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The N400 is Elicited by Meaning Changes but not Synonym Substitutions: Evidence From Persian Phrasal Verbs

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Abstract

We tested two accounts of the cognitive process underlying the N400 event-related potential component: one that it reflects meaning-based processing and one that it reflects the processing of specific words. The experimental design utilized separable Persian phrasal verbs, which form a strongly probabilistic, long-distance dependency, ideal for the study of probabilistic processing. In sentences strongly constraining for a particular continuation, we show evidence that between two low-probability words, only the word that changed the expected meaning of the sentence increased N400 amplitude, while a synonym of the most probable target word did not. The findings support an account of the N400 in which its underlying process is driven by the processing of meaning rather than of specific words.

Keywords: ERP; N400; Psycholinguistics; Semantic processing; Lexical processing

1. Introduction

The N400 brain potential reflects a language processing stage where incoming information is combined with a comprehender's current representation of the meaning of an event (Federmeier, 2022; Kutas & Federmeier, 2011). This representation guides expectations about upcoming words. Unfulfilled expectations require the representation to be updated, and the degree of this update has been associated with N400 amplitude (Rabovsky, Hansen,

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& McClelland, 2018). However, not all unfulfilled expectations trigger changes in meaning; for example, expecting the word "*couch*" and seeing the word "*sofa*" is an unfulfilled expectation about a specific word (lexical expectation), but not about the overall meaning (semantic expectation). Some accounts of the N400 predict that any unfulfilled expectation will trigger an N400 increase (Fitz & Chang, 2019), while others predict that only unfulfilled semantic expectations will do so (Rabovsky et al., 2018). In this paper, we show evidence that only unexpected words that change the expected meaning of a sentence trigger an N400 increase.

1.1. The N400 ERP component as a measure of meaning-based processing

The N400 is well-established as reflecting meaning-based processing. The component is elicited by every word in a sentence, suggesting it reflects an essential stage of language processing, and becomes smaller across the sentence as long as new words are congruous with the meaning of the sentence seen so far (Payne, Lee, & Federmeier, 2015; Van Petten & Kutas, 1991). A meaningful context is essential in generating N400 effects: Meaningless word strings, sequences of tones, and unexpected musical notes do not increase N400 amplitude (Kutas & Federmeier, 2011), but even a vague linguistic context, for example, *He went outside to…*, is sufficiently meaningful that some words become more expected than others and less expected words will increase N400 amplitude (Federmeier, Wlotko, Ochoa-Dewald, & Kutas, 2007; Kutas & Hillyard, 1984). Word pairs can be sufficient to elicit an N400 difference between conditions as long as there is a semantic relationship in one condition and not in the other (Kutas & Federmeier, 2011; Lau, Holcomb, & Kuperberg, 2013; Rolke, Heil, Streb, & Hennighausen, 2001; Vogel, Luck, & Shapiro, 1998). These findings have generated a number of explanatory theories of what the N400 represents.

The Sentence Gestalt (SG) model proposes that readers build a probabilistic representation of sentence meaning as they read and that the N400 reflects the degree of update to that representation (Rabovsky et al., 2018). Update occurs at each new word, with larger changes in expected meaning eliciting larger N400s. The SG model thus makes the empirical prediction that a new word that changes the expected meaning of the sentence will elicit an increased N400, while a synonym of the most expected next word will not.

Other accounts of the N400 make a similar prediction, partly via related mechanisms. Some propose that the N400 reflects a stage where spreading activation triggered by bottom-up processing of a word enters into a broader network of preactivated words, concepts, and relationships (Federmeier, 2022; Kutas & Federmeier, 2011). Under this account, one word may be highly preactivated given the preceding context, but synonymous words will also be highly activated, and thus substituting them would not be expected to have as large an effect on the N400 as substitution with an unactivated word. Similarly, but for different reasons, a lexical-semantic retrieval view of the N400 would predict the same effect via spreading activation that facilitates access of semantically related words (Brouwer, Crocker, Venhuizen, & Hoeks, 2017). A predictive coding account would also predict that a change in expected meaning should result in a larger N400 than a synonym substitution (Bornkessel-Schlesewsky & Schlesewsky, 2019). Under this account, the prediction error triggered by the meaning-divergent

word would affect more levels of representation (semantic and lexical) than that of the synonym (lexical only), leading to a larger N400.

