NÖRO PSİKİYATRİ ARŞİVİ
ARCHIVES OF NEUROPSYCHIATRY

REVIEW

Arch Neuropsychiatry 2021;58:249–252
https://doi.org/10.29399/npa.27422

Functional Role of the N400 and P600 in Language-Related ERP Studies with Respect to Semantic Anomalies: An Overview

Zahra SEYEDNOZADI[1], Reza PISHGHADAM[1], Morteza PISHGHADAM[2]

[1]Department of English, Ferdowsi University of Mashhad 9177948974, Iran
[2]Department of Medical Studies, Faculty of Medicine, North Khorasan University of Medical Sciences, Bojnurd 7487794149, Iran

ABSTRACT

In this study, the language-related ERP studies relevant to the functional role of the N400 and P600 in semantically anomalous sentences and the underlying reasons which may affect their functions were reviewed. Since their discovery, the N400 and P600 have been the most important language-related ERP components. The N400 has been mostly elicited as a result of processing sentences with lexical and semantic anomalies, but later on, in many studies instead of the expected lexical-semantic N400 effect, semantic anomalies elicited a P600 effect called semantic P600. However, the functional interpretation of these two ERP components has constantly been a matter of debate. Perhaps most notably, it is proposed that it is not just the N400 which is related to semantic anomalies but the P600 can also be reflected as a result of these kinds of anomalies. Reviewing the literature for explaining the functions of the two ERP components, the N400 and the P600, during the processing of semantic anomalies revealed that still there is a need for more research on language processing in order to make the researchers capable of describing the underlying factors influencing them, especially more focused investigations of the functional-anatomical and neurocomputational models may provide a clearer understanding of them. Moreover, any practical theory or model of the N400 and the P600 in language comprehension needs to consider the apparent inconsistencies in the elicitation pattern of the N400 and the P600 in order to successfully capture the full data spectrum.

Keywords: Event-related potentials, language comprehension, N400, P600

Cite this article as: Seyednozadi Z, Pishghadam R, Pishghadam M. Functional Role of the N400 and P600 in Language-related ERP Studies with Respect to Semantic Anomalies: An Overview. Arch Neuropsychitry 2021;58:249-252.

INTRODUCTION

In the course of communication, the speaker tries to make a string of words that are semantically and syntactically congruent (1). The listener also tries to incorporate the semantics, pragmatics, syntax, and prosody of the speaker's speech into meaning (2). In order to fulfill this end, the listener seems to follow these speech features, predict the upcoming speech, and involve in further processing when predictions are not compatible with what is expected (1). Many of these processes underlying language comprehension have been explained in different studies that attempt to integrate incoming knowledge during language processing (3). The different aspects of speech processing are supported by a series of cortical oscillatory and event-related potential (ERP) responses that emerge during the speech, showing the neural mechanisms that may support language comprehension (4). Hence, the neuroelectric activities of the human brain that accompany linguistic processing have been studied through the recordings of ERPs from the scalp (5). The most important language-related ERP components are the N400, a centro-parietal negativity, peaking about 400 ms, and the P600, a positive deflection in centro-parietal and sometimes frontal areas, peaking about 600 ms after the onset of the anomalous item (6).

Despite a large amount of research on the N400 and the P600 effects, as yet, there is no agreement on the functional basis of these components (1). ERP studies of semantic processing, as Newman et al. (7) described, have generally used a 'violation paradigm' to identify indexes of different temporal stages of processing. In this paradigm, subjects read or hear correctly formed sentences intermingled with sentences that have some sort of violation or incongruity of semantics. In this study, along with reviewing empirical studies considering semantic violations, we will describe the factors which may affect the functions of these two components in response to the processing of semantically anomalous sentences.

THE N400

N400 is one of the most studied language ERP components, which was first introduced by Kutas and Hillyard (5). Many studies examining the processing of semantic anomalies targeted the N400 component. Regarding the literature, the processes underlying the N400 component reflected in semantically anomalous sentences are mostly sensitive to some important factors such as contextual factors, semantic expectancy, and predictiveness.

