Research report

Phonological processing during language production: fMRI evidence for a shared production-comprehension network

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Abstract

Studies of phonological processes during language comprehension consistently report activation of the superior portion of Broca's area. In the domain of language production, however, there is no unequivocal evidence for the contribution of Broca's area to phonological processing. The present event-related fMRI study investigated the existence of a common neural network for phonological decisions in comprehension and production by using production tasks most comparable to those previously used in comprehension. Subjects performed two decision tasks on the initial phoneme of German picture names (/b/ or not? Vowel or not?). A semantic decision task served as a baseline for both phonological tasks. The contrasts between each phonological task and the semantic task were calculated, and a conjunction analysis was performed. There was significant activation in the superior portion of Broca's area (Brodmann's area (BA) 44) in the conjunction analysis, also present in each single contrast. In addition, further left frontal (BA 45/46) and temporal (posterior superior temporal gyrus) areas known to support phonological processing in both production and comprehension were activated. The results suggest the existence of a shared fronto-temporal neural network engaged in the processing of phonological information in both perception and production.

1. Introduction

Language production has been modelled by Levelt and colleagues [38,40] as a strictly serial process in which a concept (the idea) is accessed first (Fig. 1). Processing proceeds to the so-called lemma level where syntactic information is stored and becomes activated. Then, the segmental spell-out takes place, and the phonological code of the whole word is accessed. Finally, in overt production, motor programs become activated in order to articulate the intended utterance.

According to the neurocognitive model by Friederici [23–25], language comprehension also proceeds in a strictly serial manner in the opposite direction from phoneme identification to conceptual-semantic knowledge. Given these similarities in architecture, several attempts have been made to establish a functional relationship between production and comprehension. Levelt and colleagues [38,40] implemented an implicit self-monitoring mechanism that prevents the system from producing erroneous outputs by using the internal, non-peripheral part of the perception system. Hickok and Poeppel [33–35] supported the notion of a monitoring mechanism during production on the basis of neurofunctional data (which, however, is supposed to be explicit). Garrett [31], in contrast, focuses on the role of production in support of optimal comprehension performance. In line with the motor theory of speech perception [41], he argues that silent repetition of auditorily perceived verbal information improves the listener's ability to understand and anticipate what is being said. These latter psycholinguistic models

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Core processes

conceptual
preparation

↓

lexical concept

↓

lexical selection

↓

lemma

↓

morphological
encoding

↓

morpheme

↓

phonological
encoding

↓

phonological word

↓

phonetic encoding

↓

gestural code
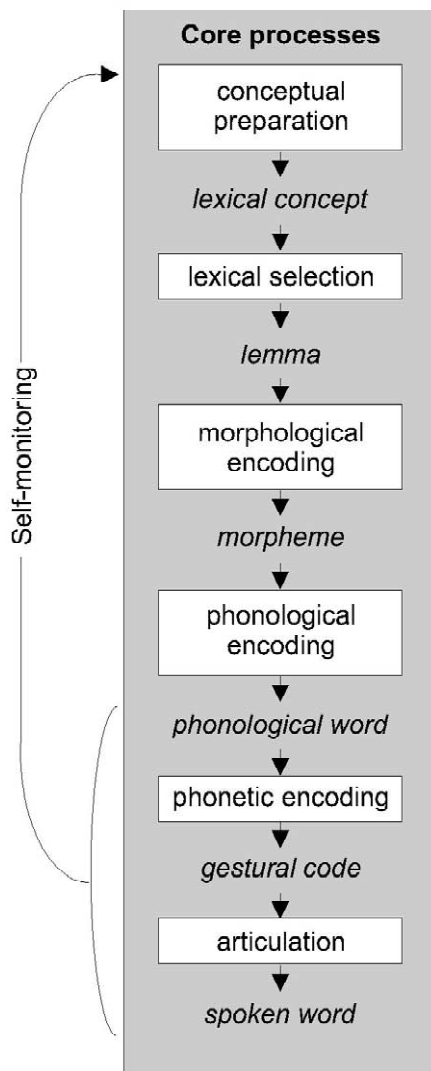
↓

articulation

↓

spoken word

Self-monitoring

Fig. 1. Core processes of language production according to the serial model as proposed by Levelt and colleagues [38,40].

suppose a close and reciprocal relationship between production and comprehension, especially in the phonological domain.

It is an interesting issue whether the functional relationship between production and perception that is assumed in psycholinguistic models is realised in the human brain. Focussing on the temporal lobe, recent studies of phonological processing in patients and healthy subjects could show the contribution of the posterior part of the superior temporal gyrus (pSTG) to both production and perception [2,6,9,11,49]. Thus, production and comprehension appear to rely at least partly on the same neural systems in the human brain.

With respect to frontal regions, functional imaging studies of language comprehension consistently reported activation in the superior posterior portion of Broca's area (a region in the left inferior frontal gyrus, approximately Brodmann's area (BA) 44) when subjects performed metalinguistic phonological decision tasks such as

phoneme monitoring, phoneme discrimination, or phoneme sequencing [11,18,21,22,50,69,70].

