

The functional neuroanatomy of morphology in language production

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ABSTRACT

The present study investigated the neural correlates of morphological priming in overt Dutch language production using a long-lag priming paradigm. Compound words were read out loud as primes that were morphologically related to picture names (e.g. the word *jaszak*, 'coat pocket' was used for a picture of a coat; Dutch *jas*), or primes were form-related, but not morphologically related monomorphemic words (e.g. *jasmijn*, 'jasmine'). The morphologically related compounds could be semantically transparent (e.g. *eksternest*, 'magpie nest') or opaque (e.g. *eksteroog*, lit. 'magpie eye,' 'corn,' for a picture of a magpie, Dutch *ekster*). These four priming conditions were complemented by two matched, unrelated conditions. The production of morphologically related, complex words but not the production of form-related words facilitated subsequent picture naming. Also, morphologically related but not form-related words led to a neural priming effect in the left inferior frontal gyrus (LIFG). The effects did not differ for transparent and opaque relations. The results point to a functional role of LIFG in morphological information processing during language production contrary to previous meta-analytic findings. Specifically, morphological priming effects in language production seem to be independent from semantic overlap. However, further research should confirm the independence of morphological and phonological factors. It is suggested that LIFG subserves word form encoding in language production.

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Introduction

Language is a characteristic feature of all humans (Hockett, 1960) and comprises largely of structured sequences of words, the building blocks of sentences. Words, in turn, comprise often times of structured sequences of morphemes. The former regularities are part of syntax; the latter are described in morphology, which deals with the internal structure of words.

Recognizing the structure of morphologically complex words is essential for meaning construction. For example, when hearing the word "worthless," the listener can apply the morphological structure *adjective* + *suffix* to understand "worthless" as indicating an entity of no significant value. In contrast, when hearing "worth less" (e.g. in a comparative sentence; "X is worth less than Y"), the listener should not apply the same morphological structure but interpret the utterance as an expression of relative value referring to two entities denoted by X and Y.

Here, we are interested in the functional neuroanatomical correlates of morphological priming in overt language production.

Compound words (e.g. coat + pocket) are concatenations of free morphemes and have an internal structure. In the present study, such compounds were used to prime the process of naming pictures in Dutch, an Indo-European language. The internal structure is hierarchical in that one constituent morpheme, the last in Dutch, determines the morphosyntactic features and the semantic category of the whole compound (Booij, 2002a; Downing, 1977). The crucial question was whether and where in the human brain morphological overlap between the compound words and the picture names would affect picture naming. To our knowledge, there is no study investigating morphological compound processing in speaking by means of functional magnetic resonance imaging (fMRI).

Language production is thought to involve a sequence of four major cognitive processes: conceptual preparation, lexical access, phonological processing, and articulation (Caramazza, 1997; Dell, 1986; Garrett, 1988; Levelt, 1989; Levelt et al., 1999). Conceptual preparation refers to the activation of the concepts that relate to the intended utterance—when naming a picture, the concept of the depicted object. The conceptual activation spreads to associated lexical representations. Next, word form encoding follows, i.e. phonological information needed for pronunciation is processed. The phonological word form is finally used for articulation by calling up the corresponding gestural scores. For the production of

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morphologically complex words, it has been suggested that these words are not planned as one chunk. Rather, they are planned serially, one morpheme after the other (Roelofs, 1996; Levelt et al., 1999). This construction of complex words from separately stored morphemes (or word stems in the case of compounds) is called the decompositional view of word production, and it has been proposed to be purely morphological, that is, without a contribution of semantic information (Roelofs and Baayen, 2002). In contrast to the decompositional view, other researchers proposed that morphologically complex words are not composed from their constituent morphemes during speaking, but rather stored and retrieved as whole units (so-called *full-listing hypothesis*; Butterworth, 1983; Bybee, 1995; Janssen et al., 2008).

Even though details of the architecture of the language production system are still debated (e.g. to what extent activation flow is cascading rather than discrete; Damian and Bowers, 2003; Jescheniak et al., 2002, 2009; Levelt, 2001; Morsella and Miozzo, 2002; Navarrete and Costa, 2005; Roelofs, 2003), it should be noted that morphological encoding follows lexical selection (Levelt et al., 1999). Accordingly, morphological structure has been allocated at the word form level (Zwitserslood et al., 2000). In terms of functional neuroanatomical localization, morphological information has been suggested to play a role in the first sub-stage of word form encoding (Indefrey and Levelt, 2004).

In a recent meta-analysis of behavioral and fMRI studies of language production, Indefrey and Levelt (2004) assessed the brain areas functionally associated with different cognitive processing stages in language production. However, the neuroanatomical correlates of morphological priming remain controversial. Based on this meta-analysis, phonological code retrieval has been localized in the left posterior superior and middle temporal gyri (so-called *Wernicke's area* together with the right supplementary motor area and the left anterior insula; Indefrey and Levelt, 2004). Since morphological information should affect the first sub-stage of phonological code retrieval, it can be predicted that morphological priming should affect neural activity in the left posterior superior and middle temporal gyri (cf. Roelofs, 2008).

Relevant studies that investigated language production – overt or covert – examined diverse inflectional mechanisms such as plural formation of nouns or first and third person verb generation (e.g. Beretta et al., 2003; Jaeger et al., 1996, 1998; Joanisse and Seidenberg, 2005; Lo Gerfo et al., 2008). The comparison and interpretation of these studies are complicated because of different methodologies and because inflectional processes may involve syntactic operations, for example related to grammatical agreement constraints (Selkirk, 1982; Di Sciullo and Williams, 1987). Since these studies presented linguistic materials to elicit a verbal response, the results may be unspecific as to whether they reflect processes of comprehension or production. Other imaging studies of pure language production, i.e. studies that avoided additional influences from comprehension processes were not concerned with morphological processes (e.g. Abel et al., 2009; De Zubicaray and McMahon, 2009; Heim et al., 2002, 2009; Kan and Thompson-Schill, 2004).

