How Different Types of Conceptual Relations Modulate Brain Activation during Semantic Priming

Olga Sachs[1,2], Susanne Weis[1], Nadia Zellagui[1,2], Katharina Sass[1,2],
Walter Huber[1], Mikhail Zvyagintsev[1,2], Klaus Mathiak[1,2],
and Tilo Kircher[3]

Abstract

■ Semantic priming, a well-established technique to study conceptual representation, has thus far produced variable fMRI results, both regarding the type of priming effects and their correlation with brain activation. The aims of the current study were (a) to investigate two types of semantic relations—categorical versus associative—under controlled processing conditions and (b) to investigate whether categorical and associative relations between words are correlated with response enhancement or response suppression. We used fMRI to examine neural correlates of semantic priming as subjects performed a lexical decision task with a long SOA (800 msec). Four experimental conditions were compared: categorically related trials (*couch–bed*), associatively related trials (*couch–pillow*), unrelated trials (*couch–bridge*), and nonword trials (*couch–sibor*). We found similar behavioral priming effects for both categorically and associatively related pairs. However, the neural priming effects differed: Categorically related pairs resulted in a neural suppression effect in the right MFG, whereas associatively related pairs resulted in response enhancement in the left IFG. A direct contrast between them revealed activation for categorically related trials in the right insular lobe. We conclude that perceptual and functional similarity of categorically related words may lead to response suppression within right-lateralized frontal regions that represent more retrieval effort and the recruitment of a broader semantic field. Associatively related pairs that require a different processing of the related target compared to the prime may lead to the response enhancement within left inferior frontal regions. Nevertheless, the differences between associative and categorical relations might be parametrical rather than absolutely distinct as both relationships recruit similar regions to a different degree. ■

INTRODUCTION

One of the most widely used and well-established tools to investigate the representation and processing of word meanings or concepts is semantic priming. A lexical decision task is very often used to assess the effects of priming: Participants are first presented with a prime word, followed rapidly (200–1000 msec) by a string of letters (target) which can be a real word or a nonword. Then, participants have to decide as quickly as possible if the target is a real word or not. A classical finding in this paradigm is that lexical decisions are made more quickly and accurately when target words are preceded by a related prime word (e.g., *doctor–nurse* vs. *bread–nurse*; for a review, see Neely, 1991), indicating facilitated word recognition.

Although decades of priming research have produced convincing behavioral correlates of semantic priming, the neural mechanisms of this phenomenon are still less understood. A number of fMRI semantic priming studies have been conducted thus far (Copland, de Zubicaray, McMahon, & Eastburn, 2007; Kuperberg, Deckersbach,

Holt, Goff, & West, 2007; Wible et al., 2006; Matsumoto, Iidaka, Haneda, Okada, & Sadato, 2005; Giesbrecht, Camblin, & Swaab, 2004; Copland et al., 2003; Rissman, Eliassen, & Blumstein, 2003; Rossell, Price, & Nobre, 2003; Kotz, Cappa, von Cramon, & Friederici, 2002; Rossell, Bullmore, Williams, & David, 2001). In general, response suppression is found in response to semantic priming. This reduced neural activity for related prime–target pairs compared to the unrelated ones was found in a variety of areas, for instance, left inferior frontal cortex, left temporal cortex, as well as bilateral middle frontal gyri and anterior cingulate (e.g., Wible et al., 2006; Matsumoto et al., 2005; Copland et al., 2003; Rissman et al., 2003; Kotz et al., 2002). This type of priming effect is thought to reflect the consequence of priming implying less effort in processing primed targets or faster processing of primed stimuli (Henson, 2003). However, a number of studies (sometimes even the same studies that found priming-related decreases in brain activation) have also found "response enhancement"—greater activation for semantically related pairs than for unrelated pairs (e.g., Copland et al., 2007; Wible et al., 2006; Rossell et al., 2003; Kotz et al., 2002). What factors lead to differences in the discovered neural priming effects is a matter of debate (Raposo, Moss,

[1]RWTH Aachen University, Aachen, Germany, [2]JARA—Translational Brain Medicine, Germany, [3]Philipps-University Marburg, Marburg, Germany

Stamatakis, & Tyler, 2006; Henson, 2003). Henson (2003) suggested that regions that show response suppression subserve the process that works for both primed and unprimed stimuli; it is just more efficient for the primed ones, and thus, requires less activity in the region. In contrast, regions that show response enhancement subserve a process that occurs only on the primed stimuli, meaning that some different process operates on the related target compared to the unrelated one. In other words, the increase in the hemodynamic response to primed relative to unprimed stimuli is a correlate of cognitive processes that involve primed words and indicates the spread of activation between related concepts (Henson, 2003; Marinkovic et al., 2003) or allocation of attentional resources (Behrmann, Geng, & Shomstein, 2004; Chein, Ravizza, & Fiez, 2003). Raposo et al. (2006) have investigated this issue further and found that semantic priming was associated with increased activation in several bilateral fronto-temporal areas, whereas repetition priming resulted in reduced activation in the left inferior frontal gyrus (IFG), bilateral parahippocampal gyrus, and right fusiform gyrus. This dissociation in neural response to semantic and repetition priming suggests that different cognitive processes are operating on evaluating targets depending on their relationship to the primes. Thus, Raposo et al. suggest that the variability in discovered neural semantic priming effects may, in part, be caused by the fact that most existing fMRI priming studies did not control for the type of semantic relationship between the prime and the target. This factor is known to play an important role in behavioral priming (e.g., Moss, Ostrin, Tyler, & Marslen-Wilson, 1995), but has received little attention in fMRI literature. Thus far, this issue has been addressed by Kotz et al. (2002), who compared associative prime–target relations (e.g., *key–chain*) with categorical relations (e.g., *cow–dog*), and found that the processing of categorical relations recruits additional areas in the right precuneus, the isthmus gyrus cinguli, and the cuneus. However, the authors do not report separate fMRI priming effects for categorically and associatively related prime–target pairs when contrasted with unrelated pairs. Instead, they contrasted all related with unrelated pairs and found response suppression in the left IFG, bilateral deep frontal operculum, and middle frontal gyri. Possibly due to the lack of differentiation between categorical and associative priming effects, they also discovered response enhancement in the left middle temporal gyrus, postcentral sulcus, and cuneus.

