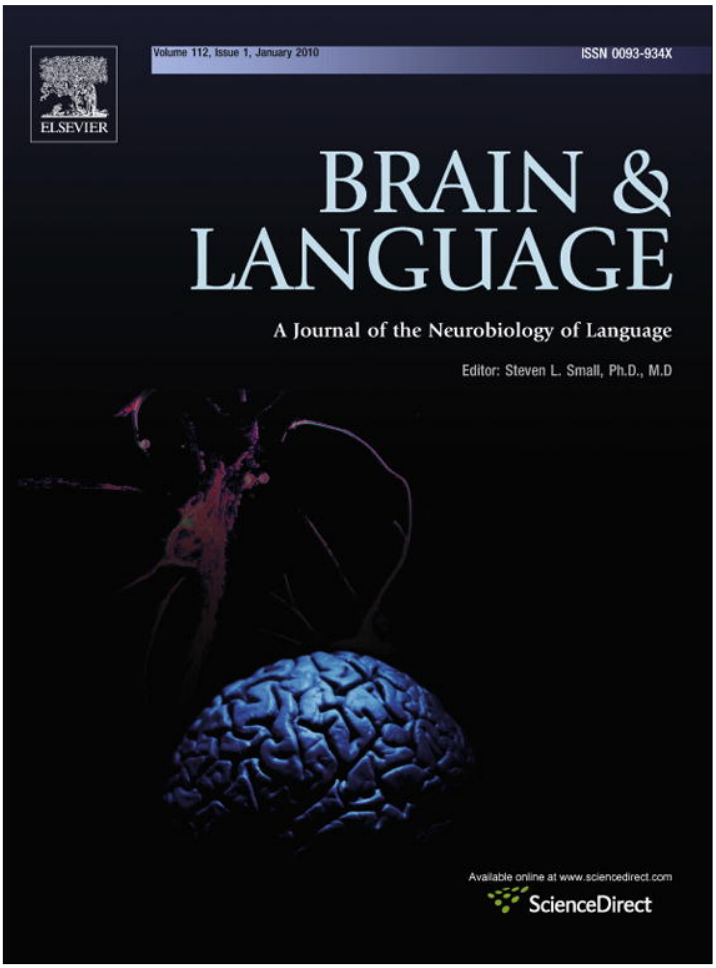
Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

http://www.elsevier.com/copyright

Author's personal copy

Brain & Language 112 (2010) 3–11

Contents lists available at ScienceDirect

Brain & Language

journal homepage: www.elsevier.com/locate/b&l

Lexicality drives audio-motor transformations in Broca's area

S.A. Kotz [a,*], A. D'Ausilio [b], T. Raettig [a], C. Begliomini [b], L. Craighero [b], M. Fabbri-Destro [b], C. Zingales [b], P. Haggard [c], L. Fadiga [b,d,*]

[a] Max-Planck Institute for Human Cognitive and Brain Sciences, Independent Research Group "Neurocognition of Rhythm in Communication", Leipzig, Germany
[b] DSBTA – Section of Human Physiology, University of Ferrara, Ferrara, Italy
[c] Institute of Cognitive Neuroscience, University College of London, London, UK
[d] IIT, The Italian Institute of Technology, Genova, Italy

ARTICLE INFO

Article history:
Accepted 17 July 2009
Available online 20 August 2009

Keywords:
Phonological priming
Motor theory of speech perception
Mirror system
Broca's area

ABSTRACT

Broca's area is classically associated with speech production. Recently, Broca's area has also been implicated in speech perception and non-linguistic information processing. With respect to the latter function, Broca's area is considered to be a central area in a network constituting the human mirror system, which maps observed or heard actions onto motor programs to execute analogous actions. These mechanisms share some similarities with Liberman's motor theory, where objects of speech perception correspond to listener's intended articulatory gestures. The aim of the current series of behavioral, TMS and fMRI studies was to test if Broca's area is indeed implicated in such audio-motor transformations. More specifically, using a classical phonological rhyme priming paradigm, we investigated whether the role of Broca's area could be purely phonological or rather, is lexical in nature. In the behavioral baseline study, we found a large priming effect in word prime/target pairs (W–W) and no effect for pseudo-words (PW–PW). Online TMS interference of Broca's area canceled the priming difference between W–W and PW–PW by enhancing the effects for PW–PW. Finally, the fMRI study showed activation of Broca's area for W–W pairs, but not for PW–PW pairs. Our data show that Broca's area plays a significant role in speech perception strongly linked to the lexicality of a stimulus.

