Repetition-priming Modulates Category-related Effects on Event-related Potentials: Further Evidence for Multiple Cortical Semantic Systems

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Abstract

■ In the present study, the significance of category-related brain activations as an index of semantic memory structure was assessed within a repetition-priming paradigm during a lexical decision task. The interpretation of category-related effects has been debated since previous studies observed category-related brain activity mainly in tasks requiring explicit semantic categorization. Furthermore, categories were frequently associated with behavioral performance differences, which could have influenced the pattern of brain activation. Event-related potentials (ERPs) to words denoting objects from artifactual (e.g., tools) and natural categories (e.g., animals) were recorded while subjects were presented with words and pseudowords as distracters, which were repeatedly presented. Category-related ERP differences emerged in the time window of the N400, an electrophysiological index of semantic processing, over occipito-parietal and fronto-central regions as well as in the following window of a late positive potential. Repetition priming modulated these category-related ERP effects whereas behavioral repetition priming (faster reactions to repeated words) was comparable for both categories. Differences in ERP repetition effects were specifically due to diminished category-related activity at repeated presentation. The present results show that category-related brain activation is not confined to tasks requiring explicit semantic categorization. Most importantly, the study demonstrates that category-related brain activation can be specifically modulated by repetition priming in the absence of corresponding behavioral performance differences. These findings therefore substantiate the significance of category-related brain activations as reflections of semantic memory structure and support the notion of multiple cortical semantic systems. ■

INTRODUCTION

The present study was aimed at substantiating the significance of category-related brain activations as an index of semantic memory structure by recording event-related brain potentials (ERPs). This line of semantic memory research was originally motivated by observations in brain-damaged patients who occasionally exhibit a selective impairment of semantic knowledge in some categories (category-specific semantic deficit). Patients with a selective loss of their semantic knowledge about natural (or animate/living) categories (e.g., animals, vegetables) have been described (e.g., De Renzi & Lucchelli, 1994; Warrington & Shallice, 1984) as showing preserved knowledge about objects from artifactual (or inanimate/nonliving) categories (e.g., tools, musical instruments). The opposite pattern has also been observed, albeit less frequently (e.g., Sacchett & Humphreys, 1992; Warrington & McCarthy, 1987).

These observations of category-specific impairments in semantic memory tasks have been taken as support for the existence of functionally and neuroanatomically distinct multiple semantic systems. It has been suggested that the semantic system is comprised of several systems that store different kinds of object attributes or features (e.g., visual, auditory, action-related, motion-related, etc.; Humphreys & Forde, 2001; Kiefer, 2001; Kiefer & Spitzer, 2001; Martin & Chao, 2001; Pulvermüller, 1999). According to the sensory/functional account of category-specific deficits proposed by Warrington and McCarthy (1987) and Warrington and Shallice (1984) different kinds of semantic attributes are of varying significance for representing objects from a given category: Action-related semantic attributes are relatively more relevant for representing artifacts whereas visual attributes are relatively more important for representing natural objects. Accordingly, damage to a particular semantic system results in a more serious impairment for a given category (or set of categories) in semantic tasks. Meanwhile, several sources at the perceptual and the semantic level of object processing have been identified, which could give rise to category-specific deficits in brain-lesioned patients and to category-related brain activations in healthy volunteers (see below). Hence, damage to a particular semantic system is only one factor among others leading to a category-specific semantic memory

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impairment (for a discussion, see Humphreys & Forde, 2001; Tyler & Moss, 2001).

Further evidence supporting the multiple semantic systems account comes from brain activation studies in healthy volunteers. Several neuroimaging studies have observed category-related[1] brain activation in semantic tasks, such as picture naming and semantic decisions (Chao & Martin, 2000; Chao, Haxby, & Martin, 1999; Perani et al., 1999; Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Martin, Wiggs, Ungerleider, & Haxby, 1996; Spitzer, Kwong, Kennedy, Rosen, & Belliveau, 1995). Artifacts such as tools frequently activated brain areas involved in action representation (premotor region, left middle temporal cortex, parietal cortex) more strongly than natural categories. Natural categories such as animals, in contrast, elicited relatively stronger activation in visual association areas of the occipito-temporal cortices. These neuroanatomical locations were taken as support for the suggestion that action-related semantic attributes are relatively more relevant for representing artifacts whereas visual attributes are relatively more important for representing natural objects (see the sensory/functional account above).

However, the reliability of category-related brain activations has been questioned since they were not consistently observed across experiments and tasks in a series of experiments with positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) (Devlin, Russell, et al., 2002). In a meta-analysis of seven PET studies involving several tasks, significant differences in category-related brain activity were only obtained for semantic decision and word-retrieval tasks, but not for lexical and orthographic tasks (Devlin, Moore, et al., 2002). If significant at all, effect sizes for category-related brain activity were quite small. Furthermore, some category-related brain activations have been attributed to differences in perceptual processing rather than to differences in semantic representations (Lloyd-Jones & Humphreys, 1997b): Increased activation in occipito-temporal regions for natural categories compared with artifacts have been related to their greater perceptual similarity (Gerlach, Law, Gade, & Paulson, 1999). Finally, category-specific deficits in patients have been related to the greater intercorrelation of semantic features (i.e., semantic similarity) for objects from natural categories (Tyler & Moss, 2001). As a consequence of this criticism, the significance of category-related effects in healthy volunteers for semantic memory organization have been questioned, and category-specific impairments in brain-damaged patients have been explained within a framework of unitary semantic system (Tyler & Moss, 2001).

In a previous ERP study, perceptual and semantic sources contributing to category-related effects have been dissociated (Kiefer, 2001). The high temporal resolution of ERPs in the range of milliseconds was used to track the time course of brain activations during ob-

ject categorization. Subjects performed a superordinate categorization task (e.g., animal–cat, tools–hammer) with pictures and words referring to artifacts and natural objects, respectively. At about 160 msec after onset of the target stimulus, ERPs between artifactual and natural categories diverged only in the pictorial modality over inferior temporo-occipital regions. Natural categories elicited a greater amplitude of the N1 ERP component, an electrophysiological index of visual processing, suggesting increased demands on perceptual processing (Tanaka, Luu, Weisbrod, & Kiefer, 1999; Mangun & Hillyard, 1995). Later, between 300 and 500 msec, in the time window of the N400, an electrophysiological reflection of semantic processing (Kutas & Van Petten, 1994; Kutas & Hillyard, 1980), scalp potentials differed between artifactual and natural categories in both the pictorial and verbal modality. Moreover, category effects on ERPs showed a comparable scalp distribution for pictures and words. Natural categories elicited a more positive potential over occipito-temporal and parietal scalp regions, hereby, specifically attenuating N400 amplitude compared with artifactual categories over this area. Artifactual categories, in contrast, were associated with a more positive potential over the fronto-central scalp also resulting in a decreased N400. The presence and the overall similarity of these category-related effects for pictures and words suggest that they arise from category-related differences in semantic processing. Furthermore, the topography of category-related ERP effects over fronto-central and occipito-temporal-parietal areas is consistent with the anatomical locations observed in neuroimaging studies reported above. Thus, the study supports the view that both perceptual and semantic sources contribute to category-related brain activation.