In general, there are two main hypotheses how categories are represented in the brain. The first theory postulates that conceptual knowledge is represented in a distributed but nonseparated semantic system (Tyler et al., 2003; Devlin, Russell, et al., 2002; Tyler, Moss, Durrant-Peatfield, & Levy, 2000), where no specific region is assigned to process concepts in any specific conceptual domain or category. The second hypothesis suggests that object knowledge is linked to our sensorial and motor experi-

ence with these objects (sensory-functional hypothesis; Warrington & Shallice, 1984). Hence, the processing of natural kinds is mainly defined by perceptual and visual attributes, whereas the processing of artifacts requires knowledge of the functional and motor features. Thus far, results of studies of representation and processing of semantic categories are often consistent with the sensory-functional hypothesis (e.g., Kalenine et al., 2009; Sachs, Weis, Krings, Huber, & Kircher, 2008; Sachs, Weis, Zellagui, et al., 2008; Devlin, Moore, et al., 2002; Perani et al., 1999; Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996). For example, Kalenine et al. (2009) used a picture matching task to examine taxonomic (e.g., *bowl–fork*) and thematic relations (e.g., *squirrel–hazelnuts*).[1] The results revealed that both category types are based on different sensory–motor processes and influence concept formation in different ways. Moreover, the results of several studies revealed that categorical relations require an additional involvement of areas in the right hemisphere (Sass, Sachs, Krach, & Kircher, 2009; Sachs, Weis, Krings, et al., 2008; Sachs, Weis, Zellagui, et al., 2008; Kotz et al., 2002). Support for these results also comes from several other semantic priming studies that used event-related potentials (ERPs) or visual half fields. The latter refer to presentation of items to the right or left visual field. They provide an optimal method to investigate hemisphere-specific processes and cerebral asymmetries. Those studies established that there is a right hemisphere advantage for the processing of categorical in comparison to associative relationships (Beeman et al., 1994; Chiarello & Richards, 1992). In addition, a lesion study of Hagoort, Brown, and Swaab (1996) revealed that patients with right hemispheric lesions produced a normal N400 priming effect while listening to associatively related prime–target pairs (e.g., *bread–butter*), but a trend toward a reduced N400 priming effect for categorically related prime–target pairs (e.g., *church–villa*). Domain-specific localization of conceptual categories is also supported by studies of brain-lesioned patients who have category-specific deficits (living vs. nonliving things, animals vs. tools; e.g., Caramazza & Shelton, 1998; Warrington & McCarthy, 1983). Nevertheless, it remains unclear whether both types of relations, that is, categorical and associative, lead to similar or different kinds of neural priming response—suppression or enhancement. Henson (2003) proposed that response enhancement arises when the target is processed differently from the prime. It is possible that members of associatively related prime–target pairs that are made up of dissimilar looking things (e.g., *dog–leash*) will also be processed differently and therefore result in response enhancement. Similar-looking members of categorically related prime–target pairs (e.g., *dog–wolf*) may undergo similar semantic processing routes and therefore lead to response suppression or even deactivation. In other words, categorically related words recruit the same processing routes and associations recruit different processing routes, resulting in response suppression and enhancement, respectively.

Moreover, a critical distinction must be made regarding the differences between automatic and controlled priming. Automatic priming mainly occurs at short stimulus onset asynchronies (SOAs) and is considered to reflect the structure of the semantic network, that is, the automatic spread of activation across semantic memory (Collins & Loftus, 1975), whereas controlled priming (at a long SOA) is considered to reflect the operation of strategic processes, that is, executive processes (e.g., expectancies; Neely, Keefe, & Ross, 1989; Becker, 1980). Nevertheless, the automatic spread of activation can still occur at a long SOA, but the controlled processes will dominate (Kuperberg et al., 2007). For example, response suppression within the fusiform gyrus is thought to reflect the automatic spread of activation at a short SOA (Gold et al., 2006; Wheatley, Weisberg, Beauchamp, & Martin, 2005), whereas response suppression within the left IFG might reflect the effects of controlled semantic expectations at a long SOA (Gold et al., 2006).

The goal of the present study was to investigate the role that different types of semantic relationships play in neural correlates of semantic priming. We set out (1) to investigate whether the type of semantic relationship between the prime and the target can influence the localization of priming effects in the brain; (2) to look at the role that semantic relations play in the resulting neural priming response—suppression or enhancement. Different semantic relations were chosen: Categorical relations were defined as an overlap in features or meaning of words (e.g., *couch–bed*) sharing similar perceptual or functional features (Devlin, Russell, et al., 2002; Grossman et al., 2002; Tyler et al., 2000). Associatively related word-pairs were defined as externally related items interacting within scenes or events (e.g., *car–garage*; Lin & Murphy, 2001) and sharing an associative relationship but no perceptual features or functional similarity. Both types of relation seem to play an important role in conceptual knowledge representation. But, thus far, very few studies (e.g., Kalenine et al., 2009; Sass, Sachs, et al., 2009; Sachs, Weis, Zellagui, et al., 2008) directly compared the neural correlates of these two types of relations. These studies have shown that associations on the one hand and categorical relations on the other hand may play complementary roles in concept formation.

