the kids used two pieces of coal. For his nose they used a groan from the fridge.	**Parietal**

Table 2 Example conditions and corresponding P600 topography (DeLong et al. 2014).

The results were consistent with general N400 findings: N400 amplitudes were smallest in expected conditions, and larger for unexpected conditions[3]. Furthermore, frontal P600 amplitudes were largest in unexpected conditions, whereas posterior P600 amplitudes were larger in implausible conditions.

Quante, Bölte & Zwitserlood (2018) replicated DeLong et al. (2014), with native German speakers, including an additional manipulation of possibility (see Table 3). This formed four conditions:

i. Expected

ii. Unexpected, plausible

iii. Unexpected, implausible, possible

iv. Unexpected, implausible, impossible

The constraint of the sentence pair (m = 77%) on the target word was similar to that in DeLong et al. (2014) (m = 85.3%) and the results largely replicated their findings. Comparatively smaller N400 responses were observed in expected conditions; frontal P600 responses were largest in unexpected conditions; and posterior P600 responses

[3] N400 findings have been reported in this paper as a reliable benchmark for the P600 findings.

Condition	Example	P600 topography
Expected	Peter gets up at dawn, drives the tractor all day and feeds his cows in the evening. On some days he would rather not be a farmer but a carefree child.	None
Unexpected	Peter gets up at dawn, drives the tractor all day and feeds his cows in the evening. On some days he would rather not be an adult but a carefree child.	**Frontal**
Implausible (possible)	Luisa's new room was very small but had high ceiling. To save space, she bought herself a pig in the store.	**Parietal**
Implausible (impossible)	Peter gets up at dawn, drives the tractor all day and feeds his cows in the evening. On some days he would rather not be a trick but a carefree child.	**Parietal**

Table 3 Example conditions and corresponding P600 topography (Quante et al. 2018).

were largest for implausible conditions. However, the study did not find a significant effect for possibility.

In combination, the results of both studies can support similar conclusions. The frontal P600 was not significantly affected by plausibility and the posterior P600 was not significantly affected by expectancy; in combination with their contrasting scalp topographies (see Figure 1) and distinct sensitivities to different stimuli, this provides additional evidence to suggest there are different neural processes involved when responding to the expectancy and plausibility of a word following a highly constraining context[4]. As these studies only investigated late positivities in highly constraining contexts, the next two experiments considered in this paper used both low and high constraint contexts to directly examine the effect. Additionally, it is important to highlight that the researchers adopt a neuro/cognitive science approach to factors affecting P600 responses; however, from this paper's linguistic perspective, through manipulating the effect of context on upcoming nouns, these studies are investigating how higher levels of representation (pragmatics) affect responses at lower levels of representation (lexicosemantics) and their subsequent interaction following unexpected or implausible stimuli.

Kuperberg et al. (2020) examined the effect of expected, unexpected and implausible words in two different contexts: low constraint and high constraint (see Table 4). This created five conditions:

[4] Although not explicitly stated, based on previous literature, the constraint of the sentence pairs in both studies is considered highly constraining.

Low Constraint:	**High Constraint:**
i) Unexpected	iii) Expected
ii) Implausible	iv) Unexpected
	v) Implausible

Context constraint	Condition	Example condition	P600 topography
High constraint: The lifeguards received a report of sharks right near the beach. Their immediate concern was to prevent any incidents in the sea.	Expected	Hence, they cautioned the swimmers.	None
	Unexpected	Hence, they cautioned the trainees.	**Frontal**
	Implausible	Hence, they cautioned the drawer.	**Parietal**
Low constraint: Eric and Grant received the news late in the day. They mulled over the information and decided it was better to act sooner rather than later.	Unexpected	Hence, they cautioned the trainees.	**None**
	Implausible	Hence, they cautioned the drawer.	**Parietal**

Table 4 Context constraint, example condition and P600 topography (Kuperberg et al. 2020).