© 2009 Elsevier Inc. All rights reserved.

1. Introduction

The problem in understanding speech is that a sequence of discrete sounds is carried in a speech stream that exceeds the temporal resolution of the auditory system. Motivated by this observation, Liberman and colleagues (Liberman, Delattre, & Cooper, 1952; Liberman, Delattre, Gerstman, & Cooper, 1956; Liberman, Harris, Hoffman, & Griffith, 1957; for a review see Galantucci, Fowler, & Turvey, 2006) suggested that vocal tract gestures generating successive speech sounds overlap temporally. Such co-articulation may help the auditory system to temporally resolve the speech segments over longer time intervals. When acoustic patterns differ but an articulatory gesture is the same (or vice versa) perception tracks articulation (Liberman et al., 1957). Building on these foundations, the "motor theory of speech perception" was born (Liberman, Cooper, Shankweiler, & Studdert-Kennedy, 1967; Liberman & Mattingly, 1985; Liberman & Whalen, 2000). Among several other propositions, this theory claims that the ultimate constituents of speech are not sounds but intended articulatory gestures that have evolved exclusively to serve language. Speech perception and speech production processes use a common repertoire of motor primitives. In other words, the listener understands the speaker when the representations of his/her articulatory gesture are activated through verbal sounds.

Despite some criticisms due to the fact that Liberman's hypothesis was never fully demonstrated, interest in these aspects of the motor theory of speech perception has recently been revived as a result of data arising from neurophysiological experiments on the monkey motor system (Galantucci et al., 2006). In monkey pre-motor area F5, hand and mouth actions are represented with a high degree of specificity. Neurons in this area discharge during grasping, holding, tearing or manipulating actions, whereas they are silent when the monkey performs actions that involve a similar muscular pattern, but are driven by a different goal (Matelli, Luppino, & Rizzolatti, 1985; Rizzolatti et al., 1988). Among the neurons of area F5 a subset of visuomotor neurons show even more interesting properties. These neurons, known as mirror neurons, are active both during observation and execution of the same grasping action (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). Thus, the monkey pre-motor cortex may transform visual information into motor

* Corresponding authors. Address: University of Ferrara, DSBTA – Section of Human Physiology, via Fossato di Mortara, 17/19, 44100 Ferrara, Italy. Fax: +39 0532 455242.
E-mail address: fdl@unife.it (L. Fadiga).

0093-934X/$ - see front matter © 2009 Elsevier Inc. All rights reserved.
doi:10.1016/j.bandl.2009.07.008

Author's personal copy

knowledge (Rizzolatti & Craighero, 2004). These functional properties of mirror neurons found in the macaque pre-motor cortex resemble some of the mechanisms of speech perception proposed by Liberman and colleagues (1967).

Neuropsychological and brain-imaging studies have provided evidence for the existence of a similar mechanism in humans, involving a cortical network formed by the rostral part of the inferior parietal lobule (IPL), the ventral pre-motor area (PMv) and the pars opercularis of the inferior frontal gyrus (IFG) (see Rizzolatti & Craighero, 2004; Turella, Pierno, Tubaldi, & Castiello, 2009). The pars opercularis of the IFG belongs to Broca's region (Amunts et al., 1999), an area classically considered as the frontal center of speech production. More interestingly, from a cytoarchitectonical point of view, this area closely resembles monkey pre-motor area F5 (Petrides, Cadoret, & Mackey, 2005; Petrides and Pandya, 1999), where mirror neurons have been found.