There is also imaging evidence about the processing of derivations in the comprehension domain, which may inform the present investigation because compounding and derivation are considered the core mechanisms of word formation. Devlin et al. (2004) investigated lexical priming and its neural substrate in a visual masked priming paradigm. When comparing form-related word pairs (e.g. corner–corn) with unrelated word pairs, neural priming occurred in the left occipito-temporal cortex. Pure semantic overlap (e.g. idea–notion) yielded a priming effect in the left middle temporal gyrus. Critically, morphologically related pairs (e.g. boldly–bold; with overlap in form and meaning) led to neural priming with an almost complete overlap in the left occipito-temporal and middle temporal areas found for pure form and semantic overlap. Based on these

results, it has been suggested that morphology emerges from the convergence of form and meaning processing (Devlin et al., 2004; see also Joanisse and Seidenberg, 2005 for inflectional morphology). Others found no effect when comparing the reading of morphologically simple and complex words, besides a word class effect (verbs vs. nouns/adjectives; Davis et al., 2004). Such results argue against an independent representation of morphological information in reading (but see Gold and Rastle, 2007).

Others investigated neural correlates of morphological priming in unmasked single word reading in English (Bozic et al., 2007). These authors used a long-lag priming paradigm in which the prime word preceded the target word by a number of intervening trials (see below). An enhanced neural response was found in the left inferior frontal gyrus (LIFG; BA 47) but no effect in the left occipito-temporal cortex when comparing the hemodynamic response for morphologically complex with simple words. Here, the neural activation for the morphologically complex words did not differ between semantically transparent (e.g. hunter) and semantically opaque words (e.g. corner).¹ However, when comparing the hemodynamic response for the prime and the target words, Bozic et al. (2007) found reduced activation in LIFG only for semantically transparent (e.g. hunter–hunt) and opaque (e.g. corn–corner) pairs which were proposed to be morphologically complex but no difference was found for form-related (e.g. scandal–scan) or purely semantically related pairs (e.g. accuse–blame). Consistent with these results, Meinzer et al. (2009) reported an involvement of the left BA 47 for the reading of German derivations that are morphologically complex. Interestingly, these authors reported an increased activity in the LIFG and left posterior middle temporal gyrus (MTG) for more complex vs. less complex derivations. Generally, these data are consistent with a role of the LIFG in morphology and morphosyntax (Marangolo et al., 2006; Marslen-Wilson and Tyler, 1998; Tyler et al., 2002, 2004; Ullman, 2001; Laine et al., 1999). Note that BA 47 is traditionally not considered to be part of Broca's area, which has been related to syntactic, phonological and semantic processing (Dronkers et al., 2007; Lindenberg et al., 2007; see Hagoort, 2005 for an alternative definition of Broca's complex).

In contrast to these comprehension studies, which mostly used meta-linguistic tasks, we are interested in morphological priming during language production. In order to avoid a meta-linguistic task and potential influences from comprehension processes, a long-lag priming paradigm was used. Prime words, i.e. compounds in our case, had to be read aloud and, seven to ten trials later, pictures (i.e. targets) had to be named overtly. That is, during a given trial only one stimulus, a word or a picture, is shown on the screen. Thus, picture naming does not coincide with reading the prime words. Importantly, when semantic, phonological and morphological priming effects in the long-lag paradigm were compared to the corresponding effects in the picture–word interference paradigm, only morphological priming effects were obtained in the long-lag paradigm (Zwitserslood et al., 2000). In contrast, in the picture–word interference paradigm, semantic, phonological and morphological effects were obtained with the same stimuli suggesting that morphological but neither semantic nor phonological effects survive an inter-trial lag of seven to ten trials. That is, effects observed in the long-lag priming paradigm cannot be explained by semantic or phonological relations between primes and targets (Feldman, 2000; Zwitserslood et al., 2000).

The paradigm's sensitivity to morphological priming of by means of compound words has been demonstrated in behavioral and electrophysiological studies (Koester and Schiller, 2008; Dohmes et al., 2004). Investigating the event-related brain potentials (ERPs) in a long-lag

¹ Words with pseudo-affixes, such as “corner” or “reason” are sometimes said to have an *apparent* morphological structure (e.g. Lavric et al., 2007; Rastle et al., 2004) or to be semantically opaque (e.g. Bozic et al., 2007). An automatic decomposition mechanism during reading would decompose these words incorrectly calling for some form of repair (Sandra, 1990; Taft, 2004).

paradigm yielded N400 effects for morphologically primed target utterances (Koester and Schiller, 2008). The onsets of the N400 effects closely matched the predicted onset of word form encoding (Indefrey and Levelt, 2004). Thus, the effects were taken as support for the paradigm's potential to trace morphological information processing in language production (i.e. the first sub-stage of word form encoding).

Based on the decompositional view of word production (Roelofs, 1996; Levelt et al., 1999) and previous findings (Meinzer et al., 2009; Bozic et al., 2007), we expect morphologically primed picture naming to affect neural processing in the LIFG but no neural priming effect for form-related prime–target pairs. In addition, morphological priming should not be modulated substantially by the semantic relation between prime and target. A recent language production study using a standard paradigm (picture–word interference) reported increased neural activity for both inhibitory and facilitatory behavioral effects (Abel et al., 2009; cf. also Spalek and Thompson-Schill, 2008). Based on these findings, we expected an increased hemodynamic response in BA 47. Additionally, the meta-analysis on the localization of language production processes and the study by Meinzer et al. led to the prediction of a neural priming effect in the left posterior MTG (BA 21; Indefrey and Levelt, 2004; Meinzer et al., 2009). To test these predictions, anatomically defined regions-of-interest (ROIs) were defined a priori based on the above-mentioned studies.

Materials and methods

Participants

Twelve right-handed native speakers of Dutch, all female, participated for monetary compensation in the experiment. They were on average 21.6 years of age (range: 19–29). All participants had normal or corrected-to-normal visual and auditory acuity and none reported a history of neurological disorder. Since there are very few studies available regarding the functional neural correlates of morphological priming in language production, we tested only one gender group to avoid potential gender differences (Gur et al., 2000; Baxter et al., 2003). Participants gave written informed consent, and the local ethics committee approved the study.

Materials

In two separate sets of stimuli, the morphological, semantic and phonological overlap was manipulated among the experimental conditions. In the critical conditions (transparent, opaque and form-related), the targets differed in their morphological and semantic overlap with the primes. In Set 1, the critical conditions (transparent and opaque) differed in semantic overlap but both overlapped morphologically. In Set 2, the critical conditions (transparent and form-related) differed semantically and morphologically. Comparable priming effects for the transparent and opaque conditions (Set 1) would indicate a morphological process because in both conditions primes and targets are morphologically but only one is semantically related. Different priming effects between these conditions suggest an additional influence of semantic information. A sole priming effect in the transparent condition (Set 2) would suggest a morphological process. Reliable priming effects of the same magnitude for the form-related and transparent conditions would indicate a phonological process because in both conditions primes and targets overlap phonologically. Note that we did not manipulate semantic and form overlap factorially as in previous studies (Devlin et al., 2004, 2006; Gold and Rastle, 2007).