Using cloze norming studies, the constraint of the preceding verb was controlled so that it did not highly predict the following target noun in the absence of a discourse context; this allowed the effect of the context to be isolated. In the low constraint context, the preceding context establishes a very open possible event. '*Eric and Grant*' are going to undertake an action, '*cautioning*'; the lexicosemantic properties of '*caution*' mean the following noun, as the direct object, has to be animate. In the high constraint context[5], the lexicosemantics of '*caution*' still require the direct object to be animate, however, '*lifeguards*', '*sharks*' and '*beach*' further constrain the event of 'cautioning' to an event that happens at a '*beach*' performed by a '*lifeguard*', caused by '*sharks*'. Therefore, following the high constraint context, the most expected continuation becomes '*the lifeguard cautioned the swimmers*'.

The results found that N400 amplitudes were smallest in high constraint, expected conditions - an expected and supported finding. Importantly, the frontal P600 was largest in high constraint, unexpected conditions; both low constraint contexts

[5] Similar to the high constraint context in both DeLong et al. (2014) and Quante et al. (2018).

and plausibility did not significantly affect the frontal P600, similar to previous findings. In contrast, posterior P600 responses were larger for implausible stimuli, with higher amplitudes in high constraint conditions compared to low constraint conditions. Notably, unlike the frontal P600, the posterior P600 was significantly affected by stimuli following low constraint contexts.

Furthermore, Brothers, Wlotko, Warnke & Kuperberg (2020) expanded on the experimental design used in Kuperberg et al. (2020) to examine how the source of contextual constraint affected P600 responses (see Table 5). The target word was preceded by either a local or global context to form six conditions:

Local context

i) Expected

ii) Unexpected, plausible

iii) Unexpected, implausible

Global context

iv) Expected

v) Unexpected, plausible

vi) Unexpected, implausible

In the local context conditions, the target word was only constrained by the lexicosemantic properties of the preceding verb '*unlocked*'. However, in the global context conditions the target word was constrained by the entire proceeding discourse context, not the preceding verb[6]; events associated with '*baking*', '*ingredients*' and '*crust*' constrained what could follow 'flattened'.

Results showed that locally constraining contexts with unexpected continuations did not elicit a frontal P600 effect; however, globally constraining contexts did. In contrast, following both local and global contexts, posterior P600 responses were elicited for implausible continuations, with no significant amplitude difference between the two contexts.[7]

Overall, results from both DeLong et al. (2014) and Quante et al. (2018) demonstrate that in highly constraining contrasts, expectancy modulates the frontal P600 and plausibility modulates the posterior P600. In addition, the results from both Brothers et al. (2020) and Kuperberg et al. (2020), suggest a highly constraining context is necessary to evoke a frontal P600 response, but it is not required to elicit a posterior P600 response. It was concluded that both "the presence of an extended linguistic context and its semantic richness" (Brothers et al. 2020: 152) contribute to the elicitation of both frontal and posterior P600 responses. However, the researchers do not explain why a low/local contextual constraint is sufficient to elicit a posterior P600 response, but not a frontal P600 response. Similar results have been observed in previous research (Kuperberg et al. 2003) and suggest this initial conclusion is a possible overgeneralisation. From a linguistic perspective, Brothers et al. (2020) show that constraints generated at lower levels of representation (lexicosemantics)

[6] The constraint of the verb in the absence of any preceding discourse was very low, controlled by cloze norming studies. This isolated the effect of the discourse context on responses to the target noun.

[7] The study also included an experiment without any preceding discourse; however, the results do not contribute anything to the frontal/posterior P600 discussion so are omitted from this review.

