N400 effects for category exemplars primed by category labels

Christina Bermeitinger

University of Hildesheim, Germany

Christian Frings

Dirk Wentura

Saarland University, Germany

Abstract. We analyzed the ERP correlates of a category priming task. In particular, participants had to judge the orthography of a target word that followed a shortly presented but clearly visible prime word. Primes and targets had a superordinate-subordinate relation (FLOWER-tulip). The behavioral effects corresponded to the typical finding – participants reacted faster to targets which were preceded by related primes (e.g., FLOWER-tulip) compared to unrelated primes (e.g., BIRD-tulip). Accordingly, the ERPs showed that unrelated prime-target trials elicited more negative going waveforms at central recording sites as compared to related trials in the N400 time window. The behavioral and the N400 priming effect were significantly correlated, thereby indicating the functional character of the ERP correlate.

Keywords: semantic priming; category priming; superordinate-subordinate relation; category-exemplar relation; event-related potentials; N400

Within semantic memory, humans represent facts and knowledge about objects or concepts in a symbolic manner without referring to a particular spatiotemporal experience. In 20th century, philosophy, linguistics, computer sciences, science of education and psychology have been engaged in the study of semantic memory (e.g., Rogers & McClelland, 2004). Yet, it is nevertheless a prevailing theme and probably one of the most debated topics of contemporary neuropsychology (e.g., Canessa et al., 2008; Laiacona, Barbarotto, & Capitani, 2006; McMullen & Purdy, 2006).

Authors' note: Correspondence concerning this report should be addressed to Christina Bermeitinger, University of Hildesheim, Department of Psychology, Marienburger Platz 22, D – 31141 Hildesheim, Germany, or via email to bermeitinger@uni-hildesheim.de.

The research reported here was supported by a grant of the Deutsche Forschungsgemeinschaft to Dirk Wentura and Christian Frings (WE 2284/5-3).

A classic task in cognitive psychology for studying the semantic memory is the semantic priming paradigm (for reviews see Neely, 1991; McNamara, 2005). The most commonly used version of this paradigm is as follows: a word-stimulus (i.e., the prime) is presented for a few hundred milliseconds and is followed by a second word-stimulus (i.e., the target), which is typically presented until participants respond. Participants pronounce the target or categorize it (for example, as a legal word or a non-word; i.e., the lexical decision task) as quickly and accurately as possible. The typical finding is that responses are faster if primes and targets are semantically related (e.g., doctor-nurse) compared to semantically un-related prime-target pairs (e.g., car-nurse). When the stimulus onset asynchrony (SOA) between prime and target is short, interpretations of the semantic priming effect in terms of strategic or executive abilities of participants can be excluded (Neely, 1977). In turn, the semantic priming effect is usually interpreted in terms of automatic memory processes.

A closer look at the semantic priming literature, however, reveals that researchers use very different relationships between prime and target (for an overview see, e.g., Hutchison, 2003; Lucas, 2000). Very often, an associative relation (e.g., bread-butter) is used. Here, the priming effect reflects environmental contingencies insofar as the prime is often followed by the target in ordinary language. However, more important for studying the organization of semantic memory seems the use of taxonomical relationships like category coordinates (e.g., rose-tulip), synonyms (e.g., afraid-scared), antonyms (e.g., day-night), superordinate-subordinate relations or category-exemplar relations (e.g., flower-tulip), perceptual properties (e.g., canary-yellow), functional properties (e.g., broom-sweep), or script relations (e.g., orchard-apple). These semantic priming effects (in the narrow sense) were all studied, although less extensively compared to associative relations (see, e.g., Hutchison, 2003, for a review).

The importance to study these kinds of relationship becomes clearer if we remind ourselves about theoretical explanations of the priming effect. The classic approach is the assumption of spreading activation in a semantic network (Collins & Loftus, 1975). Note, that originally the semantic networks were an attempt to conceptualize the hierarchical structure of semantic knowledge and not an attempt to conceptualize arbitrary contingencies in ordinary language. Thus, although associative effects can be explained by spreading activation in a network of associations, we can state that originally a theoretical conceptualisation of *semantic* relations was linked to the semantic priming effect (in the narrow sense). A prominent contemporary attempt to explain semantic priming effects are distributed network models (e.g., Masson, 1999; Plaut, 1995). Such models assume that every concept is represented by a set of distributed features which are interconnected via weighted connections. Thus, a specific concept is represented by a specific stable pattern (or vector) of these weighted connections (e.g., Rogers & McClelland, 2004). Facilitation due to semantic relatedness is explained in terms of the transition time between two stable patterns. For example, the transition from the internal representation of the superordinate concept FLOWER to a subordinate concept like TULIP is fast since the patterns of flower and tulip share several features. Again, we see a direct link between a theoretical conceptualisation of how semantic relations are encoded in semantic memory to the semantic priming effect. [1]

