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The N400 as a snapshot of interactive processing: evidence from regression analyses of orthographic neighbor and lexical associate effects

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Abstract

Linking print with meaning tends to be divided into subprocesses, such as recognition of an input's lexical entry and subsequent access of semantics. However, recent results suggest that the set of semantic features activated by an input is broader than implied by a view wherein access serially follows recognition. EEG was collected from participants who viewed items varying in number and frequency of both orthographic neighbors and lexical associates. Regression analysis of single item ERPs replicated past findings, showing that N400 amplitudes are greater for items with more neighbors, and further revealed that N400 amplitudes increase for items with more lexical associates and with higher frequency neighbors or associates. Together, the data suggest that in the N400 time window semantic features of items broadly related to inputs are active, consistent with models in which semantic access takes place in parallel with stimulus recognition.

Introduction

A concept that has classically been important to psycholinguistic theories of visual word processing is *recognition*, a process by which orthographic inputs are compared to internal representations—often items in the mental lexicon—in order to find a match to the input that can subsequently be linked with semantics. This type of staged recognition process is exemplified in Forster and colleagues' Entry Opening Model (e.g., Forster & Davis, 1984; Forster & Veres, 1998; Forster, 1999), wherein information corresponding to an orthographic input cannot be retrieved until a matching lexical entry has been identified. A similar formulation is found in the Multistage Activation Model of Besner and colleagues (e.g., Besner & Chapnik Smith, 1992; Borowsky & Besner, 1993; Plourde & Besner, 1997), in which orthographic analysis of an input must be complete (that is, the input must be recognized) before associated information can be passed forward for subsequent processing.

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Theories that require a template- or feature-matching process to be completed before semantic information can be retrieved have also been proposed for face and object recognition (e.g., for faces, Brunelli & Poggio, 1993; for objects, Poggio & Edelman, 1990).

Staged models of word processing that involve an isolated recognition process successfully explain a range of behavioral findings, notably the complex, interacting effects of frequency, context, and stimulus quality on lexical decision reaction times (e.g., Borowsky & Besner, 1993; Stoltz & Neely, 1995). However, such models make two specific predictions about the semantic processing that follows recognition that seem incongruent with data from the event-related potential (ERP) literature pertaining to the N400 component, a well-established, functionally specific marker of lexico-semantic processing (for review, see Kutas, Van Petten, & Kluender, 2007). First, if semantic access can only proceed after recognition has been successfully completed, then access should never be attempted for items without lexical representations, such as pseudowords or orthographically illegal consonant strings. Second, if semantic access is essentially limited to the process of looking up meaning information associated with a recognized lexical entry, then the largely inconsistent semantics of other orthographically or lexically associated items should never become simultaneously active. That is, for the input FORK, the semantics of the orthographically similar PORK and the lexically associated SPOON should never become active.

If the first prediction is true, and semantic access will only be attempted for items corresponding to a known lexical entry, then the N400—which has been established as a marker of attempted or successful semantic access (see, for example, Kutas & Federmeier, 2000; Federmeier & Laszlo, 2009)—should only be observed in response to items with lexical representations. However, this is not the case. Clear N400 components and N400 effects (such as reductions in amplitude with repetition) have long been observed in response to pronounceable pseudowords, such as GORK (e.g., Rugg & Nagy, 1987; Deacon, Dynowska, and Grose-Fifer, 2004; Laszlo & Federmier, 2007). This finding necessitates weakening the proposal that semantic access occurs only for lexically represented items to, at minimum, allow for attempts at semantic access for strings that are very similar to lexically represented items (i.e., pseudowords, which are often created by changing one letter of a real word). However, even this weakened proposal is incompatible with recent work from our lab, which has shown that, at least in a supportive sentence context, even meaningless, illegal letter strings (e.g., NHK) with minimum orthographic neighborhood size (i.e., Coltheart's N: the number of words that can be formed from a target by changing one of its letters) can elicit clear N400 components and N400 effects (Laszlo & Federmeier, 2008; 2009). We have argued that this pattern indicates that semantic access is attempted for *all* orthographic inputs, regardless of their lexical status, although the success of that attempted access can vary with context -- explaining why, for example, unfamiliar, orthographically illegal strings embedded in word lists have been found to not show N400 repetition effects (Rugg & Nagy, 1987), whereas, when embedded in sentences, these same types of strings do elicit N400 effects associated with similarity to a predicted completion (Laszlo & Federmeier, 2009).

Although seemingly incompatible with staged recognition models, the ERP findings are compatible with Parallel Distributed Processing (PDP) models of reading that result in some semantic features becoming at least initially active in response to all inputs (e.g., Harm & Seidenberg, 2004). In models of this type, processing that appears staged can result from nonlinear activation dynamics between orthography and semantics (Kello, Plaut, & MacWhinney, 2000). Importantly, however, even when such models exhibit stage-like behavior, this is accomplished without any formal implementation of stages and also without any formal distinction between the processing of lexically represented and unrepresented items (a distinction that is a necessary consequence of strongly staged models). Thus, data that have often been explained with staged models can also be explained with cascaded models, which, additionally, are consistent with ERP findings showing that non-lexical items engage attempts at semantic access that seem identical in timing and in nature to those engaged by lexically represented items.

The second prediction of staged models of reading outlined above is also not shared by PDP models. Because staged models assume that items are identified before semantic access begins, there is no reason to predict that semantic features of orthographically similar or lexically associated items should become active (to any significant degree) along with the features of the input stimulus. For example, having recognized an input as FORK, the system would not access semantics associated with the orthographically similar input PORK. In contrast, given the tendency of PDP models to activate similar outputs in response to similar inputs, semantic features associated with a range of items similar to the input stimulus at the orthographic or lexical levels of analysis can become active in parallel with the appropriate semantics for the input, at least transiently. Thus, in a PDP model given the input string “FORK”, both the semantics of FORK and PORK could initially become active, as both are at least partially consistent with the input (i.e., contain ORK), although, of course, the semantics of FORK are more consistent with the input and would eventually become most active.

Again, recent ERP data are more in line with the predictions of cascaded models than staged ones. In particular, Holcomb et al. (2002) found that out-of-context N400 amplitudes were larger to words and pseudowords with higher orthographic neighborhood sizes, and we have replicated that finding and shown that it extends to illegal strings of letters (Laszlo & Federmeier, 2007) and that the amplitude difference is maintained even when items are embedded in sentences (Laszlo & Federmeier, 2008, 2009). We have argued that the larger N400s to items with high N result from there being—at least initially—more semantic activation for items that are orthographically similar to many other items. That is, a high N input like CAT activates not only its own semantics, but also, briefly, the semantics of all its neighbors, whereas a low N input like OWL results in a less broad activation at the semantic level of representation. Importantly, the fact that effects of N are identical for lexical and non-lexical inputs (Laszlo & Federmeier, 2009) suggests not only that a broader range of semantic features become active in response to an input than staged models would predict, but also that lexical status *per se* is not a determining factor in this semantic level effect.

