

Parafoveal versus foveal N400s dissociate spreading activation from contextual fit

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Using concurrent electroencephalogram and eye movement measures to track natural reading, this study shows that N400 effects reflecting predictability are dissociable from those owing to spreading activation. In comparing predicted sentence endings with related and unrelated unpredicted endings in antonym constructions ('the opposite of black is white/yellow/nice'), fixation-related potentials at the critical word revealed a predictability-based N400 effect (unpredicted vs. predicted words). By contrast, event-related potentials time locked to the last fixation before the critical word showed an N400 only for the nonrelated unpredicted condition (nice). This effect is attributed to a parafoveal mismatch between the critical word and preactivated lexical features (i.e. features of the predicted word and its associates). In addition to providing the first demonstration of a parafoveally induced N400 effect, our results support the view that the N400

is best viewed as a component family. *NeuroReport* 20:1613–1618 © 2009 Wolters Kluwer Health | Lippincott Williams & Wilkins.

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Introduction

Research on the neurophysiology of language has revealed a number of language-related event-related potential (ERP) components, of which the N400 is arguably the most famous [1]. The N400, a centro-parietal negativity with a peak latency of approximately 400 ms after critical stimulus onset, is not only the first language-related component to have been discovered [2]; it has also been subjected to the most extensive investigation [3–5]. Nevertheless, the functional interpretation of the N400 remains controversial. It appears clear that it is not a language-specific component [6–8] and that it reflects lexical preactivation [3] and the degree of lexical–semantic integration effort [9,10]. However, a classification of the N400 as a purely lexical–semantic component is inaccurate, as it is also elicited in contexts, which are clearly not lexical–semantic in nature [11,12] and, conversely, it is not always engendered by semantic manipulations [13]. Seeing that the N400 is observable under these diverging circumstances, it has been proposed that the notion of an 'N400 family' may be more accurate than that of a monolithic N400 component [11,14]. Here, we provide further evidence for the N400 family view by demonstrating separable N400 subeffects

within the lexical–semantic domain. Specifically, we show that N400 effects related to lexical preactivation and semantic integration are triggered by distinct sources of input information. In addition, we provide the first demonstration that, during natural reading, lexical preactivation can lead to parafoveally induced N400 effects (i.e. effects of the critical word on the ERP time locked to the last fixation preceding the critical word).

Previous ERP studies have shown that lexical association and the ease of semantic integration into a sentence or discourse context both modulate N400 amplitude [15,16]. For example, Federmeier and Kutas [15] presented stimuli such as 'the gardener really impressed his wife on Valentine's day. To surprise her, he had recently grown some roses/tulips/palms'. At the critical word (underlined), they observed a graded N400 effect, with the smallest N400 for the expected continuation (roses), a larger N400 for an unexpected continuation of the same semantic category (tulips), and the largest N400 for an unexpected continuation of a different category (palms). This shows that the N400 correlates both with the contextually based expectation for a particular word and with the lexical–semantic associations generated by it. Strikingly, a similar pattern is observable in very highly constraining sentence contexts with a cloze probability of 1 for the expected continuation and 0 for the lexically related but unexpected continuation. This is the case in antonym constructions such as 'the opposite

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of black is white/yellow/nice' [17,18]. These results thus support the assumption that the intermediary N400 for lexically related continuations can be attributed to the spreading of activation within the mental lexicon.

Although these previous findings provide compelling evidence for association-related and prediction-related influences on the N400, they cannot determine whether both serve to modulate a single underlying mechanism (i.e. jointly define semantic integration difficulty) or whether they reflect separable underlying processes. This limitation is owing to the fact that the two information sources, namely whether a word has been preactivated and whether it is predicted by the current sentence or discourse context, have hitherto always become available through the same input item. In this study, we thus sought to test the hypothesis that lexical preactivation and predictability based semantic integration are dissociable using a natural reading paradigm and acquiring concurrent electroencephalogram (EEG) and eye movement (EM) measures.

Natural reading differs from the rapid serial visual or auditory presentation that is typically used in ERP studies on language processing in that information processing is not strictly serial. First, EMs in reading are both progressive and regressive, thus allowing for the rereading of previously processed information [19]. Second, and more importantly for present purposes, a phenomenon known as 'parafoveal preview' allows for information to be accessed from positions outside of the range of maximal visual acuity (the fovea), for example, from words adjacent to the currently fixated word [19]. EM measures suggest that, at least in Roman writing systems, the orthographic form of upcoming words is accessible parafoveally [20–22], but that full lexical access (including semantic processing) requires foveal fixation [19].