In the initial study by Kutas and Hillyard (5), it was revealed that when a contextually anomalous word appears at the end of or within a sentence,

Correspondence Address: Reza Pishghadam, Department of English, Ferdowsi University of Mashhad 9177948974, Iran • **E-mail:** pishghadam@ferdowsi.um.ac.ir
Received: 18.09.2020, **Accepted:** 11.01.2021, **Available Online Date:** 27.01.2021

a negative-going ERP component that peaks at 400 milliseconds will be produced. In the same line, recently, Cosentino et al. (8) argued that the reported N400 revealed the critical role of contextual factors in modulating the meaning of words.

In a study regarding the role of semantic expectancy, Kutas and Hillyard (9) found that the N400 amplitude decreases when the expectancy of a word increases in a given context. Most recently, Jiang and Zhou (10) also discussed that the role of expectancy is very important during semantic anomaly judgment on the size of the N400 amplitude. They revealed that an anomalous noun, which is preceded by a strong expectancy context, reflects a smaller N400 amplitude relative to an anomalous noun with an unexpected preceding context.

Considering the prediction factor, Cheimariou et al. (11) investigated the mechanisms underlying the N400 effect with respect to predictiveness and congruency. Their findings showed an interaction among predictiveness, congruency, and age. They supported the idea that lexical access and integration work in parallel and are modulated by a common prediction error. Along the same line, Szewczyk and Schriefers (12) examined if the N400 amplitude decrease for predictable words is due to the preactivation of the critical word or to the difficulty in the integration of the word with the sentence. Their results emphasized the role of prediction in sentence comprehension. In another study, Calloway and Perfetti (13) investigated whether the readers use integrative or predictive processes during the processing of semantically anomalous sentences. The results indicated that prediction and integration are both important processes in language comprehension. In detail, activation from memory and from the context words both affect each other.

Many other experiments on the N400 effect in response to semantic anomalies have examined other different factors such as level of language proficiency, emotion, age, task effects, etc. Regarding the role of proficiency, Newman et al. (14) found that different levels of processing semantic anomalies are affected by different levels of language proficiency. That is, the N400 amplitude to semantically anomalous words are larger in English language speakers with low proficiency regardless of native or second language learners. Miao (15) also discussed that language proficiency has a close correlation with brain responses to semantic anomalies. He reported similar patterns of the N400 effect in the participants with high language proficiency, but no significant effect in the low proficiency participants. Most recently, Liang and Chen (16) found that semantic incongruity reflects an N400 for bilinguals with high and low second language proficiency. However, they showed that the N400 amplitude was much larger in bilinguals with higher second language proficiency.

Regarding the role of emotion, in a recent study, Tabatabayee et al. (17) conducted an ERP study with respect to the emotioncy (emotion + frequency) model, a notion that emphasizes the role of sense-induced emotions in language processing. They revealed that involving more senses during the instruction of the target words can lead to a smaller amplitude of the N400 in response to the processing of semantically anomalous sentences containing the instructed words. Likewise, Pishghadam et al. (18) used the emotioncy model to explain the effect of sense combinations in modulating the N400 during the processing of semantically anomalous sentences. They revealed that different sense combinations did not have a significant effect on the N400 amplitude during the processing of semantic anomalies.

Considering the age factor, Abel et al. (19) asked children to identify the meaning of words presented in a text with strong contextual cues and one with not appropriate ones. Their results showed a decrease in the N400 amplitude for words in the text with a supportive context, indicating that the underlying mechanisms for word learning in children are the same as the ones related to the N400 for extracting word meaning.

In another study, Zunini et al. (20) investigated the neural correlates of semantic richness in words and its interaction with task demands targeting the N400 effect. As they discussed, the N400 amplitude decreases when the words are highly associated with the context, and they emphasized the role of different task demands on semantic richness.