The common correlate of the behavioral semantic priming effect is the so-called N400 priming effect, that is, a (relatively) more negative going ERP wave for unrelated compared to related targets with a peak at approximately 400 ms after target onset (for reviews see e.g., Kutas & Federmeier, 2000; Osterhout & Holcomb, 1995; Pritchard, Shappell, & Brandt, 1991). There is abundant evidence for N400 priming effects with associatively related prime-target pairs (e.g., Brown, Hagoort, & Chwilla, 2000; Catena, Houghton, Valdés, & Fuentes, 2009; Gomes, Ritter, Tartter, Vaughan, & Rosen, 1997; Hill, Ott, & Weisbrod, 2005; Holcomb, 1988; Kiang, Kutas, Light, & Braff, 2008; Radeau, Besson, Fonteneau, & Castro, 1998; for N400 evidence with subliminal presented primes see, e.g., Grossi, 2006; Deacon, Hewitt, Yang, & Nagata, 2000; Kiefer & Brendel, 2006; for N400 evidence for indirect semantic priming see, e.g., Kiefer, Weisbrod, Kern, Maier, & Spitzer, 1998; Kreher, Holcomb, & Kuperberg, 2006; Weisbrod, Winkler, Maier, Hill, Rösch-Ely, Kiefer, & Spitzer, 1999) whereas only a minor set of studies used categorically related prime-target pairs (e.g., Landi & Perfetti, 2007). Moreover, these studies using categorically related prime-target pairs most often used non-canonical variants of the semantic priming paradigm. In detail, in these studies, bilingual priming was investigated (e.g., Kotz, 2001), a lateralized stimulus presentation was used (e.g., Bouaffre & Faïta-Ainseba, 2007; Hagoort, Brown, & Swaab, 1996; Khateb, Michel, Pegna, Thut, Landis, & Annoni, 2001), participants had to judge whether two consecutive stimuli belong to the same semantic category (Schumacher, Wirth, Perrig, Strik, & Koenig, 2009), or the material was described only insufficiently (e.g., Koivisto & Revonsuo, 2001). Additionally, until now, we had found five studies (Deacon, Uhm, Ritter, Hewitt, & Dynowska, 1999; Heinze, Muente, & Kutas, 1998; Iragui, Kutas, & Salmon, 1996; Kiefer, 2001; Stenberg, Lindgren, Johansson, Olsson, & Rosén, 2000) which explicitly investigated superordinate-subordinate relations (e.g., bird-crow). However, all studies

[1] Of course, we might explain associative priming effects by assuming that the cognitive system has learned that a specific target pattern often follows after a specific prime pattern (e.g., bread-butter).

used non-canonical variants of semantic priming, too. That is, for example, subjects were told to try to use the prime information to predict the (category of the) target and the target had to be semantically categorized (Deacon et al., 1999) or participants were requested to decide whether the target was a member of the previously presented category or not (Heinze et al., 1998; Iragui et al., 1996; Kiefer, 2001; Stenberg et al., 2000). Additionally, Iragui et al. (1996) used spoken context phrases including the category label as primes and after the very long interval of about 1 second, the target appeared on screen and Stenberg et al. (2000) used masked target words and a very long SOA (more than 1500 ms) as well. Overall, the N400 was more negative when the second word was categorically unrelated to the first as compared to a trial in which both words were related. In addition, Deacon et al. (1999) showed that this effect was not strategic in nature. Kiefer (2001) found differences in the N400 effect for natural vs. artifactual categories, Heinze et al. (1998) found the N400 effect more pronounced for typical than for atypical members, and Stenberg et al. (2000) found it more pronounced for identified target words compared to unidentified target words.

However, it remains unclear to what extent these studies can be compared to 'classic' semantic priming studies. Note, that (for example) in a comparison task participants would likely process the first stimulus in a quite different way compared to the prime in a standard semantic priming task. In the comparison task, participants must attend to and fully analyze the first stimulus and thereafter hold in working memory the category to which the stimulus belongs (or the stimulus itself). In contrast, in the semantic priming task participants are instructed to ignore the prime and they will notice during the experiment that the prime and the target response are uncorrelated.

These differences cannot be underrated because the interpretation of the N400 effect is still under discussion. Some researchers argue that the N400 reflects the easiness with which information can be integrated into a previously created representation after the meaning of the word is already accessed (e.g., Holcomb, 1993; Rugg, 1990). This post-lexical interpretation is in contrast to interpretations that assume that the N400 is (also) related to the processing required to activate a word's meaning (for review see e.g., Kutas & Federmeier, 2000; Osterhout & Holcomb, 1995; see also e.g., Bermeitinger, Frings, & Wentura, 2008; Heil, Rolke, & Pecchinenda, 2004).

In conclusion, it is still unclear whether an N400 effect with superordinate-subordinate relationships in a standard semantic priming experiment can be observed, although we might acknowledge results from other tasks as first tentative evidence. Thus, the aim of the present study was to investigate for the first time the N400 semantic priming effect in a more conventional semantic priming task using superordinate-subordinate prime-target pairs as they appear in common language (that is, in common language, category labels and category coordinates are most often associated, too). With respect to recent results of (neuro-)psychological studies (e.g., Bermeitinger, Wentura, & Frings, 2008; Kiefer, 2001; Laws, Leeson, & Gale 2002; Wurm, Whitman, Seaman, Hill, & Ulstad, 2007) and reviews (e.g., Capitani, Laiacona, Mahon, & Caramazza, 2003; Forde & Humphreys, 1999; Martin & Chao, 2001) which reported differences between natural (i.e., biological) and artifactual (i.e., man-made) categories, we used both types of categories.

Method

Participants

Twenty-two students (11 female, 11 male) from Saarland University participated in the experiment. The median age was 22 years (ranging from 20 to 30 years). The data of two further participants were discarded due to their high mean error rate (more than 30% errors) or due to responding also to the prime's orthography. The data recording of one further participant has not been completed due to an equipment error. This participant was also excluded from the analysis. All participants were native speakers of German and had normal or corrected-to-normal vision. All subjects were right-handed and none of them reported any neurological impairment. They gave written informed consent prior to their inclusion in the study and they were paid 16 € for their participation.