Nevertheless, evidence in support of category-related brain activation as reflections of multiple semantic memory systems is still not unequivocal. It is problematic for the multiple semantic systems account that in neuroimaging studies using PET and fMRI category-related brain activations were mainly observed in naming and semantic decision tasks, that is, in tasks explicitly requiring object categorization, but not in lexical and orthographic tasks. This failure to detect category-related brain activation in these neuroimaging studies during lexical tasks is surprising to some extent because in ERP studies (Pulvermüller, Harle, & Hummel, 2000; Pulvermüller, Lutzenberger, & Preissl, 1999), reliable brain activation differences have been observed in lexical decision tasks between word categories (action verbs vs. nouns with visual associations) and between different kinds of action verbs (leg- vs. face-related actions). In one recent fMRI study (Chao et al., 1999), comparable category-related activations have been obtained for silent picture-naming, passive picture-viewing, and delayed match-to-sample tasks. However, it cannot be ruled out that subjects silently named and, thus, explic-

itly categorized depicted objects in all task conditions. Usually, the semantic meaning of stimuli is activated even when stimuli are unattended (Bentin, Kutas, & Hillyard, 1995) or not consciously perceived (Kiefer, 2002; Kiefer & Spitzer, 2000). Hence, if category-related brain activations indeed reflect semantic memory organization, they should also emerge in other tasks than those involving explicit categorization processes. Possibly, due to their limited time resolution, fMRI or PET techniques are less likely to be able to detect category-related brain activity if the signal is small or rapidly decaying over time. Although inferior in spatial resolution, ERP recordings may be superior in this respect because of their excellent time resolution.

A further limitation of previous research on category-related semantic processing in healthy subjects is that naming and categorization latencies, respectively, usually differ between artifacts and natural objects even if stimuli are matched for relevant variables such as name frequency, familiarity, and visual complexity (Kiefer, 2001; Lloyd-Jones & Humphreys, 1997a, 1997b): Artifacts are named faster at a basic (''hammer'') or subordinate level (''mallet'') than natural objects (''dog,'' ''poodle'') whereas natural objects are categorized faster at a superordinate level (''animal'') than artifacts (''tool''). These performance differences can be explained by the greater perceptual and semantic similarity of natural objects compared with artifacts (Humphreys & Forde, 2001): Similarity of natural objects renders their categorization at specific levels of abstraction (e.g., dog or poodle), which is a prerequisite for naming, more difficult because it requires fine-grained distinctions between exemplars. In contrast, similarity facilitates categorizations at more abstract levels (e.g., animal or animate/inanimate) when only broad categorical distinctions have to been made. These performance differences for natural and artifactual categories can be a potential confound in brain activation studies and are most problematic in silent naming tasks when subject's performance cannot be controlled for. It is therefore possible that category-related brain activations simply reflect performance differences due to perceptual/semantic similarity rather than semantic memory structure.

One way to overcome these limitations and to test the significance of category-related brain activations for semantic memory structure is to assess category-related effects within a repetition-priming paradigm (Roediger, Weldon, & Challis, 1989). Typically, reactions to repeated stimuli are faster and more accurate than to not-repeated stimuli (repetition priming). This facilitation of a response to a repeatedly presented stimulus suggests that reinstantiations of previously activated stimulus representations are more rapidly activated, thereby, facilitating the responses. In principle, repetition-priming effects may arise from any stage throughout the processing stream (perceptual, semantic, decision, and response stages). In line with this explanation, neuro-

imaging studies found decreased activation for repeated stimuli in visual (Buckner et al., 1998) as well as in semantic brain areas (Demb et al., 1995).

In ERPs, stimulus repetition is associated with characteristic potential modulations. Several studies have shown that repeated words elicit more positive ERPs in the N400 time window (about 300–500 msec) and in the subsequent interval (about 500–700 msec) of a late positive complex (LPC). As a consequence, N400 amplitude is attenuated and LPC amplitude is enhanced (Misra & Holcomb, 2003; Schweinberger, Pickering, Burton, & Kaufmann, 2002; Van Petten, Kutas, Kluender, Mitchiner, & McIsaac, 1991; Rugg, 1985)[2]. This effect is called ERP repetition or old/new effect. The precise functional significance of ERP repetition effects in the N400 and LPC time windows is still a matter of debate. Schweinberger et al. (2002) observed comparable ERP repetition effects in the N400/LPC time window for faces from different views of the same person and also for person names irrespective of the font, suggesting that they arise from a postperceptual, possibly semantic processing stage. Rugg, Doyle, and Wells (1995) observed that topography of ERP repetition effects can vary depending on stimulus modality (e.g., visual, auditory) or type of stimulus (word vs. pseudoword). These discrepant findings reflect the possibility that ERP repetition effects (such as reaction time, or RT, repetition priming) can arise from different stages throughout the processing stream. Hence, a variety of cognitive processes including conscious recollection of the repeated item may contribute to ERP repetition effects in general (Rugg & Nieto-Vergas, 1999).

Given the appropriate experimental design, however, repetition-priming effects can be referred to a certain processing stage (Schweinberger et al., 2002; Thompson-Schill & Gabrieli, 1999; Lloyd-Jones & Humphreys, 1997a; Vriezen, Moscovitch, & Bellos, 1995). When repetition-priming effects for words denoting objects from natural and artifactual categories are compared during a lexical decision task as in the present study, visual input (visual letter string), decision (''yes it is a word''), and motor response (button press with index finger) are identical for both categories. If neurophysiological repetition-priming effects vary as a function of category, these category-related differences must arise from differentially activated semantic representations. Hence, an interaction between category and repetition would substantiate category-related brain activations as neurophysiological reflections of semantic memory organization and would strengthen the multiple semantic systems account. Even the presence of overall performance differences between categories cannot limit the interpretation of the data, as long as category and repetition does not interact at a behavioral level. For unitary semantic memory accounts, it is difficult to explain (1) why words of a given semantic category (e.g., artifact or natural kind) should elicit activity in different brain

areas, (2) which reflects semantic processing, and (3) which is specifically reduced by repetition priming. To the best of our knowledge, ERPs have never been used before to elucidate category-related repetition-priming effects.