Context constraint	Condition	Example condition	P600 topography
Local constraint: He was thinking about what needed to be done on his way home. He finally arrived.	Expected	James unlocked the door.	None
	Unexpected	James unlocked the laptop.	None
	Implausible	James unlocked the gardener.	**Parietal**
Global constraint: Tim really enjoyed baking apple pie for his family. He had just finished mixing the ingredients for the crust.	Expected	To proceed, he flattened the dough.	None
	Unexpected	To proceed, he flattened the onlookers.	**Frontal**
	Implausible	James unlocked the gardener.	**Parietal**

Table 5 Context constraint, example condition and P600 topography (Brothers et al. 2020).

are sufficient to elicit a posterior P600 response but not sufficient to elicit a frontal P600 response; the implications are discussed below.

4 Hierarchical Generative Frameworks and Predictive Coding

As Ryskin & Nieuwland (2023: 1039) stated, "predictive coding may be a fruitful way to instantiate the computational-level proposal of a hierarchical generative framework for language comprehension". Predictive coding models are also arranged hierarchically; top-down predictions are passed down from higher levels of representation to lower levels. For example, based on the high constraint context in Kuperberg et al. (2020), a higher level of representation including '*beach*', '*lifeguard*', '*shark*' + '*Agent cautions (animate, sentient) Patient*' generates a top-down prediction to pre-activate the following word's form: '*swimmers*'. Any prediction error due to conflicting input (e.g., unexpected '*trainees*') feeds back to the higher levels and updates the system, approximating Bayesian inference (Clark 2013). Understood with a predictive coding account, the frontal P600 reflects the cost of updating the system due to an incorrect prediction and the posterior P600 reflects an "unresolved prediction error" (Kuperberg et al. 2020: 24).

In support, psycholinguistic experiments can evidence the links between P600 components and predictive coding. As research suggests that prediction is a graded process (Kuperberg & Jaeger 2016), it is reasonable to conclude that the size of a prediction error will also be graded; if P600 amplitudes reflect prediction errors, their amplitudes should also be graded. Aurnhammer et al. (2023) measured posterior P600 amplitudes in response to three sentence continuations: plausible, less plausible and implausible. The study found that posterior P600 amplitudes increased as plausibility decreased, suggesting the posterior P600 effect is a graded index of plausibility, and, therefore, could also index graded prediction errors. However, although similarities can be drawn between generative hierarchical frameworks and predictive coding accounts, no predictive coding model has distinguished between frontal and posterior P600 effects – only once a model can simulate the findings of these four P600 experiments, including the effect of contextual constraint, can the connection be made more concrete.

5 Future Considerations

Overall, when considering the four studies' results within generative hierarchical frameworks and predictive coding accounts, the frontal P600 reflects an update to the current belief system; in contrast, the posterior P600 reflects a failure to incorporate the conflict into the belief system leading to a reanalysis of the input (Brouwer et al. 2012, Kuperberg, Kreher, Sitnikova, Caplan & Holcomb 2007). However, further research is required to provide more support for these propositions; this paper will now outline two suggestions. Firstly, if the frontal P600 reflects the cost of prediction, amplitudes should be reduced when predictive processing is less likely to occur. Studies could employ the same experimental design as seen above; however, either introduce conditions that make it harder to predict (e.g., in noisy environments) or include participants where predictive processing is less likely to happen (e.g., older age, lower literacy levels or lower language proficiency). Previous literature has provided evidence that frontal P600 responses are reduced in groups where predictive processing is less likely to happen: Wlotko, Federmeier & Kutas (2012) found that older participants' frontal P600 amplitudes were reduced in response to unexpected endings when compared to younger participants. This suggests future research dissociating frontal and posterior P600 effects could directly compare younger and older participants to provide more robust evidence for frontal P600 amplitudes as the cost of incorrect predictions. Secondly, to test the claim that the posterior P600 reflects attempts at reanalysis, future studies could manipulate participants' ability to engage in reanalysis processes. Tanner, Grey & van Hell (2017) provide some guidance for designing such a study: sentences were presented at three different presentation rates, assuming that the faster the rate of presentation, the "fewer cognitive resources available to engage in reanalysis processes" (256). Results confirmed that when stimuli were presented faster, posterior P600 effects were reduced; therefore, this variable could be introduced in a similar design to those above to evidence the claim that the posterior P600 indexes reanalysis processes, assuming that in implausible conditions, faster presentation rates would reduce amplitudes.