The materials consisted of 72 black and white line drawings of common concrete objects, thirty-six for each of the two sets of stimuli (adapted from Snodgrass and Vanderwart, 1980). For both sets, each drawing was combined with three words as primes. Each drawing of Set 1 was combined with two Dutch noun–noun compound words. Both compounds contained the picture name as one constituent. One

of the two compounds was semantically related to the picture name (semantically transparent) whereas the other compound was not semantically related to the picture name (semantically opaque). For example, *eksternest* ('magpie nest') is semantically related to the picture name *ekster* but *eksteroog* ('corn') is not. All compounds in Set 1 were morphologically related to the picture name. Each drawing was also paired with a phonologically and semantically unrelated control word. Regarding Set 2, each picture was combined with a semantically transparent noun–noun compound and a form-related word that contained the full picture name form wise; the form-related words were not morphologically related to the picture names. For instance, the picture of a coat (*jas* in Dutch) was paired with the compound *jaszak* ('coat pocket') and with the morphologically unrelated, monomorphemic word *jasmijn* ('jasmine'). While both words had the same phonological overlap with the picture name, only the transparent compounds were morphologically related to the picture names. Again, each picture was also paired with a phonologically and semantically unrelated control word.

The semantic transparency of the stimuli was assessed by a group of twelve students (4 male) who did not participate in the study. They rated the semantic relation between the compounds and the corresponding picture names (e.g., *ekster*) on a 4-point scale (1 = unrelated; 4 = related). Opaque compounds (e.g., *eksteroog*) were rated as being less related (1.7) than transparent compounds (e.g., *eksternest*) from Set 1 (3.7) or Set 2 (3.8; $t(11) = 19.4$; $p < 0.001$ and $t(11) = 17.0$; $p < 0.001$, respectively).

The three priming conditions in both sets were matched for frequency, number of syllables, and number of phonemes (Table 1). Within each set, the same pictures served as targets for naming in all conditions. Therefore, picture naming is not confounded with other stimulus variables. Small differences among the prime characteristics that could not completely be avoided (e.g. number of phonemes of form-related and transparent compounds in Set 2) are highly unlikely to cause any measurable effect because primes preceded targets by 7–10 trials. Previous research demonstrated that phonological and semantic priming does not survive such a lag (Feldman, 2000; Koester and Schiller, 2008; Zwitserlood et al., 2000).

Morphological facilitation has been suggested to be independent of position of overlap (Zwitserlood et al., 2002). Therefore, compound–picture pairs were allowed to overlap either in the first or the second constituent. In Set 1, the picture names overlapped with the primes' initial constituents in 33% of the transparent and 39% of the opaque compounds. In Set 2, the picture names overlapped with the primes in 53% of the transparent compounds with the initial constituent and in 69% of the form-related words with the initial syllable. The onset of overlap in form-related words was always aligned with a syllable

Table 1

Stimulus characteristics for both sets of stimuli. (Frequency of occurrence—per one million; average begin of overlap in syllable position (average syllable number where picture names began to overlap with prime words); average inter-trial lag, i.e. the average number of trials between primes and targets; semantic relatedness judgments, 1–4). See also text.

	Frequency	Syllables	Phonemes	Begin of overlap	Inter-trial lag	Semantic relatedness
<i>Set 1</i>						
Targets	83	1.3	3.9	n/a	n/a	n/a
Primes						
Transparent	2.7	2.4	7.5	1.7	8.4	3.7
Opaque	2.7	2.6	8.0	1.6	8.4	1.7
Unrelated	2.8	1.9	5.0	n/a	8.4	1.1
<i>Set 2</i>						
Targets	67	1.0	3.2	n/a	n/a	n/a
Primes						
Transparent	2.9	2.5	7.2	1.6	8.4	3.8
Form-related	3.7	2.2	6.1	1.4	8.4	1.1
Unrelated	3.4	1.6	4.6	n/a	8.4	1.0

boundary. Another 36 comparable pictures were paired with three semantically and phonologically unrelated words each (in total 108 word–picture pairs) and used as filler items.

Experimental design and procedure

The 36 prime–target pairs per condition were presented together with 108 word–picture pairs as filler items distributed across four runs of equal length (cf. Fig. 1). The items were presented in a blocked-design. Blocks of six primes and six targets were constructed such that there was no phonological or semantic relation among the targets in a given block. Blocks of primes were separated from blocks of targets. All blocks lasted 24 s. The order of primes and corresponding targets within pairs of blocks was moderately varied in order to decrease predictability. There were six (target) blocks for every condition containing only pictures. Target blocks were always framed by four null events, i.e. fixation-only (two preceding and two following the target block). Filler items (words and pictures) were distributed only around prime blocks with a maximum of three successive filler items. Prime blocks contained only words but adjacent fillers could also be pictures. The order of prime–target block pairs was pseudorandom with no immediate repetition of any condition. As a consequence, the repetition of target pictures was randomized across participants. Each picture was presented three times during an experimental session, once for every priming condition. Each participant received a different block order.

Behavioral and (f)MRI data were acquired in two sessions, which were structurally identical with slightly varying response instructions. In the behavioral session, participants were instructed to read aloud

words and to name pictures as quickly and accurately as possible. During the fMRI data acquisition, participants had to give their verbal responses (reading and naming) when the scanner noise paused (approximately 2 s after stimulus presentation). Silent periods during the fMRI runs resulted from the bunched-early sequence (see section *fMRI data acquisition*). This delayed naming during scanning permitted the recording of participants' verbal responses and reduced motion artifacts that may result from speaking (Heim et al., 2006). As a pragmatic consequence, the trial duration of 4 s during the fMRI session could be set to 2 s during the behavioral session. Before the behavioral data acquisition, participants were familiarized with the pictorial stimuli. For this purpose all pictures were presented in a random order on the computer screen together with their corresponding names. Next, participants received 40 practice trials (20 word–picture pairs) not used in the experimental sequences. The behavioral session consisted of four blocks similar to the four runs in the fMRI session and was performed in a dimly lit and soundproof room. Participants received different stimulus sequences in the two sessions. The behavioral session lasted for about 30 min and preceded the (f)MRI session which lasted for about 60 min. Both sessions were separated by at least 30 min.