A recent fMRI study on silent picture-naming provides the first evidence for experience-dependent changes of category-related brain activation (Chao, Weisberg, & Martin, 2002): Category-related brain activity to pictures of tools and animals was specifically reduced when subjects were familiarized with the pictures 4 days ago. However, subjects intensively studied the stimuli in the learning phase, and during the test phase, familiar and unfamiliar stimuli were blocked. Therefore, it cannot be excluded that episodic memory retrieval and/or differential attentional biases to familiar and unfamiliar stimulus may partially account for the observed experience-dependent changes in brain activity.

The present study was set up to substantiate the significance of category-related brain activation as a neurophysiological index for semantic memory organization. The goals of the study were twofold: First, the question is whether category-related brain activations could be obtained within a lexical decision task, that is, a task that does not afford explicit semantic categorization. It was assessed whether category-related ERP effects as obtained in our previous study on object categorization (Kiefer, 2001) generalize to a lexical decision task. Second, it was tested whether word repetition would specifically interact with category at those electrode sites, at which category-related ERP effects are obtained. As outlined above, such a finding would strongly suggest a semantic origin of category-related brain activation.

ERPs were recorded while subjects performed lexical decisions on a continuous stream of visually presented words and pseudowords (see Figure 1). Stimuli were presented twice, presentation was repeated after three intervening stimuli. Critical words denoted objects 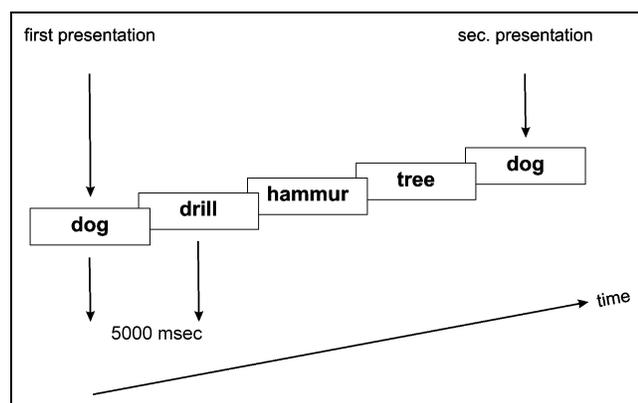from natural and artifactual categories. It was expected that category-related ERP effects as observed previously would emerge: Words from natural categories should elicit a more positive potential at occipital and parietal electrodes, whereas words form artifactual categories should be associated with a more positive potential at fronto-central electrodes. As a consequence, N400 amplitude would be attenuated at the respective electrode sites. Word repetition should also affect ERPs as observed in earlier studies (Rugg, 1985): ERPs to words at second presentation should be more positive in the N400 and LPC time windows than to words at first presentation widespread over centro-parietal scalp regions.

From these general, well-described ERP repetition effects, specific repetition effects have to be distinguished, which result in reduction of category-related activity. Most central to the aim of the study, it was hypothesized that category-related brain activity would be reduced by stimulus repetition (see also Chao et al., 2002): Category-related ERP effects at occipito-parietal (more positive ERPs to natural categories) and fronto-central electrodes (more positive ERPs to artifactual categories) should be diminished (or even nonexistent) at second compared with first presentation. As category-related activity, which is reflected by more positive-going ERPs to a given category, is expected to be obtained only at first, but not at second presentation and as the well-documented, general ERP repetition effect is associated with a more positive potential shift for words at second than at first presentation, category and repetition ERP effects will annihilate each other at those electrode sites, at which the category effect is largest. As a consequence, net scalp ERP repetition effects for a given category will be numerically reduced over that scalp region (and not increased what one might expect instead), over which category-related activity is observed. Thus, it is predicted that ERP repetition effects should be specifically smaller for natural compared with artifactual categories at occipito-parietal electrodes whereas at fronto-central electrodes ERP repetition effects should be smaller for artifactual categories.

RESULTS

Behavioral Results

Repeated measures analyses of variance (ANOVAs) were carried out on RT to the critical words and on error rate (ER), with category and repetition as factors. For RT analysis, the mean RT of the correct responses was calculated for each condition, responses longer than twice the individual mean were treated as outliers and not considered (0.45% of the data set). RT analysis only revealed a significant main effect of repetition, $F(1,19) = 84.597$, $MSE = 1585.0$, $p < .0001$). As expected, lexical decisions on words at second presentation were faster than on those at first presentation (repetition-priming effect). The main effect of category

Figure 1. Temporal sequence of events in the repetition-priming paradigm.

was only marginally significant, $F(1,19) = 4.197$, $MSE = 771.0, p = .055$, showing that reactions to natural categories were slightly faster than to artifactual categories. Most importantly, the interaction between category and repetition was not reliable ($F < 1$). Hence, behavioral repetition-priming effects were comparable for the different categories (see Figure 2).

Similar to the RT data, analysis of ER yielded a main effect of repetition, $F(1,19) = 17.608$, $MSE = 13.9$, $p < .001$. Lexical decisions to words at second presentation were less error prone than to words at first presentation (see Figure 2). All other effects were not significant ($F < 1$). Thus, a repetition-priming effect was also obtained for ER, which did not differ between categories.

Electrophysiological Data

Analyses of the ERP data were focused on the time windows of the N400 and LPC ERP components, which were known to be modulated by semantic category and by repetition priming. A broad negative deflection peaking at about 400 msec was observed at occipital, parietal, and fronto-central electrodes (see Figure 3). This negativity was attenuated for words at the second compared to at the first presentation (repetition-priming effect). According to its latency and topography this deflection was identified as an N400 ERP component (Kutas & Hillyard, 1980). Subsequent to the N400, a positivity (LPC) peaking at about 550 msec emerged, which was larger for words at the second presentation. It was assessed whether the N400 and the LPC differ in
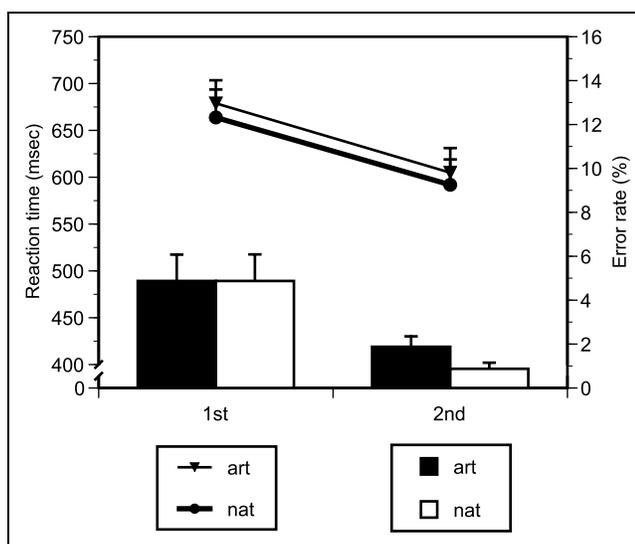