6 Limitations

So far, all accounts of the P600 group the semantic and syntactic posterior P600 effect together (see earlier discussion of Kim & Osterhout (2005)). However, there is recent evidence from hemispheric lateralisation studies to suggest that the syntactic and semantic P600 may actually be separate components. Leckey, Troyer & Federmeier (2023) found that semantic and syntactic posterior P600 responses have different sensitivities to lateralisation and familial sinistrality (family history of left-handedness or FS); for participants with no FS, morphosyntactic violations elicited different posterior P600 responses depending on which visual field stimuli were presented to; however, for participants with FS, morphosyntactic violations did not elicit a P600 effect for either field of presentation. Importantly, animacy (semantic) violations did not pattern in the same way; if the semantic and syntactic posterior P600 were the same response we would expect them to behave similarly. Therefore, this study provides preliminary evidence to suggest syntactic and semantic posterior P600 responses "may not reflect the same underlying processing" (13), challenging central assumptions made by all accounts of the posterior P600 which unify them as a single processor, including generative hierarchical frameworks.

Furthermore, it is important to note that the four studies outlined in this paper are limited in generalisability and effect size. Although supported by studies solely focusing on either the frontal or posterior P600 response, these are the only four experiments that dissociate the two P600 distributions within the same experimental design. The findings are limited to English and German speakers, but more importantly, limited by small sample sizes (n = 31). Kim, McKnight & Miyake (2024) investigated the variability of N400 and P600 using a resampling approach, finding that variability, particularly in the posterior P600 response, was substantial across magnitude, onset and scalp distributions. The study suggested that ERP research on the P600 would ideally need to include 30 participants with at least 40 trials per condition. Although DeLong et al. (2014) and Quante et al. (2018) fit this criterion, the studies manipulating contextual constraint do not. This causes an issue for the validity and reliability of the results generally, let alone connections to predictive processing. Furthermore, evidence of substantial variability in scalp distribution highlights the possibility of spatiotemporal overlap between the frontal and posterior P600, casting doubt on their disassociation within these experiments. Previous research on the P600 has highlighted how spatiotemporal overlap of the N400 and P600 can obscure findings (Delogu et al. 2021); therefore, recent research on the posterior P600 has used an experimental design that minimises N400 amplitudes to isolate posterior P600 responses (Aurnhammer et al. 2023). Although not specifically stated, the same issue is likely to occur with frontal P600 responses; however, the four studies reviewed in this paper do not account for the possible spatiotemporal overlap of the N400 with P600 components which could be confounding the results.

7 Conclusion

In conclusion, this study has critically reviewed four innovative experiments that dissociate frontal and posterior P600 responses. Broadly, they provide additional evidence to suggest that different P600 scalp distributions index independent and distinct processes in language comprehension; the frontal P600 is distinctly modulated by expectancy and the posterior P600 is distinctly modulated by plausibility. These studies have also examined the role of contextual constraint on both P600 components, finding that highly constraining contexts are required to elicit frontal P600 responses but not required to elicit posterior P600 responses; this paper has provided a novel explanation for this discrepancy. Following the connections between a hierarchical generative framework and predictive coding accounts, this paper has also critically examined the results within the current literature on predictive language processing and provided two suggestions for future research. In addition to methodological issues, this paper has also highlighted an emerging stream of research investigating hemispheric lateralisation and P600 components, challenging some core assumptions made by current accounts. Overall, the four studies reviewed in this paper dissociating frontal and posterior P600 distributions, provide new evidence to advance our understanding of the role that ERP components serve in language comprehension and the implications for prediction in language processing; however, future research should aim to test these connections and address the limitations highlighted in this paper.

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