The situation is rather different for language production. There is a high variability in the reported frontal activations related to phonological processes in different studies. Price et al. [52] sought to investigate phonological processes during production. They had subjects perform different naming task (objects, colours, letters, and words) together with an articulatory baseline task. The authors calculated the contrasts of each task against baseline and conducted conjunction analyses for pairs of contrasts. In such a conjunction analysis of the type (A–C)+(B–C) (with A and B being experimental conditions and C being the baseline task), the neural correlates of the process common to both contrasts are represented. In the conjunction analysis tracking 'phonological processing' (Experiment 5: naming objects and colours), activation in BA 46 was reported. For Experiment 4 (naming words and letters), which again tapped phonological processing, the authors found again a focus in BA 46 and, in addition, in BA 47. However, on the corresponding statistical parametric map (their Fig. 3b), there appears to be a prominent activation focus in the vicinity of Broca's area (BA 44), which is not listed in the results. Two of the picture naming studies, the one by Levelt et al. [40] (using magnetoencephalography) and the one by Murtha et al. [45] (using positron emission tomography) reported activation of Broca's area that was related to phonological processes. Chao and Martin [14] presented subjects with pictures of real objects (experimental conditions) or scrambled objects (baseline). When subjects simply looked at the objects, there was no inferior frontal activation (Experiment 1); however, if they had to name these objects silently, this evoked additional activation in Broca's area (Experiment 2). The latter results are corroborated by data by Crosson and colleagues [17] and Thompson-Schill and co-workers [60] who reported activation of BA 44 in word generation tasks in which subjects are to produce a semantically appropriate verb in response to a noun. The study by Lurito et al. [43] employed a rhyming task and a 'fluency' task in which subjects had to generate words starting with a particular phoneme and found practically identical activation foci in Broca's area in both tasks. In a study by Poldrack and colleagues [50], subjects had to count the syllables in visually presented words and pseudowords; activation in a letter-case-judgement task served as a baseline and was subtracted from the phonology-related activation. In the pseudo-word condition, there was activation in BA 44; however, in the word condition, this focus moved to BA 45.

In sum, the reported results demonstrate that no unequivocal statement about the role of Broca's area during language production is possible at the moment (see Refs. [20,21,36,50,57] for reviews on phonological processing). This may be due to the different paradigms used in the different studies, with tasks such as naming, generation, or

rhyming being closer to natural production processes, and metalinguistic decisions resembling the type of task used in comprehension studies. Thus, in order to investigate the direct relationship of the neural correlates of phonological processing during language production and comprehension, it is advisable to apply comparable paradigms in both domains.

In the field of electrophysiology, there are a number of studies investigating production processes successfully with the same kind of metalinguistic decision tasks used in the comprehension studies mentioned above. These electrophysiological studies represent one part of the crucial evidence in favour of the Levelt model [40]. van Turennout et al. [65,66] were the first to demonstrate the seriality of access to semantic, syntactic, and phonological information during language production by means of lateralised readiness potentials (LRPs). In their Experiment 1 [65], subjects had to perform a task consisting of a metalinguistic decision which was coupled with a go/no-go task. They were presented with pictures depicting either animals or objects (semantic distinction). The names of these pictures ended with one of two phonemes (phonological distinction). Subjects had to press the left button if the picture showed an animal and the right one if there was an object (decision task), but only, if the name ended with a pre-defined phoneme (go/no-go task). The LRPs were measured from the scalp from two electrodes placed over the left and right motor cortex, with a negative going difference of the potentials between the electrodes indicating the preparation of a motor response with the right or left hand, respectively. In this experiment, there were LRPs occurring in go and in no-go trials, indicating that the semantic information triggered the preparation of a motor response before the phonological information was available that determined whether or not the response really had to be executed. In their Experiment 2, the conditions were reversed such that the phonological information determined the response hand while the semantic information was the go/no-go cue. In this setting, there was an LRP only for the go trials but not for the no-go trials, indicating that, if the semantic information signalled a no-go trial, the phonological information did not evoke any motor preparation. The same pattern as in Experiment 1 was obtained with word initial instead of word final phonemes (Experiment 3). In sum, these results indicate that, in the course of the production process, semantic information is available before phonological information. As Levelt and colleagues [40] conclude, ''These findings show that, in accessing lexical properties in production, you can access a lemma property . . . and halt there before beginning to prepare a response to a word form property of the word, but the reverse is not possible'' (p. 15). In other words, the data presented by van Turennout et al. [65] show that (i) the production process is strictly serial, (ii) this process can be intentionally interrupted if all necessary information is retrieved, and (iii) explicit access to any

kind of information becoming available during this process is possible. However, the data cannot rule out the possibility that the production process runs automatically from semantics down to phonology even if phonological information is irrelevant for further actions. This issue was addressed by Jescheniak and colleagues [37] in an electrophysiological study of semantic and phonological priming during the preparation of an utterance. The authors found that, if subjects only performed a semantic judgement (real size) without preparing the utterance of the picture name, there is semantic priming, but no phonological priming. Accordingly, one can further conclude that semantic processing per se does not automatically lead to phonological processing, but only when it is required by the task.

It must be stated that the processes tapped by metalinguistic decision tasks as introduced by van Turennout and colleagues [65,66] differ from 'natural' production processes in that they require explicit judgements about information becoming available in the course of lexical access. Thus, these metalinguistic decisions may comprise more processes such as the explicit access to originally unconscious information. These issues are not yet resolved. However, Levelt and co-workers [40] explicitly accept the evidence from the LRP studies as support for their production model. This is possible under the assumption that, in order to perform the metalinguistic decision, prior access to the corresponding lexical information must have taken place and that therefore the production process is really assessed. Moreover, the results obtained with metalinguistic decision tasks during production are perfectly in line with data from tip-of-the-tongue states and behavioural (priming) data (see Ref. [40] for a review) as well as the electrophysiological data obtained by Jescheniak and colleagues, that all show a seriality in the access to semantic and phonological information. Thus, in this context, the metalinguistic decision tasks are to be taken as valid instruments to assess processes occurring in the course of language production.