Figure 2. Mean RTs (lines; $n = 20$) and ER (bars) in the lexical decision task as a function of category and repetition. The small vertical lines depict in the present and the upcoming figures the standard error of means of each condition.

topography for words from natural and artifactual categories and whether these category-related ERP effects are modulated by repetition priming. For the rationale of time window and electrode selection, see the Methods section. To reduce complexity of the result section, the main effects of hemisphere and electrode site, which are not of theoretical interest, are not reported.

N400 Time Window (350–450 msec after Stimulus Onset)

At occipito-parietal electrodes, word repetition attenuated N400 amplitude as indicated by a Repetition × Electrode interaction, $F(3,57) = 35.057$, $MSE = .63$, $\varepsilon = .634, p < .0001$. Post hoc tests showed that voltages to words at second presentation were less negative than at first presentation at the more superior occipito-parietal electrode sites only (PO1/2, PO3/4, P1/2). A Repetition × Hemisphere interaction indicated that this N400 repetition-priming effect was larger over the left than over the right hemisphere, $F(1,19) = 5.633$, $MSE = .77$, $p < .05$, although it was significant over both sides in post hoc tests. Most importantly, repetition-priming interacted with category, $F(1,19) = 6.396$, $MSE = 5.58, p < .05$. When categories were directly compared in post hoc tests, natural categories were significantly less negative than artifactual categories at first presentation. At second presentation, mean differences between categories were not statistically reliable. Hence, a category-related ERP effect was only obtained at first, but not at second presentation. As a consequence, the ERP differences between first and second presentations (N400 repetition-priming) was significant in post hoc tests for artifactual categories only, but not for natural categories (see Figure 4).

At fronto-central electrodes, repetition priming also attenuated the N400. At this electrode group, analysis revealed a significant main effect of repetition, $F(1,19) = 27.795$, $MSE = 2.77, p < .0001$, as well as its interaction with electrode site, $F(3,57) = 5.443$, $MSE = .61, \varepsilon = .731, p < .01$. In post hoc tests, mean differences between the first and second presentations were significant at all electrode sites. Category × Hemisphere, $F(1,19) = 6.407$, $MSE = .97, p < .05$, and Category × Electrode, $F(3,57) = 3.551$, $MSE = .30, \varepsilon = .818, p < .05$, interactions suggest that ERPs to natural and artifactual categories diverge over the fronto-central scalp. These interactions were further explored with post hoc tests. In contrast to the occipito-parietal electrode group, artifactual categories were associated with a less negative potential than natural categories. Mean differences reached significance at electrode site F1/F2. Moreover, there was a tendency toward a less negative potential to artifactual than to natural categories over the left hemisphere ($p = .09$). The Category × Repetition interaction only reached trend level at fronto-central electrodes, $F(1,19) = 3.310$, $MSE = .3365, p = .08$. Numerically, the
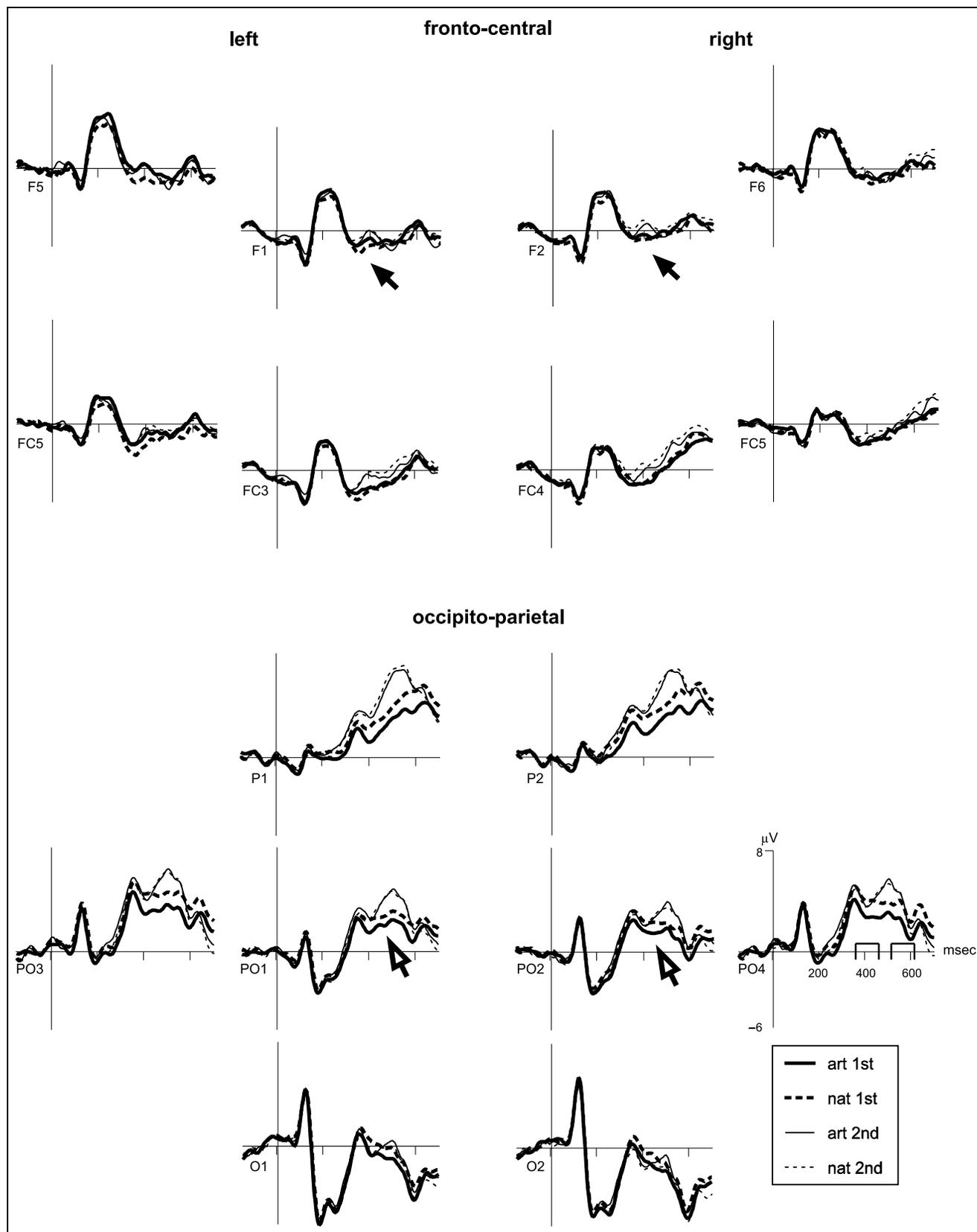
Figure 3. Selected ERP waveforms of average-referenced grand-averaged data (n = 20) for critical words as a function of object category and repetition. The long vertical line indicates the onset of the target. Negative potentials are plotted downward and positive potentials upward.