Design

Essentially, a 2 x 3 design was used. The first factor was category type (natural versus artifactual) and the second factor was priming condition (related, unrelated, neutral). Both factors were varied within-participants. The neutral condition was only included in order to lower the overall rate of related prime-target pairs and was not further analyzed. In addition, target-orthography (word versus non-word) was varied within-participants and orthogonally to the other factors. However, in accordance with other lexical decision studies, analyses were focused on word trials.

Material
The material was exactly the same as reported in Bermeitinger, Wentura et al. (2008). Essentially, we used four natural category labels – GEMÜSE (vegetables), FISCH (fish), GEWÜRZE (spices), and RAUBTIER (predator) – and four artifactual category labels – WERKZEUG (tools), KLEIDUNG (clothing), MÖBEL (furniture), and GESCHIRR (dishes) – as primes (additionally, there were neutral primes which were introduced to lower the overall proportion of related trials – the neutral primes consisted of seven randomly generated capital letters and these trials were not analyzed). Six category exemplars from each category served as target words. Pronounceable non-words were created by changing one letter of each target word (as usual for semantic priming, only trials with word targets were analyzed). Natural and artifactual targets did not differ with respect to their mean association frequency (i.e., dominance), mean length, and mean word frequency (all ps > .05). The size (i.e., the number of category coordinates which were listed for a category, see for instance Mannhaupt, 1983) of the eight categories were comparable. All stimuli were presented in light grey on a black screen and were approximately 0.5 cm (0.48° visual angle) in height.

Procedure
Participants were individually tested in an electrically shielded and sound-attenuated chamber. The experiment was run using the E-Prime software (version 1.1) with a standard PC and a 17'' CRT monitor. Viewing distance was about 60 cm. Instructions were given on the CRT screen. Participants were told that words belonging to the categories vegetables, fish, spices, and predator or belonging to the categories tools, clothing, furniture, and dishes would be presented on the screen, yet that some of these words would be written with a spelling mistake. They were requested to quickly and accurately categorize each word with regard to orthography (by pressing the right/left key with their right/left index finger for correctly/ incorrectly spelled words, respectively). The sequence of each trial was as follows: first a fixation stimulus (+) appeared at the center of the screen for 500 ms. It was followed by the prime, which was presented for 150 ms. Primes were written in capital letters (font: Fixedsys). The *related* prime was always the category name that corresponded to the target. The *unrelated* prime was always FISCH (fish) for vegetables exemplars, GEMÜSE (vegetables) for fish exemplars, RAUBTIER (predator) for spices exemplars, GEWÜRZE (spices) for predator exemplars, KLEIDUNG (clothing) for tools exemplars, WERKZEUG (tools) for clothing exemplars, GESCHIRR (dishes) for furniture exemplars, and MÖBEL (furniture) for dishes exemplars. The prime was followed by a blank screen for 150 ms (thus, the stimulus-onset asynchrony was 300 ms). Then the target appeared and remained on the screen for 800 ms. In the case of an erroneous response, an error message was given on the screen until a further button press was made. In the case of a response slower than 800 ms, a feedback message was given reminding participants of faster responding. The intertrial interval with a blank screen was 1000 ms. The factor category type (natural vs. artifactual) was varied block-wise, with block order counterbalanced across participants. Each of the two blocks comprised three sub-blocks with 48 trials each (16 related, 16 unrelated, and 16 neutral prime-target pairs; half of the trials with non-word targets). Over the course of a block (including 3 experimental sub-blocks with 48 trials each), each target appeared once in each of the three priming conditions, thus each prime-target pair appeared exactly one time over the course of the experimental trials. Within a block, each target was presented in one of the three priming conditions which resulted overall in 144 trials for each block. The sequence of priming conditions for a given target was determined by a Latin-square design (i.e., sequence of targets and conditions was balanced over participants). There was a short pause after every 24 trials. Before each block, there was a practice phase with 48 trials.

Electroencephalogram (EEG) Recording and Analyses
EEG activity was recorded continuously from 60 Ag/AgCl electrodes mounted in a preconfigured elastic cap (Easycap, Herrsching, Germany), arranged according to the extended international 10-20 system (American Electro-encephalographic Society, 1994) with a

sampling rate of 500 Hz. Impedances for all electrodes were kept below 10 kΩ. Signals were referenced on-line to the left mastoid electrode. For further analysis, electrodes were re-referenced off-line to linked mastoids. Two electrodes located medially to the right eye, one above and one below, were used to monitor vertical eye movements. Electrodes placed at the outer canthi of the eyes measured horizontal eye movements. Vertical and horizontal ocular artifacts were monitored and corrected off-line (Gratton, Coles, & Donchin, 1983).

Data were digitally filtered with Butterworth Zero Phase Filters (low cutoff: 0.1 Hz; high cutoff: 30 Hz). ERPs were obtained by averaging EEG recordings time-locked to target presentation from 100 ms prior to 900 ms after target onset. Trials with false responses or with reaction times below 200 ms or above 1500 ms or the individual Tukey criterion (see below) were rejected. Trials containing artifacts (maximum amplitude in the recording epoch ±100 µV; maximum difference between two sampling points 50 µV; maximum difference between any two sampling points within an epoch 150 µV). With respect to this artifact correction and the above response criteria, the included trials of the unrelated and the related conditions of artifactual and natural categories did not differ (artifactual categories: $M = 86.4\%$, $SD = 10.5\%$ and $M = 85.8\%$, $SD = 10.5\%$, for the related and the unrelated condition, respectively; mean difference: $M = 0.6$, $SE = 1.9$, $t(21) = 0.29$, $p = .77$; natural categories: $M = 87.3\%$, $SD = 14.3\%$ and $M = 86.0\%$, $SD = 12.9\%$, for the related and the unrelated condition, respectively; mean difference: $M = 1.3$, $SE = 1.9$, $t(21) = 0.67$, $p = .50$).