The existing results on parafoveal preview during natural reading suggest that, if lexical relatedness effects owing to spreading activation are separable from prediction-based integration effects, they may already be observable at the fixation preceding the critical word in highly constraining sentence contexts. At this point, it should be apparent from parafoveal preview that whether or not the following word is compatible with preactivated lexical – and hence orthographic – features or not. By contrast, information on whether or not the critical word fulfills the semantic prediction engendered by the sentence context should not become available until the critical word itself is fixated, as this can only be resolved by full lexical processing.

These predictions lend themselves to testing by concurrent EEG and EM measures because, in this type of experimental setup, ERPs time locked to different fixation points can potentially provide additional insights on the information processed at those points. In particular, if parafoveally perceived orthographic information mismatches preactivated lexical features, we might

expect to observe an N400 modulation reflecting this mismatch even before the critical word is fixated. In contrast to the long-held assumption that EEG measures during natural reading are precluded by the artifactual influence of EMs on the EEG, a number of recent studies attest to the feasibility of concurrent EEG–EM measures [20,23,24]. Hence, this study used this procedure to examine the processing of highly predictive sentence constructions, namely antonym relations in sentence context. As described above, the advantage of using antonym relations is that the expected continuation of a sentence such as 'the opposite of X is...' has a cloze probability of 1 whereas all alternative continuations have a cloze probability of 0 independent of their degree of lexical association with the expected antonym. The critical sentences are illustrated in (1).

- (1) Dass schwarz das Gegenteil von weiß/gelb/nett ist,
that black the opposite of white/yellow/nice is
hat Dietmar gestern behauptet
has Dietmar yesterday claimed
'Dietmar claimed yesterday that black is the opposite
of white/yellow/nice'.

If lexical preactivation and predictability based semantic integration engender N400 modulations by separable underlying processing mechanisms, fixations at the position of the critical word (white/yellow/nice) should yield an N400 effect that distinguishes between the predicted continuation (white) and the two unpredicted continuations (yellow/nice) in natural reading. By contrast, relative to the last fixation before the critical word, we should observe a parafoveally induced N400 for the unpredicted unrelated condition (nice) in comparison with the others since only in this condition the lexically preactivated information (i.e. features of the predicted word and of words lexically associated with it) is not compatible with the parafoveally accessed orthographic information of the following (critical) word.

Methods

Forty-eight right-handed native speakers of German (24 females, mean age: 23.7 years, range: 19–31) participated in the experiment after giving their informed consent.

The stimulus materials were adapted from [18] and consisted of 40 lexical sets of sentences of the type in (1). The critical word was either the predicted antonym (PRED-ANT), an unpredicted word that was semantically related to the PRED-ANT (UNPRED-REL), or an unpredicted unrelated word (UNPRED-NONREL). The 30 critical items and 150 fillers were allocated to four lists according to a Latin Square Design so that each participant read 10 sentences per condition and no item was presented twice. A comprehension question followed each trial. Note that this experimental setup (i.e. 10 sentences per condition, with only a single variant of each

lexicalization presented to a participant and with a high number of filler sentences) adheres to the standards used in psycholinguistic reading research. It serves to ensure that participants do not develop ('unnatural') reading strategies over the course of the experiment as a result of being presented with too many similar sentences. As 10 sentences per condition are relatively few from the perspective of ERP studies on language processing, we increased the signal-to-noise ratio by acquiring data from a relatively high number of participants.

EMs were recorded by an EyeLink 1000 system (SR Research, Ottawa, Ontario, Canada) with a sampling rate of 1000 Hz. A calibration routine was performed before the experiment, after a break or when necessary. The EEG was recorded from 17 Ag/AgCl scalp electrodes positioned according to the international 10–20 system (impedances < 5 k Ω , sampling rate: 250 Hz, BrainAmp amplifier). Electrodes were referenced to the left mastoid and rereferenced to linked mastoids offline (ground: AFz). The electrooculogram was recorded by three bipolar pairs of electrodes placed at the outer canthi of and above and below each eye. Critical ERPs were time locked to the first fixation on the critical word and the last fixation before the critical word.