More empirical evidences in agreement with Liberman's theory comes from a transcranial magnetic stimulation (TMS) study demonstrating that during speech perception, the listener's primary motor cortex representing tongue movements, "resonates" as if it were actually producing the speech heard (Fadiga, Craighero, Buccino, & Rizzolatti, 2002; but see Toni, de Lange, Noordzij, & Hagoort, 2008). When participants listen to speech, tongue motor evoked potentials (MEPs) are elicited by TMS of the left tongue motor representation. Results show that MEPs are larger to some word and pseudo-word types than others. For example, listening to words and pseudo-words formed by consonants (e.g., the Italian 'R' involving tongue mobilization vs. 'F'), increased tongue motor potentials. Recent work by the same group confirmed the lexical nature of this effect (Roy, Craighero, Fabbri-Destro, & Fadiga, 2008) and, very recently, that the activation of the motor cortex during speech perception is causally related to speech sound discrimination (D'Ausilio et al., 2009).

The aforementioned studies investigate the motor cortex (M1), considered the final common pathway of the motor/pre-motor cortical network. It remains unclear, however, from which brain center upstream to M1 the motor facilitation during speech perception originates. Putative candidates might be represented by Broca's area and the ventral pre-motor cortex, both because of their involvement in speech production, and because of their similarity to the monkey pre-motor region where mirror neurons were firstly discovered. However, a potential causal nature of Broca's area and the ventral pre-motor area in phonological vs. lexical speech comprehension is less clear. In fact, lesions to Broca's area are often associated with both types of comprehension deficits (Basso, Casati, & Vignolo, 1977; Moineau, Dronkers, & Bates, 2005). Repetitive TMS and fMRI studies have revealed an antero-posterior functional gradient in the inferior frontal gyrus ranging from semantic analysis to phonological processing thus suggesting that BA 44 plays a role in phonological encoding (Gold, Balota, Kirchhoff, & Buckner, 2005; Gough, Nobre, & Devlin, 2005; Vigneau et al., 2006). In order to investigate the phonological role of Broca's area in speech perception, Haggard, Craighero and Fadiga (unpublished data) applied repetitive TMS (rTMS) to Broca's area, and more specifically to BA44, in healthy participants while they were engaged in a phonological discrimination task. Their results showed that both reaction times and task accuracy were unaffected by rTMS. Therefore, it is not clear whether the *pars opercularis* (BA44) is implicated in phonological processing or word-level speech comprehension.

In the present study, we propose that lexicality could be the key component that triggers activation of Broca's area. In order to test this hypothesis, we used a task that involves phonological processing by varying the degree of lexical content (i.e., phonological priming, Emmorey, 1989). This paradigm consists of word and/or pseudo-word pairs separated by a brief time interval. The final syllables of the two stimuli forming a pair can rhyme or not. In the classic version of the phonological priming paradigm, participants perform a lexical decision regarding the second stimulus of a pair. The phonological priming effect consists of faster reaction times (RT)s when a rhyme is present (see Dufour, 2008 for a review). Although some non-linguistic strategies may partially account for this facilitation (Norris, McQueen, & Cutler, 2002), this effect is rather robust and in general has been considered the result of pre-lexical processing (Dufour, 2008). To study the role of Broca's area in encoding phonological and lexical aspects, as well as their potential interactions, we devised four combinations of word (W) and pseudo-word (PW) pairs crossed with or without a rhyme between them. We first report two behavioral experiments that tested the experimental conditions (W–W, W–PW, PW–W and PW–PW), the first engaging subjects in a lexical discrimination task, the second in a phonological one. We then applied TMS to Broca's area to verify whether TMS interferes with phonological priming. Lastly, we performed an fMRI study to test whether Broca's area is activated in phonological priming and if this activity is modulated by phonology or lexicality.

2. Behavioral experiment 1

2.1. Methods

2.1.1. Participants

Eight right-handed (Oldfield, 1971) students (four females; mean age: 26.5 ± 4.2(SD) years) from the University of Ferrara volunteered to participate. All of them were native Italian speakers. Participants were screened for neurological and other medical conditions and gave informed consent for the experimental procedures, which were approved by the local Ethics Committee.