Data were baseline-corrected with respect to the 100 ms pre-target interval. Furthermore, ERPs were averaged for the related and unrelated condition. Following suggestions by Dien and Santuzzi (2005) statistical analyses were performed by means of MANOVA. Statistical analysis of the ERP data focused on the N400 time-window between 300 and 500 using nine regions of interest (ROI): frontal-left (AF3, F7, F5, F3), frontal-midline (Fpz, F1, Fz, F2), frontal-right (AF4, F8, F6, F4), central-left (FC5, FC3, C5, C3, CP5, CP3), central-midline (FCz, C1, Cz, C2, CPz), central-right (FC6, FC4, C6, C4, CP6, CP4), parietal-left (P7, P5, P3, PO7, PO3, O1), parietal-midline (P1, Pz, P2, POz, O2), parietal-right (P8, P6, P4, PO8, PO4, O2). The resulting factors in the MANOVA were category type, side (left, midline, right), and region site (frontal, central, parietal scalp). The time-window and the regions of interest were selected based on relevant literature (e.g., Brown et al., 2000; Rossell, Price, & Nobre, 2003; Sim & Kiefer, 2005).

Results

Unless otherwise noted, all effects referred to as statistically significant throughout the text are associated with *p*-values of at least .05, two-tailed.

Behavioral effects

Mean reaction times (RTs) were derived from correct responses to word trials. The mean error rate was 6.8%. RTs that were 1.5 interquartile ranges above the third quartile with respect to the individual distribution per category type (Tukey, 1977), were above 1500 ms, or were below 200 ms were discarded (2.2% of all trials). Mean RTs and mean error rates for word targets are shown in Table 1.

Table 1. Mean response times (in ms) and error rates (in %) of word trials as a function of priming condition and category type (standard deviation in parentheses); priming effects (standard error in parentheses) are the differences between unrelated and related trials

	Priming Condition			Priming Effect
	Related	Unrelated	Neutral	
Reaction Times				
	528 (34.4)	541 (32.6)	535 (32.2)	13 (3.6)
Error Rates				
	7.3 (5.8)	8.4 (6.7)	4.8 (4.1)	1.1 (0.8)

Mean reaction times of the unrelated and the related word targets were subjected to a 2 (category type: natural versus artifactual) x 2 (priming condition: related versus unrelated) MANOVA. The main effect of category type was significant, $F(1, 21) = 17.84$, $p < .001$, $\eta_p^2 = .46$, indicating faster reactions to artifactual than natural targets. Most important, there was a significant main effect of priming condition, $F(1, 21) = 13.23$, $p = .002$, $\eta_p^2 = .39$, indicating that participants reacted faster to related than to unrelated targets. The interaction effect was not

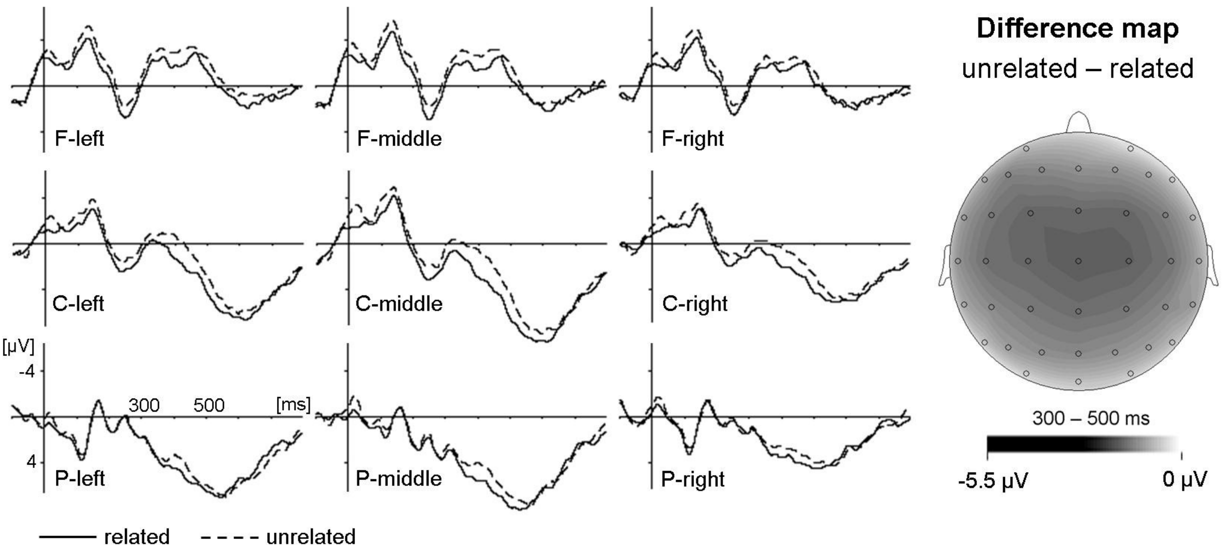

Figure 1
Grand-averaged ERP waveforms as a function of prime-target relationship (related = continuous lines, unrelated = dashed lines). For the figure, the waveforms were filtered at 9 Hz. On the right side, the difference map for the N400 effect is shown.

significant ($F < 1$). A comparable MANOVA on priming differences for arcsine transformed error rates revealed no significant effects, all Fs < 2.6, all ps > .12.

