



Research article

The priming of priming: Evidence that the N400 reflects context-dependent post-retrieval word integration in working memory



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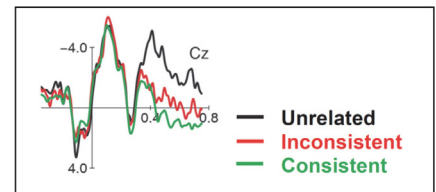
HIGHLIGHTS

- This ERP priming study shows online list effects of relational priming.
- Synonyms show more priming in a list with other synonyms.
- These effects were found despite a short SOA of 250 ms.
- N400 amplitude reductions at 400 ms overlap with ASA priming effects.
- The N400 reflects both spreading activation and post-lexical integration.

GRAPHICAL ABSTRACT

N400 priming effects:

1. Prediction (200–450 ms; WM+LTM)
2. ASA (300–500 ms; LTM)
3. Post-lexical integration (> 400 ms; WM)



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ABSTRACT

Which cognitive processes are reflected by the N400 in ERPs is still controversial. Various recent articles (Lau et al., 2008; Brouwer et al., 2012) have revived the idea that only lexical pre-activation processes (such as automatic spreading activation, ASA) are strongly supported, while post-lexical integrative processes are not. Challenging this view, the present ERP study replicates a behavioral study by McKoon and Ratcliff (1995) who demonstrated that a prime-target pair such as *finger – hand* shows stronger priming when a majority of other pairs in the list share the analogous semantic relationship (here: part-whole), even at short stimulus onset asynchronies (250 ms). We created lists with four different types of semantic relationship (synonyms, part-whole, category-member, and opposites) and compared priming for pairs in a consistent list with those in an inconsistent list as well as unrelated items. Highly significant N400 reductions were found for both relatedness priming (unrelated vs. inconsistent) and relational priming (inconsistent vs. consistent). These data are taken as strong evidence that N400 priming effects are not exclusively carried by ASA-like mechanisms during lexical retrieval but also include post-lexical integration in working memory. We link the present findings to a neurocomputational model for relational reasoning (Knowlton et al., 2012) and to recent discussions of context-dependent conceptual activations (Yee and Thompson-Schill, 2016).

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1. Introduction

The N400 component is a negative-going brain wave in event-related potentials (ERP) peaking at approximately 400 ms after

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stimulus presentation; it reflects the cost of lexical-semantic processing [1]. Its amplitude seems to decrease with increasing predictability of the target word (cloze probability) and, possibly, ease of integration into the context. This pattern holds both for sentence contexts and for priming studies in which a semantically related prime word facilitates the recognition and processing of a given target word (e.g., *doctor* – *nurse*) compared to an unrelated prime (e.g., *apple* – *nurse*). From a psycholinguistic perspective, semantic priming constitutes an important experimental paradigm, because it advances our understanding of word recognition and of the lexical-semantic network associated with the mental lexicon [2], but also because many recent approaches to sentence processing emphasize the role of expectancy based parsing [3,4]. From a neurolinguistic perspective, ERP priming studies can help clarify the specific neurocognitive processes underlying the N400 component, one of the most important physiological correlates of real-time language processing.

1.1. Priming mechanisms

In the behavioral priming literature, three different priming mechanisms have been proposed [2,5]: (1) Automatic spreading of activation (ASA) was the first such proposal [6] and assumes that semantically related ‘word nodes’ in long-term memory (LTM) are linked, such that activation of one node (e.g., *doctor*) spreads to related nodes (e.g., *nurse*) and pre-activates them, thereby facilitating subsequent lexical access. Given that ASA is viewed as fast, automatic and passive, semantic priming due to ASA is taken as mandatory at least at short stimulus onset asynchronies (SOAs) of less than 300 ms between prime and target, but it also seems to play a role at longer SOAs. (2) In contrast to ASA, the second priming mechanism is based on expectancy (prediction), is more controlled (i.e., subject to strategies), and usually gains influence at longer SOAs while it tends to be absent at short ones. Predicted target words are assumed to be active in working memory (WM) [7], such that this mechanism does not exclusively operate within the semantic network in LTM, although the corresponding word nodes in the network may receive an additional (secondary) activation boost beyond ASA. (3) The third, and perhaps least understood, mechanism is semantic matching or semantic integration, which also takes place in WM, but only after both prime and target words have already been accessed (hence the term ‘post-lexical integration’). For example, it explains the backward priming phenomenon, i.e., faster response times for word pairs in which the second stimulus primes the first one, but not *vice versa* (e.g., *box* – *lunch*). Compared to the other two mechanisms, semantic matching is most likely to inherently provide some information about the type of semantic relationship between prime and target (e.g., synonyms vs. part-whole relationships).