Figure 4. Category-related ERP repetition effects over occipito-parietal and fronto-central scalp regions averaged across sites within electrode groups.
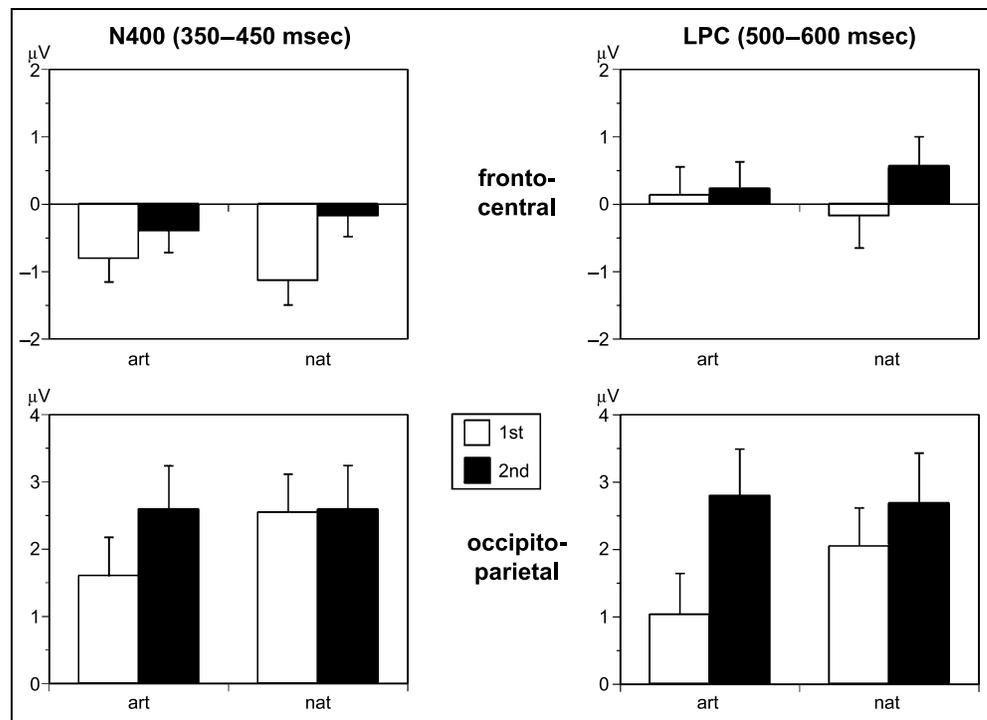
opposite pattern compared to occipito-parietal electrodes was observed: The N400 repetition-priming effect was greater for natural than for artifactual categories (see Figure 4).

LPC Time Window (500–600 msec after Stimulus Onset)

Word repetition affected ERPs at occipito-parietal electrodes also in the LPC interval. ERPs to words at second presentation were more positive than at first presentation. Analysis revealed a significant main effect of repetition, $F(1,19) = 9.279$, $MSE = 24.939$, $p < .01$, and its interaction with electrode site, $F(3,57) = 34.727$, $MSE = .68$, $\varepsilon = .677$, $p < .0001$. Mean differences between words at second and first presentation were significant in post hoc tests at all occipito-parietal electrodes sites, but magnitude of the effect was largest at parietal electrodes (P1/P2). The interaction between Category × Electrode Site also reached significance, $F(3,57) = 3.616$, $MSE = .70$, $\varepsilon = .568$, $p < .05$. Natural categories were more positive than artifactual categories at the more superior occipito-parietal electrode sites (PO1/PO2, PO3/PO4, P1/P2). Like in the N400 time window, repetition priming and category interacted with each other, $F(1,19) = 7.689$, $MSE = 6.58$, $p < .05$. Post hoc tests revealed that natural categories differed from artifactual categories only at first, but not at second presentation. Hence, the category-related ERP effect reported above was diminished by repetition priming. LPC repetition-priming effects were significant for both categories in post hoc tests. However, comparable to the results in the previous time window, rep-

etition priming was greater for artifactual than for natural categories (see Figure 4).

ERPs were also modulated by word repetition at fronto-central electrodes as shown by a Repetition × Electrode Site interaction, $F(3,57) = 5.298$, $MSE = 1.25$, $\varepsilon = .61$, $p < .05$. According to post hoc tests, voltages to words at second presentation were more positive than to words at first presentation at electrode sites FC3/FC4 and FC5/FC6. Most importantly, repetition priming interacted with category (Category × Repetition interaction; $F(1,19) = 5.233$, $MSE = 3.15$, $p < .05$). In contrast to the findings for the occipito-parietal scalp region, fronto-central LPC repetition-priming effects were observed only for natural, but not for artifactual categories (see Figure 4). In post hoc tests, voltages to words at second presentation were significantly more positive than at first presentation only for natural, but not for artifactual categories. Figure 5 shows the topography of the category-related differences in ERP repetition effects.