Each of these accounts is consistent with neuroanatomical evidence showing that the N400 is driven by cortical areas related to the access of lexico-semantic material triggered by the semantic context (Lau, Phillips, & Poeppel, 2008), although the latter accounts perhaps place more importance on the specific lexical item than the SG model. Integration accounts—which link the N400 with the ease of integrating a new word into the preceding context—would also predict that a meaning violation would be more difficult to integrate than a synonym of the expected word (Brown & Hagoort, 1993; Hagoort, Baggio, & Willems, 2009). We refer to this set of accounts as meaning-based accounts of the N400.

1.2. The N400 ERP component as lexically dependent

Another set of N400 accounts places more weight on the properties of the specific incoming word. Deacon, Dynowska, Ritter, and Grose-Fifer (2004) propose that the N400 reflects the early stages of visual- and sound-based processing of a word before the meaning of the word is accessed. Under this account, orthographic and phonological representations may be preactivated by the preceding context of a sentence, but this preactivation means that any incoming word that does not match the orthographic or phonological properties of an expected word will trigger an N400 increase, regardless of whether its meaning is consistent with the preceding context.

Fitz and Chang (2019) also propose that N400 amplitude corresponds with the match of the incoming word to the word predicted by the context of the sentence, although in contrast to Deacon et al. (2004), the N400 is elicited at the stage where the full word form has already been accessed. Under Fitz and Chang's account, meaning from the preceding context still drives activation of probable upcoming words, such that words that are semantically further away from the predicted word will trigger a larger error signal than words with closer meaning. However, even unexpected words with the same meaning as the highest probability word will trigger an increased N400. We refer to this set of accounts as lexical-semantic retrieval accounts of the N400.

1.3. Disentangling meaning-based versus lexical-semantic retrieval accounts

Despite it being a core prediction distinguishing meaning-based and lexical-semantic retrieval accounts, few studies have directly tested whether unexpected words that change the meaning of a sentence produce larger N400s than unexpected words that are synonyms of the most expected word, and whether synonyms of expected words produce an N400 increase at all. One such study found that in sentences that strongly constrained expectations for a particular word such as *On his vacation, he got some much needed rest*, only substituting *rest* for a word that changed the meaning of a sentence—such as *sun*—elicited an N400 increase, while amplitude for synonyms—such as *relaxation*—was similar to *rest* (Thornhill & Van Petten, 2012). This finding supports a meaning-based account, but similar studies using synonyms have yielded contrasting results.

In a study of processing effort in code-switching, "lexical switches" in readers' native language were found to elicit larger N400s in comparison to literal translations in their second language (Moreno, Federmeier, & Kutas, 2002). For example, seeing the unexpected word *mattress* in *He put a clean sheet on the…* (where *bed* was most expected) elicited a larger N400 than the Spanish translation for bed (*cama*), even though mattress is similar in meaning to bed in this context. Synonyms were also found to elicit larger N400s than repeated words in a study of two-sentence dialogues such as *Kathy sat in the cab/taxi. The cab came close to hitting a car* (Anderson & Holcomb, 2005). However, neither of these studies contrasted the synonym condition with a word that changed the meaning of the sentence, making it difficult to say how the lexical violation might compare to a semantic one.

In a study that did contrast meaning changes, Liu, Jin, Wang, and Xin (2011) substituted an expected target word in familiar poems with a homonym or a synonym. Both substitutions were rated as "unacceptable" by over 90% of raters, even though homonyms changed the sentence meaning relative to expectation, while synonyms did not. Only homonyms elicited an N400 relative to the most expected word. However, it is unclear whether the homonyms also made the sentence implausible, which would yield a starker contrast with a synonym than would a low-probability word that changes the meaning of the sentence without making it implausible.

In sum, evidence suggests that words changing the expected meaning of a sentence can increase N400s, but less clear is whether a purely lexical substitution elicits processing cost and if so, how much relative to semantic changes. This point is important because it distinguishes meaning-based from lexical-semantic retrieval accounts of the N400. We, therefore, conducted an experiment directly comparing semantic and lexical expectations using separable phrasal verbs in Persian.