2.1.2. Stimuli and procedure

The experimental stimuli comprised four sets of prime–target pairs consisting of disyllabic 'cvcv' or 'cvccv' words and pseudo-words (for a list of the stimuli see Table 1). The time interval between prime and target presentation (ISI) was 20 ms. Each set of 40 pairs (total $N = 160$ trials) differed in terms of the lexical content of the words, in the following pairings: (i) word/word (W–W); (ii) pseudo-word/word (PW–W); (iii) word/pseudo-word (W–PW); (iv) pseudo-word/pseudo-word (PW–PW). In half of the stimuli ($N = 20$), a phonological overlap between prime and target was present (rhyming condition), while in the other half it was absent (non-rhyming condition). Stimuli were recorded using a female and a male speaker and were randomly combined to create an experimental sequence. During experimental sessions participants lay comfortably on a reclining armchair and were required to listen carefully to the verbal stimuli delivered via headphones. Participants were asked to indicate whether a target was a word or not by pressing one of two buttons (word/pseudo-word) with their left index or middle finger. The association between fingers and lexical property was counterbalanced across participants. Stimulus randomization, response collection and event timing were controlled using custom-made software written in Basic and running under an MS-DOS environment to provide the required temporal precision.

2.2. Results

An ANOVA was run on correct responses for reaction times (RTs) with the factors CONDITION (four levels: W–W, PW–W, W–PW, PW–PW) and PRIMING (two levels: Rhyme, NoRhyme). Both main effects were significant (CONDITION: $F[3, 21] = 23.48$; $p < 0.01$; PRIMING: $F[1, 7] = 21.18$; $p < 0.0001$) and further qualified by an interaction ($F[3, 21] = 7.41$; $p < 0.01$). Post-hoc analyses

Author's personal copy

Table 1
List of Italian stimuli.

	W–W	W–PW	PW–W	PW–PW
Female				
Rhyme	Tocca – bocca	Corta – zorta	Tosse – losse	Cata –zata
	Pera – cera	Freno – preno	Stanza – vanza	Buota – suota
	Tango – fango	Tasca – masca	Bomba – comba	Cobia – robia
	Bolla – folla	Tizio – cizio	Ruga – muga	Nago – sago
	Vita – gita	Rana – mana	Spiaggia – ciaggia	Tasna – masna
	Fato – lato	Caso – zaso	Meta – reta	Ciato – viato
	Duna – luna	Magno – pagno	Vaso – paso	Stoca – ruoca
	Fare – mare	Vecchio – lecchio	Lento – rento	Dano – viano
	Zucca – mucca	Colpe – molpe	Pugno – vugno	Tecra – gecra
	Fido – nido	Toro – soro	Testa – vesta	Polta – solta
No-rhyme	Bomba – zebra	Grugno – buota	Lesta – lufo	Zangra – gispia
	Cesto – sugo	Tana – nago	Letto – stali	Fazo – rasuo
	Fiume –scuola	Media – tasna	Dopo – raga	Diase – noste
	Gara – ritmo	Strada – terto	Moro – troli	Copo – lafria
	Lago – guancia	Vela – marto	Tetro – neca	Zasta – guotra
	Mano – granchio	Moro – troli	Tino – porpo	Piusca – rieta
	Noia – cielo	Freno – tile	Prato – gondo	Brona – dasta
	Panno –capra	Terme – cagia	Piena – revia	Zugra – friepa
	Specchio – stalla	Truppa – giarti	Vela – marto	Vutra – ligri
	Topo – patto	Ragno – ligri	Sedia – zangra	Tausa – mifro
Male				
Rhyme	Tela – mela	Gioia – groia	Pano – Sano	Romba – somba
	Coda – moda	Furto – nurto	Rondo – Tondo	Drodo – strodo
	Voglie – moglie	Buccia – zuccia	Gondo – Mondo	Subo – gubo
	Maso – naso	Bava – tava	Salco – Palco	Vonna – ronna
	Godo – nodo	Scienza – vienza	Ronte – Monte	Riume – chiume
	Boia – noia	Gobba – lobba	Rupo – Pupo	Vatto – satto
	Tonno – nonno	Cervo – mervo	Tuga – Fuga	Mana – cana
	Botte – notte	Nebbia – cebbia	Vuora – Nuora	Sarga – marga
	Tacco – pacco	Sorso – porso	Redia – Media	Rome – tome
	Calo – palo	Prugna – mugna	Crada – Spada	Pospo – gospo
No-rhyme	Sabbia – tara	Cabo – lofa	Tengi – Vasca	Pona – vicco
	Lente – fiacca	Cosvo – miervo	Nala – Tromba	Trase – perra
	Pista – vitro	Tafra – gelmi	Cabra – Seta	Renio – paro
	Duna – pupo	Recuo – sapri	Pivra – Fossa	Vedia – poia
	Rospo – zona	Balui – frunto	Miecra – Piuma	Sotte – virco
	Pepe – clima	Secra – zonto	Bonto – Lupo	Peve – prago
	Frate – spugna	Fadia – gualvo	Lanto – Padre	Race – noda
	Ladro – frase	Pionto – sialva	Sulto – Cane	Malco – tarba
	Nome – squalo	Goblio – vriato	Cavria – Figlio	Roio – tera
	Latte – bolla	Lasdio – marve	Sarso – Gatto	Sestia – pome