Although effects of neighborhood density on the N400 can be taken to suggest that a range of orthographically similar and lexically associated items become active in response to any given input, it could potentially be argued that N actually reflects a property of the input item itself-- N might instead be a proxy for some information about orthographic regularity that is included in an item's lexical entry. For example, maybe the number of neighbors an item has could be an abstracted proxy for how similarly to other words that item is pronounced, and thus whether or not it can be pronounced by rule or must be considered an exception. A stronger test of the hypothesis that the N400 reflects the processing of not just an input, but also items similar to that input, could thus potentially come from examining the effect of the frequency of an item's orthographic neighbors on the magnitude of the N400 elicited by that item. Such an effect, if observed, would indicate directly that properties of items similar to an input affect its semantic processing. In fact, one study has reported such an effect, finding that items with high frequency neighbors elicited more negative N400s than items with lower frequency neighbors (Debruille, 1998). Unfortunately, however, neighbor frequency was confounded with orthographic neighborhood size in that study, making it difficult to strongly conclude that it was the frequency of an item's neighbors, and not just the number of neighbors, that affected N400 amplitude. Therefore, the first goal of the present study was to determine whether neighbor frequency has an effect on the N400 independent of the effect of N.

Further, while neighbor frequency is a property of items *orthographically* similar to an input, our second goal was to determine whether the properties of items *lexically* associated to an input might also affect its processing. Specifically, we were interested in examining the effects, if any, of the number of lexical associates and written frequency of the top associate on N400 amplitudes, as these might be considered lexical level analogues of N and neighbor frequency. For example, if FORK can activate some of the semantics of PORK by virtue of their shared orthography, can DOG also activate some of the semantics of BONE by virtue of their lexical association? The cascaded nature of the information flow between representational levels in the modeling framework that has thus far been most consistent with N400 effect patterns would seem to predict such effects—through spreading activation at the lexico-semantic level of representation – but, to our knowledge, no N400 data addressing this issue exist.

Our two experimental goals thus have much the same flavor: each is aimed at trying to determine whether or not the properties of items similar to (or linked to) an input at the orthographic or lexical level – and thus likely to become active in parallel during input processing – affect the semantic processing of that input. Evidence for such effects would support cascaded models over staged models of reading, and, in the case of the orthographic variables, this conclusion could be strengthened by an absence of an interaction with lexicality, as staged models predict important differences between lexically represented and non-represented stimuli at processing stages, such as semantic access, that are assumed to follow recognition.

We took a somewhat novel approach to these goals. The typical design of an ERP experiment aiming to examine, for example, the effect of neighbor frequency independent of the effect of N might be a factorial one wherein participants view items high and low in neighbor frequency but matched on N. Although this design would provide information about the impact of neighbor frequency on the ERP, it would do so at the expense of not affording information about the simultaneous effect of N—a downside because, of course, these variables apply to all inputs and are never processed in isolation. To address this problem, some studies have begun moving toward the use of designs that enable multiple regression analyses (e.g., King & Kutas, 1998; Hauk, Davis, Ford, Pulvermuller, & Marslen-Wilson, 2006; Hauk, Pulvermuller, Ford, Marslen-Wilson, & Davis, 2009), in order to attempt to untangle the effects of linguistic variables which tend to be highly correlated (e.g., length and word frequency, in the case of King & Kutas, 1998). Multiple regression when applied to items can afford the identification of independent effects of each variable of interest while avoiding the artificiality of attempting to examine the effects of lexical variables in isolation.

Multiple regression can be particularly useful for unraveling effects of intercorrelated item variables when combined with items-based analyses (as opposed to subjects-based analyses, which do not permit generalization across items). Despite this advantage, multiple regression has not often been used to examine dependent variables measured over items in ERP studies, because item data with satisfactory signal to noise characteristics is not generally available with the numbers of participants typically run in ERP studies (although, for an interesting exception, see Rey, Dufau, Massol, & Grainger, 2009, who extracted item ERPs representing the response to single letters or pseudoletters). In an approach similar to the one we employ in the present study, Dambacher et al. (2006) used simultaneous multiple regression to model single trial EEG collected from participants reading sentences, and supported cascaded models of word recognition over staged ones; however, high noise levels in the item ERPs—collected from only 50 participants-- resulted in relatively low R^2 values for their multiple regression models. We, therefore, sought to address this issue by collecting a large scale data set from 120 participants who viewed words, pseudowords, acronyms, and illegal strings that intentionally varied widely in their lexical characteristics (including the four presently of interest). With this data, we could form ERPs representing the responses to single items, averaged across participants (e.g., the response to the word DOG only, consisting of 120 trials—one from each participant.) This data set enables us to generalize over items in a way that is not possible in a typical ERP design where approximately 40 items per condition for approximately 20–30 participants might be collected. Figure 1 displays an unfiltered example from each item type, showing that these single item ERPs were stable, with good signal to noise ratios.

With stable ERPs available for individual items, it is then possible to obtain item-level mean N400 amplitude measures (or, of course, any other measure that can be obtained from a more typical, item-aggregated ERP). Those single item means are then eligible for regression analyses that are not possible with subject aggregated data. One drawback of this approach is that items analysis does not permit generalization across subjects. However a substantial benefit of this approach is that regression is a more powerful analysis method than analysis of variance; another is that, with multiple regression, the independent effects of multiple variables can be examined simultaneously (e.g., the effects of N and neighbor frequency.)

Given past results from factorial studies (Holcomb, Grainger, & O'Rourke, 2002; Laszlo & Federmeier, 2007; 2008; 2009), we predicted that neighborhood size would be positively correlated with N400 magnitude, independent of the lexical status of the input string. We predicted a similar relationship between number of lexical associates and N400 response to words (the only class of items for which lexical association data is available). Critically, although neighbor frequency and neighborhood size tend to be correlated, we also predicted an independent effect of orthographic neighbor frequency on N400 mean amplitude (and a similar effect of frequency of top associate), indicating that the spread of semantic activation elicited by an input is considerably broader than would be suggested under a staged account.

Methods

Participants

Data were analyzed from 120 participants (58 female, age range 18–24, mean age 19.1). Data from 6 additional participants were discarded due to either unsatisfactory levels of ocular artifact or EEG digitization equipment malfunction. All participants were right-handed, monolingual speakers of English with normal or corrected to normal vision and no history of neurological disease or defect. Participants were graduate or undergraduate students at the University of Illinois. The experimental protocol was approved by the Internal Review Board of the University of Illinois, and all participants were compensated with money or course credit.

