HHS Public Access
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Psychophysiology. Author manuscript; available in PMC 2021 July 01.

Published in final edited form as:
Psychophysiology. 2020 July ; 57(7): e13351. doi:10.1111/psyp.13351.

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The P3b and P600(s): Positive contributions to language comprehension

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Abstract

Since its discovery in the 1960s, the P300 has been contributing both directly and indirectly to language research. Perhaps most notably, it has been suggested that the P600, an ERP component that was first characterized in the context of syntactic processing, could be a variant of the P3b subcomponent of the P300. Here, we review studies on both sides of the debate. We also review the "semantic P600," a positivity with a similar time course and distribution to the P600 seen for syntactic manipulations but that is obtained in response to some types of semantic anomalies. Because most current theories of the P600 try to account for both the syntactic and the semantic variant, linking the syntactic P600 to the P3b might also imply a similar link for the semantic P600. However, we describe emerging research in our lab that casts doubt on the idea that the syntactic P600 and the semantic P600 are the same effect. We argue that grouping ERP responses primarily by domain (language vs. nonlanguage) is likely to be misleading and suggest alternative ways of determining whether ERP effects reflect similar or different processing mechanisms.

Keywords

ERPs; language/speech; P3b; P600

1 | INTRODUCTION

With the discovery of the P300 complex in the 1960s (Chapman & Bragdon, 1964; Sutton, Braren, Zubin, & John, 1965), the door was opened for the use of electrophysiological methods in the investigation of higher cognitive processes. The availability of a brain response that is modulated by an individual's interpretation of a stimulus rather than just its presence promised insights into the neural bases of aspects of human cognition that are difficult or impossible to examine with animal models … perhaps most notably language. Indeed, the use of electrophysiological methods revolutionized the study of language

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processing, and, as we review here, the P300 has played an important—and sometimes controversial—role.

1.1 | The language "oddball" and the discovery of the N400

Building on her earlier work studying the P300 using individual word stimuli (e.g., Kutas, McCarthy, & Donchin, 1977), in the early 1980s Marta Kutas expanded the classic oddball paradigm to allow the study of sentence processing. In the oddball paradigm, one type of stimulus, the so-called oddball, is less probable (and/or is prioritized by the task demands) compared to the other "standard" stimulus type. P300 responses are enhanced to oddball stimuli, in a manner inversely correlated with their probability, and the oddball paradigm has been widely employed in research using the P300. Kutas and Hillyard (1980), therefore, created sentence stimuli wherein a particular word was unexpected, either due to physical features such as font size (e.g., SHE PUT ON HER HIGH HEELED <u>SHOES</u>; note that we will underline the critical words in all examples) or because its meaning rendered it incongruous with the sentence context (e.g., HE SPREAD THE WARM BREAD WITH <u>SOCKS</u>). The physically unexpected sentence final words elicited the expected P300-like response, peaking about 560 ms after stimulus onset. However, the response that was elicited by the semantic oddballs differed in both polarity and latency. Relative to congruent sentence endings, semantic anomalies elicited a larger negative-going response, peaking around 400 ms post-stimulus onset; this response was therefore labeled the N400.

Evidence accumulated since this early study has shown that the N400 is not simply a response to semantic improbability or anomaly, as it may first have appeared. The N400, instead, is part of the normal response to words and is now widely taken to index the access of semantic information associated with incoming stimuli (see Kutas & Federmeier, 2011, for a review). The N400 is relatively facilitated (less negative) when a word is congruent in its context because there is less new information to access. Thus, what Kutas and Hillyard (1980) observed is now understood to be a facilitated N400 response in the congruent sentences, highlighting the larger N400 to the contextually unexpected words in the anomalous case. Large N400 responses can also be seen in the original data across all sentence types for content words early in the sentence (cf. Van Petten & Kutas, 1990; Payne, Lee, & Federmeier, 2015).

Even though the attempt to use an oddball P300 to uncover neural mechanisms of human language processing was not successful in the anticipated manner, by leading researchers to the N400 component, the original study was responsible for launching the now-extensive body of work using ERPs to study the neural correlates of language processing. Studies using the N400 have contributed a large body of knowledge related to the access and accrual of meaning information. The N400 has been used to show that language comprehension is incremental (Van Petten & Kutas, 1990) and involves prediction (Federmeier & Kutas, 1999a), that semantic information can be processed without conscious awareness (Luck, Vogel, & Shapiro, 1996) and in the parafovea during reading (Barber, Doñamayor, Kutas, & Münte, 2010; Kretzschmar, Bornkessel-Schlesewsky, & Schlesewsky, 2009; Payne, Stites, & Federmeier, 2016), and that language mechanisms vary across the hemispheres (Federmeier

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& Kutas, 1999b) and change over the course of normal aging (Wlotko, Lee, & Federmeier, 2010).

Although the N400 has played a critical role in shaping our understanding of how language is processed by the brain, it is important to note that the original (and sometimes lingering) conception of the N400 as a “language component” (i.e., a domain-specific response) is erroneous. The N400 is not only seen to words, but to pictorial stimuli of all kinds (line drawings, comics/cartoons, pictures of objects, natural scenes), faces, gestures, and environmental sounds (e.g., a meow)—essentially, any type of stimulus that is likely to be linked to long-term memory representations (Kutas & Federmeier, 2011). Knowledge about the N400 from this wider literature has played a critical role in building an understanding of the likely neural sources of the N400 and of the processing mechanisms it indexes. As we will argue, we believe that our understanding of other responses seen in language contexts may be similarly enhanced by moving away from domain-specific theorizing.

2 | POSITIVITIES IN LANGUAGE

Following the discovery of the N400, a number of other language-related ERP components and effects were described. Interestingly, some of these take the form of the kind of response Kutas and Hillyard originally expected for semantic anomalies: later (post-N400) positivities with a posterior scalp distribution, elicited by stimuli that are unexpected and/or difficult to process along various dimensions. The first such study was done by Kutas and Hillyard (1983), who presented participants with sentences containing violations of tense or number marking (e.g., As a turtle grows, its shell <u>grow</u> too). They observed a small N400 difference (larger for the violations than for appropriately marked words like *grows*), as well as a posterior positivity to the morphosyntactic violations.

In 1992, Osterhout and Holcomb designed an experiment to look at syntactic processing at the level of phrase structure. They showed participants nonambiguous sentences (e.g., The broker hoped <u>to</u> sell the stock) along with initially structurally similar sentences that were syntactically ambiguous (e.g., The broker persuaded <u>to</u> sell the stock was sent to jail). For these second types of sentences, readers prefer to attach the verb (*persuaded*) to the main clause (as in “the broker persuaded [someone to do something]”) rather than attaching it to the reduced relative clause (“the broker [who was] persuaded to sell the stock”). When the reader is confronted with the less expected outcome of the ambiguity (i.e., when they get the word *to* after *persuaded*), it was theorized that they would need to reanalyze (Frazier & Rayner, 1982). Osterhout and Holcomb time-locked the ERP to the word *to* in both sentence types and found that a positive-going component was seen in response to the more unexpected reduced relative sentences; see Figure 1 for an example.