1.1. The present study

In order to identify brain regions supporting phonological processing during language production and to relate the results to the data available from comprehension studies, we used the phonological task from Experiment 3 by van Turennout [65] and an adaptation [1,53,55] in a functional magnetic resonance imaging (fMRI) experiment. In this adaptation, subjects had to decide whether the initial phoneme of a picture name was a vowel or a consonant. Thus, by applying metalinguistic decision tasks, we (i) kept our production experiment as parallel as possible to the comprehension studies and (ii) benefited from the application of already well established tasks.

For the behavioural data, we expected (in accordance with the LRP data [65]) phonological processing to produce longer reaction times than semantic processing.

With respect to the imaging data, as a consequence of those psycholinguistic models of language processing assuming a common basis for production and comprehension, we expected activation for these phonological production judgement tasks in the same region that was activated by means of the same kind of task in the comprehension studies, i.e. the superior portion of Broca's area. Moreover, in accordance with comprehension and production studies [2,6,9,11,49], we expected activation in the pSTG.

2. Materials and methods

2.1. Participants

A total of eight healthy right-handed subjects (aged 24–29 years, three females) participated in the experiment. They all were native German speakers and had normal or corrected to normal vision. No subject had a known history of neurological, major medical, or psychiatric disorder; none were taking medication at the time of measurement. Informed consent was obtained from all participants.

2.2. Materials

The material of the experiment consisted of carefully selected black-on-white line drawings of 80 real objects (20 natural and 60 man-made objects) and 40 non-objects from the Snodgrass picture set. The German names of the real objects started with either a vowel or one of the phonemes /b/, /k/, and /t/, equiprobably, thus resulting in a total proportion of 25% for each initial phoneme type. Only items that yielded at least 80% correct spontaneous namings in a separate pretest were chosen for the experiment. The target picture names are listed in Appendix A.

2.3. Procedure

In an event related design, subjects performed two phonological tasks and a semantic task on pictures of real objects (PHON1, PHON2, and SEM). Moreover, they conducted a probe detection task on the non-objects. A fifth task requiring target detection served a different purpose and will not be further considered in this paper. In PHON1, subjects indicated whether or not the German picture name started with the target phoneme /b/ by pressing one of two buttons. In PHON2, subjects were requested to press the corresponding button if the initial phoneme was a vowel or a consonant. The former task was previously used by van Turennout et al. [65,66], whereas the latter task was applied by Abdel-Rahman and Sommer [1], Rodriguez-Fornells et al. [53], and Schmitt et al. [55]. Both tasks require the activation of the core processes of language production up to the phonological word (Fig. 1). In SEM, subjects decided whether the presented object was

man-made or natural. This latter task only required conceptual-semantic processes, but no phonological processing, as explained above [37]. In the probe detection task (BASE), subjects indicated whether or not a black dot was superimposed on a non-object.

These particular experimental tasks were selected for the following reasons. First, they are well established in psycholinguistic research [1,53,55] in the domain of language production. They both tap phonological processes, though possibly at different levels. While PHON1 requires the identification of the initial phoneme after the retrieval of the picture name, PHON2 required a classification of it at a more abstract level. Second, in order to overcome problems arising from the choice of baseline tasks [46,56], we decided to use the semantic decision task as a reference task that shared all formal properties with the phonological task, i.e. pseudo-randomised presentation, preparation, attention to the fixation cross, object identification, and button press. Moreover, to circumvent the short-comings of the simple cognitive subtraction logic [56], all tasks entered a conjunction analysis [51,52] (see below). In this conjunction analysis, the neural correlates underlying the processing common to both phonological tasks were assessed. The probe detection task was included as an additional control for both the phonological tasks and the semantic task. In all tasks, the proportion of targets requiring a 'yes'-response was 25%.

Right index and middle finger were used as response fingers. Left and right button presses for targets and non-targets were counterbalanced over the subjects. Each trial started with a cue in the centre of the screen that indicated which task had to be performed on the present trial. Next, a black fixation cross appeared in the same position at randomly varying SOAs (+250, +500, +750, or +1000 ms). Thereafter, the item was presented for 800 ms. The average trial length was 10 s, which allowed the fMRI signal to return to the baseline level. Subjects were instructed to react as correctly and quickly as possible. In order to optimise the subjects' performance, a 5-min training session was administered before the experiment. The items used in the training session were not part of the experimental item set. To ensure subjects were attentive during fixation between trials, the fixation cross changed its colour randomly in the time interval between the stimuli in 10% of the trials evenly distributed across items. Participants were instructed to respond to these changes as quickly as possible. Because of possible interferences of this additional task with the experimental tasks, these trials were excluded from further analyses (see Ref. [26] for this experimental set-up). Due to the relatively small size of the item set (resulting from the careful selection of the items before the experiment), all object stimuli were presented in both phonological tasks and the semantic task. In order to minimise repetition priming effects [32,71,64], the three tasks were administered in three different sessions, and subjects performed only one task together with the probe

detection task in each session. Trials and conditions were presented in pseudo-randomised order. Sessions took place with a lag of 2 weeks, and the order of the sessions was counter-balanced across subjects. Reaction times and error rates were recorded during the experiment.