Stimuli

Stimuli were 75 each words, (e.g., HAT, MAP), pseudowords (e.g., DAWK, KAK), meaningless, illegal strings (e.g., CKL, KKB), and familiar, orthographically illegal acronyms (e.g., VCR, AAA). Additionally, 150 common proper American first names (e.g., SARA, JOHN) served as targets in the substantive behavioral task, which was to monitor the stream of unconnected text for names and press a button when a name was detected. All items were between 3 and 5 letters long (mean 3.19). Words, pseudowords, illegal strings, and acronyms were the critical experimental items; no response was made to these items. Illegal strings and acronyms were composed of all consonants or all vowels. Acronym familiarity was assessed by a paper and pencil post-test (identical to that described in Laszlo & Federmeier, 2007), and only EEG responses to acronyms correctly identified by a given participant were included in the averaged ERPs computed for that participant.

Table 1 displays mean lexical characteristics of each item type (i.e., length, frequency, N, orthographic neighborhood frequency, number of lexical associates, and frequency of top associate), along with examples. Orthographic neighborhood size was the computed as the total number of words that could be formed by replacing one letter of a target item, as indicated by the Medical College of Wisconsin Orthographic Wordform Database (Medler & Binder, 2005). Neighbor frequency was, in turn, computed as the logarithm of the summed frequency of all of an item's orthographic neighbors, with frequency estimates drawn from the Wall Street Journal corpus (Marcus, Santorini, & Marcinkiewicz, 1993). An additional analysis of neighbor frequency considered only the log of the maximum frequency neighbor of each item, as opposed to the sum of the frequencies of all neighbors. Number of lexical associates was retrieved from the South Florida Free Association Norms (Nelson, McEvoy, & Schreiber, 1998), and the log frequency of each item's top lexical associate was again obtained using the Wall Street Journal corpus (Marcus, Santorini, & Marcinkiewicz, 1993).

Critical experimental items (i.e., words, pseudowords, acronyms, and illegal strings) were each repeated one time at a lag of 0, 2, or 3 intervening items, allowing us to examine the stability of any effects we might observe across presentations. Each level of repetition lag occurred an equal number of times both within and across item types. Participants did not respond to the critical items, in order to prevent contamination of the critical ERPs by response potentials. The proper names served as the targets for the behavioral task, and were only presented once. Participants responded to proper names by pressing a button with their right hand. False alarms (i.e., button presses to critical items) were not included in averaged ERPs. The experiment thus included 750 trials (2 × 300 critical items + 150 proper names). These 750 trials were broken up into 5 blocks of 150 trials with rest breaks between each block. Across the 120 participants, each of the 120 permutations of 5 block orders was presented exactly once.

Procedure

Participants were seated 100 cm away from a computer monitor and instructed that their task was to press a button whenever they were presented with a “common English proper first name,” and to minimize blinks and eye movements except during a blink interval indicated on the screen by the presence of a white cross. After a demonstration of trial structure, participants were presented with a short block of practice trials consisting of items similar to those in the experiment proper.

In both the practice and experimental blocks, a fixation arrow was continuously present in the center of the screen. Participants were instructed to keep their eyes on the fixation arrow as much as possible. Stimuli were presented one at a time in white directly above the fixation arrow on the black background of a 22 in CRT computer monitor with resolution 640 × 480. Trial structure was as follows: 500 ms warning stimulus (red cross above the fixation arrow), 500 ms stimulus presentation, 1000 ms response interval (fixation arrow present only), 1000 ms blink interval (white cross above the fixation arrow.)

After the 5 experimental blocks, participants completed the paper and pencil acronym knowledge questionnaire (described in Laszlo & Federmeier, 2007), in order to permit sorting of the acronym items as familiar or unfamiliar on an individual basis. In brief, the questionnaire required participants to indicate whether each of the acronyms and illegal strings presented in the EEG experiment were acronyms or not acronyms. If participants believed an item was an acronym, they had the option of indicating what the letters in the acronym stood for, writing a sentence showing what the acronym meant, or selecting “Don't Know,” in instances when they “had heard other people use it before, but didn't know what the letters in it stand for and couldn't use it [themselves].” Only items for which participants could identify all the letters or could write a sentence were included in subsequent ERP analyses. This method has proved reliable in the past for sorting acronym stimuli into classes distinguished in the ERP signal (Laszlo & Federmeier, 2007; 2008). On average, participants were able to correctly identify 83% of acronyms (~62 / 75).

Electroencephalogram (EEG) Recording

EEG was recorded from 6 Ag/AgCl electrodes embedded in an electrocap. We sampled from middle prefrontal, middle parietal, middle central, left middle central, right middle central, and middle occipital electrode sites. This reduced electrode montage was necessary in order to enable the collection of 120 participants in a reasonable period of time. Because our focus was on the N400 component, we chose a montage that provided good coverage of the region of the scalp where N400 effects are typically maximal (i.e., the central posterior scalp), as well as one prefrontal site to confirm the posterior distribution of observed effects.

All EEG electrodes were referenced online to the left mastoid process and then digitally re-referenced offline to the average of the left and right mastoids. The electrooculogram (EOG) was recorded using a bipolar montage of electrodes placed at the outer canthi of the left and right eyes; blinks were monitored with an electrode at the suborbital ridge. EEG and EOG were recorded with a bandpass of 0.02 to 100 Hz and sampled at a rate of 250 Hz with a gain of 10,000×. All electrode impedances were kept below 2 kΩ. Single item ERPs were computed by averaging (across the 120 subjects) at each electrode time-locked to the onset of each of the critical items (resulting in 600 single item ERPs: one for each of 2 presentations of each of 300 critical items). In addition to the single item ERPs, more traditional ERPs representing the average within subject response to, for example, all words, were also computed. Trials containing eye movement or drift artifact were rejected with a threshold individualized to each participant by inspection of that participant's raw waveforms, and blinks were corrected using a procedure described by Dale (1994). Artifact rejection resulted in an average loss of 7% of trials per participant. All ERPs contained a 100 ms pre-stimulus baseline and continued for 920 ms after stimulus onset. Measurement of ERP mean amplitude was conducted on data digitally filtered off-line with a bandpass of 0.2 to 20 Hz.

Results

Behavioral Data

Correct behavioral responses were either to press a button in the right hand in response to a name, or to press nothing in response to any other item type. Thus a hit was a button press for a name, and a correct rejection was no button press for a critical item. Participants made on average 137/150 hits ($\sigma = 10.2$), or 91% accuracy, for the names, and on average 589/600 ($\sigma = 16.5$) correct rejections, or 98% accuracy, to critical items. Overall, these results indicate that participants were appropriately attending to the substantive behavioral task, and, more importantly, that they were processing each item in the text stream.

Electrophysiological Data

Three types of analysis are reported: 1) factorial analyses including item Analyses of Variance (ANOVAs) and, where appropriate, non-parametric factorial tests, 2) single regressions over items, 3) and multiple regressions over items. In what follows, we first present factorial analyses and single regressions pertaining to each of the four single lexical factors of interest (i.e., N, neighbor frequency, number of lexical associates, and frequency of top associate). We then present multiple regressions pertaining to combinations of those variables.