Electrophysiological Results
Mean waveforms are shown in Figure 1. The 2 (category type) x 2 (priming condition) x 3 (side: left, midline, right) x 3 (region site: frontal, central, parietal) MANOVA on mean amplitudes in the N400 time-window between 300 and 500 ms revealed a significant main effect for the factor priming condition, $F(1, 21) = 11.29$, $p < .01$, $\eta_p^2 = .35$, indicating overall a more negative going wave for unrelated compared to related targets. Additionally, there was a significant interaction of priming condition and region site, $F(2, 20) = 9.39$, $p = .001$, $\eta_p^2 = .48$. Post-hoc tests revealed a significant (according to the Bonferroni-Holm adjusted α-level) N400 effect only at the central region site, $t(21) = 3.86$, $p < .001$, but no significant N400 effect at frontal and parietal regions ($t(21) = 1.97$, $p = .06$ and $t(21) = 1.80$, $p = .09$, respectively). The interaction of priming condition and side was also significant, $F(2, 20) = 4.27$, $p < .05$, $\eta_p^2 = .30$. Post-hoc tests revealed significant (according to the Bonferroni-Holm adjusted α-level) N400 effects at all three sides (left: $t(21) = 2.88$, $p = .009$, midline: $t(21) = 3.61$, $p = .002$, right: $t(21) = 3.03$, $p = .006$), only the mean priming differences between midline and right side differed significantly ($t(21) = 2.94$, $p = .008$, with a larger priming effect at midline regions; the other differences were not significant, both ps > .13). Additionally, there was a significant interaction of category type and region site, $F(2, 20) = 4.61$, $p < .05$, $\eta_p^2 = .32$, indicating the largest difference between natural and artifactual waveforms at central region sites; however, when each region site was separately analyzed, the difference between natural and artifactual waveforms was never significant (all ps < .18). No other main or interaction effect including the factors category type and/or priming condition reached significance, all ps > .21.

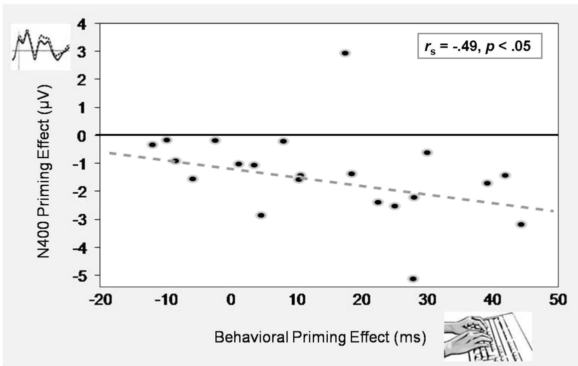

Figure 2
Correlation and individual distribution of the behavioral priming effect (mean RT to unrelated targets minus mean RT to related targets; in ms) and the N400 priming effect (mean voltage to unrelated targets minus mean voltage to related targets in the time-window between 300 and 500 ms after target-onset at the central-midline ROI; in µV). Note, the larger the N400 priming effect is, the more negative the difference is. Therefore, the negative correlation means that the larger the behavioral priming effect is, the larger the N400 priming effect is.

Finally, we correlated the behavioral priming effect with the N400 priming effect at the central-midline ROI (note that at this ROI the largest N400 priming effect emerged compared to all other ROIs). In fact, both priming effects were significantly correlated at $r_s = -.49$, $p < .05$ (see Figure 2). The larger the behavioral priming effect was, the larger was the N400 priming effect thereby indicating the functional character of the ERP correlate.

Discussion

We investigated the behavioral and the N400 priming effect in a semantic priming task with a superordinate-subordinate relation between the prime and the target. The data showed a behavioral priming effect which was accompanied by a significant N400 effect; both priming effects were not moderated by the type of category (artifactual versus natural). The N400 priming effect was largest at the central electrode site and the midline side. In addition, the N400 effect was significantly correlated with the semantic priming effect in response times, hereby indicating that the N400 taps the process that contributes to the behavioral priming effect.

There were slight differences between the waveforms of natural and artifactual targets which resulted in an interaction of category type and region site. This result could be related to the findings of Kiefer (2001) who found also differences between artifactual and natural categories. However, in slight contrast to Kiefer, first, we found the largest difference between artifactual and natural waveforms at central electrodes but no influence of the factor side (i.e., hemisphere) and second, the priming effects found in the present experiment were not moderated by the category type. Principally, this difference in the topography does not preclude the same neuronal generators in both cases (e.g., Alain, Achim, & Woods, 1999; Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001; Shibasaki, 2008). In particular, with the problem of source localisation in the EEG in mind (e.g., Osterhout & Holcomb, 1995), any definite conclusion concerning the different topographies may require fMRI data. However, cautiously, our finding could be interpreted as evidence that the processes or brain regions related to classic semantic priming (see below) do not differ between artifactual and natural categories, but the processes or brain regions required for the direct comparison of a target and the previous presented category might differ for natural and artifactual categories.

The present finding is especially important for closing a gap in the literature. It is the first time that an N400 was observed in parallel to a canonical version of a semantic priming effect based on superordinate-subordinate relationships. Interestingly, we found an interaction of priming condition and region site; the difference between the related condition and the unrelated condition was significant only at central electrodes. In turn, at the central electrode site, the N400 was clearly obvious.

One caveat might be seen in the repeated presentation of primes and targets. However, a study of Frenck-Mestre, Besson and Pynte (1997) investigated the N400 in dependence of repetition of category labels and exemplars. Here, they found equal sized N400 effects irrespective of the amount of repetition. Therefore, an interpretation of our results in terms of repetition of primes and targets seems inadequate.