1.4. The current experiment

We addressed the hypothesis that in sentences with highly predictable continuations, an unexpected word that changes the expected meaning of the sentence will elicit a larger N400 than an unexpected word that is a synonym of the most expected word. We also tested the SG model hypothesis that there should be no difference in the N400 between expected words and unexpected words that are synonyms of expected words. We used Persian phrasal verbs as a way of maximizing the predictive nature of the sentences. Persian phrasal verbs consist of a verb and a nonverbal element that form a tight probabilistic dependency, similar to English particle verbs like *take out*, where the full meaning is only interpretable from both elements (Dabir-Moghaddam, 1997; Samvelian & Faghiri, 2013, 2014). The tight dependency stems from the fact that Persian phrasal verbs are highly frequent, idiomatic structures whose second element becomes highly predictable from the sentence context. Manipulating the identity of the second element to have a synonymous or different meaning to that of the most predictable word thus constitutes a manipulation of expectancy, which we categorize as lexical versus semantic for the purposes of the current study, although cognitive representations are likely not categorical. Further information about Persian phrasal verbs can be found in the Supplementary Information (S1).

We created sentences where the clause-final verb was either the most probable verb given a clause-medial noun and the context, a verb that completed the noun-verb dependency with the same meaning as the most probable verb, or a verb that changed the meaning but was still semantically plausible. An equivalent example in English would be "*The teacher filled the form out*," where *out* is the most probable continuation but substituting *in* for *out* would yield the same meaning. In contrast, substituting *on* for the more probable *off* in "*The woman asked her husband to turn the music off*" changes the meaning of the event. Previous research suggests that the possibility of a phrasal or particle verb construction triggers the preactivation of plausible clause-final particle or verb representations (Husain, Vasishth, & Srinivasan, 2014; Safavi, Husain, & Vasishth, 2016; Stone, von der Malsburg, & Vasishth, 2020). We utilized this property of phrasal verbs to encourage prediction of the upcoming verb, in order to maximize potential N400 effects.

We developed the stimuli in a 2 × 2 design contrasting expectedness of the target word (expected/unexpected) and the type of unexpectedness (semantic/lexical; Table 1), although note that expectedness was operationalized as the continuous variable cloze probability in the statistical analysis. In line with meaning-based accounts of the N400, particularly the SG model, we expected an interaction between expectedness and the type of unexpectedness, such that there would be a difference in N400 amplitude between low cloze (unexpected) and high cloze (expected) target words in the different meaning condition (d vs. c), but not between low cloze and high cloze target words in the same meaning condition (b vs. a).

2. Methods

2.1. Participants

Electroencephalogram (EEG) recordings were obtained from 35 right-handed Persian native speakers with normal or corrected-to-normal vision at the University of Potsdam. Participants were monolingual Persian speakers before the age of 6, recruited via public notices in Persian expat groups in Potsdam and Berlin. Exclusion criteria included participation in the offline cloze test, or the presence of a psychological or neurological disorder. Four participants were excluded due to technical problems or a question response accuracy below 70%, leaving data from 31 participants for analysis (mean age = 32 years; $SD = 6$ years; range = 18–44 years; 17 male). The experiment was conducted in line with the Declaration of Helsinki as part of a larger project approved by the Ethics Committee of the University of Potsdam. All participants gave written informed consent to participation and were reimbursed financially.

2.2. Materials

The experimental items presented to participants were 80 sentence quartets (Table 1), although the final analysis was only conducted on the 67 items that best met the requirements of the study design.[1] Summary statistics of the cloze probability, frequency, and orthographic neighborhood of the target verb are in Table 2. Cloze test responses were used to select target

Table 1
Example stimulus

(a) Expected, same meaning condition				
Dokhtarake kuchak ba shirinzabaniye khod	**dele**	hame ra	**bord**	va
The girl little with sweet-tongue (of) her	**heart** (of)	everyone	**won**	and
pishe mehmanan neshast.				
with guests sat.				
Translation: The little girl won everybody's heart by her sweet way of speaking and sat with the guests.				
(b) Unexpected, same meaning condition				
Dokhtarake kuchak ba shirinzabaniye khod	**dele**	hame ra	**roboud**	va
The girl little with sweet-tongue (of) her	**heart** (of)	everyone	**stole**	and
pishe mehmanan neshast.				
with guests sat.				
Translation: The little girl stole everybody's heart by her sweet way of speaking and sat with the guests.				
(c) Expected, different meaning condition				
Dokhtar ba pushidane lebase gerangheimatash	**dele**	hame ra	**bord**	va
The girl with wearing (of) clothes expensive (of her)	**heart** (of)	everyone	**won**	and
ehsase rezayat kard.				
feeling satisfied did.				
Translation: The girl won everybody's heart by wearing her expensive clothes and felt satisfied.				
(d) Unexpected, different meaning condition				
Dokhtar ba pushidane lebase gerangheimatash	**dele**	hame ra	**souzand**	va
The girl with wearing (of) clothes expensive (of her)	**heart** (of)	everyone	**burned**	and
ehsase rezayat kard.				
feeling satisfied did.				
Translation: The girl made everybody jealous by wearing her expensive clothes and felt satisfied.				