List of the stimuli used in the behavioral and TMS studies. Half of them were read by a female and the other half by a male speaker. Each column contains one of the four stimulus categories, half rhyming, half not.

(Duncan, $p < 0.05$ corrected) performed on the results indicate strong and statistically significant facilitation (phonological priming effect) for the following pairs: W–W ($p < 0.0001$), PW–W ($p < 0.005$), W–PW ($p < 0.05$), but no phonological priming effect for PW–PW ($p = 0.96$) pairs (Fig. 1A).

2.2.1. Interim summary

An interesting finding emerges from the analysis of the first behavioral data set: the presence or absence of lexical content modulates phonological priming. When neither a target nor a prime is lexical (PW–PW pairs) the presence of a rhyme does not facilitate the recognition of a target, suggesting that phonological priming requires lexical access. Norris et al. (2002) suggest that part of the facilitation effect in a primed lexical decision task is strategic as subjects are biased to say "yes" to targets that rhyme with their respective primes. Such a bias should affect all types of pairs in lexical decisions as a rhyme was present in all four conditions. However, both PW–W and W–PW pairs were not critically affected by such a bias in the current investigation. In order to ensure that the result was not simply a task-related lexical effect, we therefore performed an experiment in which participants were asked to perform a phonological discrimination task instead of a lexical decision task.

3. Behavioral experiment 2

3.1. Methods

3.1.1. Participants

Six right-handed (Oldfield, 1971) students (three females; 27.3 ± 5.4(SD)) from the University of Ferrara volunteered to participate in the study. All of them were native Italian speakers. Participants were screened for neurological and other medical conditions and gave informed consent for the experimental procedures, which were approved by the local Ethics Committee.

3.1.2. Stimuli and procedure

A subset (140 trials) of the initial stimulus set was tested in a phonological discrimination task. Participants were asked to detect if the final vowel of the target stimulus was /a/ or /o/. In all other aspects the procedure was to the same as in Experiment 1.