Summary of Event-related Potential Results

As expected, ERPs differed as a function of semantic category, hereby replicating earlier findings (Kiefer, 2001). Natural categories were associated with relatively greater positive potentials than artifactual categories over the occipito-parietal scalp, which resulted in a decreased N400 and in an increased LPC amplitude. Artifactual categories, in contrast, elicited a decreased N400 over the fronto-central scalp. Repetition also affected ERPs as expected: N400 amplitude was decreased, and LPC amplitude was increased for words
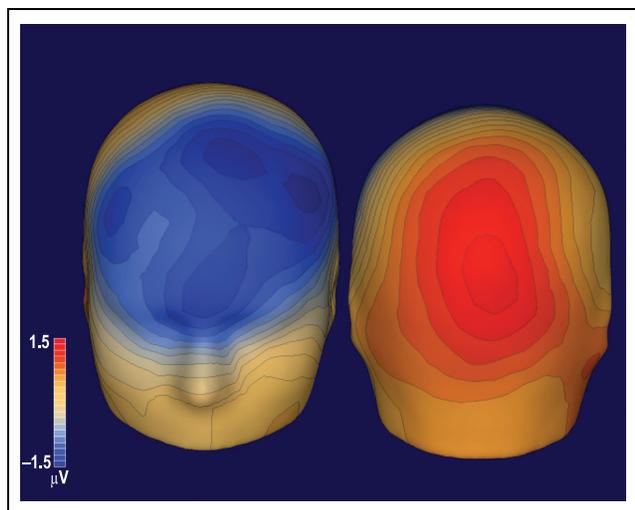
Figure 5. Topography of category-related ERP repetition effects at 550 msec (red: natural < artifactual; blue: artifactual < natural). Shown are spline interpolated potential differences between categories (artifactual minus natural) of the ERP repetition effect (second minus first presentation).

at second compared to first presentation. Most importantly, repetition and category interacted with each other. The observed interactions between category and repetition were mainly due to the occurrence of the above-described category-related ERP differences only for words at first, but not at second presentation. As a consequence, the net ERP repetition effect was greater for artifactual than for natural categories over the occipito-parietal scalp, whereas over the fronto-central scalp net ERP repetition effects were greater for natural than for artifactual categories. The Category × Repetition Priming interactions exhibited different time courses at occipito-parietal and fronto-central electrodes. Although this interaction was reliable at occipito-parietal electrodes in both the N400 and LPC time windows, at fronto-central electrodes it was significant only in the LPC time window.

DISCUSSION

The present study was set up to investigate the significance of category-related brain activation as a neurophysiological index for semantic memory organization. ERPs to words denoting objects from artifactual and natural categories were recorded within a repetition-priming paradigm during a lexical decision task. It was assessed whether category-related brain activation previously mainly observed in tasks requiring explicit semantic categorization could be replicated within a lexical decision task. Furthermore, it was asked whether category-related brain activation is specifically reduced by word repetition. As processes elicited by lexical decisions to words from natural and artifactual catego-

ries are comparable with respect to the perceptual, decisional, and response level, ERP differences in repetition priming must arise from a semantic processing stage. Hence, an interaction between category and repetition would substantiate category-related brain activations as neurophysiological reflections of semantic memory organization and would strengthen the multiple semantic systems account.

The results of the present study are clearly in accord with the predictions of the multiple semantic systems account. Comparable with our earlier ERP study on object categorization (Kiefer, 2001), natural categories were associated with a relatively greater positive potential over occipito-parietal regions in the N400 and the LPC time windows. Artifactual categories, in contrast, elicited a relatively greater positivity over fronto-central regions in the N400 time window. The present study shows that category-related brain activations can also be obtained in lexical decision tasks when semantic meaning is only implicitly accessed. They are not confined to tasks requiring explicit semantic categorization. The results therefore substantiate category-related brain activations as a reflection of semantic memory organization.

In brain-damaged patients with category-specific deficits, semantic processing is typically assessed with tasks requiring explicit semantic categorization such as picture naming or picture–word matching (e.g., Warrington & McCarthy, 1987; Warrington & Shallice, 1984). It is an open question whether these patients would also exhibit an impairment in a lexical decision task. As the lexical decision task can be performed correctly by solely relying on the mental lexicon without the necessity to explicitly access semantic memory, it is possible that a category-specific semantic deficit would be less pronounced or even absent. However, intact performance in neuropsychological patients in the lexical decision task would not imply that category-related brain activity during this task is without significance for theories of semantic memory organization. On the contrary, the present observation of category-related brain activity in healthy volunteers demonstrates that words from different semantic categories differentially activate semantic networks in distinct brain regions even if semantic access is not task-relevant. This rules out the possibility that category-related brain activation is simply contingent upon particular task requirements.

Although the localizational value of ERPs has to be viewed with caution (Nunez, 1981), the topography of the category-related ERP effects is consistent with findings from neuroimaging studies, which suggest that the processing of natural categories depends more on visual semantic knowledge stored in occipito-temporal areas, whereas for the processing of artifactual categories, action-related knowledge represented close to the motor areas in frontal cortex is relatively more important (Kellenbach, Brett, & Patterson, 2003; Chao et al., 2002; Phillips, Noppeney, Humphreys, & Price, 2002; Chao &

Martin, 2000; Perani et al., 1999; Thompson-Schill, Aguirre, D'Esposito, & Farah, 1999; Martin et al., 1996; for an overview, see Martin & Chao, 2001).

Our findings are at variance with previous neuro-imaging studies, which failed to detect reliable category-related brain activations in perceptual and lexical tasks (Devlin, Moore, et al., 2002; Devlin, Russell, et al., 2002). Possibly, ERP recordings, due to their high temporal resolution, more likely capture small, fast-decaying signals in the brain compared with neuroimaging techniques such as fMRI and PET, which depend on the relatively slow changes of blood flow (Kiefer & Spitzer, 2000).

The observed ERP and behavioral repetition-priming effects in the present study are in line with previous behavioral (Vriezen et al., 1995; Scarborough, Gerad, & Cortese, 1979) and electrophysiological studies (Schweinberger et al., 2002; Van Petten et al., 1991; Rugg, 1985). Reactions to repeated words were faster and more accurate than to not-repeated words. In the ERP recordings, repeated words elicited a more positive potential than not-repeated words over occipito-parietal and fronto-central electrode sites in the N400 and LPC time windows. As already mentioned in the introductory session, these general repetition effects probably arise from a variety of processing stages (visual, semantic, response, and decision stages) including conscious recollection of the repeated stimulus (episodic memory). In line with this interpretation, Chao et al. (2002) observed increased hippocampal and parahippocampal activity to repeated items (besides of an increase and decrease of brain activity due to stimulus repetition in visual and semantic brain areas in occipito-temporal and frontal cortex).

Although the behavioral repetition-priming effects were comparable in magnitude for artifactual and natural categories, ERP repetition-priming effects varied as a function of category as predicted by the multiple semantic systems account. Most importantly, category-related activity (i.e., more positive ERPs to a given category) was reduced by repetition priming. Only at first presentation, ERPs between natural and artifactual categories diverged from each other as described above, at second presentation ERPs to categories were comparable. As both category and classical stimulus repetition effects elicit positive potential shifts in the ERP, the measurable net ERP repetition effect (potentials to repeated words more positive than to not-repeated words) is specifically smaller at those electrode sites, at which the category effects are largest. For that reason, at occipito-parietal electrodes, ERP repetition-priming effects were smaller for natural than for artifactual categories. At fronto-central electrodes, ERP repetition-priming was smaller for artifactual than for natural categories. These category differences in ERP repetition effects were mainly due to category-related activity for not-repeated words (i.e., at first presentation), which was reduced for repeated presentation. Thus, compara-ble to the study of Chao et al. (2002), the present results reflect a decrease of category-related brain activity due to stimulus repetition.