Note. The phrasal verb construction is bolded and the target verb is underlined.

Table 2
Summary statistics of the target verb for the 67 analyzed items

Condition	Cloze probability	Frequency	Orthographic neighborhood	Rated as having the same meaning
(a) Expected	0.59 (0.16)	0.06 (0.06)	0.48 (0.83)	80.00 (13.20)%
(b) Unexpected, synonym	0.10 (0.09)	0.05 (0.05)	0.32 (0.22)	
(c) Expected	0.56 (0.17)	0.07 (0.09)	0.36 (0.51)	20.50 (23.10)%
(d) Unexpected, different meaning	0.07 (0.06)	0.05 (0.03)	0.50 (0.98)	

Note. The mean cloze probability of the second-best completion in the expected conditions (a) and (c) was 0.18 ($SD = 0.08$) and 0.19 ($SD = 0.08$), respectively. Means are presented with standard deviations in brackets. The final column shows the mean percentage of agreement in judgments about how similar the meaning of the sentence pairs was (a vs. b and c vs. d).

words: two verb continuations that had approximately the same high cloze probability (> 0.5) for conditions a/c and approximately the same low probability (< 0.1) for b/d. Within each experimental item, the difference in cloze probabilities was approximately the same between conditions a/b as between c/d. Native-speaker ratings confirmed that within each experimental item, the selected verb continuations yielded the same or similar meaning in conditions a/b and different meanings in conditions c/d. Further detail on the meaning assessment and stimuli development can be found in the Supplementary Information (S2).

2.3. Procedure

2.3.1. EEG recording procedure

The presentation paradigm was created using OpenSesame (Mathôt, Schreij, & Theeuwes, 2012). Participants saw the 80 critical experimental items and 80 filler sentences with a range of structures with and without phrasal verbs. The 80 critical experimental items were split into four lists in a Latin square design and presented in randomized order with the fillers. After 50% of the fillers, participants answered a Yes/No comprehension question. The experiment began with eight practice trials. Each trial began with a fixation cross of 500 ms followed by a blank screen of 300 ms. A sentence then appeared word-by-word in the center of the screen. Each word was presented for a minimum of 350 ms plus 20 ms per letter. The interstimulus interval was 300 ms. Breaks were offered every 36 sentences. The whole experimental recording session lasted approximately 50 min.

EEG was recorded in an electrically shielded cabin using a 32-channel ActiCAP system and BrainVision Recorder Version 1.0 with a 1000 Hz sampling rate and an online bandpass filter of 0.02–1000 Hz. Electrodes were placed according to the international 10–20 system (Jasper, 1958) and referenced online to the left mastoid. Impedances for all electrodes were kept below 10 kΩ. Electrodes were placed on the outer canthi of both eyes to record horizontal eye movements.

2.3.2. EEG preprocessing

Preprocessing was conducted using *eeguana* (Nicenboim, 2018) in *R* (R Core Team, 2020). Raw EEG data were downsampled to 500 Hz and filtered using a zero phase finite impulse response (FIR) filter with a bandpass of 0.01–30 Hz. All electrodes were re-referenced to the average of the mastoids. Blinks were corrected using independent component analysis (ICA). For the ICA, downsampled data were separately filtered with a bandpass of 1–30 Hz (Winkler, Debener, Müller, & Tangermann, 2015), re-referenced to the average of the mastoids, and segmented into sentences. ICA was applied and the mixing matrix for each subject was extracted and applied to their 0.01–30 Hz filtered data. Blink components were manually identified. Epochs containing the target verbs were extracted from the ICA-corrected sentence segments, starting 200 ms prior to word onset and ending 1000 ms post-onset. The remaining artifacts were rejected automatically if exceeding a voltage difference of over 100 μV in a time window of 150 ms or a voltage step of over 50 μV/ms. In total, 2% of the data was rejected leaving approximately 500 segments per condition. The target epochs were baseline-corrected relative to the 200 ms prestimulus interval.