Because various existing fMRI semantic priming studies were conducted under controlled processing conditions using a long SOA of 600–1000 msec (Copland et al., 2007; Kuperberg et al., 2007; Wible et al., 2006; Matsumoto et al., 2005; Giesbrecht et al., 2004; Rissman et al., 2003; Kotz et al., 2002), we decided to use a long SOA of 800 msec to allow for a better comparison with existing studies. Moreover, some studies manipulating the SOA demonstrated that associative effects occur mainly for short and categorical effects only for long SOA (e.g., Hutchison, 2003; Kotz et al., 2002). Additionally, it is assumed (Koivisto, 1998) that the processing of categorical relations requires postlexical mechanisms that occur mainly at a long SOA.

Therefore, to ensure that a priming effect occurs for both types of relation and to bias toward controlled processing, we decided to use long SOAs. Overall, the novelty of our design compared to existing studies lies in the use of a long SOA addressing controlled lexico-semantic processing and the variation of prime–target relationship. On a neural level, we expected that categorically related prime–target pairs are likely to recruit additional right hemispheric areas (fronto-temporal and parietal; Sachs, Weis, Krings, et al., 2008; Sachs, Weis, Zellagui, et al., 2008; Kotz et al., 2002), reflecting the rather effortful processing of categories in comparison to associations (e.g., Kotz et al., 2002; Beeman et al., 1994; Chiarello & Richards, 1992) and the perceptual similarity between members of the same category items (sensory-functional hypothesis; Warrington & Shallice, 1984). In contrast, associations might lead to more left hemispheric signal changes (especially in fronto-temporal regions; Sass, Krach, Sachs, & Kircher, 2009), reflecting the retrieval of semantic information and the processing of semantic associations (Kircher, Sass, Sachs, & Krach, 2009; Sass, Krach, et al., 2009; Sachs, Weis, Zellagui, et al., 2008; Wible et al., 2006; Copland et al., 2003; Chiarello & Richards, 1992). Less clear are the predictions concerning the kind of neural priming effects that the two semantic relation types will lead to. Still, our working hypothesis is that members of categorically related prime–target pairs will lead to response suppression due to their perceptual and functional similarity, whereas dissimilar-looking members of associatively related pairs will lead to response enhancement.

METHODS

Participants

Sixteen healthy male subjects participated in the study. All of them were right-handed according to the Edinburgh Inventory of Handedness (Oldfield, 1971). Their mean age was 27 years ($SD = 4.7$) and they all spoke German as their native language. All participants had normal or corrected-to-normal vision, gave informed consent, and were paid €10 for participation in the study. The study was approved by the local ethics committee.

Stimuli and Design

Subjects performed a lexical decision task that is commonly used in semantic priming research. In this task, subjects are first presented with a prime word in the center of the computer screen (e.g., *couch*), followed by a target word (e.g., *pillow*) that could either be a word or a nonword. Subjects were instructed to read the first word and to decide as fast as possible if the second string of letters was a real word in German or not.

Four main experimental conditions were used: (1) 30 associatively related, for instance, *couch–pillow*; (2) 30 categorically related, for example, *couch–bed*; (3) 60 unrelated, for example, *couch – bridge*; (4) 120 nonword trials,

for example, *couch–sibor*. Prime words were kept constant in each condition to make sure that the only factor that was varied is the type of relationship between the prime and the target. The same target words were used in the associatively related and in the associatively unrelated condition (but paired differently to rule out any relation between prime and target words). The same was true for the categorically related and unrelated prime–target pairs. This design was used to make sure that any priming effects that we find were due exclusively to the relationship between related prime–target pairs and not due to the systematic presentation of different target words in the unrelated condition. Although the repetition of target words (even in new pairings with prime words) can potentially introduce the confound of repetition priming, this confound is likely to be cancelled out in our design. Due to careful pseudorandomization of the trial presentation order, we ensured that half the targets are first presented in the related condition and the other half in the unrelated condition, so there should not be any systematic effects of repetition of targets, such as when the target is always presented first in the related and second in the unrelated condition.

For each of the 30 German prime words, an associative and a categorical target was found that formed either an associative or a categorical relation with the prime. All categorical targets were related to the prime on the superordinate level (e.g., *bus* and *car* are both members of the superordinate category *vehicles*). All associative targets shared either a functional or a part–whole relationship with the target (we also made sure that the "part" could also exist as an independent object without the "whole"). The categorical and associative prime–target pairs were taken from those used in previous published studies (Sass, Sachs, et al., 2009; Sachs, Weis, Krings, et al., 2008) or were developed for the current study. To ensure that associative and categorical targets had an equally strong and salient relationship with a prime word, 15 pretest participants were asked to rate the relationship between potential associative targets and their primes on a scale from 1 to 7 on the basis of how well they form an external or complementary relationship and co-occur and interact together in space and time. A definition of categories was used to rate the relationship between potential categorical targets and their primes, that is, how similar they are in their perceptual, biological, or func-

tional properties. Based on the results of this pretest, we selected only those associative and categorical targets that scored 5 or higher. The selected associative and categorical targets did not differ in their average rating (M_{assoc} = 6.24, SD = 0.53; M_{cat} = 6.31, SD = 0.46, p = .30). The unrelated targets scored 2 or less on the same test (M_{unrel} = 1.08, SD = 0.12). Nonwords were all pronounceable German words that were constructed by changing one or two consonants in real target words. They were matched to real word targets for word length. All selected stimuli belonged to the same overall conceptual domain (all words depicted only artifacts), were concrete, and imageable (all words were concrete objects that are easy to visualize). The CELEX lexical database (Baayen, Piepenbrock, & Rijn, 1993) was used to control for the average word frequency of German words used in categorical and associative trials (M_{assoc} = 15.50, SD = 28.62; M_{cat} = 23.04, SD = 48.06, p = .24). All stimuli were also controlled for word length (M_{assoc} = 5.80, SD = 1.25; M_{cat} = 5.87, SD = 1.18, p = .42). As described before, the unrelated condition was created by combining target words from the related conditions with different unrelated priming words. This was done so that lexical factors could not influence the results of the study (see Table 1 for examples of the stimuli used in the experiment).