The observed positivity was sustained but had a midpoint around 600 ms, a characteristic that led the component to be termed the P600.[1] A similar response was also seen in the Osterhout and Holcomb study to the overtly ungrammatical sentences, such as at *was* in

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[1] Other studies published shortly after the initial discovery called this response the syntactic positive shift or SPS (e.g., Hagoort, Brown, & Groothusen, 1993); however, the field has largely converged on referring to it as a P600.

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"The broker hoped to sell the stock was sent to jail." As will be described in more detail, the P600 has come to be well characterized as part of the response to syntactic violations and dispreferred syntactic structures of a variety of types, in multiple languages.

Based on these kinds of findings, initial views understood the N400 and P600 as responses that indexed different language subprocesses, such that semantic processing difficulties yield effects on the N400, whereas syntactic processing difficulties yield effects on the P600 (although syntactic violations, less consistently, also elicit N400-like effects and semantic violations sometimes elicit late positivities, usually labeled as late positive complex [LPC] effects). However, as Figure 1 also illustrates, an early 2000s experiment yielded results wherein a P600-like component could be seen in response to language violations that seemed semantic in nature.

In this experiment, Kuperberg and colleagues (Kuperberg, Sitnikova, Caplan, & Holcomb, 2003) presented participants with three sentence types: standard sentences (e.g., For breakfast, the boys would only <u>eat</u> toast and jam), thematic role animacy violations (e.g., For breakfast, the eggs would only eat toast and jam), and nonthematic role pragmatic violations (e.g., For breakfast, the boys would only <u>bury</u> toast and jam). Given what was known at the time, it was expected that an N400 would be elicited by the animacy violations as well as the pragmatic violations at the critical verb (*eat* or *bury*). Yet, although an N400 effect was observed for the pragmatic violations (bigger N400 to *bury* than *eat*), a posterior, post-N400 positivity was elicited when the ERP was time-locked to the critical verb in the animacy violation sentences.

This positivity was similar in distribution to the typical syntactic P600, and it also fell within the expected time window for the P600. Kuperberg and colleagues (2003) interpreted these findings by suggesting that semantic animacy information allows for the building of a thematic structure for the sentence. In the example above, they theorized that within this structure the word *eggs* would be expected to take the role of theme within the sentence, and so when *eggs* is placed into the agent role, the resulting discrepancy is unexpected within the unfolding structure, and the component that has come to be labeled the semantic P600 is seen.

Thus, several responses that have been characterized in the context of language comprehension bear some similarity to the classic P300 response: they are positive-going responses to events that are unexpected (and possibly attention grabbing), often with a wide-spread distribution that is larger over the back of the head. The question of whether the relationship between these positivities and the P300 is more than superficial (i.e., whether these language-related P600s might actually be P300 responses) has sparked an ongoing, decade-long debate. In the remainder of this article, we shall give an overview of that debate, discuss why it matters, and describe some emerging data that suggest there may be a need to refine the question moving forward.

2.1 | Seminal studies: The P300

Before discussing the debate about the relationship between the P600 and the P300, it is useful to briefly examine how an understanding of each of these components has evolved

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within their separate literatures. We focus here on the subcomponent of the P300 that is known as the P3b (as opposed to the P3a: Snyder & Hillyard, 1976; Squires, Squires, & Hillyard, 1975).

Figure 1 shows a classic P3b as it appears when elicited through the use of a simple oddball task. In neurotypical adults, the P3b has a posterior distribution, and its latency is variable, depending on the complexity of the dimension(s) along which stimuli are being evaluated (Kutas et al., 1977). For relatively easy discriminations, latencies of 300–400 ms are typical, and the latency gets longer as complexity/difficulty of stimulus evaluation increases. The amplitude of the P3b is modulated by several different aspects of the stimuli and task conditions. It is larger to stimuli that are relevant to the task being completed (Duncan-Johnson & Donchin, 1977) and larger to stimuli that are more salient and are being actively attended to (Donchin & Cohen, 1967). It is also larger to stimuli that are less probable both globally and locally (Squires, Wickens, Squires, & Donchin, 1976). The P3b is specifically sensitive to subjective probability, meaning that the probability of the category to which a stimulus belongs (or is thought to belong) in the context of the task is more important than the objective probability (Courchesne, Hillyard, & Courchesne, 1977).

A number of theories have been put forward to explain the functional and/or neural bases of the P3b. Although an exhaustive review of these theories is beyond the scope of this article, we will highlight a few that are most relevant for comparisons with language positivities. One long-standing theory is that of context updating (Donchin, 1981). Context updating proposes that, when processing information, people develop a model of their environment, maintained in working memory. Incoming information that triggers a revision of this model (i.e., an updating of the context) elicits a P3b. Context updating naturally explains the sensitivity of the P3b to probability. In an oddball task, for example, encountering a series of standards creates a context, such that further iterations of this standard will not provide much new information. However, when the infrequent oddball is encountered, the model must be updated, yielding a larger P3b. Higher global, local, or temporal probability increases the likelihood that an oddball will already have been encountered within the span of the currently maintained context (a span that varies as a function of working memory resources: Brumback, Low, Gratton, & Fabiani, 2005), such that encountering another oddball would entail less updating.

Some views also emphasize the role that attention plays in the elicitation of the P3b; whereas in tasks that are fairly nondemanding, P3b amplitudes are large and latencies are relatively short, and as attentional demands increase, P3bs get smaller and later (Kok, 2001). Thus, the P3b has been argued to arise when attentionally mediated processes promote memory operations in temporo-parietal areas (Polich, 2007).

Whereas context updating, and other theories, view the P3b as reflecting the processing consequences associated with evaluating a stimulus, some emerging views link the component directly to decision making (Twomey, Murphy, Kelly, & O’Connell, 2015). In particular, at the neurobiological level, Nieuwenhuis, Aston-Jones, and Cohen (2005) have argued that the P3b reflects the phasic response of the locus coeruleus-norepinephrine (LC-

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NE) system, which, in turn, has been theorized to reflect the results of decision-making processes.