In general, the results match assumptions of distributed network models of semantic priming (e.g., Masson, 1999). These models assume that semantic priming effects arise due to faster transformations of the pattern representing the prime to the pattern representing the target. However, distributed network models assume slightly different processes for category and associative priming. In the case of category priming, the transformation from the prime to the target pattern is faster when both patterns share many common features. Thus, when both concepts are related, many features of the target pattern are already activated due to the prime pattern resulting in faster identification of the target stimulus. In contrast, in the case of associative priming, the transformation in related trials is faster since the cognitive system has learned that a specific concept (here the target) usually follows another specific concept (i.e., the prime) and hence the generation of the target pattern is facilitated. In principle, associative priming is assumed to occur due to some kind of learning processes (e.g., Masson, 1999).

With respect to these theoretical points regarding slight differences between category priming and associative priming, one could note that the topography of the N400 effect in our data was somewhat different to the typical topography of the N400 in priming studies using exclusively associatively related prime-target pairs. Typically, with associative priming, the N400 priming effect is most pronounced at central and parietal sites (e.g., Brown et al., 2000; Chwilla, Hagoort, & Brown, 1998; Kiang et al., 2008). In contrast, with a superordinate-subordinate relation, we found a significant N400 priming effect most pronounced only at central electrodes but no significant N400 effect at parietal electrodes. Again, the difference in the topography does not preclude the same neuronal generators in both cases (see above). However, with respect to the existing body of evidence on the N400, one may speculate on the existence of two different processes both reflected in a N400 component but with different topographies. The N400 was originally interpreted as purely reflecting the integration process of the target word into a context (for example the prime-context; e.g., Holcomb, 1993; Rugg, 1990). Yet, contemporary accounts on the N400 (e.g., Bermeitinger, Frings et al., 2008; Kutas & Federmeier, 2000) argued that the N400 can reflect the activation of a word's meaning instead of (or in addition to) the integration of the target word into the previous context. Interestingly, there is some tentative evidence that both processes elicit N400 effects with different topographies. The activation of a words' meaning seems to be most prominent at parietal sides (Bermeitinger, Frings et al. 2008; Deacon et al., 1999; Heil et al., 2004; Holcomb, Reder, Misra, & Grainger, 2005) whereas the integration process seems to be stronger at frontal and fronto-central recording sides (e.g., Willems, Özyürek, & Hagoort, 2008). If we assume that differences in the topography really reflect two different mechanisms, we might speculate that pure (supraliminal) associative priming may be based on integration *and* activation processes whereas the (supraliminal) category priming effect seems to be based more on the integration process. Thus, probably, the more association between prime and target, the more the effect would be at parietal sites.

Concerning the debate on the N400 effect, we can add several points to the ongoing debate on the character of the N400 effect. Of course, with respect to the idea presented above, we may speculate that different topographies in different studies might yield evidence for two processes adding to the N400 effect and further that these processes can be separated by topographical analyses. Additionally, we found a significant correlation between two effects or constructs, i.e. the behavioral performance and the N400 effect. Thus, our data confirm and enhance the evidence that the N400 priming effect is a functional correlate of behavioral priming in general. This correlation of individual behavioral performance and the N400 effect fosters the view that the N400 really is related to semantic processes and that individual differences in N400 effects are not simply due to artifactual effects (as for example skull thickness), but reflect variability in cognitive processing occurring during the execution of the experimental task. Thus, potentially, the N400 could be used for a deeper understanding of the nature of individual differences in semantic processing (for the logic of individual differences to constrain cognitive theories see also Vogel & Awh, 2008). However, further work is needed to explore whether these individual differences are due to underlying constructs as different personality variables (e.g., intelligence), or due to intraindividual changes across time.

In conclusion, by using a superordinate-subordinate relationship between primes and targets, we were the first ones to ever observe a N400 effect for this kind of priming task. This is by all means a noteworthy result since for the claim that the N400 taps the processes contributing to behavioral semantic priming – also confirmed by the correlation between behavioral and electrophysiological effects – , the N400 priming effect should be found in all conditions in which the behavioral effect is usually observed.

References

Alain, C., Achim, A., & Woods, D. L. (1999). Separate memory-related processing for auditory frequency and patterns. *Psychophysiology*, *36,* 737-744.

Bermeitinger, C., Frings, C., & Wentura, D. (2008). Reversing the N400: Event-related potentials of a negative semantic priming effect. *NeuroReport*, *19*, 1479-1482.

Bermeitinger, C., Wentura, D., & Frings, C. (2008). Nature and facts about natural and artifactual categories: Sex differences in the semantic priming paradigm. *Brain and Language*, *106*, 153-163.

Bouaffre, S., & Faïta-Ainseba, F. (2007). Hemispheric differences in the time-course of semantic priming processes: Evidence from event-related potentials (ERPs). *Brain and Cognition*, *63*, 123-135.

Brown, C. M., Hagoort, P., & Chwilla, D. J. (2000). An event-related brain potential analysis of visual word priming effects. *Brain and Language, 73*, 158-190.

Canessa, N., Borgo, F., Cappa, S. F., Perani, D., Falini, A., Buccino, G., et al. (2008). The different neural correlates of action and functional knowledge in semantic memory: An fMRI study. *Cerebral Cortex*, *18*, 740-751.