THE P600

P600 is another language-related ERP component that has been analyzed in different studies throughout the years since it has been discovered. Many studies discovered that certain types of semantically anomalous sentences that are syntactically congruent did not elicit an N400 effect but a P600 effect instead (21). Hence, the studies in which semantic incongruities have elicited P600 effects instead of N400 ones tried to find the underlying processes regarding this phenomenon (22). In the following section, the new concept of semantic P600 will be discussed.

Semantic Illusion or Semantic P600 Effects

In contrast to the dominant belief, which has been considered the P600 effect as a result of a purely syntactic violation, researchers using ERPs to study language comprehension were confronted with a phenomenon they called 'Semantic Illusion', which is originated from a study by Erickson and Mattson (23). Some studies have called this phenomenon a 'semantic P600 effect', emphasizing the non-syntactic nature of the evoked late positivities (21). The semantic illusion occurs when a semantically anomalous, syntactically well-formed sentence elicits a P600 effect but no N400 effect (24). The researchers assumed that the absence of the N400 effect is due to the independent semantic analysis without reference to the sentence structure, which leads to the illusion that the sentence is correct, but after some milliseconds, the reader understands that their interpretation is wrong and leads to an increase in the P600 amplitude (25). Some processing models have been proposed as an explanation for this phenomenon. Most of these models are of two kinds: multi-stream models and single-stream ones, which will be discussed in the next section.

Multi-Stream and Single-Stream Models

The multi-stream models typically consider two or more processing systems for sentence processing and challenge the previous sentence processing theories, which emphasize the dominance of syntactic representations over semantic ones. As Leckey and Federmeier (26) noted, these accounts provide evidence that different kinds of language processing difficulties lead to different functional and neural effects, reflecting in the N400 and P600 components. In contrast, single-stream models propose that different ERP components (the N400 and P600) reflect in response to the different parts of a unified processing stream. For example, the single-stream model, which was introduced by Brouwer et al. (24) has given a retrieval role to the N400 and an integration role to the P600. The multi-stream models considering semantic anomalies include the Semantic Attraction account (22), the Monitoring Theory (27), the Continued Combinatory Analysis (28), and the Processing Competition model (29).

In the Semantic Attraction model, Kim and Osterhout (22) explained the semantic P600 effect through the semantic attraction. In fact, from their point of view, the semantic attraction between a verb and its argument can be so strong that it overrides the syntactic evaluation.

In the next model, The Monitoring Theory, van Herten et al. (27) proposed that when the reader is presented with semantically anomalous sentences, the brain reanalyzes the memory trace of the perceptual input to check for the possibility of a processing error. As a result, full syntactic

analysis indicates a semantic anomaly, whereas the word-based heuristic leads to a plausible interpretation, so the two processing streams come to the conflicting interpretations of a sentence; the processor monitors the conflict and tries to resolve these conflicts through reanalysis that reflects in the P600 amplitude increase.

Moreover, in the Continued Combinatory Model, Kuperberg (28) suggested that language processing goes along with two competing streams. The first stream is based on semantic memory, and the second one is based on morphosyntactic rules and also the semantic-thematic constraints. She believed that the conflict between the output of these two competing and, at the same time, interactive neural streams leads to the P600 effect.

Kos et al.'s (29) Processing Competition Model is also a two-stream model with a syntactic and a semantic stream. Both streams simultaneously try to interpret a sentence, and if the processing of the sentence leads to a conflict between the two streams, the one which has the weakest support is responsible for resolving the conflict. For example, if semantic cues are strong, the syntactic stream is activated and leads to a P600 effect. If, on the other hand, syntactic cues are strong, the semantic system is activated and reflects an N400 effect.

In addition to these multi-stream models, Brouwer et al. (24) introduced a new single-stream model called Retrieval-Integration (RI) model. First, in the same vein with previous findings (30, 31), they suggested that the N400 component reflects the retrieval of lexical-semantic information, but after that, the integration of the retrieved word into the unfolding utterance reflects in the P600 amplitude. Also, Delogu et al. (6) provide support for the retrieval-integration account of the N400 and the P600. Their findings suggested that the N400 reflects context-sensitive lexical retrieval processes, and the observed P600 effects can be in line with the integration view. Most recently, Shayesteh et al. (32) also found a late positive component (LPC) in addition to the N400 effect they found in response to semantically incongruent sentences, and they corroborated the previous studies which related this late positive component to the later stages of semantic integration processes.