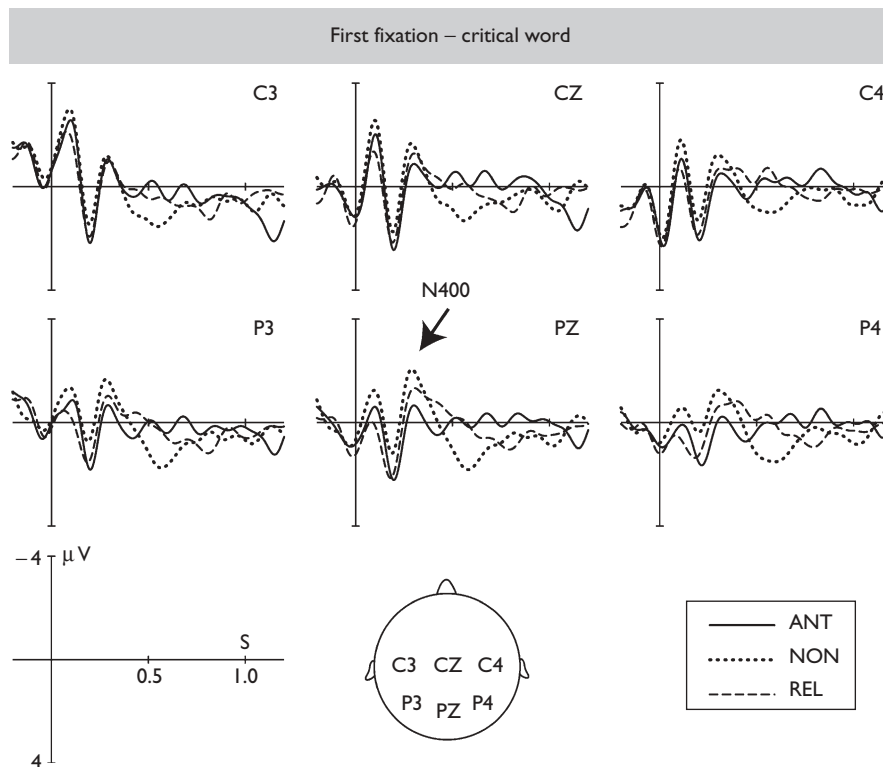
ERP and EM data were analyzed using repeated measures analyses of variance involving the factor CONDition (PRED-ANT vs. UNPRED-REL vs. UNPRED-NONREL) and, for the ERPs, the topographical factor region of interest (ROI). ROIs were defined as follows: left-central (C3, T7), right-central (C4, T8), left-posterior (P3, P7), and right-posterior (P4, P8). Only central and posterior electrode sites were analyzed, as (i) the N400 is known to have a centro-parietal distribution [3] and (ii) this served to exclude possible EM artifacts at frontal sites.

Midline analyses are not reported here for reasons of brevity, but confirmed the findings of the lateral analyses. Whenever the main effect of COND reached significance, pairwise comparisons between conditions were computed, with significance levels adjusted according to a modified Bonferroni procedure.

Results

Visual inspection of ERPs time locked to the first fixation on the critical word (Fig. 1) suggests that both unpredicted (nonantonym) conditions differed in N400 amplitude from the predicted (antonym) condition and that the unpredicted unrelated words additionally triggered a late

Fig. 1



Grand average event-related potentials (ERPs) ($N=48$) time locked to the first fixation on the critical word. ERPs for the predicted antonym condition (ANT) are depicted by the solid line, whereas those for the unpredicted related (REL) and unpredicted nonrelated (NON) conditions are depicted by the dashed and dotted lines, respectively. Negativity is plotted upwards.

positivity. Here, we only report analyses for the N400 (250–400 ms) in accordance with the question under consideration. For analyses of the late positivity (which replicate earlier findings in antonym paradigms, *c.f.* Ref. [18]), see Supplemental Digital Content 1, <http://links.lww.com/WNR/A15>. The time windows for the statistical analysis were chosen on the basis of visual inspection as ERP component latency is known to change with the modality of presentation [1] and there are no previous results on a comparable manipulation using natural reading. However, note that the choice of N400 time window is highly compatible with previous examinations of semantic congruity in antonym paradigms using auditory [17] or rapid serial visual presentation [18], in which N400 effects were observed between 200 and 440 ms post critical word onset.