Capitani, E., Laiacona, M., Mahon, B., & Caramazza, A. (2003). What are the facts of semantic category-specific deficits? A critical review of the clinical evidence. *Cognitive Neuropsychology*, *20*, 213-261.
Catena, A., Houghton, G., Valdés, B., & Fuentes, L. J. (2009). Unmasking word processing with ERPs: Two novel linear techniques for the estimation of temporally overlapped waveforms. *Brain Topography*, *22*, 60-71.
Chwilla, D. J., Hagoort, P., & Brown, C. M. (1998). The mechanism underlying backward priming in a lexical decision task: Spreading activation versus semantic matching. *Quarterly Journal of Experimental Psychology*, *51A*, 531-560.
Collins, A. M., & Loftus, E. F. (1975). A spreading-activation theory of semantic processing. *Psychological Review*, *82*, 407-428.
Deacon, D., Uhm, T. J., Ritter, W., Hewitt, S., & Dynowska, A. (1999). The lifetime of automatic semantic priming effects may exceed two seconds. *Cognitive Brain Research*, *7*, 465-472.
Deacon, D., Hewitt, S., Yang, C., & Nagata, M. (2000). Event-related potential indices of semantic priming using masked and unmasked words: Evidence that the N400 does not reflect a post-lexical process. *Cognitive Brain Research*, *9*, 137-146.
Forde, E. M. E., & Humphreys, G. W. (1999). Category-specific recognition impairments: A review of important case studies and influential theories. *Aphasiology*, *13*, 169-193.
Frenck-Mestre, C., Besson, M., & Pynte, J. (1997). Finding the locus of semantic satiation: An electrophysiological attempt. *Brain and Language*, *57*, 406-422.
Gomes, H., Ritter, W., Tartter, V. C., Vaughan, H. G., & Rosen, J. J. (1997). Lexical processing of visually and auditorily presented nouns and verbs: Evidence from reaction time and N400 priming data. *Cognitive Brain Research*, *6*, 121-134.
Gratton, G., Coles, M. G. H., & Donchin, E. (1983). A new method for off-line removal of ocular artefact. *Electroencephalography and Clinical Neurophysiology*, *55*, 468-484.
Grossi, G. (2006). Relatedness proportion effects on masked associative priming: An ERP study. *Psychophysiology*, *43*, 21-30.
Hagoort, P., Brown, C. M., & Swaab, T. Y. (1996). Lexical-semantic event-related potential effects in patients with left hemisphere lesions and aphasia, and patients with right hemisphere lesions without aphasia. *Brain*, *119*, 627-649.
Heil, M., Rolke, B., & Pecchinenda, A. (2004). Automatic semantic activation is no myth: Semantic context effects on the N400 in the letter-search task in the absence of response time effects. *Psychological Science*, *15*, 852-857.
Heinze, H. J., Muente, T. F., & Kutas, M. (1998). Context effects in a category verification task as assessed by event-related brain potential (ERP) measures. *Biological Psychology*, *47*, 121-135.
Hill, H., Ott, F., & Weisbrod, M. (2005). SOA-dependent N400 and P300 semantic priming effects using pseudoword primes and a delayed lexical decision. *International Journal of Psychophysiology*, *56*, 209-221.
Holcomb, P. J. (1988). Automatic and attentional processing: An event-related brain potential analysis of semantic priming. *Brain and Language*, *35*, 66-85.
Holcomb, P. J. (1993). Semantic priming and stimulus degradation: Implications for the role of the N400 in language processing. *Psychophysiology*, *30*, 47-61.
Holcomb, P. J., Reder, L., Misra, M., & Grainger, J. (2005). The effects of prime visibility on ERP measures of masked priming. *Cognitive Brain Research*, *24*, 155-172.
Hutchison, K. A. (2003). Is semantic priming due to association strength or feature overlap? *Psychonomic Bulletin & Review*, *10*, 785-813.
Iragui, V., Kutas, M., & Salmon, D. P. (1996). Event-related potentials during semantic categorization in normal aging and senile dementia of the Alzheimer's type. *Electroencephalography and Clinical Neurophysiology*, *100*, 392-406.
Khateb, A., Michel, C. M., Pegna, A. J., Thut, G., Landis, T., & Annoni, J. M. (2001). The time course of semantic category processing in the cerebral hemispheres: An electrophysiological study. *Cognitive* Brain *Research*, *10*, 251-264.
Kiang, M., Kutas, M., Light, G. A., & Braff, D. L. (2008). An event-related brain potential study of direct and indirect semantic priming in schizophrenia. *The American Journal of Psychiatry*, *165*, 74-81.
Kiefer, M. (2001). Perceptual and semantic sources of category-specific effects: Event-related potentials during picture and word categorization. *Memory & Cognition*, *29*, 100-116.
Kiefer, M., & Brendel, D. (2006). Attentional modulation of unconscious 'automatic' processes: Evidence from event-related potentials in a masked priming paradigm. *Journal of Cognitive Neuroscience*, *18*, 184-198.
Kiefer, M., Weisbrod, M., Kern, I., Maier, S., & Spitzer, M. (1998). Right hemisphere activation during indirect semantic priming: Evidence from event-related potentials. *Brain and Language*, *64*, 377-408.
Koivisto, M., & Revonsuo, A. (2001). Cognitive representations underlying the N400 priming effect. *Cognitive Brain Research*, *12*, 487-490.
Kotz, S. A. (2001). Neurolinguistic evidence for bilingual language representation: A comparison of reaction times and event-related brain potentials. *Bilingualism: Language & Cognition*, *4*, 143-154.
Kreher, D. A., Holcomb, P. J., & Kuperberg, G. R. (2006). An electrophysiological investigation of indirect semantic priming. *Psychophysiology*, *43*, 550-563.
Kutas, M., & Federmeier, K. D. (2000). Electrophysiology reveals semantic memory use in language comprehension. *Trends in Cognitive Sciences*, *4*, 463-470.
Laiacona, M., Barbarotto, R., & Capitani, E. (2006). Human evolution and the brain representation of semantic knowledge: Is there a role for sex differences? *Evolution and Human Behavior*, *27*, 158-168.
Landi, N., & Perfetti, C. A. (2007). An electrophysiological investigation of semantic and phonological processing in skilled and less-skilled comprehenders. *Brain and Language*, *102*, 30-45.
Laws, K. R., Leeson, V. C., & Gale, T. M. (2002). The effect of 'masking' on picture naming. *Cortex*, *38*, 137-147.
Logothetis, N. K., Pauls, J., Augath, M., Trinath, T., & Oeltermann, A. (2001). Neurophysiological investigation of the basis of the fMRI signal. *Nature*, *412*, 150-157.
Lucas, M. (2000). Semantic priming without association: A meta-analytic review. *Psychonomic Bulletin & Review,* *7*, 618-630.
Mannhaupt, H. R. (1983). Produktionsnormen für verbale Reaktionen zu vierzig geläufigen Kategorien [German category norms for verbal items in 40 categories]. *Sprache & Kognition*, *2*, 264-278.