For all analyses, the N400 was measured as mean amplitude in a 250–450 ms post stimulus onset window, relative to a 100 ms pre-stimulus baseline. The N400 was measured over the middle parietal channel only. The reduced electrode montage made analyses including data from each of the 6 electrode channels relatively uninformative; all reported effects were qualitatively similar across all five central-posterior channels.

Orthographic Neighborhood Size

We began with a 2 × 2 item ANOVA with factors of orthographic neighborhood size (high or low) and lexical type (lexical: word and acronym, or nonlexical: pseudoword and illegal string). This ANOVA revealed a main effect of N ($F1, 296 = 159.7$, $p < 0.0001$), but no effect of lexical type ($F = .19$) and no interaction ($F = 1.1$). Indeed, as is depicted in Figure 2, the relationship between N and N400 amplitude is nearly identical for the two lexical types. The single regression correlations of N on N4 mean amplitude for lexical and nonlexical items are $r = -.61$ ($r^2 = .37$, $p < 0.0001$) and $r = -.49$ ($r^2 = .24$, $p < 0.0001$), respectively. The equivalence of the N effect for lexical and nonlexical items – and the strong effect of N on N400 amplitude – is reiterated in Figure 3, which shows item ERPs for a low, mid, and high N item from each lexical category separately. Because the N effect is so similar across lexical category, in what follows we will sometimes collapse across lexical category when considering N effects (for example, when collapsed across lexical category, the single correlation of N with N400 mean amplitude has $r = -.55$, $r^2 = .30$, $p < 0.0001$).

The same pattern of N effect was also observed on second presentation. An identical item ANOVA with factors of N (high or low) and lexical type (lexical or nonlexical) revealed a main effect of N ($F1,296 = 39.6$, $p < 0.0001$), but no main effect of lexical type ($F = 6.3$) and no interaction between the two ($F = .26$). The single regression correlations of N with N4 amplitude were mildly reduced but still highly reliable on second presentation. For lexical items, $r = -.43$ ($r^2 = .19$ $p < 0.0001$), and for nonlexical items $r = -.33$ ($r^2 = .11$, $p < 0.0001$). Thus, across both first and second presentation, items with high N elicited more negative N400s than did items with low N, regardless of lexical type.

Neighbor Frequency

Our analysis of neighbor frequency effects mirrored our analysis of N effects. Again, we began with an item ANOVA with factors of (summed) neighbor frequency (high or low) and lexical type (lexical or nonlexical), which revealed a main effect of neighbor frequency ($F1,296 = 53.0$, $p < 0.0001$), but no main effect of lexical type ($F = .15$) and no interaction ($F = .81$). The single regression correlations of summed neighbor frequency with N4 amplitude were also both strongly reliable (for lexical items, $r = -.48$, $r^2 = .23$, $p < 0.0001$; for nonlexical items, $r = -.39$, $r^2 = .15$, $p < 0.0001$.) As was the case with the effect of N, the effect of orthographic neighbor frequency was nearly identical across lexical types. The strikingly similar pattern is displayed in Figure 4.

An identical ANOVA conducted with a neighbor frequency measure consisting of the frequency of each item's highest frequency neighbor (as opposed to the summed frequency of all its neighbors) yielded the same pattern of results, with a main effect of maximum neighbor frequency ($F1,296 = 21.66$, $p < 0.0001$) but no main effect of lexical type ($F = .13$) and no interaction between the two ($F < 0.1$). Similarly, the single regressions of maximum neighbor frequency with N4 amplitude were reliable for both lexical types (for lexical items $r = -.28$, $r^2 = .08$, $p < 0.001$; for nonlexical items $r = -.25$, $r^2 = .06$, $p = .002$). Figure 5 displays waveforms evincing the neighbor frequency effect, aggregated over items and lexical types. As with N, items with higher neighbor frequencies elicit larger N400s, regardless of lexical type.

Also as in the case of N, the same pattern of effects was observed on second presentation. An item ANOVA with factors of neighbor frequency (high or low) and lexical type (lexical or nonlexical) again revealed a strongly reliable main effect of neighbor frequency ($F1,296 = 27.8$, $p < 0.0001$), but no main effect of lexical type ($F = 3.14$) and no interaction ($F = 2.83$). Also as with N, on second presentation the correlations between neighbor frequency and N4 amplitude were reduced, but still highly reliable, for both lexical types (for lexical items, $r = -.39$, $r^2 = .15$, $p < 0.0001$; for nonlexical items $r = -.34$, $r^2 = .12$, $p < 0.0001$). Thus, just as with N, items with higher neighbor frequency elicit larger N400s on both first and second presentation, regardless of lexical type.

We again conduced an identical set of analyses using the frequency of the most frequent neighbor (as opposed to the summed frequency of all neighbors) on seceond presentation. An item ANOVA with factors of max neighbor frequency (high or low) and lexical type (lexical or nonlexical) showed that with this measure of neighbor frequency, on second presentation, there was no main effect of either neighbor frequency or lexical type, and no interaction between the two (for neighbor frequency, $F = 1.72$, for lexical type $F = 2.87$, for the interaction $F = 0.67$.) Accordingly, the single correlations between N4 mean amplitude and max neighbor frequency were not reliable for either lexical or nonlexical items (for lexical items, $r = -0.08$, $p = 0.31$; for nonlexical items $r = -0.05$, $p = 0.56$).

Number of Lexical Associates

61 of our lexical items were included in the South Florida Free Association Norms (Nelson, McEvoy, & Schreiber, 1998), and a median split of the N4 mean amplitude data when sorted by number of lexical associates put 27 items in the “high number of lexical associates” category and 28 in the “low number of lexical associates” category. Because there were different numbers of items in the two categories, we used a nonparametric rank sum test (equivalent to a Mann-Whitney U test) to examine whether or not there was a factorial effect of number of lexical associates on first presentation. The rank sum test was only marginally reliable ($p = .12$). However, the more powerful single regression of number of lexical associates with N4 mean amplitude was reliable ($r = -.34$ $r^2 = .12$, $p = .008$). Thus, similar to the analogous effect of orthographic neighborhood size, items with more lexical associates elicit more negative N400s. Figure 6 displays this relationship.

On second presentation, an equivalent rank sum test performed on a median split of the N4 mean amplitude data sorted by number of lexical associates was reliable ($p = .02$), as was the single regression of number of lexical associates with N4 mean amplitude ($r = -.41$, r^2

= .17, $p = .001$). On second presentation, as on first presentation, items with more lexical associates elicited a more negative N400.