Some Recent Empirical Studies on the Semantic P600 Effect

In recent years, many other experiments have been conducted in support of the semantic P600 notion. For instance, Shen et al. (33) used a semantic violation paradigm and source localization analysis in order to examine the functional significance of the semantic P600 effect. The results corroborated the other findings that the P600 is not just the result of syntactic processing, but it can also be reflected in semantic processing. Sikos et al.'s (34) findings are in line with theories that consider the P600 effect as a result of the conflict between syntactic and semantic processing (22). Indeed, they provided evidence for the previous studies which emphasize the role of semantic cues during sentence interpretation (35). For the first time, Zheng and Lemhofer (36) investigated the semantic P600 effect in the second language (L2) population. They argued that L2 learners could find the conflict in syntactically correct but semantically implausible sentences, and they show the same neural responses, a P600 effect, as the native speakers do. In a very recent study on second language learners, Pishghadam et al. (18) argued that the LPC effect, as a later manifestation of the P600, might be the result of reanalysis in participants when confronted with a conflict in the semantic representation of the sentence and what they have expected.

SUMMARY AND CONCLUSION

During the past decades, from the invention of ERPs, the study of language processing has evolved a great deal. Various linguistic processes have been investigated, and some ERP components such as the N400 and the P600 have been discovered, providing important implications for the neural study of language comprehension. Numerous studies considered the N400 as the most important component reflected in response to the processing of semantically anomalous sentences. The most prominent factors which have been mostly investigated as the ones influencing the functional basis of the N400 component in response to semantic anomalies seem to be predictiveness, semantic expectancy, and contextual factors. As Lau et al. (31) indicated, it seems that the most factors which affect access and integration also affect the N400 amplitude. In the lexical access view, it is assumed that the N400 is elicited in response to the activation of long-term memory, finding compatible entries with the initial input. In the integration view, it is postulated that the N400 reflects the unification of the chosen lexical item with the other parts of the available context. In contrast to the dominant literature, some studies (37, 38) revealed that these two prominent processes are not separable, and they are cascading processes. Thus, it can be concluded that the factors mentioned influencing the N400 effect, such as prediction, context relations, and semantic expectancy, may have been affected by each other, but more research is needed to be able to prove such a claim. Furthermore, the studies reviewed here showed that some other factors such as language proficiency, emotion, age, and task manipulations could affect the N400 amplitude in semantic anomaly studies.

As it has been shown, the researchers questioned the dominance of the N400 in semantic anomaly studies, and they found out that it is not just the N400 effect that is reflected during the processing of semantically anomalous sentences but also the P600 effect may show up. In this respect, many researchers have considered it as an important component in interpreting semantic anomalies, and they have proposed different models, multi-stream and single-stream models, in order to find an explanation for the emergence of a P600 effect in response to semantic anomalies. Also, some later studies have been conducted to put proof on the concept of semantic P600.

Overall, although an exhaustive review of all the studies regarding the N400 and the P600 components with respect to semantic anomalies was not possible, it was attempted to include the most relevant ones. From all the above-reviewed studies, it can be concluded that despite the researchers' attempt for explaining the functions of the two ERP components (i. e., the N400 and the P600) in processing the sentences with semantic anomalies, there is still a need for more research on language processing in order to make the researchers capable of describing the underlying factors influencing these two ERP components, especially more focused investigation of the functional-anatomical and neurocomputational models may provide a clearer understanding of them. Moreover, any practical theory or model of the N400 and the P600 in language comprehension should consider the apparent inconsistencies in the elicitation pattern of the N400 and the P600 in order to successfully capture the full data spectrum.

Peer-review: Externally peer-reviewed.