2.2 | Seminal studies: The P600

2.2.1 | Syntactic P600—Following the initial description of the syntactic P600 by Osterhout and Holcomb (1992), this response has been characterized across a number of studies using different languages and a variety of stimulus types, and it has been attested for listening as well as word-by-word reading (Hagoort & Brown, 2000). In the original study, the experimenters used phrase structure violations to elicit the P600, and since then similar stimuli and conditions have replicated these findings in English (Ainsworth-Darnell, Shulman, & Boland, 1998) as well as Dutch (Hagoort, Brown, & Groothusen, 1993) and German (Friederici, Hahne, & Mecklinger, 1996; Hahne & Friederici, 1999). Investigations have also been made into different types of syntactic violations, with late posterior positivities not just being seen to violations of phrase structure but also to violations of subjacency (Neville, Nicol, Barss, Forster, & Garrett, 1991), subject-verb number agreement (Hagoort & Brown, 2000; Osterhout & Mobley, 1995), German case inflection (Münte, Heinze, Matzke, Wieringa, & Johannes, 1998), and Dutch verb inflection (Gunter, Stowe, & Mulder, 1997).

Although many studies have predominantly made use of specific syntactic violations, it is also important to note that the P600 can be elicited by structures that are grammatical but induce processing difficulties. For example, the P600 is larger (at *imitate*) to “Emily wonders who the performers in the concert imitate for the audience’s amusement” than “Emily wonders whether the performers in the concert imitate a pop star for the audience’s amusement.” This makes clear that the P600 is not simply indexing the appreciation of a syntactic error as such (Kaan, Harris, Gibson, & Holcomb, 2000). Moreover, although most experiments have used sets of disconnected sentence stimuli to characterize the P600, there is also evidence that the P600 is elicited during the reading of more natural prose, suggesting that it is not just an artifact of the experimental conditions often required by the ERP method (Osterhout, Allen, McLaughlin, & Inoue, 2002).

2.2.2 | Semantic P600—The semantic P600 has also been further studied since it was originally reported by Kuperberg and colleagues (2003). In addition to work in English, the semantic P600 has been characterized in Dutch (Van Herten, Kolk, & Chwilla, 2005), Spanish (Stroud & Phillips, 2012), and Chinese (Chow & Phillips, 2013), attesting to its generalizability. The original results have been replicated and built upon in the Kuperberg lab, showing, among other things, that the semantic P600 often makes up part of a biphasic response, being seen alongside an N400 in a number of studies (e.g., Kuperberg, Caplan, Sitnikova, Eddy, & Holcomb, 2006; Kuperberg, Choi, Cohn, Paczynski, & Jackendoff, 2010).

Several papers have reported similar results with English materials, including Kim and Osterhout (2005), who suggested that the semantic P600 results from cases in which there is a semantics-based “attraction” between the verb and its argument (e.g., The hearty meal was devouring …) but not in cases where the semantic relationship between the noun and the

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verb is weaker (e.g., The dusty tabletops were devouring …). They propose that, in cases of strong semantic attraction, plausibility overrides syntactic structure and the verb is misinterpreted (e.g., in the above case, *devouring* would be interpreted as *devoured*), leading to a syntactic error and, as a consequence, a P600. In other words, Kim and Osterhout (2005) hypothesize that there is a single type of P600, elicited by syntactic processing difficulty, and that in some cases syntactic misparsed words arise because other parts of the language processing system (e.g., semantics) yield competing interpretations. However, other work has argued that attraction cannot explain all cases in which a semantic P600 response is observed (e.g., Van Herten et al., 2005; Van Herten, Chwilla, & Kolk, 2006).

2.2.3 | Nonlinguistic P600s—Although most studies reporting a P600 response are in the domain of language, late posterior positivities (with waveform features similar or identical to those characterized for the P600) have also been observed in nonlinguistic domains and have sometimes also been labeled as P600s. For example, P600s are observed to violations of visual narrative structure in comics (Cohn, Jackendoff, Holcomb, & Kuperberg, 2014; Cohn & Kutas, 2015), and, more generally, late positive potentials are seen to violations of the components within scenes and events (Sitnikova, Holcomb, Kiyonaga, & Kuperberg, 2008; Võ & Wolfe, 2013; these have also sometimes been linked to the “LPC” effects that have been observed to classic semantic anomalies in some studies, as reviewed in Van Petten & Luka, 2012). P600-like effects are also seen to harmonic anomalies in music (Patel, Gibson, Ratner, Besson, & Holcomb, 1998) and to violations of learned structure within simple nonlinguistic sequences (Christiansen, Conway, & Onnis, 2012; Lelekov-Boissard & Dominey, 2002).

2.2.4 | Theories of the P600—Despite the general morphological/topographical similarity between the P600 and domain-general components like the P3b and the elicitation of P600-like responses to nonlinguistic stimuli, the fact that the P600 was initially observed in a language context has led to language-dominant theories of the component. Moreover, the appealing simplicity of a semantic component (N400) and a syntactic one (P600) has meant that theories not only hinge on the factors that lead to a P600 modulation but often also on the contrast between manipulations that affect the N400 versus the P600 (or, in some cases, that might elicit both types of effects). As such, many of the P600 accounts suggest that sentence processing involves two (or more) processing streams (e.g., Bornkessel-Schlesewsky & Schlesewsky, 2008; Hahne & Friederici, 1999; Kim & Osterhout, 2005; Kos, Vosse, Van Den Brink, & Hagoort, 2010; Kuperberg, 2007; Van Herten et al., 2006). These theories often split the proposed two streams into a semantic and a syntactic processing route, with P600 modulations then arising from the syntactic processing route, and they posit varying accounts of how this could contribute to the P600 effects that are seen to garden-path sentences as well as those to syntactic violations. Some theories, for example, focus on syntactic reanalysis (Hahne & Friederici, 1999; Kim & Osterhout, 2005) and others on the difficulty of integration/unification (Hagoort & Brown, 2000; Kaan et al., 2000).

Recent multistream models accommodate semantic as well as syntactic P600 findings (e.g., Bornkessel-Schlesewsky & Schlesewsky, 2008; Kos, Vosse, Brink, & Hagoort, 2010; Kuperberg, 2007). For example, Kuperberg proposes a semantic stream in conjunction with

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combinatorial streams (which include both syntactic and thematic processing). In the case of a conflict between these streams, further analysis must take place, and this continued analysis is proposed to be reflected in the P600 component. Such multistream models fairly naturally account for the fact that different kinds of language processing difficulties yield functionally and neurally dissociable effects, manifesting in different ERP signatures. Yet, as detailed by Brouwer, Fitz, and Hoeks (2012), such accounts have difficulty explaining the full range of results and predicting when particular manipulations will yield both an N400 and a P600 effect, rather than just one or the other. Such models also do not yet fully explain how there can be individual differences in whether N400s or P600s are elicited to exactly the same type of language manipulation (Tanner & Van Hell, 2014).