Frequency of Top Associate Effects

A median split of the item N4 mean amplitude data when sorted by frequency of top lexical associate put 30 items in the "high frequency of top lexical associate" category and 30 items in the "low frequency of top associate" category. Although the number of items in the high and low categories was thus balanced in this comparison, for analogy with the analyses of the effects of number of lexical associates, we again used rank sum tests in our factorial analysis of the effects of frequency of top associate. A rank sum test on the effect of frequency of top associate on N400 amplitude on first presentation was reliable ($p = .03$), and, accordingly, so was the single regression correlation of frequency of top associate with N4 amplitude ($r = -.27$, $r^2 = .07$, $p = .04$). Figure 6 depicts the effect of frequency of top associate side by side with the effect of number of lexical associates.

On second presentation, the effect of frequency of top associate on N4 mean amplitude was not reliable either in the factorial analysis (rank sum $p = .38$) or the single regression correlation ($r = -.13$, $p = .32$.)

Multiple Regressions

Of particular interest was to use multiple regression to enable examination of the unique effects of each of our variables of interest. We conducted two multiple regression analyses: one pertaining to orthographic variables and one pertaining to lexical variables. Included in the orthographic analysis were N and neighbor frequency (which are strongly correlated in this dataset: $r = .64$, $p < 0.001$). Included in the lexical analysis were number of lexical associates and frequency of top associate (which are more weakly correlated in this datasest: $r = .19$, $p = .14$).

Because the effects of N and neighbor frequency are so similar across the lexical and nonlexical item types, we collapsed across lexicality in the analysis of orthographic factors. (In addition to this lack of interaction in the N4 window, we also observed no differences between these item types in the immediately preceding, P2 (175–225 ms, middle prefrontal channel) window ($t_{298} = .09$, $p = .93$)). Automated stepwise multiple regression revealed that the most reliable predictor of N4 amplitude was N, followed by neighbor frequency. Alone, N explained 30.6% of variance in N400 mean amplitude ($F_{298} = 131.58$, $p < 0.0001$). With the variance from N already explained, the stepwise procedure did add neighbor frequency to the model, which explained an additional 1.2% of variance ($F_{297} = 69.37$, $p < 0.0001$). Thus, when combined, these two factors explain 31.8% of variance in N400 mean amplitude. Neighbor frequency was added to the model after N even when length was additionally added to the pool of lexical variables available to the stepwise procedure—a supplemental analysis we conducted because length and N are strongly correlated in this dataset ($r = -.27$, $p < 0.0001$). Additionally, a simultaneous multiple regression including length, N, and neighbor frequency was highly reliable ($F_{296} = 53.72$, $p < 0.0001$).

Because both N and neighbor frequency also influenced N400 amplitudes for repeated items, we performed the same regression analysis on data from the second presentation of each item, again collapsed across lexicality. Automated stepwise multiple regression revealed that the most reliable predictor of N4 amplitude was again N, followed by neighbor frequency. Alone, N explained 14.8% of variance in N400 mean amplitude (F_{298} =, $p < 0.0001$). With the variance from N already explained, the stepwise procedure again added neighbor frequency to the model, which explained an additional 2.5% of variance (F_{297} =, $p < 0.0001$). Thus, when combined, these two factors explain 17.3% of variance in N400 mean amplitude to items that have been repeated.

An identical automated stepwise multiple regression conducted over lexical variables (number of lexical associates and frequency of top lexical associate for all 61 items for which this information was available) revealed that number of lexical associates was a better predictor of N4 amplitude than was frequency of top associate. Alone, number of lexical associates explained 11.5% of variance in N4 mean amplitude ($F_{59} = 7.65$, $p = .008$). With the variance due to number of lexical associates already explained, adding in frequency of top associate explained an additional 4.1% of variance ($F_{58} = 5.37$, $p = .007$). Thus, when combined, these two factors explained 15.6% of variance in N400 mean amplitude. Number of lexical associates was strongly correlated with written frequency in this dataset ($r = .35$, $p = .006$), but an additional automated stepwise procedure conducted with number of lexical associates, frequency of top associate, and written frequency as predictor variables added number of lexical associates to the model after variance due to frequency was explained. In this case, neighbor frequency was added only if a less conservative entry criterion was used (p in < 0.10). Thus, the independent contributions of item frequency and neighbor frequency are more difficult to disentangle. The simultaneous regression with all three variables was also reliable ($F_{57} = 3.60$, $p = .02$).

Discussion

Our goal was to discover whether properties of items related to an input item—either orthographically or lexically—would have any effect on the magnitude of the N400 ERP component elicited by that input. We were motivated to this goal by recent evidence suggesting that the range of information activated by a particular input may be considerably broader than is assumed in classical, staged models of reading—especially at the semantic level of representation. Thus, we looked for N400 effects of orthographic neighborhood size and neighbor frequency (either summed or maximum) and what we thought of as their lexical correlates, namely number of lexical associates and frequency of top associate. We found effects of all four factors, consistent with the hypothesis that orthographic inputs activate not only directly associated semantic information but also information associated with items related to the input on at least two levels of representation (orthographic and lexical), and that this information is accessed in a cascaded, not staged, fashion.

We replicated and extended previous findings showing a relationship between orthographic neighborhood size and N4 amplitude (Holcomb et al., 2002, Laszlo & Federmeier 2007; 2008; 2009) with high N items eliciting larger N400s than low N items. Our use of regression analysis on individual item ERPs showed clearly that this is a graded effect, and a strong one, with just over thirty percent of unique variance in N400 mean amplitude explained by N alone. Furthermore, this relationship was statistically indistinguishable for lexically represented items (words, acronyms) and items without lexical representation (pseudowords, illegal strings of letters)—although, of course, non-lexical items are discriminated from lexical items in portions of the ERP subsequent to the N400 window.

The finding that number of orthographic neighbors strongly affects N400 amplitude already hints that semantic information associated with orthographically similar items becomes active in parallel with that for a given input. However, as we described in the introduction, N alone could potentially be thought of as a proxy for some property of lexically represented items such as how likely they are to be pronounced similarly to other words– although it is then difficult to explain the identical N effects we observed for non-lexical items. Nevertheless, the present data revealed an even stronger finding in support of the hypothesis that items orthographically related to an input affect that input's semantic processing. In particular, we found that items with orthographic neighbors that are high in lexical frequency tend to elicit N400s with larger amplitude than items with neighbors that are low in frequency. Multiple regression analysis revealed that even though N and neighbor frequency are strongly correlated, neighbor frequency explains an additional, unique portion of variance in N400 amplitude. To our knowledge, this is the first time that neighbor frequency has been shown to affect the N400 independent of N (c.f. Debruille, 1998).