Author Contributions: Concept- RP, ZS; Design- ZS; Supervision- ZS, RP Resource- RP; Materials- (-); Data Collection and/or Processing- MP; Analysis and/or Interpretation- ZS, RP, MP; Literature Search- ZS; Writing- ZS, RP; Critical Reviews- ZS, RP, MP.

Conflict of Interest: No.

Financial Disclosure: This work was supported by grants-in-aid of research from Ferdowsi University of Mashhsd, Iran (grant number 48316) and the Cognitive Sciences and Technologies Council (CSTC), Iran (grant number 7568).

REFERENCES

1. Bridwell DA, Henderson S, Sorge M, Plis S, Calhoun VD. Relationships between alpha oscillations during speech preparation and the listener N400 ERP to the produced speech. Sci Rep 2018;8:1–10. [Crossref]

2. Kutas M, Federmeier KD. Thirty years and counting: Finding meaning in the N400 component of the event-related brain potential ERP. Annu Rev Psychol 2011;62:621–647. [Crossref]
3. Hinojosa JA, Martin-Loeches M, Rubia FJ. Event-related potentials and semantics: An overview and an integrative proposal. Brain Lang 2001;78:128–139. [Crossref]
4. Maess B, Mamashli F, Obleser J, Helle L, Friederici AD. Prediction signatures in the brain: Semantic pre-activation during language comprehension. Front Hum Neurosci 2016;10:591. [Crossref]
5. Kutas M, Hillyard SA. Reading senseless sentences: Brain potentials reflect semantic incongruity. Science 1980;207:203–205. [Crossref]
6. Delogu F, Drenhaus H, Crocker MW. On the predictability of event boundaries in discourse: An ERP investigation. Mem Cognit 2018;46:315–325. [Crossref]
7. Newman AJ, Pancheva R, Ozawa K, Neville HJ, Ullman MT. An event-related fMRI study of syntactic and semantic violations. J Psycholinguist Res 2001;30:339–364. [Crossref]
8. Cosentino E, Baggio G, Kontinen J, Werning M. The time-course of sentence meaning composition. N400 effects of the interaction between context-induced and lexically stored affordances. Front Psychol 2017;8:813. [Crossref]
9. Kutas M, Hillyard SA. Brain potentials during reading reflect word expectancy and semantic association. Nature 1984;307:161–163. [Crossref]
10. Jiang X, Zhou X. An alternative structure rescues failed semantics? Strong global expectancy reduces local-mismatch N400 in Chinese flexible structures. Neuropsychologia 2020;140:107380. [Crossref]
11. Cheimariou S, Farmer TA, Gordon JK. Lexical prediction in the aging brain: The effects of predictiveness and congruency on the N400 ERP component. Aging Neuropsychol Cogn 2019;26:781–806. [Crossref]
12. Szewczyk JM, Schriefers H. The N400 as an index of lexical preactivation and its implications for prediction in language comprehension. Lang Cogn Neurosci 2018;33:665–686. [Crossref]
13. Calloway RC, Perfetti CA. Integrative and predictive processes in text reading: The N400 across a sentence boundary. Lang Cogn Neurosci 2017;32:1001–1016. [Crossref]
14. Newman AJ, Tremblay A, Nichols ES, Neville HJ, Ullman MT. The influence of language proficiency on lexical semantic processing in native and late learners of English. J Cogn Neurosci 2012;24:1205–1223. [Crossref]
15. Miao J. An ERP study of semantic anomalies in second language processing. In: Liu D, Alippi C, Zhao D, Hussain A, editors. Advances in Brain Inspired Cognitive Systems. Berlin: Springer; 2013. p.38–45.
16. Liang L, Chen B. The impact of language proficiency on the time course and neural basis of L2 semantic access in bilinguals. Int J Bilingual 2020;24:840–860. [Crossref]
17. Tabatabayee Farani S, Pishghadam R, Khodaverdi A. Sensory emotion in words: Evidence from an ERP study in light of the emotioncy model. Basic Clin Neurosci (in press). [Crossref]