Procedure

An event-related design was used to present associatively related, categorically related, unrelated, and nonword trials in a pseudorandomized order to participants. Four pseudorandomized versions of the experiment (same trials, but in a different succession) were counterbalanced across subjects to avoid a systematic effect of conditions on each other. Each subject received one of the four pseudorandomized versions. Presentation of stimuli was controlled by a computer using the Presentation 10.1 software package (Neurobehavioral Systems; www.neurobs.com/). Subjects lying in the scanner viewed the computer screen through MR-compatible video goggles (VisuaStim XGA, Resonance Technology, Inc.; www.mrivideo.com/).

Each trial started with a fixation cross (800 msec), followed directly by the presentation of the prime word (800 msec). As soon as the prime word disappeared, the target word (or nonword) was presented for 1000 msec, followed by the # sign that was shown for the jittered time

Table 1. Sample Stimuli Used in the Experiment

Associatively Related Condition [English Translation]	Categorically Related Condition [English Translation]	Unrelated Condition [English Translation]	Nonword Condition [English Translation]
Topf–Herd [pot–stove]	Topf–Kessel [pot–kettle]	Topf–Nagel [pot–nail]	Topf–Dalen [pot–dalen]
Jacke–Knopf [jacket–button]	Jacke–Weste [jacket–vest]	Jacke–Flasche [jacket–bottle]	Jacke–Neuz [jacket–neuz]
Schrank–Kleid [wardrobe–dress]	Schrank–Kommode [wardrobe–dresser]	Schrank–Saphir [wardrobe–sapphires]	Schrank–Inster [wardrobe–inster]

range of 2.5–8 sec. Thus, the average intertrial interval was 5000 msec. Subjects had to decide as fast as possible whether the second string of letters was a real word in German or not. They were instructed to press the right button of the parallel port device when the target was a real word in German and to press the left button when the target was not a real word as soon as the target appeared. The pressing was done with the index and middle fingers of the left hand to avoid the motor-related activation in the left hemisphere.

MRI Acquisition

All scanning was performed on a 3-T scanner (Gyroscan Achieva, Philips Medical Systems, Best, The Netherlands) using standard gradients and a circular polarized phase array head coil. For each subject, we acquired two series of functional volumes of T2*-weighted axial EPI scans including five initial dummy scans parallel to the AC/PC line with the following parameters: number of slices (NS), 31; slice thickness (ST), 3.5 mm; interslice gap (IG), 0.35 mm; matrix size (MS), 64×64; field of view (FOV), 240×240 mm; echo time (TE), 30 msec; repetition time (TR), 2 sec.

fMRI Data Analysis

MR images were analyzed using Statistical Parametric Mapping software (SPM2; www.fil.ion.ucl.ac.uk) running on MATLAB 6.5 (Mathworks Inc., Sherborn, MA).

After discarding the first five volumes, all images were realigned to the first image to correct for head movement. Unwarping was used to correct for the interaction of susceptibility artifacts and head movement. After realignment and unwarping, the signal measured in each slice was shifted relative to the acquisition time of the middle slice using a sinc interpolation in time to correct for their different acquisition times. Volumes were then normalized into standard stereotaxic anatomical MNI space by using the transformation matrix calculated from the first EPI scan of each subject and the EPI template. The default settings for normalization in SPM2 with 16 nonlinear iterations and the standard EPI template supplied with SPM2 were used. Afterward, the normalized data with a resliced voxel size of $4 \times 4 \times 4$ mm were smoothed with a 10-mm FWHM isotropic Gaussian kernel to accommodate intersubject variation in brain anatomy. The time-series data were high-pass filtered with a high-pass cutoff of 1/128 Hz. The autocorrelation of the data was estimated and corrected for.

We modeled the expected hemodynamic response at target onset for each event-type (categorically related target, associatively related target, unrelated target, and nonword target). The hemodynamic response was modeled by two response functions, a canonical hemodynamic response function (HRF; Friston et al., 1998) and its temporal derivative. The temporal derivative was included in the model to account for the residual variance resulting from small temporal differences in the onset of the hemodynamic response, which is not explained by the canonical HRF alone. The functions were convolved with the event-train of stimulus onsets to create covariates in a general linear model. Subsequently, parameter estimates of the HRF regressor for each of the different conditions were calculated from the least mean squares fit of the model to the time series. Parameter estimates for the temporal derivative were not further considered in any contrast.

An SPM2 random effects group analysis was performed by entering parameter estimates for all conditions into a within-subject one-way ANOVA. We expected the differences between processing of categorical as opposed to associative categories to be quite small. Still, we were interested in studying effects across the whole brain instead of restricting the search volume to predefined regions of interest. Therefore, we chose to employ Monte Carlo simulation of the brain volume to establish an appropriate voxel contiguity threshold (Slotnick, Moo, Segal, & Hart, 2003). This correction has the advantage of higher sensitivity to smaller effect sizes, while still correcting for multiple comparisons across the whole brain volume. Assuming an individual voxel type I error of $p < .005$ (Sachs, Weis, Zellagui, et al., 2008), a cluster extent of 12 contiguous resampled voxels was indicated as necessary to correct for multiple voxel comparisons at $p < .05$. The reported voxel coordinates of activation peaks were transformed from MNI space to Talairach and Tournoux (1988) atlas space by nonlinear transformations (www.mrc-cbu.cam.ac.uk/Imaging/mnispace.html). This was done to be able to use the Talairach and Tournoux atlas to identify the anatomical brain region for the activation peaks.