Single stream accounts, in contrast, propose that the N400 and P600 arise from different aspects of a unified processing stream. For example, in the Brouwer et al. (2012) account (instantiated in the neurocomputational model of Brouwer, Crocker, Venhuizen, & Hoeks, 2017), the N400 reflects semantic access, which is followed by the P600, reflecting the integration of that accessed information into an ongoing sentence structure. This model thus makes the strong claim that language processing is always accompanied by both types of activity, and that cases—such as semantic anomaly—that do not (always) elicit post-N400 effects actually reflect processing differences on the P600 (which this model proposes should be assessed relative to the prior N400 peak, not relative to the baseline).

One commonality between recent multiple and single stream theories is that, in focusing on the difference between the streams/subprocesses that characterize the N400 versus the P600, both types of models have tended to group the syntactic and semantic P600s together, explaining both under the same theoretical umbrella. In so doing, the theories have made the —often tacit—assumption that the functional and neural underpinnings of the two types of P600 are similar. Indeed, both components not only arise in the context of language manipulations but also have a similar time course and distribution. Nonetheless, direct empirical support for this link has been lacking in the literature. Moreover, the kind of morphological similarity that has led many researchers to group the two P600s together has also compelled a comparison between these language positivities and the P3b—a comparison that has been more controversial.

3 | DEBATE: IS THE P600 A FORM OF A P3B?

The debate about whether the P600 is actually a manifestation of the P3b in the context of language is not a new one, and, as a result, there is much evidence on both sides. Before considering this evidence, however, it is worth considering the implications of this debate. From one perspective, the grouping together or splitting apart of the P3b and the P600 is of little importance. Regardless of its similarity (or not) to the P3b, the P600 is a marker that can capture differences between the processing of syntactically congruent, preferred, or probable structures relative to incongruent, dispreferred, or less probable structures, making it a useful measure for understanding the online processing of syntax (and other structured/analytical/combinatorial language processes) and how that processing changes with experience, context, and task demands, in a wide variety of populations.

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However, aside from general scientific interest, there are other reasons to want to know if the components are in fact related. The first of these reasons is purely pragmatic. As outlined above, the P3b has been heavily studied since its discovery in the 1960s, and, as a result, there is a lot of information available about the component, including where it might be generated in the brain (see Hansenne, 2000; Polich, 2012; Soltani & Knight, 2000), how it changes with age (e.g., Fabiani & Friedman, 1995; Fabiani, Friedman, & Cheng, 1998; Friedman, Kazmerski, & Fabiani, 1997), and if/how it differs in various clinical populations (Clark, McFarlane, Weber, & Battersby, 1996; Jeon & Polich, 2003; Polich, 2012; Röschke & Wagner, 2003).

The literature provides knowledge about the sensitivity of the P3b to chemicals and hormones, for example, the effects of caffeine (Kawamura, Maeda, Nakamura, Morita, & Nakazawa, 1996; Seidl, Peyrl, Nicham, & Hauser, 2000) and menstrual cycle (e.g., Fleck & Polich, 1988; Johnston & Wang, 1991), as well as theories about the neurotransmitters and systems involved (Nieuwenhuis et al., 2005). If it is the case that the P600 shares important overlap with the P3b, then the wider body of available information about the P3b could be used to target future research into P600-eliciting stimuli and provide interesting and testable hypotheses about the neurophysiology of language processing.

The relationship between the P600 and the P3b also bears on an important larger question about the domain specificity of the processes used to comprehend and produce language. Language has often been put forward as an example of a cognitive ability that is special, requiring processing abilities and biological structures/mechanisms distinct from other cognitive skills (e.g., Hauser, Chomsky, & Fitch, 2002), especially those required for processing language structure. Thus, while the apparent domain generality of some aspects of semantic processing, as evidenced by findings in the N400 literature, may not be particularly controversial, the question of whether syntactic processing (if this is what the P600 is taken to index) might be similarly domain-general is much more theoretically laden. If the P600 is indeed a specialized response for processing language structure, this would support the idea that syntactic processing might have unique, dedicated neurophysiology. On the other hand, if one of the primary electrophysiological responses associated with syntactic manipulations is a form of the P3b, a component that is clearly domain-general, this might tend to support views that posit that language processing is built from domain-general skills (e.g., MacDonald, Pearlmutter, & Seidenberg, 1994).

Next, therefore, we overview the empirical evidence that is relevant to the question of whether the P600 might be a variant of the P3b. In the interest of transparency, we will begin by making clear that we come down on the side of thinking that the P600 is functionally and neurally related to the P3b. However, in order to present a balanced argument, we will first discuss the research that has been used to support the idea of a distinct P600, and, where appropriate, we will provide a critique of these interpretations. We will then discuss empirical evidence that directly supports a link between the two components.

Osterhout, McKinnon, Bersick, and Corey (1996) conducted an early experiment to examine the relationship between the P600 and the P3b, by designing stimuli expected to elicit a P3b, due to a physically unexpected event, a P600, from a syntactic violation, or both.

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Participants were presented with typical sentences (e.g., The doctors believe the patient will recover), sentences that contained a syntactic error in the form of a number agreement violation (e.g., The doctors believes the patient will recover), sentences that contained a physically unexpected (in this case, uppercase) word (e.g., The doctors BELIEVE the patient will recover), and sentences that contained both of these (e.g., The doctors BELIEVES the patient will recover). Osterhout and colleagues found a late positivity to both the number agreement violations and to the physical anomalies. Replicating the typical distribution of the P3b and the P600, both positivities had posterior scalp distributions (although the P3b was found to have a more right-lateralized scalp distribution). However, the responses differed in latency: the physical anomaly positivity peaked at around 500 ms and the number agreement violations peaked 100 ms later (cf. Figure 1).

Although Osterhout and colleagues interpreted this latency difference as supporting the separability of the two responses, it could also be a function of the more complex processing that is presumably required to perceive and evaluate number agreement violations compared to the unexpected use of uppercase, given that P3b latency is known to vary with stimulus evaluation difficulty (as in Kutas et al., 1977). The P600 response was also more sensitive to task relevance (which is, however, known to affect the P3b as well; Duncan-Johnson & Donchin, 1977), being larger when people were asked to make acceptability judgments than when simply reading.

Finally, the sentences that contained both the number agreement violation and the physically unexpected word showed a larger positivity than that seen to either violation type alone. The authors took this pattern as evidence that the two responses arose from different neural generators, whose independent contributions created an additive effect at the scalp. However, this conclusion has also been questioned, most notably by Coulson, King, and Kutas (1998), who pointed out that by including two anomalies (physical and syntactic) in the same sentence, the authors were simply making the stimuli more salient—a factor that is known to augment P3b amplitudes (Donchin & Cohen, 1967).