Although lexical frequency effects on the N400 have often been in the form of amplitude reductions (more positivity) to high as opposed to low frequency words, the effect of neighbor frequency we observe here is different, with more negative responses when neighbors of input items have high lexical frequency. However, this pattern may reflect a similar underlying mechanism. Traditional N400 frequency effects are often interpreted as reflecting the “ease” with which an item becomes active, with higher frequency words being easier to activate than lower frequency words. This higher ease of activation may reflect a greater tendency for the neighbor to become active when an item containing some of its orthographic features is encountered. In other words, the neighbor item is a better “lure” when it is of higher frequency. This explanation seems consistent with the finding in the behavioral literature that the lexical decision task takes longer for items with high frequency neighbors than with low frequency neighbors (e.g., Grainger, 1990), which has been interpreted as representing “interference” by the high frequency neighbors (Grainger, 1990). In the data described here, because higher frequency neighbors are more likely to become active in response to a given input, the net amount of semantic information evoked by that input is greater, resulting in larger N400 amplitude.

We also found corresponding effects from items lexically associated with an input, which we believe to be novel to the N400 literature. In particular, N400 amplitudes were larger for words with higher numbers of lexical associates, suggesting again that inputs evoke semantic activity associated with a *set* of items that are similar or interconnected at lower processing levels. Some items elicit a greater spread of activation at the lexical level, and, in turn, a greater net level of initial activity in the semantic system. Analogous to the pattern seen for orthographic neighbors, we also found that N400 amplitudes are larger for items whose top associate is higher in lexical frequency. We were not able to statistically disentangle effects that might be due to frequency of a word's top associate from effects that might arise from the frequency of the word itself; however, it is worth noting the direction of the effect, if due to word frequency rather than frequency of the top associate, goes in the opposite direction from that typically observed, as in this case more frequent words (with more frequent top associates) elicited a larger (rather than a smaller) N400. The effects of lexical association were smaller than the effects of orthographic similarity, perhaps reflecting their second-order nature. That is, whereas it is reasonable to assume that orthographic neighbors are activated directly by the input (i.e., the presence of “ORK” in the input FORK directly causes some co-activation of PORK), the activation of lexical associates must be mediated, such that the activation of, for example, SPOON is dependent on the activity associated with FORK.

The distinction between measures that reflect properties of a subset of the network—such as N and number of lexical associates—and measures that instead represent the properties of single items—such as neighbor frequency and frequency of top associate—is critical to explaining the different impact of repetition on neighbor or associate effects, as compared with neighbor or associate frequency effects. Effects of both N and number of lexical associates were maintained across repetitions. However, effects of neighbor frequency were only maintained when a measure of lexical frequency summed across all an item's neighbors was used. When max neighbor frequency—a measure more similar to the frequency of a single, top associate—was used, an effect of neighbor frequency was no longer observable on second presentation. Because both N and number of lexical associates are properties of the structure of the comprehension network, it makes sense that these factors would have an impact every time an input is encountered (and, indeed, N effects have been shown persist even for the final words of highly constraining sentences; Laszlo & Federmeier, 2009)— a single presentation of an item does not affect the entire system it is embedded in in a persistent way. In contrast, effects that arise due to baseline activity of particular items – for example, frequency effects – can be over-ridden by the processing context (e.g., Van Petten & Kutas, 1990). Thus, it makes sense that the effect of frequency of an orthographic or lexical associate is reduced (in fact, statistically eliminated) with repetition, as first order lexical frequency effects of input items (i.e., not even second order effects of associates of items) have been found to be similarly context sensitive (Van Petten & Kutas 1990).

Taken all together, the findings that semantic processing, as indexed by the N400, is modulated by the number of items that share orthographic features with an input and the number that are lexically associated with that input, as well as by lexical properties (such as frequency) of those orthographically or lexically related items strongly suggest that semantic access does not serially follow a recognition process in which the input has been mapped onto a single, stored representation. In models of that type (e.g., Forster & Davis, 1984; Borowsky & Besner, 1993), semantic processing should be limited to lexically represented items, and only semantic features directly associated with a recognized input should become active. That is to say, no semantic processing should be observed for nonlexical items like our pseudowords and illegal strings. Instead, it seems that activity is elicited in the semantic system for both lexical and nonlexical inputs, and that this activity is cascaded from lower-level (orthographic, lexical) processes, such that semantic features associated with a range of similar (or associated) inputs becomes active in parallel, beginning around 250 ms post-stimulus onset. Although serial models do not predict this pattern, it is entirely consistent with cascaded models, which do not require lexical access to be complete (or ultimately successful) in order for semantic processing to begin.

In arguing against models where semantic access is gated by recognition, these data are also inconsistent with views of the N400 that derive from such models, especially those that map the N400 onto some aspect of "post-lexical" processing (e.g., Brown & Hagoort, 1993; Sereno, Rayner, & Posner, 1998). For example, Hagoort and colleagues, (2009) have linked the N400 with post-recognition processes that integrate the (already accessed) meaning of the current word with sentence- and discourse-level representations. It seems difficult, under this kind of view, to explain how items with no lexical representation-- such as pseudowords and orthographically illegal strings-- can show identical, graded N400 effects to those shown by lexically represented items. Furthermore, the N400's sensitivity to number of neighbors and associates and to properties of those items is inconsistent with the assumption that the meaning information associated with a given input has already been accessed by the time the N400 is measured.

Instead, the present data – in the context of the full set of variables known to modulate the N400 (for a review, see, e.g., Kutas & Federmeier, 2000)– are more consistent with views that link the N400 to early aspects of semantic access (e.g., Kutas & Federmeier, 2000; Van Berkum, 2009; Federmeier & Laszlo, 2009; Lau, Phillips, & Poeppel, 2008), on the assumption that semantic access takes place in a cascaded processing stream and is distributed over time. Under such views, while linguistic effects can still be observed in the ERP prior to the N400 epoch—for example discrimination between pseudohomophones and orthographically matched controls (Grainger, Kiyonaga, & Holcomb, 2006) or discrimination between words and nonwords in the lexical decision task (Kiyonaga, Midgley, Holcomb, & Grainger, 2007)—they are interpreted not as evidence for early lexical access, but instead as representing complex perceptual or formal analysis, with the N400 still representing the first point in time at which amodal, position invariant representations come into contact with semantics (e.g., Grainger & Holcomb, 2009). For example, in the bi-modal interactive activation model (BIAM), which instantiates the principles of interactivity proposed in Rumelhart & McClelland's Interactive Activation model (McClelland & Rumelhart, 1981; Rumelhart & McClelland, 1982), visual word recognition proceeds first through visual feature analysis around 100 ms post stimulus onset, then subsequently through position dependent and position invariant orthographic analysis at approximately 200 ms and 250 ms respectively. The position invariant orthographic analysis outputs representations akin to visual wordforms around 300 ms, and processing of these visual wordforms is only advanced enough to begin contacting semantics around 400 ms—that is, the time of the N400 (Grainger & Holcomb, 2009, Massol, Grainger, Dufau, & Holcomb, 2010). In addition to being more compatible with the present data than post-lexical views, models like the BIAM are consistent with what is known about the neural generators of early ERP components elicited during word reading (e.g., Marinkovic, Dhond, Dale, Glessner, Carr, & Halgren, 2003; Tse, Lee, Sullivan, Garnsey, Dell, et al., 2007)—an important constraint on cognitive models of any kind.