RESULTS
Behavioral Data
Accuracy

The percentages of lexical decision errors were entered into repeated measures ANOVA to analyze whether the type of prime–target relationship (associatively related, categorically related, or unrelated) influenced the number of errors made. We found that there was no effect of relationship on the accuracy rates [$F(2, 30) = 2.29$, $p = .12$] with further planned contrasts indicating that there was no difference in the percentage of errors that subjects made in the categorically and in the associatively related condition [$M_{cat} = 2.71\%$, $SD = 2.78\%$; $M_{assoc} = 1.46\%$, $SD = 2.71\%$; $t(15) = 1.69$, $p = .11$]. Incorrect responses were excluded from further analyses.

Reaction Time

Reaction time was measured from the moment the target was presented until the subject made a correct response. Reaction times in the associatively related, categorically related, and unrelated condition were entered into a

repeated measures ANOVA that has shown a main effect of relatedness [$F(2, 30) = 11.54, p < .001$]. Planned contrasts were conducted to calculate associative and categorical priming effects—the difference in the reaction time between unrelated and related conditions. Subjects responded faster in the associatively related than in the unrelated condition [$M_{assoc} = 669.56$ msec, $SD = 54.21$ msec; $M_{unrel} = 714.38, SD = 60.31; t(15) = 4.44, p < .001$], showing a semantic priming effect of 44.82 msec. Responses in the categorically related condition were also faster than responses in the unrelated condition [$M_{cat} = 670.23$ msec, $SD = 56.16$ msec; $M_{unrel} = 714.38, SD = 60.31; t(15) = 4.44, p < .001$], with the categorical priming effect of 44.15 msec. A further t test of priming effect sizes in categorical and associative conditions has indicated that the associative priming effect was not significantly different from the categorical priming effect [$t(15) = 0.092, p = .928$].

Imaging Data

Categorical Priming Effect: Unrelated > Categorically Related

To calculate the categorical priming effect, we subtracted the categorically related condition from the unrelated condition. This contrast revealed one cluster of activation in the right middle frontal gyrus [MFG] (24 voxels). The opposite contrast (categorically related > unrelated) revealed no significant difference. The activations were further investigated by plotting parameter estimates for each one of the conditions. We established that there was a decrease of signal (a deactivation) in the related condition compared to the unrelated one (see Figure 1).

### Associative Priming Effect: Associatively Related > Unrelated

Because the subtraction of associatively related trials from unrelated trials did not yield any areas of activation, we investigated the opposite contrast: associatively related > unrelated. This contrast resulted in one activation cluster in the left IFG (58 voxels). Analysis of parameter estimates in this cluster revealed that there was an increase of activity in the related condition compared to the unrelated one (see Figure 2).

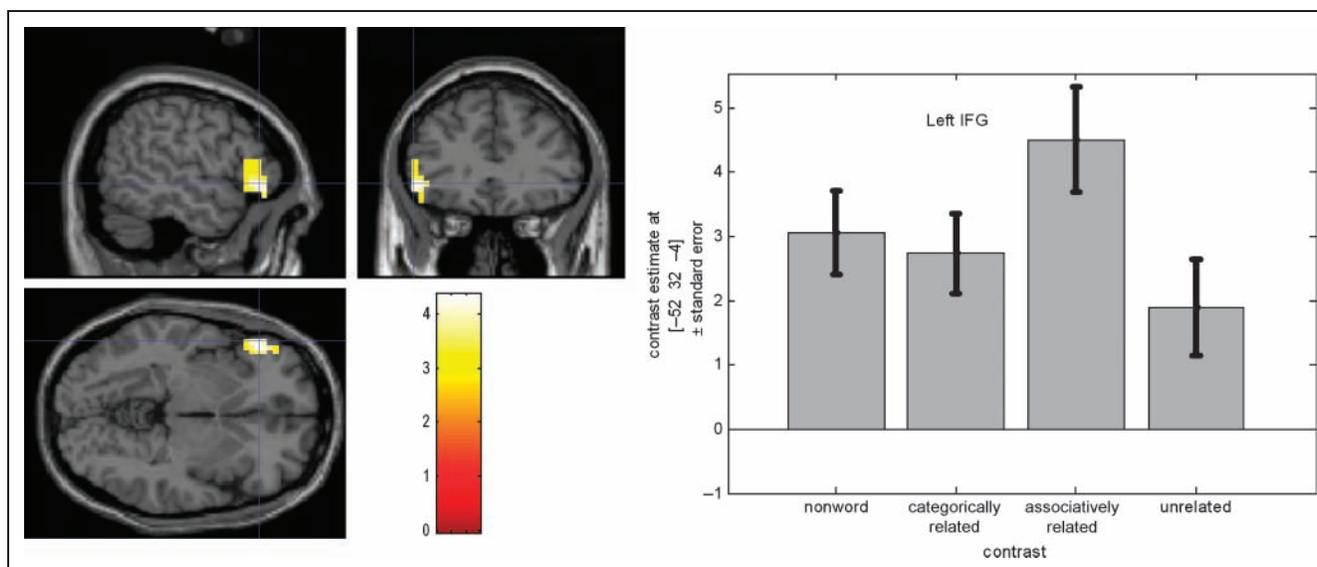### Categorically Related > Associatively Related

A direct contrast between categorically and associatively related trials revealed one activation cluster in the right insular lobe. Only categorically related trials showed increased activation in the right insula lobe, the opposite subtraction (associatively related > categorically related) yielded no difference. Parameter estimates showed that the observed difference resulted from the increase of signal in the categorically related condition and a decrease in the associatively related condition (see Figure 3). Table 2 presents the exact coordinates, statistics, and cluster sizes.