18. Pishghadam R, Jajarmi H, Shayesteh S. Sense combinations influence the neural mechanism of L2 comprehension in semantically violated sentences: Insights from emotioncy. J Neurolinguistics 2021;58:100962. [Crossref]
19. Abel AD, Schneider J, Maguire MJ. N400 response indexes word learning from linguistic context in children. Lang Learn Dev 2018;14:61–71. [Crossref]
20. Zunini RAL, Baart M, Samuel AG, Armstrong BC. Lexical access versus lexical decision processes for auditory, visual, and audiovisual items: Insights from behavioral and neural measures. Neuropsychologia 2020;137:107305. [Crossref]
21. Brouwer H, Crocker MW, Venhuizen NJ, Hoeks JC. A neurocomputational model of the N400 and the P600 in language processing. Cogn Sci 2017;41:1318–1352. [Crossref]
22. Kim A, Osterhout L. The independence of combinatory semantic processing: Evidence from event-related potentials. J Mem Lang 2005;52:205–225. [Crossref]
23. Erickson TD, Mattson ME. From words to meaning: A semantic illusion. J Mem Lang 1981;20:540–551. [Crossref]
24. Brouwer H, Fitz H, and Hoeks J. Getting real about semantic illusions: Rethinking the functional role of the P600 in language comprehension. Brain Res 2012;1446:127–143. [Crossref]
25. Hoeks JC, Brouwer H. Electrophysiological research on conversation and discourse. Holtgraves T, editor. The Oxford handbook of language and social psychology. New York, NY. Oxford University Press; 2014. p.365–386. [Crossref]
26. Leckey M, Federmeier KD. The P3b and P600(s): Positive contributions to language comprehension. Psychophysiology 2019;56:10. [Crossref]
27. Van Herten M, Chwilla DJ, Kolk HH. When heuristics clash with parsing routines: ERP evidence for conflict monitoring in sentence perception. J Cogn Neurosci 2006;18:1181–1197. [Crossref]
28. Kuperberg GR. Neural mechanisms of language comprehension: Challenges to syntax. Brain Res 2007;1146:23–49. [Crossref]
29. Kos M, Vosse T, Van den Brink D, Hagoort P. About edible restaurants: Conflicts between syntax and semantics as revealed by ERPs. Front Psychol 2010;1:222. [Crossref]
30. Kutas M, Federmeier KD. Electrophysiology reveals semantic memory use in language comprehension. Trends Cogn Sci 2000;4:463–470. [Crossref]
31. Lau EF, Phillips C, Poeppel D. A cortical network for semantics:(de) constructing the N400. Nat Rev Neurosci 2008;9:920–933. [Crossref]
32. Shayesteh S, Pishghadam R, Khodaverdi A. FN400 and LPC responses to different degrees of sensory involvement: A study of sentence comprehension. Adv Cogn Psychol 2020;16:45–58. [Crossref]
33. Shen W, Fiori-Duharcourt N, Isel F. Functional significance of the semantic P600: Evidence from the event-related brain potential source localization. NeuroReport 2016;27:548–558. [Crossref]
34. Sikos L, Duffield CJ, Kim AE. Grammatical predictions reveal influences of semantic attraction in online sentence comprehension: Evidence from speeded forced-choice sentence continuations. Lang Cogn Neurosci 2016;31:1055–1073. [Crossref]
35. Kim A, Sikos L. Conflict and surrender during sentence processing: An ERP study of syntax-semantics interaction. Brain Lang 2011;118:15–22. [Crossref]
36. Zheng X, Lemhöfer K. The "semantic P600" in second language processing: When syntax conflicts with semantics. Neuropsychologia 2019;127:131–147. [Crossref]
37. Van den Brink D, Brown CM, Hagoort P. The cascaded nature of lexical selection and integration in auditory sentence processing. J Exp Psychol Learn Mem Cogn 2006;32:364–372. [Crossref]
38. Rabovsky M, Hansen SS, McClelland JL. Modelling the N400 brain potential as change in a probabilistic representation of meaning. Nat Hum Behav 2018; 2:693–705. [Crossref]