As far as I know, this is the first demonstration of category-related ERP repetition-priming effects, an observation that has also general relevance for research on ERP repetition effects. As already mentioned, classical ERP repetition effects are associated with a broad positive potential shift over the posterior and central scalp for repeated compared with not-repeated stimuli. These repetition effects are interpreted as reflecting easier access to visual representations, to semantic memory, and/or to episodic memory retrieval (see the paragraph above and the Introduction section). This general result pattern is relatively unspecific, because it occurs for repetitions of a variety of stimuli. The present study shows that in addition to these rather unspecific effects repetition may reduce positive potential shifts over relatively circumscribed scalp regions that are thought to mirror stimulus-specific processing (referred here as category-related). As a consequence, typical ERP repetition effects are masked or reduced at the corresponding electrode sites. This observation has relevance for future studies on ERP repetition-priming. First, when the topography of ERP repetition effects is compared across experiments or studies, the precise composition of the stimulus material (e.g., proportion of words referring to artifacts or natural objects) has to be taken into account (for topographic differences in repetition-priming effects between words and nonwords, see Rugg, Doyle, et al., 1995). Second, besides of only being a potential confound, research could explicitly exploit category-related repetition effects (e.g., different word classes, different classes of emotional stimuli, etc.) to explore the nature of underlying stimulus representations.

The present findings are compatible with those of a recent fMRI study (Chao et al., 2002) on experience-dependent modulation of category-related brain activation. In a training session, subjects were intensively familiarized with a set of pictures of tools and animals, respectively, by requiring them to perform naming, delayed match-to-sample, and one-back tasks. Four days later, in the test session, subjects were presented with blocks of old and new pictures, respectively, from the tools and animals categories, respectively. Brain activation images were taken when subjects silently named the pictures. Activity for old pictures of a given semantic category was particularly reduced in brain areas, which showed category-related activation, that is, a greater fMRI signal to one category. Naming old pictures of tools particularly diminished activity in the premotor, middle temporal, and parietal regions whereas naming old pictures of animals reduced activity in lateral temporal cortex.

The present study confirms and extends these previous findings in several ways. First, in the present study, repeated and not-repeated stimuli from the different

categories were presented in a randomized order so that any attentional biases that could have compromised the results can be excluded. In the study of Chao et al. (2002), in contrast, stimuli of the different conditions were blocked. Second, the lexical decision task of the present study does not require explicit semantic categorization and allows monitoring of behavioral performance in contrast to silent naming. Third, the use of words in our study (in contrast to pictures) excludes the possibility of perceptual differences between categories to have influenced the results. Fourthly, in the present study, a typical repetition-priming paradigm with only one previous presentation was used. In the study of Chao et al., in contrast, subjects were repeatedly and intensively familiarized with the pictures that could have enhanced episodic memory retrieval during the test session. In fact, naming old pictures was associated with increased hippocampal activation. Finally, due to the high temporal resolution of ERPs, the present study provides information how category-related repetition effects unfold over time.

Over occipito-parietal regions, the interaction between category and repetition due to reduced category-related activity for repeated words from natural categories reached significance in both the N400 (350–450 msec) and LPC (500–600) time windows. Over fronto-central regions, the corresponding interaction due to reduced activity for repeated words from artifactual categories emerged later in the LPC time window. These time-course differences suggest that repetition effects for natural categories in occipito-temporal regions develop more rapidly than repetition effects for artifactual categories in frontal brain regions. There is evidence from a behavioral study (Flores d'Arcais, Schreuder, & Glazenborg, 1985) that visual semantic knowledge is faster activated than functional semantic knowledge (for domain-specific repetition priming, see Thompson-Schill & Gabrieli, 1999). The earlier onset of repetition effects for natural than for artifactual categories in the present study could well reflect the temporal dynamics of accessing different knowledge aspects.

It should be noted at this place that the distinction between natural and artifactual categories as well as between visual and functional/action-related knowledge is a simplification. A much greater variety of knowledge aspects is involved in the representation of objects from different categories (McRae & Cree, 2002), and research is only at the beginning to identify their neural substrate. Furthermore, as it has been already outlined in the Introduction section, different relevance of particular knowledge aspects for semantic categories is only one factor among others potentially contributing to category-related effects in neuroimaging and behavioral studies.

Although the present study shows that category-related brain activations can be obtained within a lexical decision task and are not confined to semantic catego-

rization, I do not suggest that category-related semantic processing is task-independent. The multiple semantic systems account implicates that category-related brain activity may be modulated by task demands. A specific task (e.g., perceptual feature verification) may require the retrieval of visual semantic knowledge regardless of the category involved, so that category-related differences in brain activation may disappear. In fact, recent neuroimaging evidence suggests such interactions between task and category (Devlin, Moore, et al., 2002; Phillips et al., 2002).

Note in this context that my view of semantic memory organization does not imply that there is a "tool" or "animal center" in the brain (however, see Caramazza, 2000; Caramazza & Shelton, 1998). The activation pattern across all semantic systems with its activation peaks and valleys is thought to represent an object of a given category (Chao et al., 2002; Martin & Chao, 2001). Thus, representation of semantic knowledge is both distributed and localized (Kiefer, 2001; Kiefer & Spitzer, 2001): It is distributed as it comprises multiple semantic systems in neuroanatomically distinct brain areas. It is localized as a given cortical area codes a particular knowledge aspect.

In conclusion, the interactions between category and repetition ERP effects observed in the present study strongly support the multiple systems account and are difficult to reconcile with the view of a unitary semantic system. It is difficult to explain within a framework of a distributed, but unitary semantic system (Tyler & Moss, 2001), which is thought to be accessed regardless of semantic category, why category-related ERP effects emerge for not-repeated words and why they are reduced for repeated stimuli. As behavioral repetition-priming effects were similar for both categories, the present category-related ERP repetition effects cannot be attributed to differences in behavioral performance. The present results therefore strengthen the multiple semantic system account of category-related brain activation. In line with others (Humphreys & Forde, 2001; Martin & Chao, 2001; Pulvermüller, 1999; Warrington & Shallice, 1984), I propose that semantic knowledge is represented in multiple cortical areas, which code different knowledge aspects or features (e.g., visual, auditory, action-related, etc.). These multiple semantic systems are modality-specific in the sense that they code semantic knowledge derived from a particular sensory or action channel (Barsalou, Simmons, Barbey, & Wilson, 2003).