Martin, A., & Chao, L. L. (2001). Semantic memory and the brain: Structure and processes. *Current Opinion in Neurobiology*, *11*, 194–201.

Masson, M. E. J. (1999). Semantic priming in a recurrent network: Comment on Dalrymple-Alford and Marmurek. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *25*, 776-794.

McMullen, P. A., & Purdy, K. S. (2006). Category-specific effects on the identification of non-manipulable objects. *Brain and Cognition*, *62*, 228-240.

McNamara, T. P. (2005). *Semantic priming: Perspectives from memory and word recognition*. New York: Psychology Press.

Neely, J. H. (1977). Semantic priming and retrieval from lexical memory: Roles of inhibitionless spreading activation and limited-capacity attention. *Journal of Experimental Psychology: General*, *106*, 226-254.

Neely, J. H. (1991). Semantic priming effects in visual word recognition: A selective review of current findings and theories. In D. Besner, & G. W. Humphreys (Eds.), *Basic processes in reading: Visual word recognition* (pp. 264-336). Hillsdale, NJ: Erlbaum.

Osterhout, L., & Holcomb, P. J. (1995). Event-related potentials and language comprehension. In M. D. Rugg, & M. G. H. Coles (Eds.), *Electrophysiology of mind: Event-related brain potentials and cognition* (pp. 171-215). New York: Oxford University Press.

Plaut, D. C. (1995). Semantic and associative priming in a distributed attractor network. *Proceedings of the Annual Conference of the Cognitive Science Society*, *17*, 37-42.

Pritchard, W. S., Shappell, S. A, & Brandt, M. E. (1991). Psychophysiology of N200/N400: A review and classification scheme. In J. R. Jennings, P. K. Ackles, & M. G. H. Coles (Eds.), *Advances in psychophysiology: A research annual* (pp. 43-106). Philadelphia, PA.: Jessica Kingsley Publishers.

Radeau, M., Besson, M., Fonteneau, E., & Castro, S. L. (1998). Semantic, repetition and rime priming between spoken words: Behavioral and electrophysiological evidence. *Biological Psychology*, *48*, 183-204.

Rogers, T. T., & McClelland, J. L. (2004). *Semantic cognition: A parallel distributed processing approach.* Cambridge, MA: MIT Press.

Rossell, S. L., Price, C. J., & Nobre, A. C. (2003). The anatomy and time course of semantic priming investigated by fMRI and ERPs. *Neuropsychologia*, *41*, 550-564.

Rugg, M. D. (1990). Event-related brain potentials dissociate repetition effects of high- and low-frequency words. *Memory & Cognition*, *18*, 367-379.

Schumacher, R., Wirth, M., Perrig, W. J., Strik, W., & Koenig, T. (2009). ERP correlates of superordinate category activation. *International Journal of Psychophysiology*, *72*, 134-144.

Shibasaki, H. (2008). Human brain mapping: Hemodynamic response and electrophysiology. *Clinical Neurophysiology*, *119*, 731-743.

Sim, E. J., & Kiefer, M. (2005). Category-related brain activity to natural categories is associated with the retrieval of visual features: Evidence from repetition effects during visual and functional judgments. *Cognitive Brain Research*, *24*, 260-273.

Stenberg, G., Lindgren, M., Johansson, M., Olsson, A., & Rosén, I. (2000). Semantic Processing Without Conscious Identification-Evidence from Event-Related Potentials. *Journal of Experimental Psychology: Learning, Memory and Cognition*, *26*, 973-1004.

Tukey, J. W. (1977). *Exploratory data analysis.* Reading, MA: Addison-Wesley.

Vogel, E. K. & Awh, E. (2008). How to Exploit Diversity for Scientific Gain: Using Individual Differences to Constrain Cognitive Theory. *Current Directions in Psychological Science*, *17*, 171-176.

Weisbrod, M., Winkler, S., Maier, S., Hill, H., Roesch-Ely, D., Kiefer, M., & Spitzer, M. (1999). Electrophysiological correlates of direct versus indirect semantic priming in normal volunteers. *Cognitive Brain Research*, *8*, 289-298.

Willems, R. M., Özyürek, A., & Hagoort, P. (2008). Seeing and hearing meaning: ERP and fMRI evidence of word versus picture integration into a sentence context. *Journal of Cognitive Neuroscience*, *20*, 1235-1249.

Wurm, L. H., Whitman, R. D., Seaman, S. R., Hill, L., & Ulstad, H. M. (2007). Semantic processing in auditory lexical decision: Ear-of-presentation and sex differences. *Cognition & Emotion*, *21*, 1470-1495.