2.4. Data acquisition and analysis

The experiment was carried out on a 3T scanner (Medspec 30/100, Bruker, Ettlingen). A standard birdcage head coil was used. Visual stimuli were presented on a screen positioned at the head end of the magnet bore. Subjects viewed the screen through mirror glasses. Cushions and stereotactic fixation were used to reduce head motion. T1-weighted MDEFT [62] images (data matrix 256×256, TR 1.3 s, TE 10 ms) were obtained with a non slice-selective inversion pulse followed by a single excitation of each slice [47]. For registration purposes, a set of T1-weighted EPI images were taken with TE 30 ms, flip angle 90°, acquisition bandwidth 100 kHz. The inversion time was 1200 ms, with a TR of 45 s and four averages. The functional data were recorded using a gradient-echo EPI sequence with TE 30 ms, flip angle 90°, TR 1 s, acquisition bandwidth 100 kHz. The matrix acquired was 64×64 with a FOV of 19.2 cm, resulting in an in-plane resolution of 3×3 mm. A total of 12 slices were recorded (6-mm thickness, 2-mm skip). The data processing was performed using the software package LIPSIA [42]. Functional data were corrected for motion using a matching metric based on linear correlation. To correct for the temporal offset between the slices acquired in one scan, a sinc-interpolation based on the Nyquist-Shannon-Theorem was applied. A temporal highpass filter with a cut-off frequency of 1/100 Hz was used for baseline correction of the signal and a spatial Gaussian filter with FWHM 5.64 mm was applied. The increased autocorrelation due to filtering was taken into account during statistical evaluation. To align the functional data slices with a 3D stereotactic co-ordinate reference system, a rigid linear registration with six degrees of freedom (three rotational, three translational) was performed. The rotational and translational parameters were acquired on the basis of the MDEFT and EPI-T1 slices to achieve an optimal match between these slices and the individual 3D reference data set. This 3D reference data set was acquired for each subject during a previous scanning session. The MDEFT volume data set with 160 slices and 1-mm slice thickness was standardised to the Talairach stereotactic space [58]. The rotational and translational parameters were subsequently transformed by linear scaling to a standard size. The resulting parameters were then used to transform the individual pre-processed 2D data sets using trilinear interpolation, so that the resulting 3D data sets were aligned with the stereotactic co-ordinate system.

The statistical evaluation was based on a least-squares estimation using the general linear model for serially autocorrelated observations [27,29,30,68]. The design matrix was generated using basis functions [28]. These functions were synthetic haemodynamic response functions composed of three gamma functions and their derivatives [30]. The derivatives can be interpreted as a shift of the response in time. In our analysis, they were treated as confounds. The model equation, including the observation data, the design matrix and the error term, was convolved with a Gaussian kernel of 4-s FWHM dispersion. The model includes an estimate of temporal autocorrelation that is used to estimate the effective degrees of freedom. For each subject, two contrasts were specified (PHON1–SEM, PHON2–SEM), and a conjunction analysis of the type (PHON1–SEM)+(PHON2–SEM) was applied [51,52]. As an additional control, the same contrasts were also calculated against the probe detection baseline (PHON1–BASE, PHON2–BASE, conjunction [(PHON1–BASE)+ (PHON2–BASE)]), and the contrast SEM–BASE was calculated. Group analysis was performed applying a Gaussian test for individual statistic parametric maps (SPM$\{t\}$) [7]. Due to the small number of subjects, no data were excluded from the analyses. In order to assess differences between the two phonological tasks, spherical regions of interest (ROIs) with a radius of 3 mm were defined in each individual SPM$\{t\}$ around the activation foci that reached significance in the conjunction analysis, and paired t-tests were calculated separately for each ROI [7].

3. Results

3.1. Behavioural data

After substituting outliers with values exceeding the criterion of mean±2 S.D. by the mean of the corresponding experimental condition, repeated-measurements ANOVAs with the factor 'task' were carried out separately for reaction times and error rates. For the reaction times, there was a significant effect of 'task' ($F_{(2,14)}=36.19$, $P<0.001$). Consecutive paired t-tests revealed significant differences between all tasks (PHON1–PHON2: $t_{(7)}= -3.95$, $P<0.006$; PHON1–SEM: $t_{(7)}=8.31$, $P<0.001$; PHON2–SEM: $t_{(7)}=7.22$, $P<0.001$). For the error rates, there was no significant effect for the factor 'task' ($F_{(7)}= 2.27$, $P<0.140$) (Table 1).

Table 1
Mean reaction times, error rates, and SD (in parentheses) as a function of task (SEM, semantic decision [natural or man-made?]; PHON1, phonological decision [/b/ or not?]; PHON2, phonological decision [vowel or not?])

	Reaction times (ms)	Error rates (%)
SEM	646 (10)	3 (3)
PHON1	812 (62)	8 (2)
PHON2	1015 (140)	13 (17)

Table 2
Mean Z-scores of regions of interest (ROI) during phonological processing as revealed by the conjunction analysis ([PHON1−SEM]+[PHON2−SEM])

| ROI (BA)	Coordinates (x, y, z)			Mean Z-score
L IFG (44)	−49	18	23	3.4
L IFG (45/46)	−34	36	17	3.5
R PrCG (6/4)	46	9	29	3.5
L STG (22/39)	−43	−56	20	3.8
L MTG (21)	−49	−47	0	3.4

Coordinates refer to the Talairach space [58]. Abbreviations: L, left; R, right; BA, Brodmann's area; IFG, inferior frontal gyrus; IFS, inferior frontal sulcus; PrCG, precentral gyrus; STG, superior temporal gyrus; MTG, middle temporal gyrus; SMG, supramarginal gyrus.