However, even if post-lexical theories of the N400 are correct, and lexical access does take place prior to 400 ms (despite being opaque to ERPs, MEG, and EROS; although see Shtyrov, Kujala, & Pulvermuller, In Press, for counterarguments to this claim), the present data clearly indicate that during the N400 time window, the system is in a state wherein lexical and nonlexical items are treated identically, as indicated by the indistinguishable effects of N and neighbor frequency we observed for words and nonwords, and wherein activity reflects the structure of the input network, not just the properties of the input item itself. To our knowledge, no implemented or proposed model of serial word recognition would be expected to show such effect patterns in a post-recognition time window.

Instead, we have previously suggested (Federmeier & Laszlo, 2009) that the basic temporal properties of the N400 inherently argue against the idea that the processing it indexes is dependent on a discrete recognition process, since recognition, both theoretically and empirically, would seem to take varying amounts of time for different types of stimuli and in different types of contexts, whereas the N400 manifests striking temporal stability. If, then, semantic access is not dependent on recognition, it follows that all types of stimuli might elicit N400 activity to some degree—as was observed here. Furthermore, the present data suggest that activity in the N400 time window can reflect initial semantic activation states, that is, those which emerge before activity in orthographic levels of processing has reached a stable point. Thus, although the comprehension system will eventually reach a state in which only the orthographic features comprising F-O-R-K, and the corresponding semantic features of FORK are strongly activated (or in which the system has determined that, for example, that there is no stable semantic representation associated with the input GORP), activity in the N400 time window is sensitive to points in processing earlier that this, when semantic information associated with a distributed set of co-activated representations comes online in parallel. Within the PDP modeling framework, this same point might be stated as suggesting that the N400 represents activity taking place in the semantic level of representation before either the orthographic or semantic layers have settled. The N400 might thus be well described as providing a temporally delimited “snapshot” of activity elicited by a given input in a distributed, cascaded, semantic system.

Conclusion

Using a regression approach to examine effects of correlated variables on ERP responses to single items, we observed strong, independent effects of orthographic neighborhood size, neighbor frequency, number of lexical associates, and frequency of top associate on the amplitude of the N400 component—the latter three, to our knowledge, for the first time in the literature. This pattern supports a view of the N400 as indexing fairly early aspects of distributed semantic activation arising in a cascaded processing system. In turn, this data, in combination with the larger literature, are consistent with parallel distributed processing models of language comprehension, which are characterized by interactive dynamics and recurrent architecture. Such models can typically never be said to be doing only “semantic” processing or “orthographic” processing, as activation flows through all levels of representation in a parallel fashion. Thus, a snapshot of the model at any particular moment in time reflects activity in all levels of representation — much as, as suggested by the current data, the N400 represents a snapshot of late orthographic and early semantic processing occurring in parallel.

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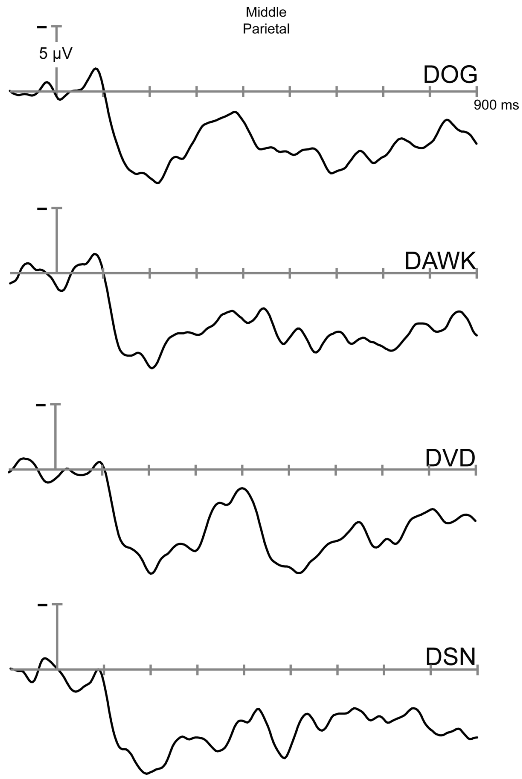

Figure 1.

Example single item ERPs: Each ERP is an average of one EEG sweep over the middle parietal channel from each of 120 participants in response to a single item: the word DOG, the pseudoword DAWK, the acronym DVD, and the illegal string DSN. In this figure, as in all subsequent ones, negative is plotted up. These ERPs are unfiltered, which makes it evident that the signal to noise characteristics of the single item ERPs are satisfactory.

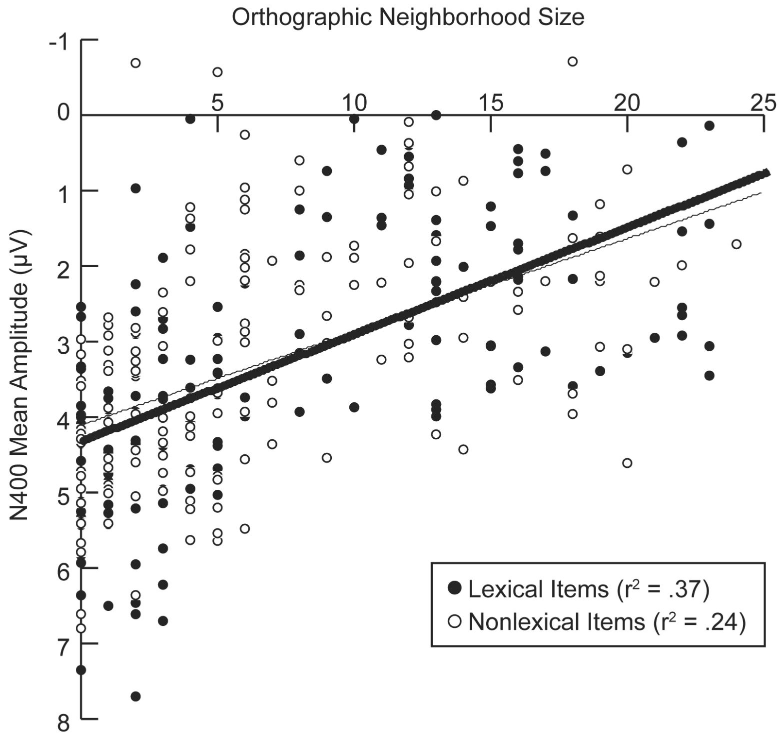

Figure 2.

Equivalency of N effect across lexical types: Item N400 mean amplitude (250–450 ms) over the middle parietal channel is plotted against orthographic neighborhood for lexical items (filled circles) and nonlexical items (empty circles). Single regression trend lines for the relationship between N4 mean amplitude and N are also plotted for each item type. The function relating N400 amplitude to N is nearly identical for the two item types.