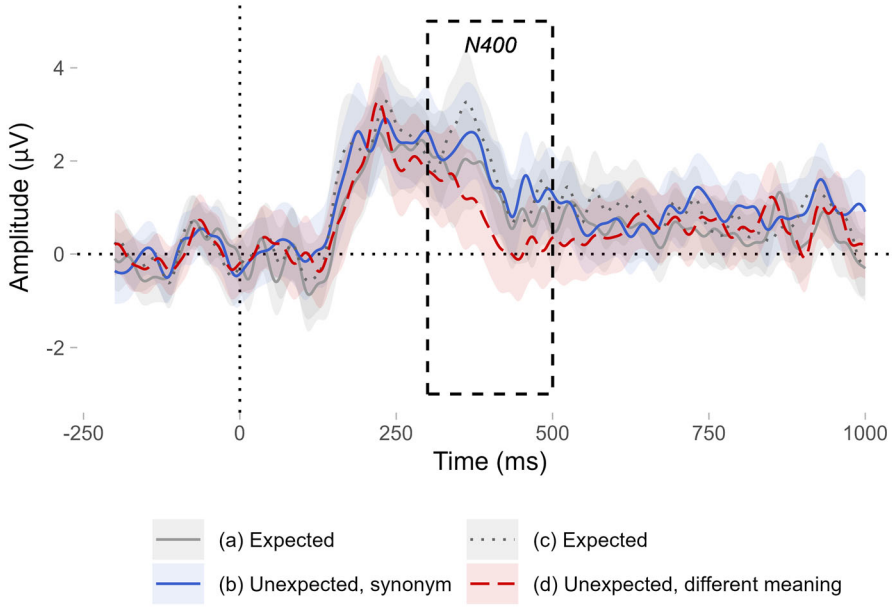

Fig. 1. Average ERP amplitude at the target word. Average amplitude across the centro-parietal scalp region of interest in each condition. Ribbons indicate 95% confidence intervals. The dashed box indicates the 300–500 ms time window. Expected and unexpected conditions are plotted by median split cloze probability within the two meaning conditions (same, different) to align with the analysis.

2.4. Analysis

A linear mixed effects model with maximal variance-covariance matrices for by-subject and by-item random effects was fit in *brms* (Buerkner, 2018) in *R* (R Core Team, 2020). The dependent variable was the average N400 amplitude over electrodes Cz, CP1/2, P3/4, and Pz in the time window 300–500 ms after target word onset. The two main independent variables were cloze probability (scaled and centered) and unexpectedness type (sum contrast coded lexical −0.5, semantic 0.5). Frequency and orthographic neighborhood were added as scaled, centered predictors to account for the difference between the target words (the phonological neighborhood was not added as it correlated highly with the orthographic neighborhood, $r =$ .72). Priors encoding our expectations about the range of plausible effect sizes were informed by the effects observed in previous analyses (Nicenboim, Vasishth, & Rösler, 2020; Stone, Nicenboim, Vasishth, & Rösler, 2023), but were not strictly informative to account for the different experimental design. Support for our hypotheses was assessed using Bayes factors. The data, code, and experimental materials can be found at https://osf.io/vwgfk/.

3. Results

Fig. 1 shows that event-related potential (ERP) amplitude in the N400 window was most negative for semantically unexpected words and comparable for all other conditions.