3.2. Imaging data

In the conjunction analysis, the superior portion of Broca's area (BA 44) was significantly activated. Further foci were observed in other parts of the left inferior frontal gyrus (IFG), the right precentral gyrus (PrCG) and left temporal and parietal areas (superior temporal gyrus (STG), middle temporal gyrus (MTG), and supramarginal gyrus (SMG)) (Table 2 and Fig. 2). A similar pattern of activation was observed in both single contrasts. In the contrast PHON1−SEM, frontal activations were in the left IFG in Broca's area (BA 44) and BA 45/46, the left middle frontal gyrus (MFG), the left PrCG and precentral sulcus (PrCS). Temporal and parietal areas showing activation were the left STG and MTG (Table 3 and Fig. 2). In the contrast PHON2−SEM, there was again activation in Broca's area (BA 44) ($P<0.002$) and further left frontal regions including the MFG, SFG, PrCG and posterior cingulate gyrus. Temporal activation foci were in the left STG and the superior temporal sulcus (STS) (Table 4 and Fig. 2). In the ROI analysis, there was a significant difference between the two phonological tasks for the activation focus in the superior BA 44 ($t(7)=3.24$,
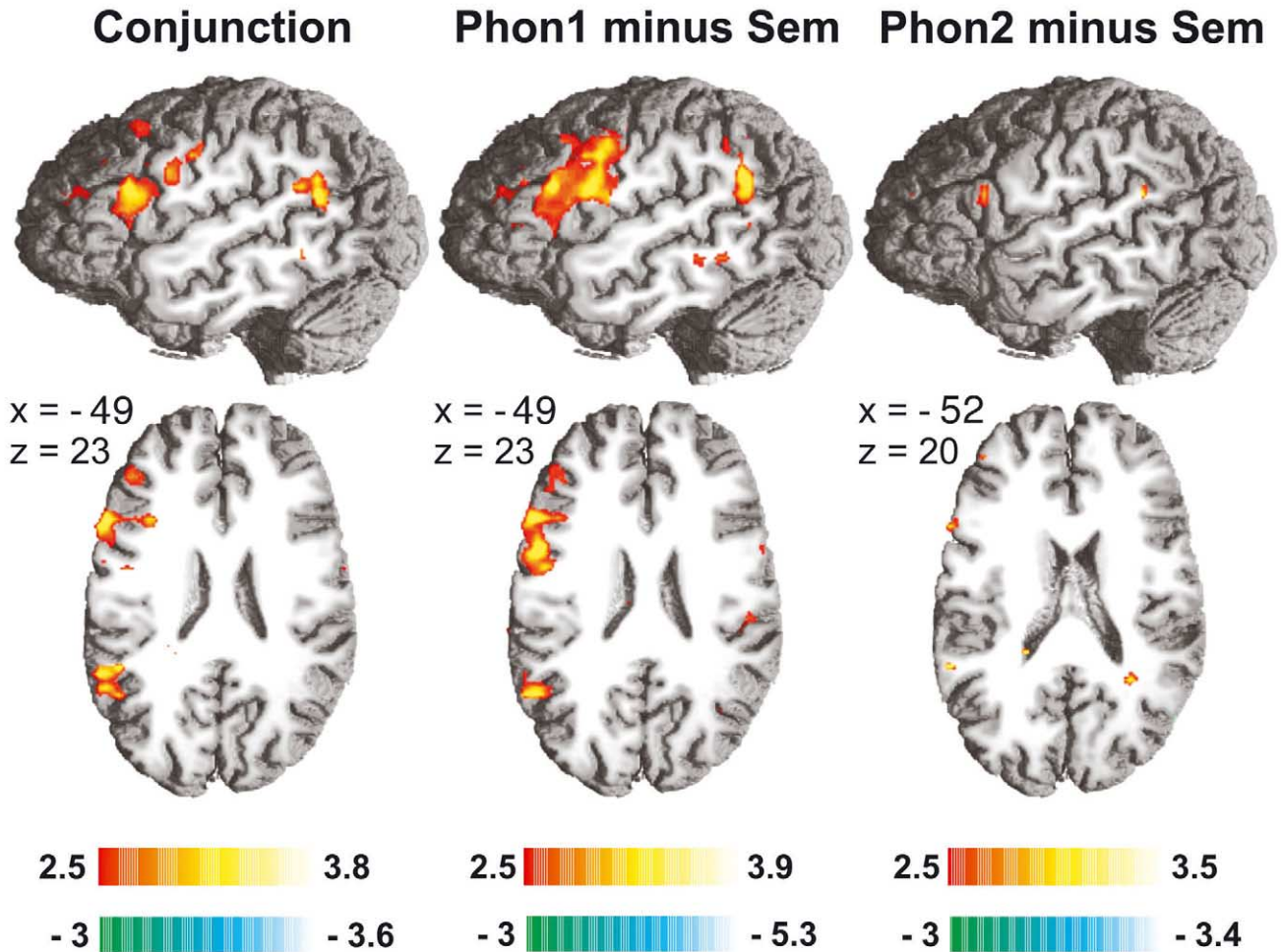
Fig. 2. Statistical parametric maps (SPM{z}) of the activations in the experimental contrasts, superimposed onto a high-resolution 3D MDEFT scan of a representative individual brain. The co-ordinates of each particular section in the sagittal slices (top row) and the transaxial slices (bottom row) are indicated by the corresponding x- and z-value in Talairach co-ordinate space [58]. The coloured scale bars indicate the activation strength. (For a complete list of activations see Table 2). Left column: conjunction analysis of both contrasts (PHON1−SEM)+(PHON2−SEM); middle column: PHON1−SEM; right column: PHON2−SEM. (For the task specifications, refer to the Materials and methods section in the text.).