In each trial, a fixation cross was presented for 250 ms followed by a blank screen for 250 ms. After the blank screen, a word or a picture (white on black background; cf. Fig. 1) was presented in the center of the screen for 400 ms. Reaction times in the behavioral session were measured relative to the onset of picture presentation. The trial duration was set to 2 s in the behavioral session and to 4 s in the fMRI session. The fixation cross presentation was temporally jittered in 4 levels; it was presented after 0, 100, 200, or 300 ms in the behavioral and after 0, 250, 500, or 750 ms in the fMRI session. Jittered presentation times were used to reduce predictability of next trial's onset. Jitter levels and trial duration were reduced in the behavioral session compared to the fMRI session to counteract a very low presentation rate and a potential reduction in participants' sustained attention. No feedback was provided during the experiment. The stimulus presentation and the vocal recordings were controlled by Presentation® software (version 9.13; www.neuro-bs.com).

fMRI data acquisition

Structural and functional MRI was performed on a Siemens Magnetom Allegra scanner with a magnetic field strength of 3.0 T. Functional data were collected with an echo planar imaging sequence in 32 transversal slices in an interleaved fashion (with no inter-slice gap; repetition time [TR]=4000 ms; echo time [TE]=30 ms; flip angle = 90°; slice thickness = 3.5 mm; field of view [FoV]=224 mm; in-plane resolution = 3.5 × 3.5 mm). Single volumes were acquired within the first 2000 ms of each TR. Participants were instructed to respond during the remaining 2000 ms in which no data acquisition took place. Each run began with presentation of the instruction (for 2 TRs) and 2 additional filler trials to allow for magnetic saturation. High-resolution anatomical images were collected using a T₁-weighted 3D-MPRAGE sequence (TR = 2250 ms; TE = 2.6 ms; flip angle = 9°; slice thickness = 1 mm; FoV = 256 mm; voxel resolution = 1.0 × 1.0 × 1.0 mm) covering the whole brain between the second and third functional runs. Participants wore earplugs and headphones for hearing protection and head motion was restricted by foam pads (Heim et al., 2006).

Data analyses

For the behavioral analyses, six word–picture pairs were discarded (e.g., 'donkey', 'kat', 'cat', 'parel', 'pearl' and 'wagen', 'vehicle' from Set 1; 'klink', 'door handle' and 'lam', 'lamb' from Set 2) because more than half of the participants responded incorrectly to these pictures. Mean picture naming latencies were submitted to by-participant (*F*₁) and

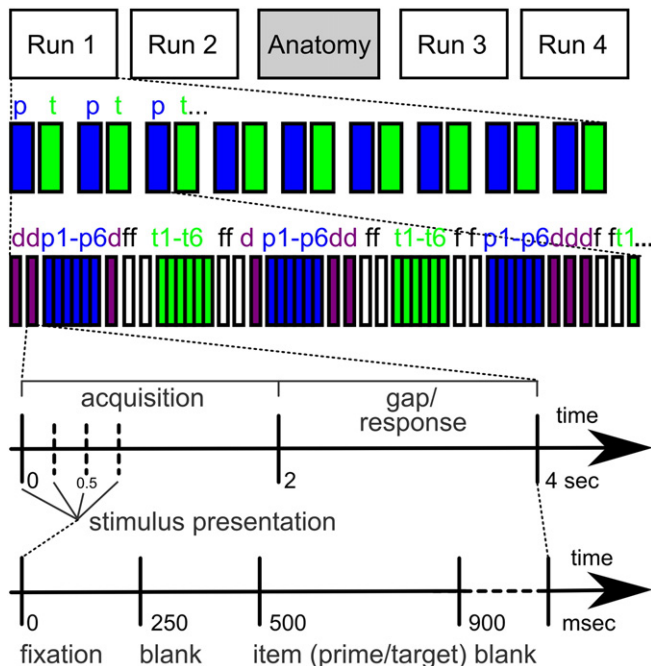


Fig. 1. Schematic illustration of the blocked-design. The experiment consisted of four functional runs with a structural scan between runs two and three. Each run contained 18 blocks, i.e. nine prime–target block pairs; primes (p) in blue, targets (t) in green. Two runs comprised of all three conditions from one set of stimuli; the other two runs comprised of the three conditions from the other stimulus set (counterbalanced across participants). Thus, there were 18 block pairs for each stimulus set which resulted in 6 block pairs per condition (three per set). Each block pair included 12 stimuli (6 primes and 6 targets) corresponding to 36 target stimuli per set. Prime blocks (p1–p6) were preceded and followed by a variable number of max. three filler items (d = distracter, purple) which could be words or pictures. Target blocks (t1–t6) were 'framed' by four fixation scans (f, white). Each volume acquisition took 2 s and was followed by 2 s of silence in which participants should respond to the stimuli. Stimulus presentation was jittered (0, 250, 500, 750 ms after the begin of volume acquisition). Only target blocks were analyzed. See also text.

by-item (F_2) repeated measurement ANOVAs with the factor Prime Type (3). Differences in mean RTs were evaluated in by-participant (t_1) and by-item (t_2) t -tests. Original degrees of freedom and Greenhouse–Geisser corrected p -values are reported where appropriate. Trials involving incorrect responses (9.8%) were excluded from the analyses.

Offline fMRI data analysis was performed using MATLAB 7.2 (<http://www.mathworks.co.uk/>) and SPM5 (<http://www.fil.ion.ucl.ac.uk/spm/>). The first 4 volumes of each functional run were discarded to minimize T1-saturation effects. Pre-processing included the standard procedures of realignment (rigid body transformation of all volumes to the first volume), co-registration with the corresponding structural MR images for normalization to the Montreal Neurological Institute (MNI) space. Subsequently, the functional MR images were spatially smoothed with an isotropic 3D Gaussian filter kernel of 10 mm full-width at half maximum (Xiong et al., 2000). Head movements were below 3 mm for all translation and below 3° for all rotation parameters; one participant showed a head movement of 8 mm along the Z-axis and 8° rotation (pitch) of which 4 mm translation and 3° rotation occurred in one block break, i.e. not during functional scans.