Perhaps more compelling evidence for the separability of the two components comes from studies looking into the neural generators of these effects. Despite the wealth of studies involving the P3b, its underlying neural correlates are not agreed upon, and little is known about the neural generators of the P600. The P3b has been argued to have several different generators, including medial temporal lobe structures and the temporal parietal junction (for reviews on the neural generators of the P300, see Hansenne, 2000; Soltani & Knight, 2000), and although one study found increased activity in the right medial parietal cortex in response to classic P600 eliciting stimuli (Kuperberg et al., 2003), an enhanced understanding of the underlying neural generators of the P600 is an important step in resolving the issue of separability.

To begin to address this question, researchers have turned to patient studies. In one such study, patients with left perisylvian damage were divided into agrammatic and nonagrammatic groups, and then they, along with age-matched controls, were presented with spoken Dutch sentences containing grammatical violations in the form of an agreement violation (e.g., The girls pay the baker and takes the bread home) or a word order violation

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(e.g., The thief steals the expensive very clock from the living room; Hagoort, Wassenaar, & Brown, 2003). In response to these violations, both the nonagrammatic aphasics and the controls elicited a late positivity (P600). However, the agrammatic patients showed a response that was more N400-like, suggesting that these patients were relying on semantic information to understand the sentence structure. The authors suggested that the lack of P600-like response in the agrammatic patients indicates that the neural generators for the P600 may be within the areas damaged in these patients. However, it is also possible that the damaged areas are critical for appreciating the violation but that the generation of the P600 is downstream of that. This particular experiment is also difficult to interpret in the context of the debate because the same patients were not tested for their ability to elicit a P3b.

Another experiment that remedied this latter issue tested for both the P3b and the P600 in patients who were grouped depending upon whether they had basal ganglia damage or damage to temporo-parietal regions (Frisch, Kotz, von Cramon, & Friederici, 2003). Both groups were presented with an auditory oddball and spoken German sentences that contained verb inflection violations. Frisch and colleagues found that both patient groups elicited a P3b to the oddball task but that only the temporo-parietal patients showed a P600 effect to the grammatical violations. They therefore concluded that the basal ganglia are an important area for the generation of the P600 but not for the P3b. Again, however, with a single dissociation, it is difficult to know whether the damage is affecting the source of the component itself or a specific, critical precursor to what is then a more domain-general response.

From the above literature, we can see that, although the research that supports splitting the P3b and the P600 into two separate components is compelling, it is not definitive. We now turn to the other side of the debate, looking at evidence that supports a link between the two components. Similarities in the time course, polarity, and typical topography between the P3b and the P600 are well established and were alluded to even by Osterhout and Holcomb (1992). Although these similarities are important markers, what is more notable is that the P600 and the P3b are also sensitive to very similar manipulations. To begin with, the amplitude of the P3b is known to be modulated by the salience and probability of the eliciting stimuli, and the violations that are often used in P600 experiments are by definition salient in their incorrectness and low probability in the world.

Coulson et al. (1998) directly tested the sensitivity of the P600 to experimental probability by manipulating the frequency of grammatical errors in different blocks of an experiment. They found increased positivity to less probable sentence types, both for improbable syntactic violations as well as for grammatical sentences, when those were improbable. Moreover, the response to lower probability events of both types (a response that thus might be argued to be a P3b) was indistinguishable in timing or distribution from the response to ungrammaticality (independent of probability)—that is, the P600. The same is also true of the level of task relevancy, another variable known to affect the P3b (Duncan-Johnson & Donchin, 1977). In studies wherein syntactic violations are relevant to the task (e.g., because participants are required to make judgments), the P600 is larger than when they are not (Hahne & Friederici, 2002; Osterhout et al., 2002, 1996).

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The latency of the P600 is later than the typical latency of the P3b in a simple oddball task. However, before the discovery of the P600, it was already known that, unlike some of the other cognitive components (such as the N400), P3b latency is not tightly yoked to the onset of the eliciting stimulus but instead is related more strongly to the participant's response to the stimulus, in particular varying with factors affecting the time course of stimulus evaluation (Courchesne, Hillyard, & Courchesne, 1977; Nieuwenhuis et al., 2005; Verleger, 1988). Given that the processes involved in detecting a syntactically low probability or anomalous event are likely to take more time than those involved in detecting a simple perceptual deviant, this latency difference is arguably not only readily explainable but also actually theoretically predicted. Indeed, P3b latency in the single-word oddball task used by Kutas and colleagues (1977) varied between just before 400 ms to over 700 ms and was around 600 ms on average (i.e., similar to a typical P600 latency) for tasks involving the detection of a synonym or a variable name.

Perhaps more important than the absolute latency of the P600 is the question of whether that latency shows the kind of variability that has been established for the P3b. Single-trial analyses of the P3b have found that it is closely aligned with reaction time (e.g., Makeig et al., 1999), at least under conditions in which accuracy rather than speed is prioritized (e.g., Kutas et al., 1977) and wherein reaction times are not highly dominated by response selection demands (McCarthy & Donchin, 1981). Thus, an important question for linking the two potentials is whether the latency of P600 also varies with response latency, rather than being more stably associated with stimulus onset, as competing accounts might predict (see discussion in Sassenhagen, Schlesewsky, & Bornkessel-Schlesewsky, 2014).

To test this, Sassenhagen and colleagues used a single trial analysis that assessed alignment of the P600 latency with the stimulus and with the response. In this experiment, participants heard sentences that contained morphosyntactic violations (gender mismatches) and semantic violations. The average ERP revealed the expected N400 effect associated with the semantic violations and a P600 effect for the morphosyntactic violations. Whereas the latency of the N400 was found to be consistently aligned with the onset of the critical word, the latency of P600 was instead tightly aligned with the button press response that participants used to indicate if the sentence was correct or incorrect. Moreover, on a single-trial level, the button press response occurred during the elicitation of the P600, not after—thus inconsistent with accounts that posit that the processes involved in the P600 are a necessary part of syntactic analysis (which would therefore need to be completed and followed by response selection and execution to permit an accurate judgment response).

In addition to the similarity in factors affecting P600 and P3b amplitude and latency, there is also similarity between the two responses at the level of scalp distribution. In typical young adult samples, the P3b has been found to peak over posterior areas of the scalp (e.g., Fabiani, Karis, & Donchin, 1986; Friedman et al., 1997). That the P600 has a similar distribution is not in and of itself strong evidence that the components are related, as multiple differentiable neural sources could lead to similar scalp distributions. Again, therefore, the question is whether the distribution of the P3b and P600 are modulated in similar ways. One factor known to affect the distribution of the P3b is normal aging, with older adults showing a

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more frontal distribution in response to standard oddball tasks (Fabiani & Friedman, 1995; Fabiani et al., 1998; Friedman et al., 1997).