Author's personal copy

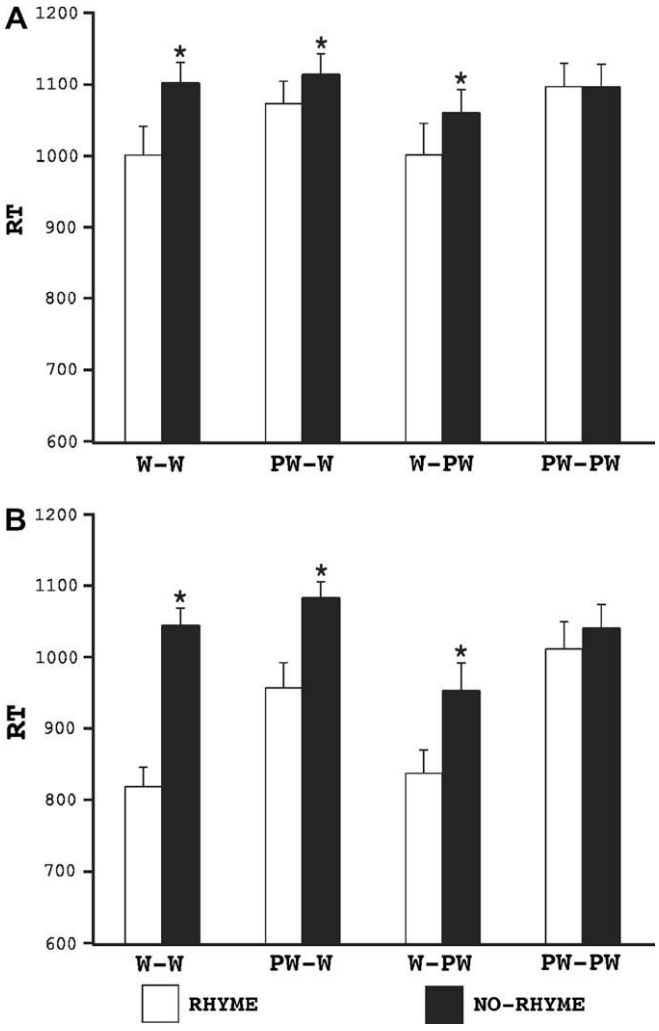


Fig. 1. Results of the behavioral studies. Reaction times (RTs ± SEM in milliseconds) for the behavioral lexical decision experiment (A). Reaction times (RTs ± SEM in milliseconds) for the behavioral vowel decision experiment (B). White bars: presence of rhyme between prime and target. Black bars: absence of rhyme. Asterisks on the black bar indicate the presence ($p > 0.05$, Duncan's test) of a phonological priming effect (response to rhyming target faster than response to non-rhyming target) in the respective condition. W–W, prime word/target-word; W–PW, prime-word/target-pseudo-word; PW–W, prime-pseudo-word/target-word; PW–PW, prime-pseudo-word/target-pseudo-word.

3.2. Results

An ANOVA was run on correct responses for reaction times (RTs) with the factors CONDITION (four levels: W–W, PW–W, W–PW, PW–PW) and PRIMING (two levels: Rhyme, NoRhyme). Both main effects were significant (CONDITION: $F[3, 15] = 69.89$; $p < 0.0001$; PRIMING, $F[1, 5] = 67.06$; $p < 0.0005$) and further qualified by a two-way interaction of the two factors ($F[3, 15] = 13.19$; $p < 0.0005$). Post-hoc tests (Duncan, $p < 0.05$ corrected) confirmed the results of the first experiment (W–W: $p < 0.00005$; PW–W: $p < 0.0005$; W–PW: $p < 0.0005$; PW–PW: $p = 0.21$).

3.2.1. Interim summary

Considering that in the second experiment, participants judged if the last vowel of the target was /a/ or /o/, this task is devoid of any explicit lexical decision. The fact that analogous results were found for both tasks supports the conclusion that the absence of phonological priming for the pseudo-word/pseudo-word pairs is task independent (Fig. 1B).

4. TMS experiment

4.1. Methods

4.1.1. Participants

Sixteen right-handed (Oldfield, 1971) students (eight females; 24.7 ± 5.1(SD)) from the University of Ferrara volunteered to participate in the TMS study. All of them were native Italian speakers. Participants were screened for neurological and other medical conditions and gave informed consent for the experimental procedures, which were approved by the local Ethics Committee.

4.1.2. Stimuli and procedure

The experimental stimuli were the same as in Behavioral Experiment 1. Participants lay comfortably on a reclining armchair, with their head stabilized by a headrest, and were required to listen carefully to the verbal stimuli delivered via headphones. Participants were requested to perform a lexical decision task as described in Behavioral Experiment 1.