The fMRI data were statistically analyzed in a two-step approach using the general linear model (Friston et al., 1995). At the participant level ($N=12$), all picture presentations according to the six experimental conditions were included as explanatory variables and modeled as separate events with a duration of one TR before they were convolved with the canonical hemodynamic response function. That is, only overt naming responses (target blocks) were analyzed. Each participant's movement parameters (translation and rotation) from the motion correction algorithm were included as regressors of no interest to account for small head movements. At the group level, the average activation levels (beta weights) were entered into a random effects analysis. The estimated activation levels per participant and condition were tested in paired t -tests ($df=11$) in the a priori constructed, i.e. independently of the results defined ROIs. Each item set was tested for an overall priming effect (primed vs. unprimed conditions). In subsequent analyses, it was determined between which conditions within an item set a priming effect occurred. All local maxima are reported as MNI coordinates.

Region of interest analyses

As laid out in Introduction, a priming effect may be expected for the LIFG (BA 47) and left posterior MTG (BA 21). Consequently, a region of interest (ROI) analysis was performed in the LIFG and the left posterior MTG. The ROIs for left BA 47 and left BA 21 were defined anatomically using the WFU PickAtlas (Lancaster et al., 2000; Maldjian

et al., 2003, 2004). The data were thresholded at $p<0.001$ (uncorrected) and the significance level was set to $p=0.05$ when correcting for multiple comparisons (FWE).

Whole-brain analyses

Furthermore, a whole-brain analysis was performed at a more lenient threshold to test whether the priming conditions activated other regions differentially. Here, the results of the random effects analysis were thresholded at $p<0.01$ (uncorrected). Given this intensity threshold, an activated cluster would need to comprise of 1350 adjacent voxels in order to reach a corrected alpha level of $p<0.05$ at the cluster-level (correction for multiple comparisons; Poline et al., 1997).

Results

Behavioral data

The behavioral data, obtained outside the scanner, are shown in Table 2. The overall error rate was 9.8%. RTs were analyzed with a one-way ANOVA (3 levels) for Set 1 and showed a main effect of Prime Type ($F(1,22)=16.4$, $p<0.001$, $\varepsilon=0.89$; $F(2,62)=5.1$, $p<0.05$, $\varepsilon=0.73$). Subsequent t -tests revealed that picture naming was significantly facilitated when preceded by morphologically related primes in comparison to unrelated primes irrespective of whether related primes were semantically transparent ($t(11)=6.5$, $p<0.001$; $t(31)=2.4$, $p<0.05$) or opaque ($t(11)=3.6$, $p<0.01$; $t(31)=3.2$, $p<0.01$, both one-tailed). The transparent and the opaque conditions did not differ from one another (both $ts<1.5$; ns).



For Set 2, the same one-way ANOVA yielded a main effect of Prime Type ($F(1,22)=5.4$, $p<0.05$, $\varepsilon=0.98$; $F(2,66)=3.4$, $p<0.05$, $\varepsilon=0.88$). Subsequent t -tests showed that semantically transparent primes facilitated picture naming only marginally ($t(11)=1.6$, $p=0.07$; $t(33)=1.5$, $p=0.08$, one-tailed). In contrast, form-related primes did not facilitate picture naming (both $ts<1.7$; ns, two-tailed). The transparent and form-related conditions differed from one another ($t(11)=3.5$, $p<0.01$; $t(33)=2.2$, $p<0.05$). Picture naming was faster in the transparent than in the form-related condition.

fMRI data

Fig. 2 illustrates regions that were found to be more responsive to naming pictures than during fixation (so-called *task network*). These task-related activations occurred bilaterally in the occipital cortex (inferior and middle occipital gyrus), temporal cortex (superior and middle temporal gyrus and fusiform gyrus), parietal cortex (superior

Table 2

Stimulus examples, reaction times in ms, errors rates in percent (standard deviations in parentheses), and RT differences (unrelated – primed) in the behavioral session.

Prime Type	Example (prime)	Example (target)	Δ RT	RT	Error rates
Set 1					
Transparent	<i>eksternest</i> (magpie nest)		31	599 (101.0)	7.5 (6.0)
Opaque	<i>eksteroog</i> (corn)		23	607 (97.2)	7.3 (6.1)
Unrelated	<i>gnoom</i> (hobgoblin)		n/a	630 (104.0)	13.5 (17.0)
Set 2					
Transparent	<i>jaszak</i> (coat pocket)		14	592 (92.2)	5.0 (3.2)
Form-related	<i>jasmijn</i> (jasmine)		— 13	619 (85.1)	11.0 (10.1)
Unrelated	<i>otter</i> (otter)		n/a	606 (88.0)	14.6 (11.2)

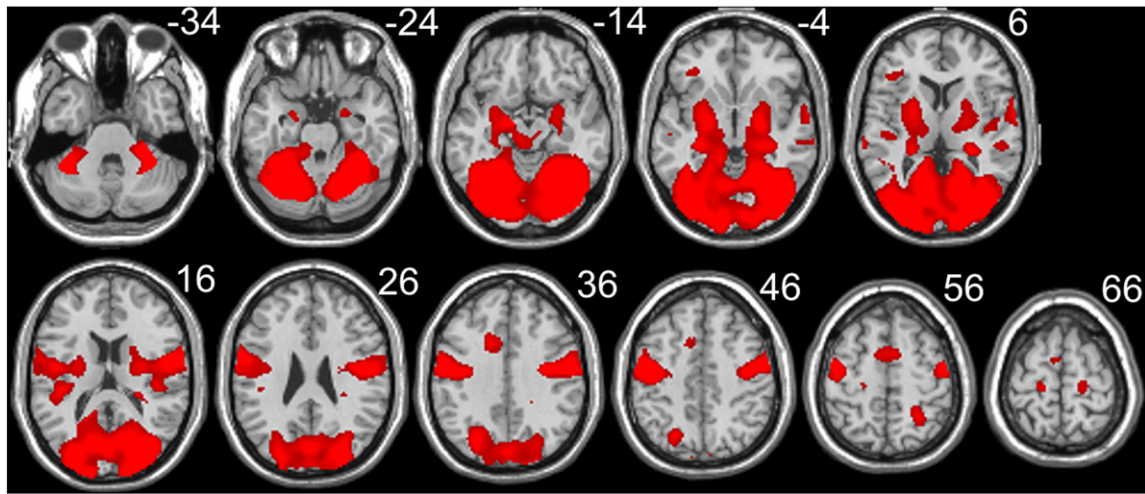


Fig. 2. Regions more activated by picture naming compared with fixation, $p < 0.001$ uncorrected. Shown are axial slices between Z-coordinates -34 and 66 (in 10 mm steps). Activations are superimposed on a single subject MNI template.

parietal lobe), frontal cortex (precentral and medial frontal gyrus), the cingulate cortex, subcortical structures (thalamus, insula, putamen, and globus pallidus) and the cerebellum. In the left hemisphere, there was also activation in the superior and inferior frontal gyrus and the rolandic operculum. Two activation clusters were found in the LIFG centered around $[x\ y\ z] = -36\ 32\ 2$ and $-32\ 34\ 0$ (both BA 47). These areas seem to be involved in visual object recognition and spoken word production. The activation pattern is largely overlapping and, hence, consistent with previous investigations of overt language production (e.g. Christoffels et al., 2007; Spalek and Thompson-Schill, 2008).