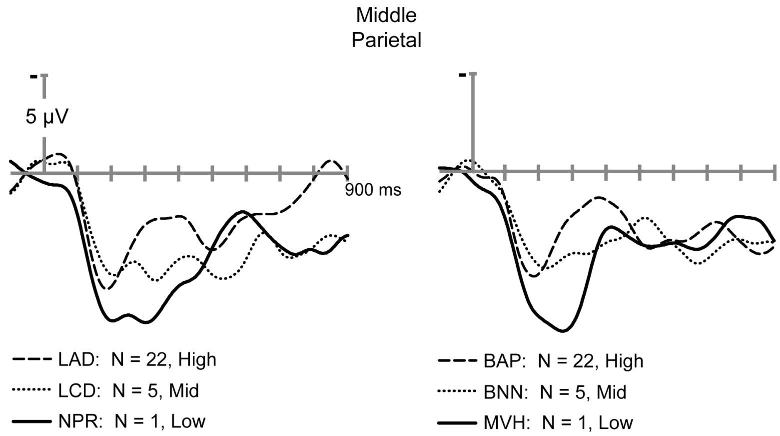

Figure 3.

N effect in item ERPs: Left, the ERPs elicited by lexical items with Ns of 1, 5, and 22: the word LAD, and the acronyms LCD and NPR (Liquid Crystal Display and National Public Radio). Right, ERPs elicited by nonlexical items with the same Ns: the pseudoword BAP and the illegal strings of letters BNN and MVH. Individual N is strong predictor of N400 amplitude, regardless of lexical type.

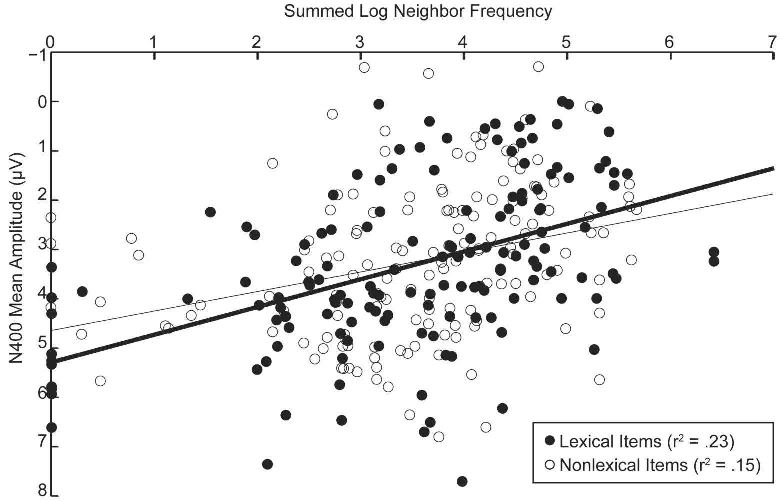

Figure 4.

Equivalency of neighbor frequency effect across lexical types: Item N400 mean amplitude (250–450 ms) over the middle parietal channel is plotted against neighbor frequency for lexical items (filled circles) and nonlexical items (empty circles). Single regression trend lines for the relationship between N4 mean amplitude and neighbor frequency are also plotted for each item type. The function relating N400 amplitude to neighbor frequency is nearly identical for the two item types.

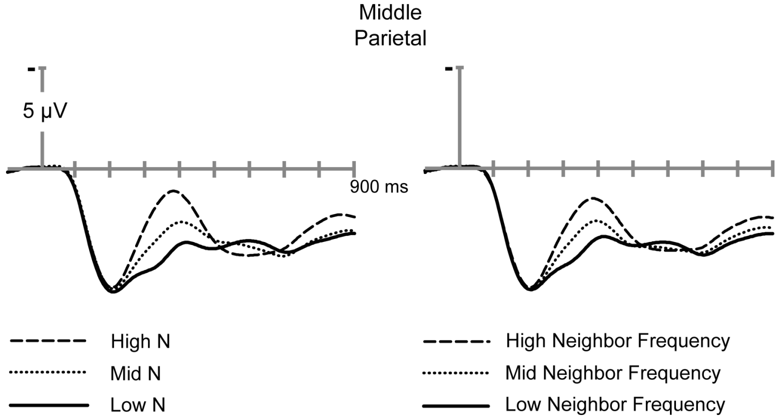

Figure 5.

Effects of N and neighbor frequency: Left, grand average ERPs elicited in response to items with high, mid, or low orthographic neighborhood size (N). Right, grand average ERPs elicited in response to items with high, mid, or low neighbor frequency. All ERPs are from the middle parietal channel, and are averaged over both lexical and nonlexical items. In part because the two variables are highly inter-correlated, the effects are quite similar.

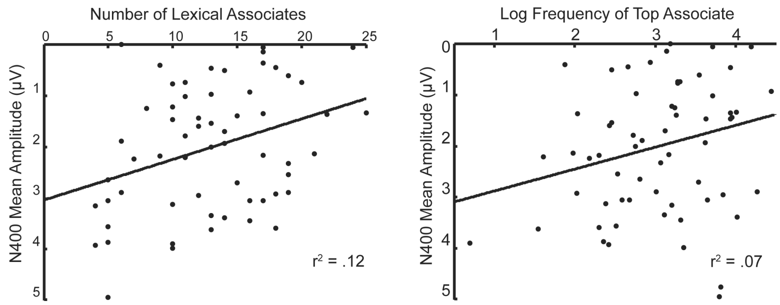

Figure 6.

Effects of number and frequency of lexical associates: Left, a scatter plot showing the relationship of N400 mean amplitude (250–450 ms) and number of lexical associates at the single item level. Right, an identical scatter plot showing the relationship of N400 mean amplitude and log frequency of top lexical associate. Items with more lexical associates and items with more frequent lexical associates both elicit more negative N400s.

Table 1

Selected Lexical Characteristics: By design, the lexical characteristics of the items included in the single item ERP corpus varied broadly. N was estimated from the Medical College of Wisconsin Orthographic Wordform Database (Medler & Binder, 2005). All frequency estimates were drawn from the Wall Street Journal Corpus (Marcus, Santorini, & Marcinkiewicz, 1993). Number of lexical associates was estimated from the South Florida Free Association Norms (Nelson, McEvoy, & Schreiber, 1998).

Item Type	Examples	Length	Log Written Frequency	N	Log Neighborhoo d Frequency	Number of Lexical Associates	Log Frequency of Top Associate
Word	HAT, MAP	3.2	2.39	12.99	4.32	10.53	2.45
Pseudoword	TUL, KAK	3.2	--	11.04	4.12	--	--
Acronym	VCR, AAA	3.2	0.96	1.93	2.71	--	--
Illegal String	CKL, KKB	3.2	--	2.4	2.96	--	--