Table 3
Mean Z-scores of regions of interest (ROI) during phonological processing as revealed by the contrast PHON1–SEM

ROI (BA)	Coordinates (x,y,z)			Mean Z-score
L IFG (44)	−49	18	23	3.4
L IFG (45/46)	−37	33	14	3.2
L MFG (9)	−43	18	29	3.9
L MFG (6)	−25	0	47	3.7
L PrCS (44/6)	−46	6	23	3.3
L PrCG (6)	−43	0	38	3.6
L STG (22)	−49	−53	29	3.4
L MTG (21)	−49	−44	−2	3.3

Coordinates refer to the Talairach space [58]. Abbreviations: L, left; BA, Brodmann's area; IFG, inferior frontal gyrus; MFG, middle frontal gyrus; PrCG, precentral gyrus; PrCS, precentral sulcus; STG, superior temporal gyrus; MTG, middle temporal gyrus.

Table 4
Mean Z-scores of regions of interest (ROI) during phonological processing as revealed by the contrast PHON2–SEM

ROI (BA)	Coordinates (x,y,z)			Mean Z-score
L IFG (44)	−52	15	20	3.0*
L MFG (9)	−40	21	32	3.1
L SFG (8)	−5	41	38	−3.4
L PrCG (6)	−31	−2	32	3.2
L pCG	−14	−41	8	3.4
L STG (22)	−52	−44	20	3.4
L STS (22/21)	−34	−41	8	3.2

Coordinates refer to the Talairach space [58]. (*P<0.002). Abbreviations: L, left; BA, Brodmann's area; IFG, inferior frontal gyrus; MFG, middle frontal gyrus; SFG, superior frontal gyrus; PrCG, precentral gyrus; STG, superior temporal gyrus; STS, superior temporal sulcus; pCG, posterior cingulate gyrus.

$P<0.014$), with PHON1 yielding a higher amount of activation than PHON2 (Table 5).

As argued above, the semantic judgement task does not involve any phonological processing. However, in order to ensure that in SEM there were really no activations related to phonological processing, contrasts of all conditions against BASE were also calculated. For SEM–BASE, there was no activation exceeding the threshold of $Z>3.09$ ($P<0.001$). At a more lenient threshold, there was activation in the left BA 47 (co-ordinates: −44, 26, 0; $Z=2.2$) and the left superior occipital gyrus (SOG; co-ordinates:

Table 6
Mean Z-scores of regions of interest (ROI) during phonological processing as revealed by the contrast PHON1–BASE

ROI (BA)	Coordinates (x,y,z)			Mean Z-score
L IFG (44)	−43	15	23	3.2
L MFG (9)	−37	15	29	3.3
L MFG (9)	−40	12	35	3.2
L frontal operculum (45)	−37	21	8	3.2
R PoCG (4)	43	−14	32	−3.8
R SOG (19)	34	−71	23	−3.5
L cerebellum	−10	−56	−3	3.6
R cerebellum	7	−56	0	4.0

Coordinates refer to the Talairach space [58]. Abbreviations: L, left; R, right; BA, Brodmann's area; IFG, inferior frontal gyrus; MFG, middle frontal gyrus; PoCG, postcentral gyrus; SOG, superior occipital gyrus.

−18, −88, 23; $Z=2.7$). In the contrasts of the phonological tasks against BASE, there was the following pattern of activation. For PHON1–BASE, there was left frontal activation in BA 44, the frontal operculum (BA 45), and the MFG (BA 9). Moreover, there were foci in the right postcentral gyrus and SOG and bilaterally in the cerebellum (Table 6). For PHON2–BASE, there was bilateral activation in BA 44. Additional foci were in the left anterior insula, head of the left caudate nucleus, and left lingual gyrus (Table 7). The conjunction analysis (PHON1–BASE)+(PHON2–BASE) yielded activation in inferior frontal regions in the left and right BA 44, the left deep frontal operculum, and the right BA 45. Further foci lay bilaterally in the heads of the caudate nuclei and the cerebellum as well as in the pons (Table 8).

Table 7
Mean Z-scores of regions of interest (ROI) during phonological processing as revealed by the contrast PHON2–BASE

ROI (BA)	Coordinates (x,y,z)			Mean Z-score
L IFG (44)	−40	18	23	3.2
R IFG (44)	40	15	11	3.3
L aIns	−31	24	2	3.1
L CH	−10	12	11	3.1
L LG	−4	−83	5	3.2

Coordinates refer to the Talairach space [58]. Abbreviations: L, left; R, right; BA, Brodmann's area; IFG, inferior frontal gyrus; aIns, anterior insula; CH, caudate head; LG, lingual gyrus.

Table 5
Results from the blob analysis in the significant regions of interest (ROI) as identified in the conjunction analysis (cf. Table 2)

ROI (BA)	PHON1 Mean (SD)	PHON2 Mean (SD)	t-Value (df)	P
L IFG (44)	83 (42)	39 (40)	3.24 (7)	0.014
L IFG (45/46)	70 (50)	19 (42)	2.19 (7)	0.065
L PrCG (6/4)	46 (33)	6 (40)	1.75 (7)	0.123
L MTG (21)	36 (32)	−1 (27)	2.13 (7)	0.071
L STG (22/39)	40 (30)	26 (46)	0.67 (7)	0.526

Displayed are the mean activation strength (arbitrary units) and the corresponding standard deviations (SD) as a function of the ROI and the task (PHON1/PHON2); the empirical t-value and degrees of freedom (df); and the resulting P-value. Abbreviations: L, left; BA, Brodmann's area; IFG, inferior frontal gyrus; PrCG, precentral gyrus; MTG, middle temporal gyrus; STG, superior temporal gyrus.