METHODS

Subjects

Twenty-five right-handed (according to Oldfield, 1971) students from the University of Ulm participated in the experiment. Participants were native German speakers

without any signs of neurological or psychiatric disorders and with normal or corrected-to-normal vision. Data of five participants had to be excluded from analysis because of excessive ocular artifacts in the electroencephalogram (EEG) recordings (less than a minimum of 60% artifact-free trials). The remaining 20 subjects (11 women and 9 men) had an average age of 24 years (range 20–29).

Procedure

Subjects were presented with a pseudorandomized sequence of words and pseudowords as stimuli in the center of the computer screen. Each trial started with a fixation cross for 500 msec, thereafter, a stimulus was shown for 400 msec, and the screen went blank for 2000 msec. After an intertrial interval of 2500 msec, during which three asterisks were displayed, the next trial started. All stimuli were displayed in white font against a black background on a computer monitor synchronous with the screen refresh (refresh rate = 16.67 msec). Participants were instructed to decide as fast and as accurately as possible whether the stimulus was a real word and had to respond by pressing one of two buttons with the right index or the middle finger, respectively. They were also told that stimuli may be sometimes presented repeatedly. They were instructed not to pay attention to the repetitions, but to focus on the lexical decision task.

Critical words consisted of 80 names of common objects. Half of the objects belonged to artifactual categories (10 items from the categories of tools, furniture, transportation, and musical instruments, respectively) and the other half were from natural categories (10 instances from the categories of animals, plants, fruits, and vegetables, respectively). All stimuli were drawn from an earlier study (Kiefer, 2001).

These critical stimuli were selected such that names from natural and artifactual categories did not differ from each other significantly in typicality [according to Kiefer, 2001; natural: 4.71, artifactual: 4.59; $t(1,78) = 0.853$], word length [natural: 6.9 letters, artifactual: 7.2; $t(1,78) = -0.846$], and word frequency [according to Ruoff, 1990; natural: 8.08/500,000, artifactual: 9.53/500,000; $t(1,78) = -0.409$]. Eighty legally spelled pseudowords derived from real object names (40 natural kinds and 40 artifacts different from critical stimuli) by exchanging one letter served as distracters. At a distance of 95 cm, the viewing angle for the stimuli subtended about $3°$ horizontally and $1°$ vertically.

Within the stimulation sequence, critical words as well as pseudoword distracters were presented twice (see Figure 1). Second presentation (repetition priming condition) followed first presentation after three intervening stimuli. Forty more words and pseudowords, respectively, were used as fillers and shown only once. These filler stimuli were included so that participants were not able to predict a repeated presentation with certainty. From the total of 400 stimuli, two pseudorandomized sequences fulfilling the repetition lag restrictions were constructed and were divided into five blocks of 80 trials. An equal number of participants were randomly assigned to the two stimulus sequences. Between blocks, participants were able to rest. At the beginning, 25 training trials similar to the experimental trials were run. The entire experimental session required about 2 hr and 30 min to complete.

Event-related Potential Recording, Signal Extraction, and Statistical Analysis

Scalp potentials were collected using a equidistant montage of 64 sintered Ag/AgCl electrodes mounted in an elastic cap (Easy Cap, Falk Minow Systems, Munich, Germany). An electrode between Fpz and Fz was connected to the ground and an electrode between Cz and FCz was used as recording reference. Eye movements were monitored with supra- and infraorbital electrodes and with electrodes on the external canthi. Electrode impedance was kept below 5 kΩ. Electrical signals were amplified with Synamps amplifiers (low-pass filter = 70 Hz, 24 dB/octave attenuation; 50 Hz notch filter) and continuously recorded (digitization rate = 250 Hz), digitally band-pass filtered (high cut-off: 16 Hz, 24 dB/octave attenuation; low cut-off: 0.2 Hz, 24 dB/octave attenuation), and segmented (150 msec before to 700 msec after the onset of the target). Only EEG segments to the critical words were further analyzed. EEG data were corrected to a 150-msec baseline before the onset of the stimulus. Artifact-free EEG segments to trials with correct responses were averaged synchronous to the onset of the stimulus separately for each experimental condition. To obtain a reference independent estimation of scalp voltage, the average reference transformation was applied to the ERP data (Kiefer, Marzinzik, Weisbrod, Scherg, & Spitzer, 1998; Bertrand, Perrin, & Pernier, 1985).

Mean voltages were analyzed statistically in two time windows of interest. The first time window (350–450 msec after onset of the critical word) covered the N400 peak, the second time window (500–600 msec after onset of the critical word) was centered around the peak of the LPC elicited by repeated words. As in the previous study (Kiefer, 2001), two scalp regions-of-interest, each of them being represented by four pairs of contralateral electrodes, were selected for analysis: fronto-central (electrode sites: FC3/FC4, FC5/FC6, F1/F2, F5/F6) and occipito-parietal (electrode sites: O1/O2, PO1/PO2, PO3/PO4, P1/2). Repeated measures ANOVAs were performed separately for each scalp region and time window with repetition (first vs. second presentation), category (artifacts vs. natural kinds), hemisphere, and electrode site as within-subjects factors (p level of .05). When appropriate, degrees of freedom were adjusted according to the method of Greenhouse–Geisser, and

the Greenhouse–Geisser ε as well as the corrected significance levels are reported. Significant interactions were further explored with Fisher LSD post hoc tests. The recommendation by Urbach and Kutas (2002) not to scale ERP data for topographic ERP analysis was followed because these authors have convincingly shown that different spatial configurations of neural generators cannot reliably be inferred from different scalp topographies even after amplitude normalization.

Acknowledgments

Notes

1. In this context, I prefer the more general term *category-related* to *category-specific* because activity in a given brain area is frequently simply greater to a certain category than to other categories. The term *category-specific* implies that a given brain area may selectively respond to one category, which is rather rarely the case.

2. It has been debated that repetition priming effects in the N400 and LPC time windows may reflect separable cognitive and neural processes (for a discussion, see, Misra & Holcomb, 2003; Van Petten et al., 1991). However, as this issue is not central to the topic of the present study, I will use the terms *N400* and *LPC repetition priming* only to indicate the respective time windows without any reference to possible functional distinctions.

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