Relatively few studies have looked at the P600 in older adults. However, Kemmer, Coulson, De Ochoa, and Kutas (2004) presented older adult participants with sentences containing number agreement violations (e.g., Industrial scientists develops many new consumer products) and pronoun-antecedent agreement violations (e.g., The grateful nieces asked themselves how she could repay her aunt). They observed a P600 in older adults with similar amplitude and latency to that in younger adults—but, indeed, with a pronounced frontal shift. We replicated this finding in an experiment that used word–class violations (e.g., the eat). Whereas younger adults showed the typical posterior distribution in their P600 responses (Lee & Federmeier, 2015), older adults' P600s showed a broader, frontally shifted distribution (Leckey & Federmeier, 2017).

The similarity in the effect of aging on the distribution of the P600 and P3b across the two literatures is striking, but no study has directly compared the distribution of the two, so in ongoing work, we set out to do just that. Younger and older adults performed a simple visual oddball task consisting of target letters interspersed with standard letters (to elicit a P3b) as well as a sentence reading task. We used the sentences from Kuperberg et al. (2006), which added a morphosyntactic violation condition (e.g., For breakfast, the boys would eats toast and jam), designed to elicit a syntactic P600, to the three sentence types from Kuperberg and colleagues (2003) described previously. Thus, we expected to be able to characterize a syntactic and semantic P600 and a basic oddball P3b response in all participants, as well as an anomaly N400. Indeed, in both younger and older adult groups, we found an N400 to the pragmatic violations, which was later but similar in distribution in the older compared to the younger group. Replicating prior work looking at aging effects on the P3b, we found a robust P3b oddball in both participant groups, but with a frontal distributional shift in the older adults. Importantly, we also found a frontal shift in the P600 to the morphosyntactic violations, replicating Kemmer et al. (2004) and our own prior work.

4 | THE SYNTACTIC AND SEMANTIC P600S … SEPARABLE COMPONENTS?

Both younger and older adults also elicited the expected semantic P600, and Figure 2 shows the interesting difference between the two groups. For young adults, the distribution of the syntactic and semantic P600 was similar (as has been seen in prior work): bilaterally posterior for both (although it should be noted that the syntactic P600 was overall larger than the semantic P600). However, the semantic P600—which has never before been characterized in older adults—retained a more posterior distribution, in contrast to the syntactic P600, which showed the anticipated age-related frontal shift. Hence, in addition to further replicating the syntactic P600 frontal shift, these results suggest the possibility that the semantic P600 is perhaps different in origin to its syntactic counterpart.

There is little work that empirically tests the similarity of the syntactic and semantic P600, beyond noting their basic morphological resemblance (in young adults, at least) and the fact that both are elicited in the context of sentence processing. However, there are some existing

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findings that perhaps point to differences between the two. One such example is that the semantic P600 has been elicited in both active and passive tasks (Kolk, Chwilla, van Herten, & Oor, 2003). This is in contrast to the syntactic P600, which is largely attenuated (Osterhout et al., 2002) or absent (Hahne & Friederici, 2002) in cases wherein participants are not explicitly asked to make judgments on content. Not only is this a potentially important distinction between the semantic and syntactic P600s, but it also further ties the latter to the P3b, which, as previously noted, is well known for its sensitivity to task demands.

With the aim of explicitly comparing the semantic and syntactic P600s, we decided to examine the tendency of the two hemispheres to elicit the two responses, as we had previously characterized the syntactic P600 in terms of laterality in both younger (Lee & Federmeier, 2015) and older (Leckey & Federmeier, 2017) adults. In this experiment, we used the Kuperberg and colleagues (2006) stimuli with young adult participants, lateralizing the critical verb to the left or right visual field, thereby biasing processing to the right and left hemispheres, respectively.

Figure 3 shows the results at a representative channel. Replicating the pattern seen for a syntactic P600 to word order violations in Lee and Federmeier (2015), we find that, in strongly right-handed (RH) young adults (without familial sinistrality), the syntactic P600 to morphosyntactic violations is lateralized to the left hemisphere, with RH-biased processing manifesting an N400 response. However, in contrast, the thematic role violations, which elicit a semantic P600 with central presentation, elicit a bilateral N400 response in both visual fields—not a positivity. This pattern, in which neither hemisphere stimulated selectively shows the response seen with central (and, therefore, bihemispheric) stimulation, has been observed previously for other components. For example, Wlotko and Federmeier (2007) observed that a late frontal positivity, which has been characterized in response to plausible but unexpected words in contexts that strongly constrain for a different word, was absent with selective presentation to either visual field. Hence, the semantic P600 may similarly require joint processing across the hemispheres and/or central (foveal) attentional resources. Regardless of the precise reasons for the difference, however, these data reveal an additional dissociation between the semantic and syntactic P600s. The tentative conclusion based on the two experiments outlined above is thus that the syntactic and semantic P600s may not be reflecting the same processing.

5 | CONCLUSIONS: ORGANIZING THE “FAMILY” OF LATE POSITIVE COMPONENTS

Although this is the first proposal that the semantic and syntactic P600s may differ in important ways, it is not the first suggestion that the P600 might constitute a family of functionally dissociable components. The early reanalysis and repair view of the P600 led different groups to suggest that, based on differential scalp topography, there was a distinction between these two processes and the positivities that reflected them. Friederici, Hahne, and Saddy (2002) presented participants with syntactic violations as well as complex syntactic structures. They reported that, in case of violations, where repair was required, the

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resulting P600 had a posterior distribution; however, in response to complex syntactic structures, the reanalysis required led to a more frontally distributed P600. Along similar lines, Hagoort and Brown (2000) put forward the idea that there were different subcomponents within the P600, with a more widely distributed initial phase being modulated by integration complexity followed by a second, more posterior effect, reflecting reanalysis. More recently, Tanner, Grey, and van Hell (2017) manipulated retrieval interference and the time allowed for reanalysis and found that, although both manipulations modulated the P600, they did so in a way that was not interactive—again pointing to the possibility of multiple distinct P600 effects.

Clearly, more data will be necessary to determine whether there are subclasses of effects that have been termed syntactic P600s and whether the semantic P600 might be related to one or more of them or is functionally/mechanistically distinct. At this point, however, it seems clear that the field could benefit from a reconsideration of how these components are identified and classified. In this article, we have described several components that share surface similarity in the ERP waveform (positivities, with a generally posterior distribution, that emerge after sensory components and with a broad and/or variable latency) and that have a general functional similarity in being enhanced to stimuli that are relatively unexpected and/or that would tend to elicit some kind of updating. These include the P3b, the syntactic P600(s), and the semantic P600, as well as variations of what has been termed the LPC. In thinking about these responses, the field has tended to use domain as a primary organizing principle, grouping together the syntactic and semantic P600s and, in some cases, subsets of the LPC effects, by virtue of the fact that they are elicited in the context of language—and, correspondingly, theorizing about them largely separately from the P3b and from other late positivities elicited in nonlanguage contexts. We have attempted to show here how this domain-based bias can be misleading, making the field both slow to accept accumulating evidence for similarity between the P3b and the syntactic P6 and unlikely to seek out evidence for differences between the semantic and syntactic P600 (and other possible functional subdivisions within these effect classes).