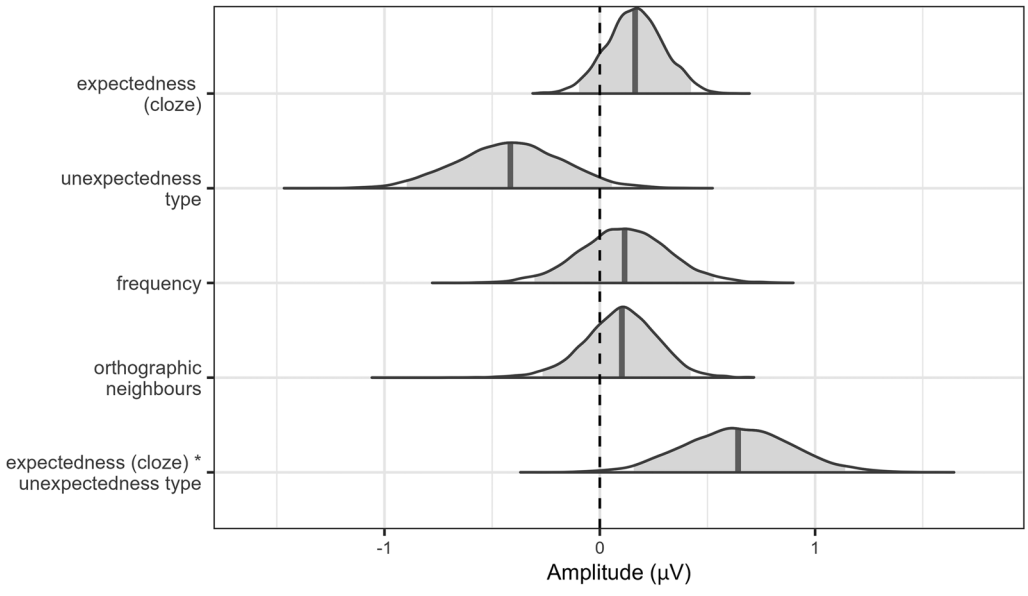

Fig. 2. Posterior probability estimates. Posterior probability distributions represent the effect size estimated for each predictor shown. The vertical line represents the mean and the shaded area is the 95% quantile credible interval.

The model-estimated interaction suggested that the change in amplitude as cloze probability (expectedness) increased was greater in the semantic than the lexical condition, $\hat{\beta} = 0.64\ \mu V$ with a 95% quantile credible interval of $[0.16,\ 1.14]\mu V$. The Bayes factor at a prior of *Normal*(0,1) was 8, suggesting moderate evidence (8:1) in favor of the interaction (Jeffreys, 1939; Lee & Wagenmakers, 2013). Since the Bayes factor is sensitive to the choice of prior, a sensitivity analysis can be found in the Supplementary Information (S3) showing that other prior choices would not have changed our conclusion. The model posterior estimates are plotted in Fig. 2. Fig. 2 does not suggest a main effect of any predictor except perhaps unexpectedness type, although the 95% credible interval included zero as a probable effect size.

Separate models indicated moderate evidence against a difference in amplitude associated with cloze probability at the target within the lexical condition (b vs. a), $\hat{\beta} = -0.16,\ 95\%\ CrI = [-0.53,\ 0.21]\ \mu V, BF_{10} = 0.26$, but indicated moderate evidence for a larger N400 for lower cloze (more unexpected) targets within the semantic condition (d vs. c), $\hat{\beta} = 0.49,\ 95\%\ CrI = [0.14,\ 0.85], BF_{10} = 8$.

4. Discussion and conclusions

In an experiment using Persian phrasal verbs strongly constraining expectations for a specific target word, we show evidence that only unexpected words that changed the

expected sentence meaning elicited an increased N400 relative to the most expected word. There was evidence against an N400 effect for unexpected words that were synonymous with the most expected word. These findings are consistent with meaning-based accounts proposing that the N400 reflects a process where meaning is updated, accessed, or integrated (Bornkessel-Schlesewsky & Schlesewsky, 2019; Brouwer et al., 2017; Brown & Hagoort, 1993; Federmeier, 2022; Hagoort et al., 2009; Kutas & Federmeier, 2011; Lau et al., 2008; Rabovsky et al., 2018).

The findings also converge with evidence that the N400 shows a graded response to words in accordance with how semantically related they are to the most expected word. For example, in a context about wanting to make a hotel look more like a tropical resort, the most expected word following the fragment "*[so] they planted rows of…*" was *palms*, which elicited a smaller N400 than *pines*—a member of the same semantic category (i.e., tree). *Tulip* elicited the largest N400 as the least semantically related (Federmeier & Kutas, 1999). Similar graded results for words with and without semantically overlapping features have been observed elsewhere (Boudewyn, Long, & Swaab, 2015; Ito, Corley, Pickering, Martin, & Nieuwland, 2016; Szewczyk & Federmeier, 2021; Thornhill & Van Petten, 2012). However, the design of these studies necessitated that the target words had different cloze probabilities, meaning that less semantically related words were also generally less expected. Our results build on these findings by demonstrating that even between two low-probability words, it is still the word with less semantic overlap that increases N400 amplitude, supporting a primarily meaning-driven process underlying the N400.