ROI analyses

Inside the scanner, when participants responded during pausing scanner noise, the overall error rate was 1.2%. Relatively low error rates resulted from the delayed response as participants had to await the scanner to pause. Given our specific a priori hypothesis, we first tested whether our ROI in LIFG responds differently to morphological priming in Set 1 (semantically transparent and opaque minus unrelated condition). The ROI analysis revealed a significantly higher activation for the primed conditions ($Z = 3.78$; $p < 0.05$, FWE corrected). In further analyses, the contrast for the semantically transparent minus the unrelated condition yielded a significantly higher activation level for the primed condition ($Z = 3.44$; $p < 0.05$, FWE corrected). Similarly, the contrast for the semantically opaque condition yielded a significantly higher activation level ($Z = 3.32$; $p < 0.05$, FWE corrected). The contrast between the semantically transparent minus opaque conditions did not reveal a significant difference in activation level nor did the reversed contrast.

For Set 2, we also explored the effect of morphological priming in LIFG (semantically transparent minus form-related and unrelated conditions). In this analysis, however, no voxel crossed the intensity threshold. Additional exploratory contrasts (transparent minus unrelated; transparent minus form-related; and form-related minus unrelated conditions) did not reveal a significant difference in neural activation between these conditions.

Analyzing the predicted ROI in left MTG yielded no significant activation differences for the contrasts between primed and unprimed conditions, neither in Set 1 nor in Set 2. Additional exploratory analyses in this ROI did not reveal any priming effect for the opaque or the transparent conditions of Set 1 and not for the form-related or transparent condition of Set 2 either.

Whole-brain analyses

Whole-brain analyses were also performed to test for activation differences outside LIFG. The contrast of primed minus unrelated conditions in Set 1 (semantically transparent and opaque minus unrelated) revealed one cluster in LIFG that was marginally significant on the cluster-level (Fig. 3 and Table 3; note that for presentation purpose no cluster extent threshold was set). The effect sizes depicted as bar plots in Fig. 4 confirm that both the transparent and the opaque priming conditions (Set 1) elicited a stronger activation compared with the matched, unrelated condition. Another cluster of activation was seen in LIFG and left middle frontal gyrus (LMFG; BA 46/9), which, however, did not approach the cluster-size threshold. There was no indication of neural activity in (posterior) temporal lobes.

In order to test whether there are voxels that are differentially activated by the opaque and transparent conditions, further contrasts

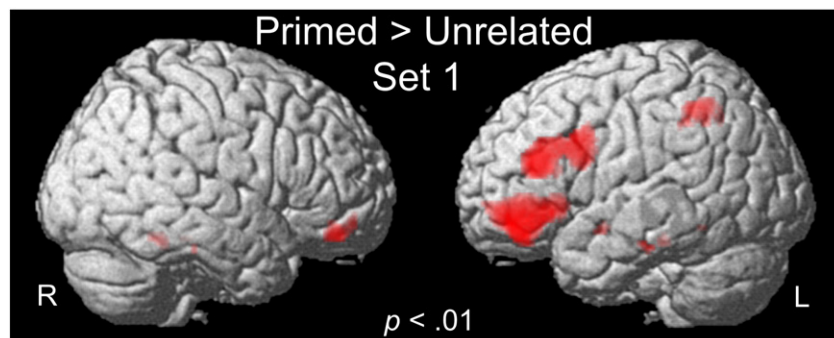


Fig. 3. Surface rendering of regions more activated in morphologically primed (transparent and opaque) conditions relative to the unrelated condition in Set 1, $p < 0.01$ (uncorrected; $k = 0$). Activations are superimposed on a standard single subject MNI template. Only the cluster in LIFG approached significance.

Table 3

Localization of the peak activations and cluster size (clusters with more than 500 adjacent voxels) for the whole-brain analysis for Set 1 (primed–unrelated). The intensity threshold was set at 0.01. In Set 2, no cluster reached significance or a similar size.

Region	Cluster-level			MNI coordinates		
	Z	P_{corr}	Size	x	y	z
LIFG	3.78	0.059	1290	−42	38	−4
LIFG/LMFG	3.43	0.162	958	−46	32	20

were calculated. A direct comparison of the opaque and the transparent conditions (opaque minus transparent and vice versa) showed no cluster that differed significantly in activation between these conditions. Furthermore, a conjunction analysis (Nichols et al., 2005; Price and Friston, 1997) was performed to test if the activation in BA 47 was present for both conditions. This conjunction analysis revealed shared effects (17 voxels) only for left BA 47 around MNI coordinates [x y z] −44 38 −4 ($Z=3.25$; $p_{\text{uncorrected}} < 0.001$; see Fig. 5).

The equivalent contrast for Set 2 (semantically transparent minus form-related and unrelated) did not reveal any significantly activated cluster. Neither the semantically transparent nor the form-related condition contrasted with the unrelated condition revealed any significantly activated voxel. Overall, using a higher intensity threshold ($p < 0.001$) did not reveal further areas of activation in addition to the activation in left IFG and MFG.

Discussion

The present study explored the functional neural correlates associated with one processing step in overt language production, namely morphological encoding. Morphological priming effects point to specific neural activity in the LIFG, specifically Brodmann area 47. Thus, the results support the prediction for LIFG but not for the left posterior MTG.