DISCUSSION

The present study addressed the question of whether the type of semantic relationship between words, categorical or associative, plays a role in the neural correlates of semantic priming. We found that prime–target pairs that are categorically related lead to similar behavioral priming effects as the associatively related pairs. However, the
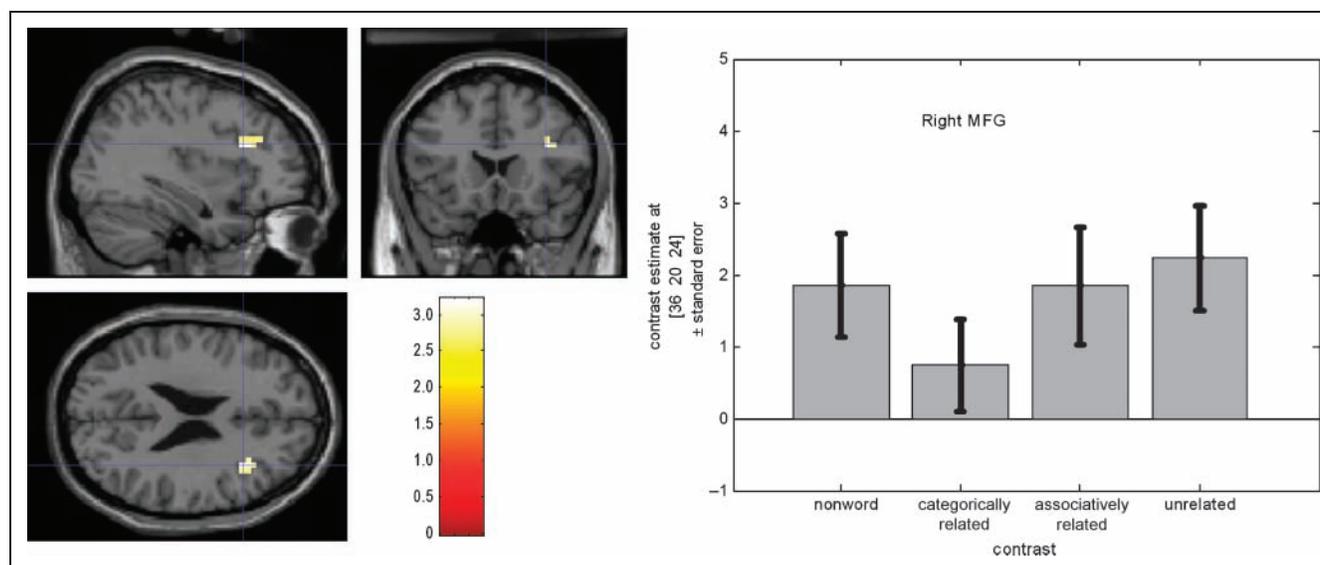
Figure 1. Areas of activation and parameter estimates for the contrast of unrelated prime target pairs minus categorically related prime target pairs. The activation map is shown overlaid onto a selected section of a canonical single-subject T1-weighted volume. The position of the selected section corresponds to the biggest clusters of activation corrected at $p < .05$ across the whole brain. Scale bar shows t values for contrasts. Plots of mean parameter estimates with standard error bars showing response amplitude in the right MFG for each condition: nonwords, categorically related pairs, associatively related pairs, and unrelated pairs. Labeling of the y-axis is in arbitrary units.
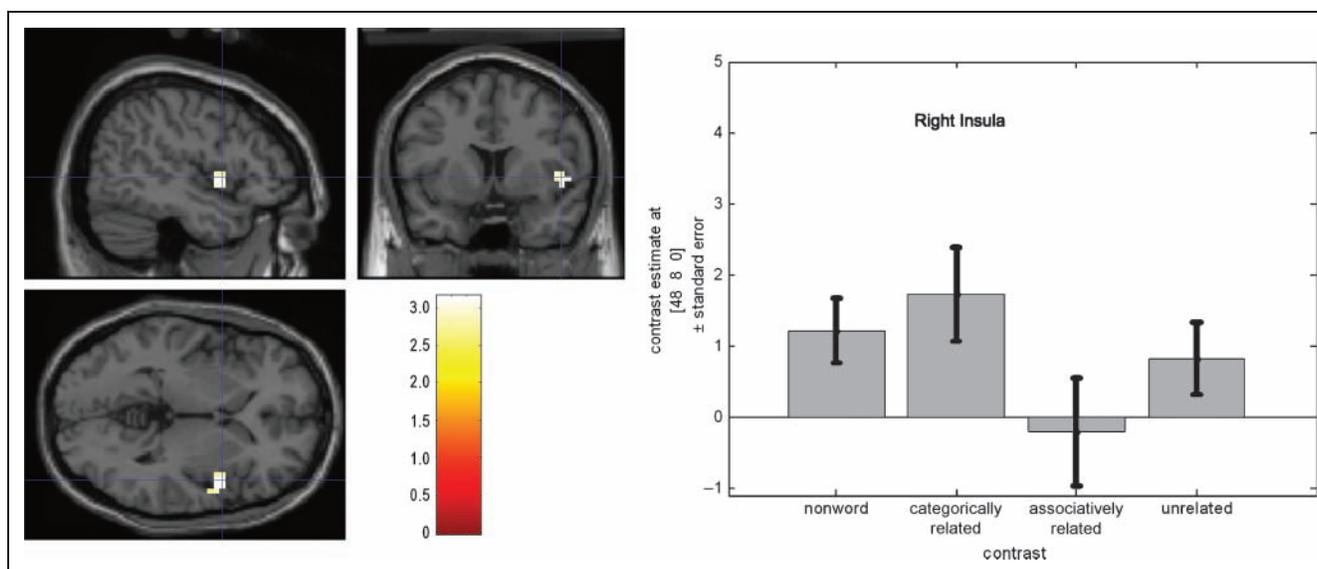
Figure 2. Areas of activation and parameter estimates for the contrast of associatively related prime target pairs minus unrelated prime target pairs. The activation map is shown overlaid onto a selected section of a canonical single-subject T1-weighted volume. The position of the selected section corresponds to the biggest clusters of activation corrected at $p < .05$ across the whole brain. Scale bar shows t values for contrasts. Plots of mean parameter estimates with standard error bars showing response amplitude in the left IFG for each condition: nonwords, categorically related pairs, associatively related pairs, and unrelated pairs. Labeling of the y-axis is in arbitrary units.