The graded response of the N400 to semantic overlap has led to the assumption that reading words within a context triggers the activation not just of the corresponding words in memory, but also of related words and concepts. How this activation translates to N400 amplitude is still an open question: one limitation of the current study is that it is not able to distinguish between whether activation lessens the degree of sentence meaning update or implicit semantic prediction error (Rabovsky et al., 2018), facilitates lexico-semantic access (Brouwer et al., 2017; Federmeier, 2022; Kutas & Federmeier, 2011; Lau et al., 2008), lessens the effect of precision-weighted prediction error (Bornkessel-Schlesewsky & Schlesewsky, 2019), or facilitates integration (Brown & Hagoort, 1993; Hagoort et al., 2009). One finding in the current study that may distinguish at least the SG model from other accounts is the evidence that lexical substitutions did not elicit any N400 effect at all. The SG model predicts that this should be the case, whereas the remaining accounts might predict a graded effect based on the overlap of semantic, lexical, orthographic, and other features.

The evidence against an expectedness effect in the lexical condition also contradicts lexical accounts of the N400 and it is unclear how these accounts would accommodate the current findings (Deacon et al., 2004; Fitz & Chang, 2019). One possibility is that there was a small lexical effect but the sample size of 31 was not sufficient to detect it. Some ERP studies have noted that small effects (if present) may be difficult to detect even with large sample sizes (Nicenboim et al., 2020; Nieuwland et al., 2018; Stone et al., 2023). Even within the meaning-change condition, the size of the N400 effect was not especially large ($0.49\ \mu V$) relative to previous studies. This is likely because the target word was plausible—plausible continuations semantically related to the best completion are known to elicit smaller N400s

than incongruent or unrelated continuations (Federmeier & Kutas, 1999; Kuperberg, Brothers, & Wlotko, 2020; Kutas & Hillyard, 1984; Thornhill & Van Petten, 2012). However, the effect in the current study was still smaller than that of related completions in previous studies. Due to differences between studies, we do not wish to overinterpret variability in effect size or morphology of the N400, but we propose a tentative hypothesis: The small effect in the current study could be due to the target word being a verb rather than a noun; there is indeed some evidence that verbs elicit smaller N400 amplitudes (Federmeier, Segal, Lombrozo, & Kutas, 2000; Khader, Scherag, Streb, & Rösler, 2003; see also Vigliocco, Vinson, Druks, Barber, & Cappa, 2011). Semantic representations of nouns in memory may be more feature-based than verb representations and thus an unexpected noun may mismatch with the most expected noun along more dimensions than an unexpected verb, even if plausible. If so, the plausible but unexpected nouns used in previous studies may have elicited a larger N400 than our plausible but unexpected verb. The use of a verb could, therefore, also have affected our ability to detect an effect in the lexical condition. The current results, therefore, do not completely rule out that lexical substitutions can affect N400 amplitudes, but the evidence against an effect makes this interpretation unlikely based on the current data.

Another possibility is that a lexical unexpectedness effect was not observed because we dichotomized word meaning into synonymous and nonsynonymous. As noted by Thornhill and Van Petten (2012), in reality, true "synonymousness" of two words is unlikely and even disfavored by language evolution (Manin, 2008). What is considered synonymous or not, and to what degree, also likely differs between individual readers. It may, therefore, be more plausible that meaning is continuously represented and so future studies might consider a continuous measure such as cosine similarity to better disentangle the contributions of lexical word form and semantics to N400 amplitude.

In sum, the increased N400 for meaning-based changes but not synonym substitutions in the current study supports a primarily meaning-driven process underlying N400 amplitude. While the exact mechanism remains unclear, the result is that reading is most disturbed by changes to the expected meaning of a sentence rather than changes to the specific, expected word forms that appear.

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Note

1 Evidence supporting the hypotheses was actually stronger when using our original set of 80 items (see *Supplementary Information [S2 and S4]* for details), presumably due to higher power, but we nonetheless opted for keeping our design as clean as possible for the main analyses.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Supplementary information