Behaviorally, picture naming was facilitated by the preceding production of morphologically related compound words in Set 1, but the facilitation missed the statistical threshold in Set 2. Importantly, the facilitation did not differ between the semantically transparent and opaque conditions. The form-related condition did not produce a facilitation effect. If anything, it produced a (numerical) slowing of picture naming. This data pattern is very similar to previous morphological priming effects for the production of compound words and derivations (Dohmes et al., 2004; Koester and Schiller, 2008; Zwitserlood et al., 2002).

These data are consistent with the claim that the processing of morphological information has a neural correlate that is independent of semantic and phonological information processing (Roelofs and Baayen, 2002; cf. Aronoff, 1994). In contrast, connectionist approaches propose that morphological effects can be reduced to a

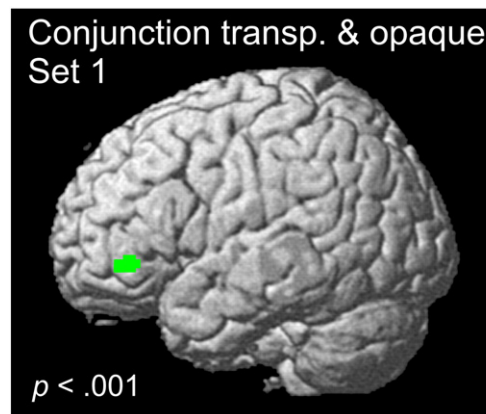


Fig. 5. Surface rendering of regions activated by transparent and opaque priming conditions in Set 1 (conjunction analysis; $p < 0.001$, uncorrected; $k = 0$). Activations are superimposed on a standard single subject MNI template.

combination of semantic and phonological processes (e.g. Gonnerman et al., 2007; Joanisse, and Seidenberg, 2005). In the present study, semantic similarity between primes and targets did not modulate the facilitation effect substantially. Therefore, we argue that the present morphological priming effect cannot be explained by semantic factors. To rule out phonological factors, further confirmation is needed although mere form overlap, i.e. phonological information, did not lead to facilitated processing of the target.

Regarding the neuroanatomy, an involvement of the LIFG in language production is well documented, starting with the work by Paul Broca (1861/2003). A meta-analytic study on the neural correlates of language productions suggests that LIFG subserves syllabification and possibly phonetic encoding whereas word form encoding was assigned to temporal areas (Indefrey and Levelt, 2004). Here, we observed an increased neural activity during picture naming in BA 47 if picture names were morphologically related to previously uttered compound words. As with the response latencies, the neural activation in LIFG (BA 47) was not modulated significantly by the semantic relatedness between prime words and target picture names. Transparent and opaque primes led to a similar neural effect in Set 1 only in BA 47. Also, mere form overlap between prime and target (Set 2) did not yield a neurofunctional effect in this or another ROI. Moreover, the whole-brain analyses did not yield any indication of a neurofunctional effect in any other brain area than LIFG. The activation pattern is comparable to previous findings in the comprehension domain (Bozic et al., 2007; Marangolo et al., 2006; Meinzer et al., 2009) but dissimilar to the earlier meta-analytic results of language production (Indefrey and Levelt, 2004). Note that Indefrey and Levelt's study did not focus specifically on morphological processing as the first sub-stage of word form encoding. The whole-brain analysis yielded no indication of a morphological effect in the middle occipital gyrus, either, as previously reported by Gold and Rastle (2007) for visually masked priming of words.

The present results suggest that LIFG (BA 47) is involved in morphological encoding. Specifically, we tentatively propose that activity in LIFG (BA 47) reflects the computation of a morphological, i.e. a hierarchical structure (of compounds and derivations) rather than mere storage of lexical–semantic entries. If BA 47 subserves the storage and/or access of lexical–semantic entries (Copland et al., 2007; De Zubicaray and McMahon, 2009; Price, 2010; Wiggs et al., 1999), its activity should have been modulated in the present study by the semantic relation between primes and targets because the semantic relation was stronger for transparent than opaque prime–target pairs. However, this was not the case; the opaque and transparent conditions led to comparable activity in LIFG. Also, semantic retrieval of words has been related to neural activity in LIFG and MTG, not solely to activity in

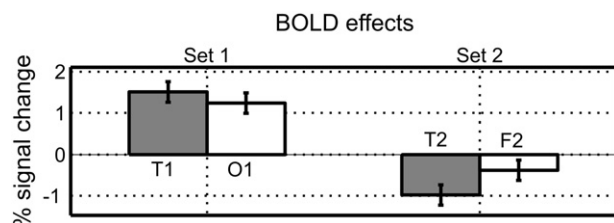


Fig. 4. Bar plot of the effect size for the four priming conditions in the peak voxel −42 38 −4 (LIFG). The priming effect is significant in Set 1 and comparable for the transparent and the opaque conditions. Further analyses showed that the priming effect was due to an activation of the transparent and opaque conditions and not due to a deactivation of the unrelated condition. Note: T—transparent, O—opaque, F—form-related.

LIFG (e.g. Price, 2010). The proposed neural implementation of morphological encoding is in accordance with the decompositional view of speaking (Bien et al., 2005; Levelt et al., 1999; cf. Caramazza et al., 1988; Koester et al., 2007; Taft and Forster, 1976) because the results point to a potential neural substrate of morphological composition in speaking. Although the present result is not compatible with a strict version of the *full-listing hypothesis* (Butterworth, 1983; Bybee, 1995; Janssen et al., 2008), it does not rule out full listing in a weaker form. For example, morphologically complex words with high frequencies or with irregular forms (e.g. “passersby,” “assistant attorneys general” or “teaspoonfuls”) may still be stored holistically.

Similar to our results, LIFG (BA 47) is also involved in the comprehension of complex words (Bozic et al., 2007; Meinzer et al., 2009). Clearly, reading and producing morphologically complex words differ on a number of cognitive processes, but the computation of the internal word structure is common to both processes. It is necessary irrespective of the ‘processing direction,’ i.e. independently of whether a complex word is segmented or whether multiple morphemes are composed into one complex word. In either case the internal word structure is relevant, for interpretation in comprehension and for expressing the intended meaning in production. Thus, the present data suggest that BA 47 is involved in the computation of word internal structure during language production. Here, this was shown for Dutch, an Indo-European language and it would be very informative to investigate morphological aspects of language production in other language families (cf. Bick et al., 2008, 2009; Palti et al., 2007 for comprehension in Hebrew).