neural priming effects associated with categorical and associative priming were different, both regarding their localization in the brain and the type of priming response elicited—suppression or enhancement. Processing of prime–target pairs that are categorically related resulted in the neural suppression effect in the right MFG, that is, pairs such as *couch–bed* produced less activation in the right MFG than unrelated pairs, such as *couch–bridge*. In contrast, associatively related prime–target pairs resulted in response enhancement effect in the left IFG, that

is, pairs such as *couch–pillow* produced stronger activation in the left IFG than unrelated pairs, such as *couch–bridge*. A direct contrast between categorically and associatively related pairs revealed additional activation for categorically related trials in the right insula, whereas the opposite subtraction (associatively related > categorically related) yielded no difference.

Thus, although the processing of categorical and associative semantic relations was not different on the behavioral level, it showed the predicted differences on the

Figure 3. Areas activation and parameter estimates for the contrast of categorically related prime target pairs minus associatively related prime target pairs. The activation map is shown overlaid onto a selected section of a canonical single-subject T1-weighted volume. The position of the selected section corresponds to the biggest clusters of activation corrected at $p < .05$ across the whole brain. Scale bar shows t values for contrasts. Plots of mean parameter estimates with standard error bars showing response amplitude in the right insula lobe for each condition: nonwords, categorically related pairs, associatively related pairs, and unrelated pairs. Labeling of the y-axis is in arbitrary units.

Table 2. Results of fMRI Semantic Priming Effects

Anatomical Region	BA	Coordinates			Z	No. Voxels
		x	y	z		
Unrelated > Categorically Related						
Middle frontal gyrus (R)	8	36 [36]	20 [20]	21 [24]	3.13	24
Associatively Related > Unrelated						
Inferior frontal gyrus (L)	47	−51 [−52]	31 [32]	−5 [−4]	4.16	58
Categorically Related > Associatively Related						
Insular lobe (R)		48 [48]	8 [8]	0 [0]	3.08	18

Significance level and the size of the respective activation cluster (number of voxels) at $p < .05$, corrected.

Coordinates are listed in Talairach and Tournoux (1988) atlas space with MNI coordinates in brackets. BA is the Brodmann's area nearest to the coordinate and should be considered approximate.

neural level. Categorically related prime–target pairs recruited right lateral frontal areas, producing a response suppression effect, whereas associatively related pairs produced a response enhancement effect in the left lateral frontal cortex. This pattern is in line with earlier studies (e.g., Sachs, Weis, Krings, et al., 2008; Sachs, Weis, Zellagui, et al., 2008; Kotz et al., 2002) reporting right hemispheric involvement for categorical relations. Therefore, the suppression might be caused by perceptual and functional similarity of categorically related words. In contrast, associatively related pairs are connected by their external or complimentary relations, requiring a different processing of the related target as response to the (associative) relationship to the prime, thus leading to the response enhancement.

It is important to note that this dissociation was found using priming parameters that encourage controlled processing of the semantic relationship between the prime and the target, allowing for postlexical semantic integration. Copland et al. (2007), who used similar parameters and also found increased activation for the related prime–target pairs in the left IFG, suggest that controlled semantic priming may reflect the conscious detection of semantic relationships between words. This idea is further supported by the fact that response enhancement for associatively related pairs was found in the left IFG, an area associated with the executive control of retrieval and selection from the semantic memory (e.g., Rossell et al., 2003; Cabeza & Nyberg, 2000; Demb et al., 1995), and controlled semantic processing and monitoring (e.g., Schacter & Buckner, 1998). However, this explanation does not account for a reversed pattern of activation that we found under the same experimental conditions for categorically related pairs. Our tentative interpretation of increased activation for unrelated compared to categorically related pairs is that their shared perceptual and functional similarity has led to a greater efficiency during semantic retrieval,

that is, the access to unrelated targets is more demanding and requires more effort in accessing the target word in the semantic memory storage leading to enhanced activation. The role of the right MFG, where this additional activity for unrelated pairs took place, supports this interpretation. This area, particularly in the right hemisphere, has been associated with extensive mental search in the semantic network, higher retrieval effort, and decision uncertainty (Sass, Sachs, et al., 2009; Kuperberg, Lakshmanan, Greve, & West, 2008; Sachs, Weis, Zellagui, et al., 2008; Tivarus, Ibinson, Hillier, Schmalbrock, & Beversdorf, 2006; Kotz et al., 2002; Rugg & Wilding, 2000; Grabowski, Damasio, & Damasio, 1998). Furthermore, this is in line with the sensory-functional hypothesis of Warrington and Shallice (1984), as categorical relations share a greater perceptual similarity than associations. In addition, response enhancement is thought to reflect the cognitive processes that index the spread of activation (Henson, 2003). This spread of activation occurs between connected words and "can […] be viewed as indication of changes in the mental lexicon, but only as far as the activation level on a lexical node is concerned" (Heim, Eickhoff, Friederici, & Amunts, 2009). To sum up, in line with our hypotheses, we found response suppression for categorically related words reflecting the consequence of priming (Henson, 2003) that might occur specifically for category members, that is, it might be easier to process similar-looking objects that recruit similar processing routes and, therefore, it is easier to process related than unrelated targets. Associations led to response enhancement reflecting the spread of activation between connected nodes and the perceptual dissimilarity between prime and target, that is, they are processed differently requiring different processing routes, resulting in enhanced activation for related in comparison to unrelated word pairs. An alternative explanation for our findings might be that the activation of the IFG is related to an integration of lexical information that is

retrieved from the mental lexicon [i.e., to detect the relationship between associatively related items, it is necessary to "construct" the relation between the prime and the target (semantic unification; Hagoort, 2005]. In contrast, as categorically related items are conceptually related and activate overlapping semantic areas, this process might not be required for categorical relations.