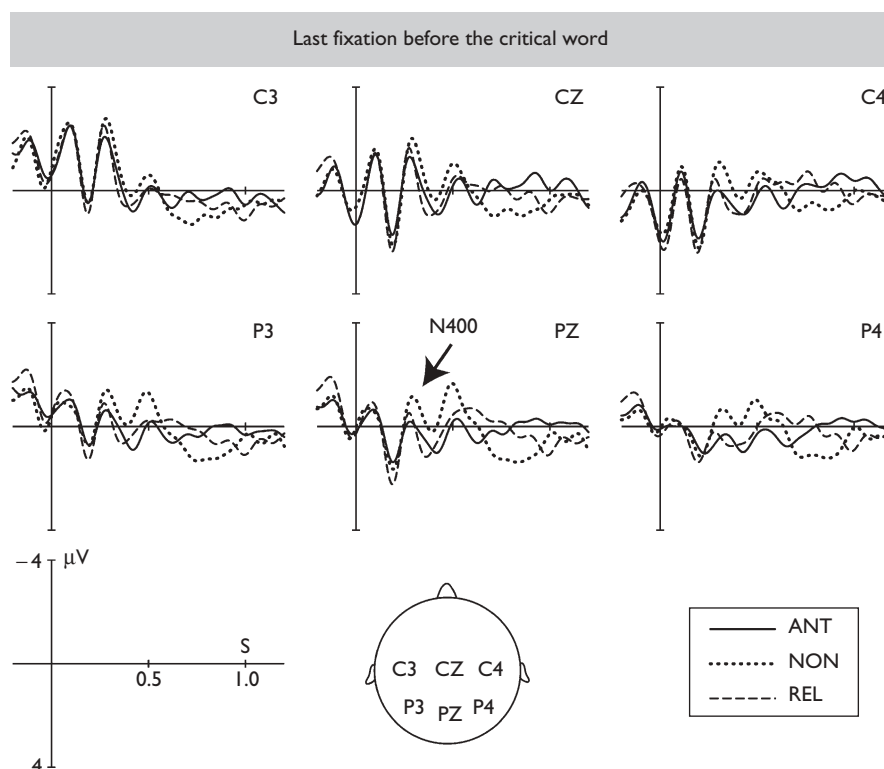
The analysis of the N400 time window revealed an interaction of ROI \times COND [$F(6,282) = 7.81$, $P < 0.0001$] which was as a result of significant effects of COND in both the posterior ROIs [left: $F(2,94) = 4.85$, $P < 0.01$; right: $F(2,94) = 8.15$, $P < 0.0001$]. Pairwise comparisons showed that PRED-ANT differed significantly from both UNPRED-REL [right-posterior: $F(1,47) = 7.77$, $P < 0.01$] and UNPRED-NONREL [left-posterior: $F(1,47) = 10.44$,

$P < 0.01$; right-posterior: $F(1,47) = 15.55$, $P < 0.0001$], which in turn did not differ from one another (all P values > 0.11).

Visual inspection of ERPs relative to the last fixation before the critical word (Fig. 2) indicates that the nonrelated condition engendered an N400 in comparison with the two other conditions. This impression was confirmed by the statistical analysis (250–400 ms), which revealed an effect of COND [$F(2,94) = 6.22$, $P < 0.01$]. Subsequent pairwise comparisons showed that UNPRED-NONREL differed significantly from PRED-ANT [$F(1,47) = 8.88$, $P < 0.01$] and UNPRED-REL [$F(1,47) = 8.90$, $P < 0.01$], which did not differ from one another ($F < 1$).

Relevant aspects of the EM record are shown in Table 1. In addition to the mean durations of the first fixation in the critical region and the last fixation before the critical region, the table lists the mean launch position of the last saccade before entering the critical region. This information is relevant because it has been suggested that apparent effects of parafoveal information on fixations before a critical word ('parafoveal-on-foveal effects') may result from the undershooting of saccades targeted at the critical word and, hence, from foveal processing [25].

Fig. 2



Grand average event-related potentials (ERPs) ($N=48$) time locked to the last fixation before the critical word. ERPs for the predicted antonym condition (ANT) are depicted by the solid line, whereas those for the unpredicted related (REL) and unpredicted nonrelated (NON) conditions are depicted by the dashed and dotted lines, respectively. Negativity is plotted upwards.

Table 1 Relevant eye movement results for this study

Condition	First fixation		Last fixation		Launch site	
	Mean	SD	Mean	SD	Mean	SD
PRED-ANT	213	63	183	57	7.7	5
UNPRED-REL	232	69	190	61	7.6	5
UNPRED-NONREL	229	70	186	53	7.8	5

First fixation on the critical region (in ms), last fixation before entering the critical region (in ms), and launch site of saccade targeting the critical region (in characters; relative to the first character of the critical region).

PRED-ANT, predicted antonym; SD, standard deviation; UNPRED-NONREL, unpredicted nonrelated; UNPRED-REL, unpredicted related.

Here, an explanation along these lines is ruled out by the fact that the mean launch site of the saccade to the critical word was almost eight characters to the left of it (i.e. too far removed for foveal processing). Mean launch sites did not differ across conditions ($F < 1$).