The computation of morphological structures (of compounds and derivations) might rely at least partly on separate neural mechanisms than the processing of syntactic structures. It can be argued that morphological and syntactic structures are computed by non-identical neural mechanisms because syntactic processes are unable to manipulate the internal structure of words (Booij, 2002b; Anderson, 1992). Accordingly, syntax has been associated functionally with other parts of LIFG, namely BA 44/45 (Friederici, 2002; Hagoort, 2005; Grodzinsky and Santi, 2008). The present results give a tentative indication that derivation and compounding (as mechanisms of word formation proper) may be processed by partly different neural mechanisms (BA 47; cf. Marangolo et al., 2006; Bozic et al., 2007; Meinzer et al., 2009) than inflections which are closely related to syntactic functions (BA 44/45; e.g. Laine et al., 1999; Sahin et al., 2009). Of course, hierarchical sequence processing might serve domain-general rather than specifically linguistic functions, but such domain-general aspects have been suggested for BA 44/45 and right hemispheric structures (e.g. Friederici, 2006; Bahlmann et al., 2009; Marangolo and Piras, 2010).

In the present study, the exclusive priming effects in Set 1 (behavioral and on the neural level) might be due to differences between the stimuli in the two sets. Naturally, different stimuli may diverge in a number of features ranging from visual to conceptual aspects even though stimuli were thoroughly matched. We do not think that differences in semantic relations can explain the different results for the two stimulus sets. For example, opaque and transparent primes (Set 1) differed significantly in their semantic relations to the targets but elicited a comparable neural effect in the same brain region. This suggestion of (other) diverging features between the sets is supported by the results of a concomitantly performed ERP study with a similar design (Koester and Schiller, 2008) in which the behavioral facilitative effect of semantically transparent primes in Set 2 approached significance similarly to the behavioral priming effect in the present experiment for Set 2. In that study, reliable ERP effects were obtained for both sets, and one may wonder whether the differential sensitivity of neurocognitive methods also plays a role.

It might be argued that the present LIFG activation reflects phonological processes because the transparent priming condition in Set 2 led only to faster responses compared to the form-related

condition and marginally faster responses compared to the unrelated condition; semantically transparent primes in Set 2 did not lead to a neural priming effect. That is, the present data considered in isolation cannot strictly rule out a contribution of phonological processes. However, together with further data obtained with the same experimental paradigm, we consider this explanation highly unlikely because phonological (and semantic) effects observed in an immediate picture-word interference paradigm do not survive a longer inter-trial interval as used in the present long-lag paradigm, i.e. seven to ten trials between prime and target (Dohmes et al., 2004; Feldman, 2000; Zwitserlood et al., 2000). Furthermore, recent ERP results using the same stimuli as the present work (Koester and Schiller, 2008) suggest that the priming effects are not phonological in nature as the transparent but not the form-related condition yielded a reliable N400 effect.

In reading, Bozic et al. (2007) reported also a deactivation for target reading compared with unprimed word reading (the primes) although this effect was more extended (BA 44, insula, Rolandic operculum, and BA 6). Even though it has been suggested that priming leads to deactivation on the neural level, increased neural activity has also been observed for priming (Henson, 2003). Since these observations were not based on pure language production studies, the tentative relation of deactivation and facilitated behavioral responses may not hold for language production. For example, using an implicit object-naming paradigm, Van Turenout et al. (2000) reported increased neural activity for repeated object presentation in the left insula for a comparable delay, but no reduction in neural activity for LIFG. In another study, activation and deactivation were found in LIFG for different priming conditions (phonological, semantic, and syntactic; Heim et al., 2009). Finally, Abel et al. (2009) found increased neural activity associated with both inhibitory and facilitative behavioral effects in a standard language production paradigm.

The increased neural activity in picture naming might reflect a functional difference between language comprehension and production (cf. Spalek and Thompson-Schill, 2008). Given the currently unclear relation of BOLD signal changes and behavioral measures for pure language production, two potential explanations may be given: First, the increased activity in LIFG (BA 47) might reflect an increase in allocated processing resources to the morphological encoding during complex word production. Such increased processing resources may lead to reduced response latencies. The second alternative is that, the increased neural activity may index the inhibition of a previously used morphological structure (the prime) that was associated with the currently to-be-produced word (the target). This inhibition could lead to the disinhibition of the morphological encoding stage, i.e. the preparation of the current verbal response. Such a disinhibition of the morphological encoding process would also result in decreased response latencies. The disinhibition account would imply a deactivation in another cortical area responsible for morphological encoding. Since we do not have evidence for such a deactivation, we favor the morphological encoding account for the activity in LIFG (BA 47). However, these interpretations remain speculative and have to await future confirmation.

Compared to fMRI data, ERPs have a higher temporal resolution. ERP data obtained with a similar paradigm showed N400 effects for morphological priming (Koester and Schiller, 2008). The onset of these N400 priming effects (350 ms) is in close agreement with Indefrey and Levelt's (2004) temporal estimate of morphological encoding. These corresponding results suggest that the LIFG activation and the N400 priming effect reflect the same process of language production. The suggestive mapping of LIFG's function and N400 priming effect is further supported by reports of a significant contribution of LIFG (incl. BA 47) to the surface N400 effect (Hagoort et al., 2004; Maess et al., 2006). As far as the surface N400 effect for morphological priming can be related to the present LIFG activity, the temporal characteristics of these N400 effects support a functional role of LIFG in morphological processing.

Further work is needed to clarify psycholinguistic similarities and differences between compounding and derivation (cf. [Park-Diener and Simpson, 2010](#); [Marslen-Wilson et al., 1994](#)). Although both are means of word formation, they also differ in that derivations are typically formed by affixation (or circumflexion) and involve bound morphemes requiring subcategorization of their stems ([Booij, 2002a](#)). Compounds, in contrast, involve free morphemes and do not require subcategorization. Also, if morphological information is processed independently at the neural level, it should be possible to dissociate it from other lexical processes, such as lexical-semantic integration within compounds ([Koester et al., 2009](#)).

In summary, the present study investigated the processing of morphological information in speaking. Morphological priming in picture naming led to increased neural activity in LIFG (BA 47). This result underlines the functional importance of LIFG for morphological processing in language production and calls for further investigations of the neural correlates of language production. More specifically, our results bear relevance for the understanding of compound processing, an elementary mechanism of word formation. Overall, LIFG (BA 47) appears to contribute functionally to word form encoding in language production and not to be worthless for morphological processing.

Acknowledgments

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