1.2. Priming effects on the N400

To what extent the three proposed priming mechanisms contribute to N400 amplitude reduction has been controversial for more than twenty years. Automatic priming via ASA had been generally assumed, until Brown and Hagoort [8] reported that masked priming at short SOAs resulted in behavioral priming effects, but not in a reduction of the N400 amplitude. Similarly, Chwilla and colleagues [9] found that performing physical letter case discrimination during reading completely eliminated N400 priming effects even between strongly related prime-target pairs. The authors interpreted this finding as evidence that post-lexical semantic integration (and not ASA) underlies N400 priming effects and was successfully prevented by their task. Alternatively, the nature of their task may not have promoted semantic network activation, thereby preventing ASA from taking place. Indeed, other

researchers maintain that N400 priming effects are primarily (or even exclusively) driven by ASA. For example, Deacon and colleagues [10] and Kiefer [11] observed N400 priming effects with very short SOAs (<70 ms) in a masked priming paradigm, suggesting that the underlying mechanism must have been ASA. Similarly, Brouwer and colleagues [12] suggest that the N400 is exclusively linked to lexical retrieval, while (post-lexical) semantic integration is supposed to be reflected by the P600 component. Moreover, as neuroimaging studies found consistent priming effects for the brain structure assumed to house the lexical semantic network (e.g., the posterior part of the middle temporal gyrus, pMTG), the influential review paper by Lau and colleagues [13] argued that retrieval-related processes including ASA are likely to always contribute to N400 priming effects, irrespective of SOA duration. In contrast, they emphasize that the data reviewed “do not provide any conclusive evidence to support the integration account of the N400 effect” [p. 928], although they acknowledge this possibility cannot be ruled out by the data. Turning to future research, they suggest that “paradigms that selectively manipulate integrative processes at different levels of representation [...] will be needed” [p. 929].

A more recent ERP article by Lau et al. [7] extended the 2008 article by clarifying that activation-based N400 effects during initial word retrieval in LTM may also include prediction-based priming. The authors manipulated the proportion of semantically related prime-target pairs (10% versus 50%) in two experimental blocks, where the higher proportion should encourage participants to use strategies to predict the target word. Their 600 ms SOA was long enough for participants to profit from strategies. Indeed, while the low-proportion condition only showed the classical (presumably ASA-driven) N400 reduction between 300 and 500 ms, in the high-proportion condition an additional – and earlier – ERP priming effect was found between 200 and 450 ms. The latter also reduced the N400 amplitude and was attributed to higher target predictability. The authors argue that while WM-mediated contextual prediction mechanisms go beyond passive spreading activation (ASA), ultimately both types of priming “facilitate lexical access in exactly the same way and have the same neural effects in temporal cortex” (Ellen Lau, personal communication, February 2017), thereby reducing the N400. Thus, even though the observed prediction effects are said to involve WM, they do not seem to shed any light on the “integration account of N400 effects”.

1.3. Present study

In order to fill this gap, our current ERP study aims at investigating the specific contribution of post-lexical semantic matching to N400 effects. The design was inspired by McKoon and Ratcliff’s behavioral study [14], which tested various semantically related prime-target pair lists. Each list was dominated by a specific kind of semantic relationship (e.g., one list with synonyms such as *far* – *distant* or *room* – *space*, another list with part-whole relationships such as *finger* – *hand* or *blade* – *knife*, and yet other lists with opposites, category-member relationships, etc.). Importantly, they moved some of these highly related prime-target pairs from their original list into another list, e.g., a few synonyms into the part-whole list (and vice versa), and found that priming effects on these items were dramatically reduced or even absent. In other words, *far* seems to prime its synonym *distant* more strongly if a majority of other prime-target pairs in the list are also synonyms. Such a contextual effect is very difficult to explain in terms of ASA for two reasons: First, ASA priming relies on node (word or concept) pre-activation, not on the links connecting them. Secondly, neither the activation levels of a prime-target pair in LTM nor the semantic links between them should change just because *other* words being processed happen to have similar links between them. With long SOAs, McKoon and Ratcliff’s contextual list effect could possibly be

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