In contrast with most other fMRI studies of lexical priming, the present results did not show activation of areas in the left temporal lobe. This could be caused by several factors. First, priming effects could be quite small. To enhance effects, it is possible to restrict the search volume to predefined regions of interest, but in the current study, we were interested in studying the whole brain. Therefore, the absence of temporal activity might be due to our design, the small effects, and the whole-brain analysis. Second, we still found activation of the left IFG for associations, a region typically implicated by the majority of semantic priming studies. Hence, our study highlights the role of the IFG during controlled semantic priming. Third, the use of categorically and associatively related stimuli within one session could lead to specific influences on each other. For example, in an earlier study (Sachs, Weis, Krings, et al., 2008), we found that a right hemispheric network including the right MFG is recruited when subjects made a categorical choice in the presence of associative alternatives, that is, constructing "categorical" categories requires activation of right frontal areas. In addition, the activation of right frontal areas was found to be implicated in the processing of abstract nouns and verbs (Grossman et al., 2002; Perani et al., 1999), leading to the conclusion that forming categories "requires assessing a more abstract relationship between the target and the matchword." This process can also be more effortful and require the "recruitment of the right hemisphere" (Sachs, Weis, Zellagui, et al., 2008). Finally, other studies hypothesized that right frontal regions reflect the processing of categorical relations (Sachs, Weis, Krings, et al., 2008; Sachs, Weis, Zellagui, et al., 2008; Kotz et al., 2002). These studies suggest that activations in the right frontal regions reflect the perceptual similarity between categorically related items (sensory-functional hypothesis; Warrington & Shallice, 1984) and the more effortful processing of categorical in comparison to associative relations (e.g., Kotz et al., 2002; Beeman et al., 1994; Chiarello & Richards, 1992). In sum, we found activation of the left IFG for associations—a typical region found by several earlier semantic priming studies—reflecting the processing and integration of semantic information. Furthermore, when comparing categorical and associative relations, it seems plausible to expect the right frontal activation in response to categories rather than classical left fronto-temporal regions. Our results therefore support earlier studies that also found right hemispheric involvement.

Thus, our results suggest that controlled processing of categorical and associative semantic relations may involve qualitatively different neural mechanisms, accounting for diverse findings that so far emerged from the semantic priming literature. The difference between categorical and associative relations is further highlighted by our finding of increased activation for categorically related pairs in the right insula when directly contrasted with associatively related pairs. This region is associated with high working memory load and attentional components (Sabb, Bilder, Chou, & Bookheimer, 2007), leading to the conclusion that it is not specific to lexical–semantic processing alone (Gold et al., 2006). We assume that categorical relations induce postaccess search strategies (Chwilla & Kolk, 2002; Balota & Lorch, 1986) and necessitate additional attentional demands when compared to the associative relations. This conclusion is supported by the fact that the right hemisphere is assumed to maintain more diffuse semantic activations of a broader semantic field (Jung-Beeman, 2005; Kircher, Brammer, Tous Andreu, Williams, & McGuire, 2001; Beeman & Chiarello, 1998). Because categories might be held together by a more abstract relationship between the prime and the target, recruitment of the right frontal areas is required (Sachs, Weis, Krings, et al., 2008). Overall, we hypothesize that the right hemispheric activation (frontal and insula) is necessary to compensate for a less efficient routine in recognizing categorical relations in comparison to associations and, therefore, the processing of categorical relations seems to be more effortful (Sass, Sachs, et al., 2009; Kotz et al., 2002).

In summary, our study provides novel evidence for the role played by the type of semantic relationship in the neural correlates of semantic priming, elicited under controlled processing conditions (i.e., SOA of 800 msec). When other factors, such as overall conceptual domain, word frequency, and the strength of semantic relation are controlled for, differences were found between categorical and associative priming effects. Categorically related pairs resulted in response suppression in the right MFG, whereas associatively related pairs lead to response enhancement in the left IFG, all of this in the absence of any behavioral dissimilarity between the two types of priming relations. This finding begins to account for the widely diverging results of fMRI semantic priming studies that have hardly controlled for the type of semantic relationship shared by the stimuli. In addition, these differences might be parametrical rather than absolutely distinct. The parameter estimate of the right MFG (Figure 1) is graded, that is, the response suppression is stronger for categorical primes but also, in tendency, present for associative primes. Similarly, the response enhancement in the left IFG is biggest for associative primes, but also present for categorical primes (Figure 2). Therefore, it does not seem to be the case that only categorically related items share surface features, whereas associatively related items do not, but rather they do so to a different degree, that is, specific influences might be relevant for the kind of signal changes in the brain (e.g., perceptual similarity). Moreover, our results set up new questions for further research: What exactly are the mechanisms relating conceptual

relationship and neural response enhancement and suppression effects? What is the relationship between behavioral and neural priming effects? Does increased activation imply more effort/higher integration load? Answering these questions will help us understand not only the neural mechanisms behind semantic priming but also the general issue of how word meanings are organized and connected to each other in the brain.

Acknowledgments

Reprint requests should be sent to Katharina Sass, Department of Psychiatry and Psychotherapy, RWTH Aachen University, Pauwelsstr. 30, D-52074 Aachen, Germany, or via e-mail: ksass@ukaachen.de.

Note

1.   It is important to note that taxonomic categories often referred as "categorically" related concepts and thematic categories as "associates." In the current study, we predominantly used the terms "categorical" and "associate" relations according to the more common way in neuroimaging literature.

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