Table 8
Mean *Z*-scores of regions of interest (ROI) during phonological processing as revealed by the conjunction analysis ([PHON1–BASE]+[PHON2–BASE])

ROI (BA)	Coordinates (*x,y,z*)			Mean *Z*-score
L IFG (44)	−43	21	14	3.5
L IFG (44)	−43	18	23	3.5
L frontal operculum (45)	−31	24	14	4.0
R IFG (44)	37	18	5	3.8
R IFG (45)	37	24	14	3.2
L CH	−10	9	5	3.6
R CH	7	12	8	3.4
Pons	−4	35	0	4.0
L cerebellum	−19	−59	0	3.7
R cerebellum	7	−62	3	3.2

Coordinates refer to the Talairach space [58]. Abbreviations: L, left; R, right; BA, Brodmann's area; IFG, inferior frontal gyrus; CH, caudate head.

4. Discussion

In the present fMRI study, subjects performed two phonological decision tasks on the initial phoneme of the name of a picture (PHON1: /b/ or not?; PHON2: vowel or not?). These tasks necessarily require the initiation of the core processes of language production up to the retrieval of the phonological word (Fig. 1). A semantic decision task (SEM: natural or man-made) requiring only conceptual processes served as a baseline task, a probe detection task (BASE) as a further control. In the behavioural data, there was no significant difference with respect to the error rates, suggesting equal difficulty among the tasks. For the reaction times, there was a significant difference between each phonological task and SEM as well as between PHON1 and PHON2. This expected pattern of longer reaction times for phonological relative to semantic processing during language production is a behavioural replication of the electrophysiological data obtained by van Turennout et al. [65] with semantic and phonological decision tasks on picture names. With respect to the reaction times difference between the two phonological tasks, no prediction had been made on the basis of the production model proposed by Levelt et al. [38,40] as both tasks tap the same processing level during production. Nonetheless, the data are in accordance with the electrophysiological studies. Using a phoneme discrimination task (/k/ or /s/; /v/ or /h/), van Turennout et al. [65,66] observed a difference between go- and no-go trials in the time window between 400 and 410 ms, indicating the availability of the phonological information. Schmitt and colleagues [55], who had their subjects perform a vowel/ consonant classification rather than a phoneme discrimination task, obtained this difference between the go- and the no-go LRP somewhat later, namely at 460 ms. Thus, the classification between vowels and consonants (as required in the study by van Turennout [65,66] and in PHON2 in

the present study) results in longer latencies in both the LRP and the reaction time data.

With respect to the imaging data, the obtained results are in line with the hypothesis. As predicted, the conjunction analysis of both phonological tasks revealed activation in the same region of Broca's area (i.e. the superior portion of BA 44) which has often been reported in studies of language comprehension [11,18,21,22,50,69,70] (e.g. Burton et al. [11]: −47, 17, 24; Démonet et al. [18]: −50, 18, 20; Zatorre et al. [70]: −35, 20, 21). Moreover, this activation was present in the two contrasts between each phonological task and SEM. These results allow the conclusion that phonological processing in production as well as in comprehension (when measured with decision tasks) similarly relies on Broca's area. This pattern of activation was confirmed in the additional contrasts of all tasks against the probe detection task. The contrasts PHON1–BASE and PHON2–BASE as well as their conjunction revealed comparable activations in the superior portion of BA 44, whereas, in accordance with the hypothesis, no such activation was observed for semantic processing (SEM–BASE) [63,67].

However, why did the two phonological tasks result in a statistically different amount of activation in the superior portion of Broca's area (as revealed by the blob analysis; Table 5)? The function of this difference should be related to the behavioural data which indicate equal task difficulty (error rates) but longer processing times (reaction times). One explanation could be that, after the retrieval of the phonological code, two different processes take place. As the results by Burton et al. [11] demonstrate, the discrimination between the (initial) phonemes of two CVC-syllables consisting of different phonemes in otherwise non-identical syllables (dip-ten), but not between the voicing of the (initial) consonants when all other features of the syllables are identical (dip-tip) requires involvement of the superior BA 44. In PHON1, this is exactly what the subjects have to do. The features of the initial phoneme of the picture name have to be checked against the target phoneme /b/. If this phonetic feature check is positive, a 'yes'-response is given. But in order to perform this discrimination, all features have to be checked separately against the template /b/, and only if the conjunction of all phonetic features yields a positive result, the 'yes'-response is adequate. For the classification task PHON2, this process is different. After the retrieval of the phonological code of the picture name, there is not one unique set of features establishing the yes/no-criterion. Rather, the properties of the initial phoneme must match those of any phoneme in the set of vowels in order to trigger a 'yes'-response. Thus, the process does not require the binding of the same amount of information as in PHON1 for a single decision, but rather a search in the set of vowels which, in turn, may be more time consuming but not necessarily more effortful. This interpretation, which is in line with both the behavioural data and the imaging results, is

supported by other studies that demonstrate a positive relationship between the amount of processing resources and the activation in frontal areas (e.g. [59]). The difference between the two phonological tasks, and the particular involvement of the cortex at the junction of the precentral sulcus and the inferior frontal sulcus for PHON2 compared to PHON1 may be related to the task differences as this cortex has been identified to reflect aspects of task management [8]. In any case, due to the logic of the conjunction analysis, the general interpretation of the presented data on phonological processing in Broca's area during language production does not rely on the differences between PHON1 and PHON2 as these may be task related, but rather on the processes common to both tasks. Therefore, we will now turn to the other common activations in both tasks.