Statistical analyses (by participants and items) of the first fixation on the critical word showed a main effect of COND [$F_1(2,94) = 12.02$, $P < 0.0001$; $F_2(2,78) = 10.54$, $P < 0.0001$]. Pairwise comparisons revealed differences between PRED-ANT and UNPRED-REL [$F_1(1,47) = 22.45$, $P < 0.0001$; $F_2(1,39) = 16.72$, $P < 0.0001$] and PRED-ANT and UNPRED-NONREL [$F_1(1,47) = 12.83$, $P < 0.001$; $F_2(1,39) = 14.10$, $P < 0.001$], but not between UNPRED-REL and UNPRED-NONREL ($F < 1$). Hence, both nonantonym conditions showed longer first fixation times on the critical word than the antonym condition. For the last fixation before the critical region, there were no significant differences in fixation durations ($P > 0.27$).

Discussion

We have presented a concurrent EM and ERP study on the processing of antonym relations during natural reading. ERPs time locked to the first fixation on the critical word revealed an N400 for both unpredicted (nonantonym) conditions. This pattern was mirrored by the EM record, which showed longer first fixations for nonantonyms versus antonyms. Relative to the last fixation before the critical region, by contrast, ERPs showed an N400 for the unpredicted nonrelated condition in comparison with the unpredicted related and predicted antonym conditions. Here, fixation durations did not differ across conditions.

These results are significant for two reasons. First, they provide the first demonstration of a parafoveally induced N400 effect. Second, they support the hypothesis that N400 modulations owing to lexical activation spread and contextual prediction can be dissociated from one another. These two observations are closely intertwined, as the dissociation between the two types of N400 modulations was based on the fact that only spreading activation seems to be able to influence parafoveally induced effects, whereas contextual integration requires

foveal processing. Although both the unpredicted continuations showed an N400 at the position of the critical word in comparison with the PRED-ANT, ERPs at the last fixation before the critical word showed an N400 effect for the unpredicted and unrelated condition, in which the upcoming critical word was neither identical with the predicted continuation nor lexically related to it. As the N400 effect at the critical word was independent of the degree of relatedness to the expected continuation, it seems to reflect either the mismatch between the contextually induced prediction and the current input or the difficulty of semantic integration that arises from this mismatch. By contrast, the N400 effect at the last fixation before the critical word cannot be explained by predictability because both the nonantonym conditions were equally unpredictable. Rather, the fact that the related but unpredicted continuation patterned with the expected antonym continuation at this point provides converging support for the assumption that the preactivation of features of the expected target word also led to the activation of features of semantically related words (e.g. white/yellow).

The information engendering the N400 at the last fixation before the critical word must have been registered parafoveally, as the location of this fixation was sufficiently far removed from the critical word to rule out foveal processing (*c.f.* Table 1). In our view, orthographic feature matching provides the most parsimonious interpretation of this effect, as (i) there is robust evidence for the parafoveal uptake of orthographic [20–22] but not semantic information [19] and (i) the observation of a second N400 effect for the unrelated condition at the critical word suggests that it was not processed completely on the preceding fixation.

Interestingly, the dissociation between spreading activation (relatedness) and predictability that was observed in the ERPs did not manifest itself in the EM record. Although the prediction effect was observed in first fixations at the critical word, there was no effect of relatedness (neither at the critical position nor for the preceding fixation). Possibly, the parafoveal information came in too late to prolong the last fixation before the critical region: saccade planning requires approximately 150–180 ms and can no longer be terminated once the signal to move the eyes has been sent to the oculomotor system. An alternative explanation is that the eyes are an input-oriented processing system, which, in reading, is concerned with optimizing the information uptake of the neural language comprehension system (*c.f.* the reinforcement learning approach in [26]). Relatedness is not relevant for this optimization (or considerably less so than predictability), as only the PRED-ANT serves to complete the sentence in a meaningful way; both non-predicted continuations are equally nonsensical. Although an explanation along these lines is clearly speculative at

present, it provides an interesting and potentially fruitful new perspective on discrepancies between ERP and EM data on language comprehension [27]. It suggests that we may do well to consider, in future research, what motivation there is for the eyes to move as they do during reading, rather than assuming that their movements are directly coupled to the underlying neural processing mechanisms.

Conclusion

Our findings from natural reading show (i) that N400 effects can be induced by parafoveal information uptake and (ii) that N400 effects owing to spreading activation reflect a separable underlying process to N400 effects engendered by semantic predictability. These results corroborate the view that the N400 is best viewed as a component family rather than as a monolithic effect. The dissociability of the two processes is supported by the observation that only one of them (predictability) is observable in the EM record, a fact that we attribute to the differential function of the eyes and the brain in information processing.

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