In determining how these components relate to one another—or do not—we suggest that the field consider other organizing principles. In his 1980 Presidential Address discussing the P300, Donchin emphasized the need to understand ERP components in terms of the underlying processes that generate them, rather than their correlations with specific behaviors—or, we might add, domains (Donchin, 1981). It is possible that there are processes specific to language. However, the fact that comprehending language necessarily also draws on a myriad of more general processing resources means that one cannot, by default, assume that effects elicited within language are likely to arise from domain-specific sources. Thus, it is fruitful to consider the role that domain-general processes might play in yielding the ERP effects that have been observed in the context of language processing.

Although a process-based taxonomy of ERP components is a laudable goal, it is of course the case that designing experiments to target specific underlying processes can be challenging. Here, we have tried to highlight what we see as some promising approaches toward that goal. Because normal aging is associated with changes in core neurocognitive processes and abilities (see, e.g., Fabiani, 2012, for a review), studying the effects of age on

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sets of putatively related (or unrelated) ERP effects has the potential to reveal not only which effects do or do not change in tandem, but also what resources (e.g., working memory capacity, inhibitory processing) each subset of effects might tap into. Studies of individual differences could offer similar opportunities (see review by Tanner, Goldshtein, & Weissman, 2018). We showed that another way to assess similarities and differences between ERP effects is through the study of hemispheric differences. Different patterns of response as a function of presentation visual field across different ERP effects can provide evidence for underlying differences in neural generators/mechanisms. Moreover, given that there are well-established hemispheric processing biases for a number of types of cognitive processes (see extensive review in Hellige, 1993), such patterns can provide clues about the nature of the processes that might underlie subclasses of ERP effects and the resources (such as central/joint attention) that each might require.

Funding information

James S. McDonnell Foundation, National Institutes of Health (grant AG026308) (to K.D.F.).

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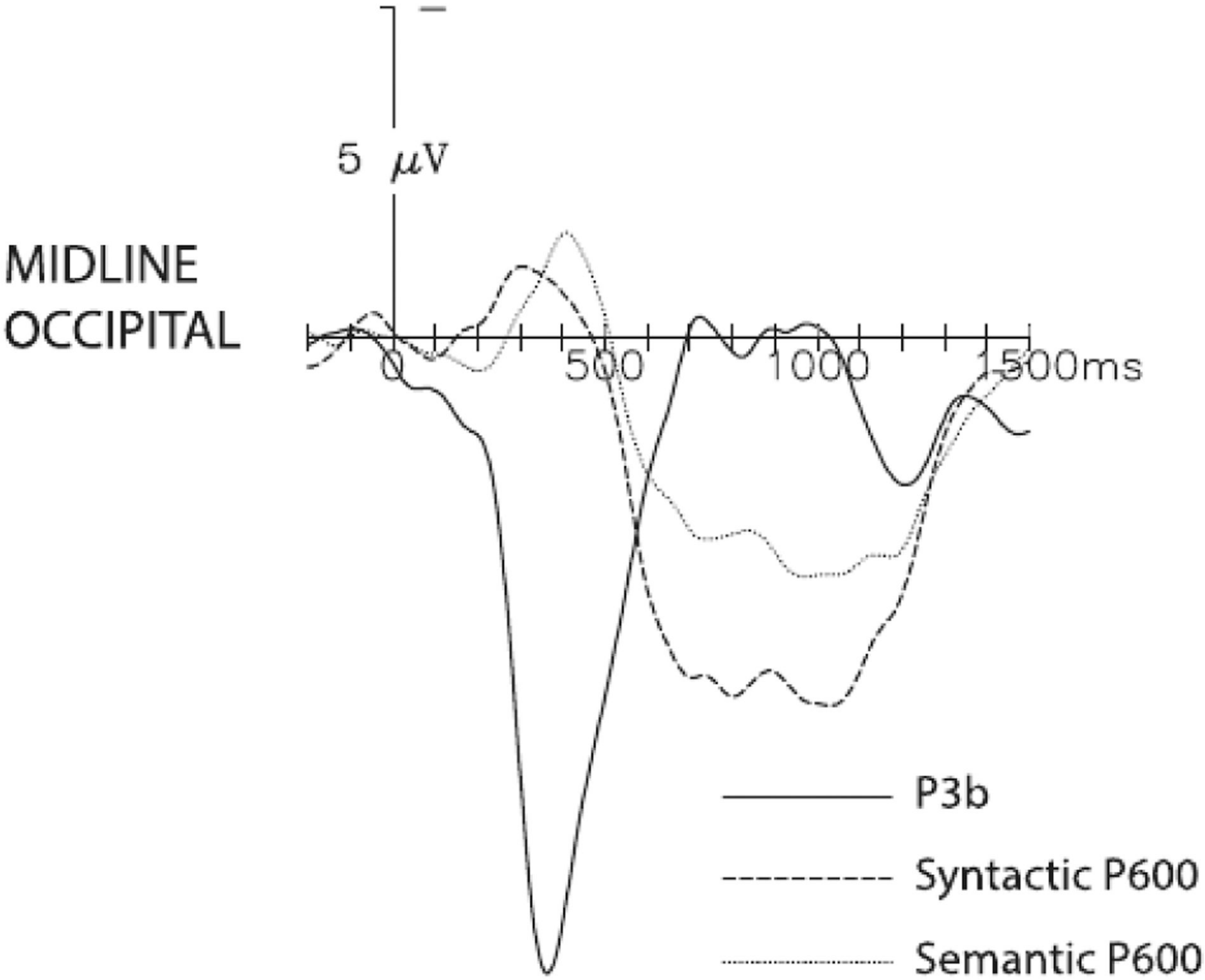

FIGURE 1.