In the conjunction analysis, there were some further activation foci in frontal and temporo-parietal areas. First, there was activation more anteriorly in the inferior frontal gyrus (IFG) at a location (BA 45/46) that has earlier been reported to contribute to phonological processes during language production [52] and comprehension [71] as well as phonological working memory [3,71]. Interestingly, the studies reporting this activation made use of different experimental paradigms, including natural processing during naming [52], phonological decision, and rehearsal [3,71]. On the basis of these results, one can further assume the domain- (production/comprehension) and task- (natural/strategic) independent contribution of this more anterior portion of the IFG (the pars triangularis) to phonological processing.

Among the other brain structures that showed activation for phonological processing, there is the right precentral gyrus (PrCG) and the left middle frontal gyrus (MFG). Activation in these areas has been related to phonological working memory processes [4,16]. Baker and colleagues [5] reported activation in the right PrCG when verbal material was encoded successfully. Clark and co-workers [15] found evidence for the involvement of the MFG in phonological working memory [10,19,52–55,61]. The posterior STG (pSTG) appears to play a significant role in phonological processing during both comprehension and production [2,9,11,13,34,44,49]. Hickok et al. [34] report pSTG activation in a silent object naming task. Similarly, Burton and colleagues [12] found involvement of the pSTG when subjects repeated heard words relative to uttering 'crime' as a response to reversed speech stimuli. Anderson and co-workers [2] could demonstrate that direct cortical stimulation of the pSTG leads to deficits resembling those in conduction aphasia. Buchsbaum et al. [9] provided evidence that pSTG activation is related to both comprehension (listening to speech) and production (covertly reproduce speech). In line with these results, Poeppel [49] demonstrated that patients with pure word deafness often suffer from lesions to the pSTG. Thus, for phonological processing, the pSTG appears to be the

functional counterpart to Broca's area as an interface between production and comprehension.

In sum, the network that showed up in the conjunction analysis can be attributed to phonological processing, with activation in the pSTG and the IFG being related to the phonological encoding and (especially the activation in BA 44) the decision process, while the foci in the MFG and PrCG appear to reflect phonological working memory processes. These working memory processes are necessary for the subjects to keep the target as well as the initial phoneme in mind to be able to map them onto each other in order to perform the correct button press.

5. Conclusion

We were able to show that, during language production, the superior portion of Broca's area plays an important in phonological processing. These results are compatible with the available data in the domain of language comprehension and provide some further evidence that there is a shared fronto-temporal neural network for both language production and comprehension, with phonological processes being supported by the pSTG and the superior portion of Broca's area.

6. Uncited references

[39]; [48]

Appendix A. German target picture names and their English translations

AMBOSS (ANVIL)	BÜGELEISEN (FLAT IRON)	KUH (COW)
AMPEL (TRAFFIC LIGHT)	BÜROKLAMMER (PAPER CLIP)	OFEN (OVEN)
ANANAS (PINEAPPLE)	BUS (BUS)	ORDEN (MEDAL)
ANGEL (FISHING ROD)	EICHHÖRNCHEN (SQUIRREL)	ORGEL (ORGAN)
APFEL (APPLE)	EIMER (BUCKET)	TAFEL (BLACKBOARD)

AQUARIUM (FISH BOWL)	ELEFANT (ELEPHANT)	TANNE (FIR)
ARMBRUST (CROSSBOW)	IGEL (HEDGEHOG)	TASSE (CUP)
ASCHENBECHER (ASHTRAY)	IGLU (IGLOO)	TELLER (PLATE)
AUTO (CAR)	KÄFER (BUG)	THRON (THRONE)
BAGGER (EXCAVATOR)	KÄFIG (CAGE)	TIGER (TIGER)
BALKON (BALCONY)	KAMM (COMB)	TOASTER (TOASTER)
BANANE (BANANA)	KÄNGURUH (KANGAROO)	TOMATE (TOMATO)
BANK (BENCH)	KANONE (CANON)	TOPF (POT)
BARREN (BAR)	KASSE (CASH)	TRAKTOR (TRACTOR)
BAUM (TREE)	KATZE (CAT)	TRAUBE (GRAPE)
BESEN (BROOM)	KEGEL (PIN)	TRESOR (SAFE)
BETT (BED)	KERZE (CANDLE)	TRICHTER (FUNNEL)
BIRNE (PEAR)	KETTE (CHAIN)	TROMMEL (DRUM)
BLATT (LEAF)	KIRSCHE (CHERRY)	TROMPETE (TRUMPET)
BLUME (FLOWER)	KLAVIER (PIANO)	TUBE (TUBE)
BOJE (BUOY)	KLEID (DRESS)	TULPE (TULIP)
BRILLE (GLASSES)	KNOPF (BUTTON)	TUNNEL (TUNNEL)
BRÜCKE (BRIDGE)	KOFFER (SUITCASE)	TÜR (DOOR)
BRUNNEN (WELL)	KORB (BASKET)	TURM (TOWER)
BUCH (BOOK)	KORKEN (CORK)	U-BOOT (SUBMARINE)
BÜGELBRETT (IRONING BOARD)	KREISEL (SPINNER)	UHR (CLOCK)
	KRONE (CROWN)	

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