Grand-averaged difference waveforms showing a typical P3b effect, syntactic P600 effect, and semantic P600 effect at the midline occipital site. Negative is plotted up. P3b eliciting task was a standard visual oddball (low probability - high probability). P600 eliciting tasks were taken from Kuperberg et al. (2006). From these stimuli, morphosyntactic violations were used to elicit the syntactic P600 (violation - grammatical sentence), and animacy violations were used to elicit the semantic P600 (violation - grammatical sentence)

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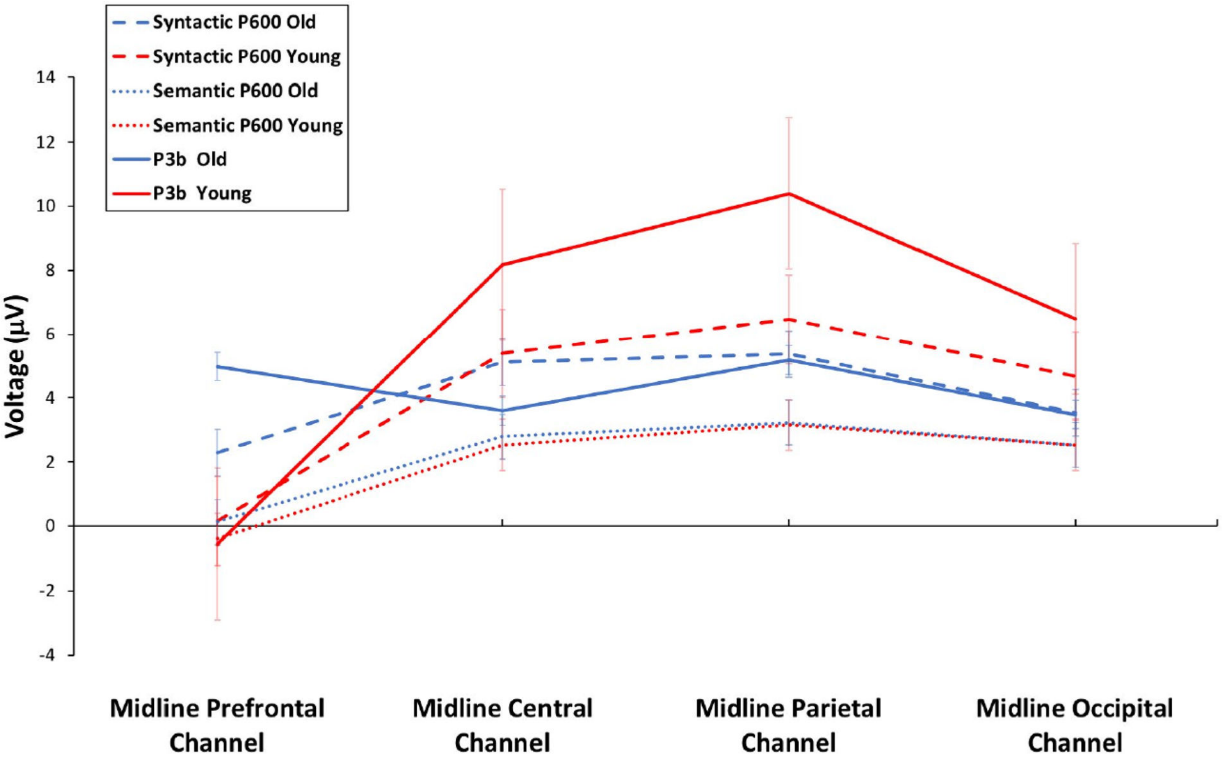

FIGURE 2.

Distribution of the syntactic P600 effect, the semantic P600 effect, and the P3b effect at all midline channels. The syntactic P600 and P3b effects show a frontal shift, with reduced voltages over midline posterior channels and increased voltages at the midline frontal site for the older adult compared to the young adult group. The semantic P600 effect is similar for both age groups across all four of the midline channels. Error bars show standard error

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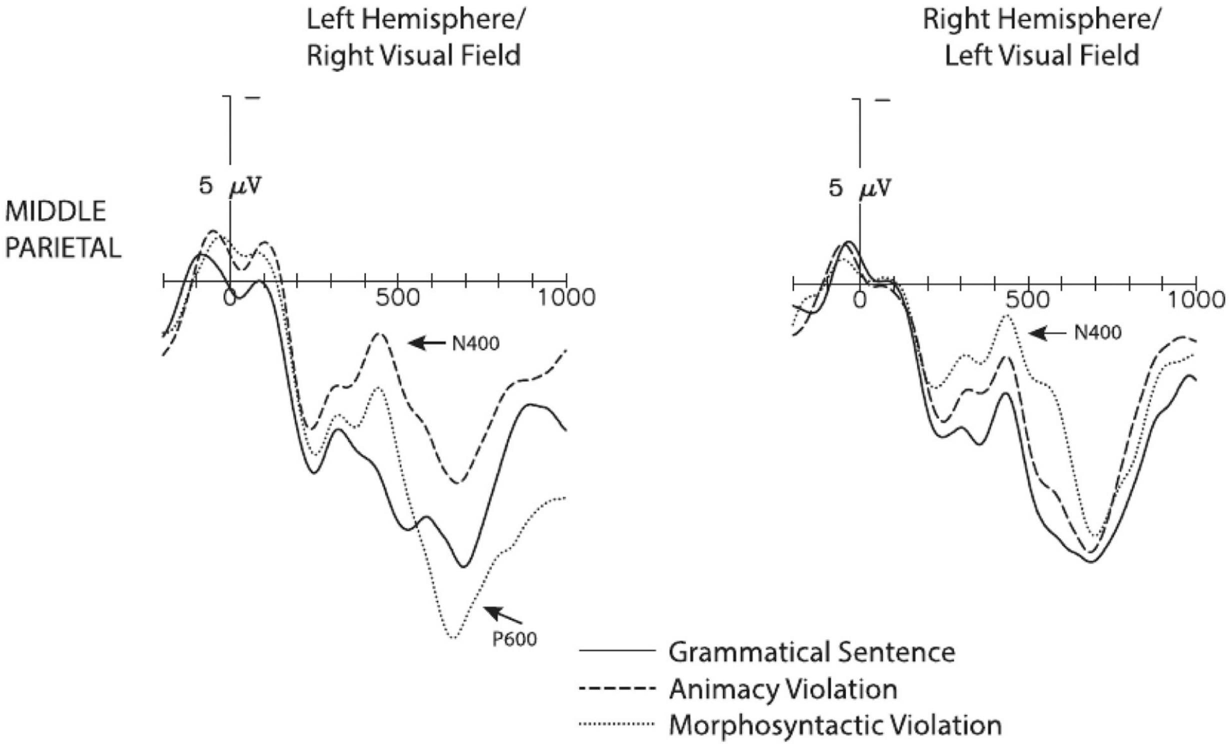

FIGURE 3.

Grand-averaged ERP waveforms for grammatical sentences, animacy violations, and morphosyntactic violations at the midline parietal site. Negative is plotted up. Results for initial presentation to the left hemisphere are shown on the left, and results for the right hemisphere are shown on the right. For left hemisphere/right visual field presentation, both the animacy violations and the morphosyntactic violations elicit an N400 effect, and the morphosyntactic violations also elicit a P600 effect. For right hemisphere/left visual field presentation, both animacy violations and morphosyntactic violations elicit only an N400 effect