4.1.3. Transcranial magnetic stimulation

Single pulse monophasic TMS (Magstim 200, Magstim Ltd., UK) was randomly administered in 50% of the trials using a custom-made BASIC script running under MS-DOS. TMS was delivered in the middle of the 20 ms delay between prime and target words, thus ensuring that the TMS click (duration 5 ms) did not overlap with the verbal stimuli. Stimulation intensity was set at 60% of the stimulator output via a 70 mm diameter 8-shaped coil.

Stimulation was applied to both Broca's area and to a control region (see below) in two separate sessions. Participants were subdivided into two groups. The first group ($n = 8$) underwent stimulation corresponding to the left Broca's area (pars opercularis), the second group ($n = 8$) to the posterior superior parietal lobule (control site). To avoid mislocalization of the target brain region, each participant underwent magnetic resonance imaging (MRI) scanning, and the position of the participant's scalp overlapping the target sites was assessed using custom-made neuro-navigation software. A 6-DOF electromagnetic tracker (Flock of Birds, Ascension Technology) was attached to the participant's forehead by an elastic band to compensate for head movements, and three fiducial points (bilateral tragus and nasion) were located by pointing to them with a stylus equipped with a second tracker. Then, the same fiducial points were identified on the participant's MRI, and the two coordinate systems were registered. Finally, for each point identified by the stylus on the participant's scalp, the software presented the corresponding location (three MRI sections) in real time.

4.2. Results

A pre-processing phase eliminated data two standard deviations above or below the participant's average RTs. The analysis of the TMS data set was restricted to the interaction between lexical and phonological processes. To do this, we analyzed the W–W and PW–PW conditions that had shown maximal differences in priming in the two behavioral experiments (results of all four conditions are presented in Table 2). Single two-tailed Paired Student's *t*-tests (corrected for multiple comparisons with the Bonferroni method) were used to analyze the rhyming effect. RT differences between rhyming and non-rhyming pairs were used as a measure of facilitation induced by the presence of a rhyme. The difference between W–W and PW–PW was significant both at the control site ($t[7] = 3.79$; $p = 0.007$) and in the "no" TMS trials ($t[7] = 4.03$; $p = 0.005$). In contrast, the stimulation of Broca's area ($t[7] = 1.69$; $p = 0.136$) did not result in significant differences between the two trial types. Additionally, stimulation of Broca's area increased the phonological

Author's personal copy

Table 2
TMS study results.

	W–W	PW–PW	W–PW	PW–W
Broca's area	127.20	83.15	23.12	76.53
SEM	22.03	14.59	17.11	15.94
Control area	151.02	6.20	66.63	100.74
SEM	27.06	14.86	11.99	9.63
No TMS	110.40	10.40	22.83	105.34
SEM	26.57	12.78	17.30	23.72

Summary of TMS results. Phonological priming when TMS stimulation was applied to Broca's area, to a control site (posterior parietal) or not applied. The priming effect was measured for W–W, PW–PW as well as PW–W and W–PW pairs. Mean RT difference between Rhyme and No-Rhyme trials are shown with the SEM.

priming effect for PW–PW trials compared to the control site ($t[7] = 4.74$; $p = 0.002$) and no stimulation ($t[7] = 4.63$; $p = 0.002$). Therefore, the pattern of performance observed after stimulation of Broca's area diverged from the results obtained when stimulation was applied to a control site or in absence of any stimulation.

4.2.1. Interim summary

These data suggest that TMS to Broca's area interferes with the lexical–phonological interaction reported in the behavioral experiments. This interaction induced considerable phonological facilitation when W–W pairs were presented and no phonological modulation when listening to PW–PW pairs. Conversely, TMS to Broca's area significantly increased the rhyme-induced facilitation for the PW–PW pairs (see Fig. 2).

5. fMRI experiment

5.1. Methods

5.1.1. Participants

Sixteen right-handed (Oldfield, 1971) students (nine males, seven females; Mean Age: 25.25 ± 4.4(SD)) from the University of Leipzig volunteered to participate in the present study. All participants were native German speakers. Participants were screened for neurological and other medical conditions and gave informed consent for the experimental procedures, which were approved by the local Ethics Committee.

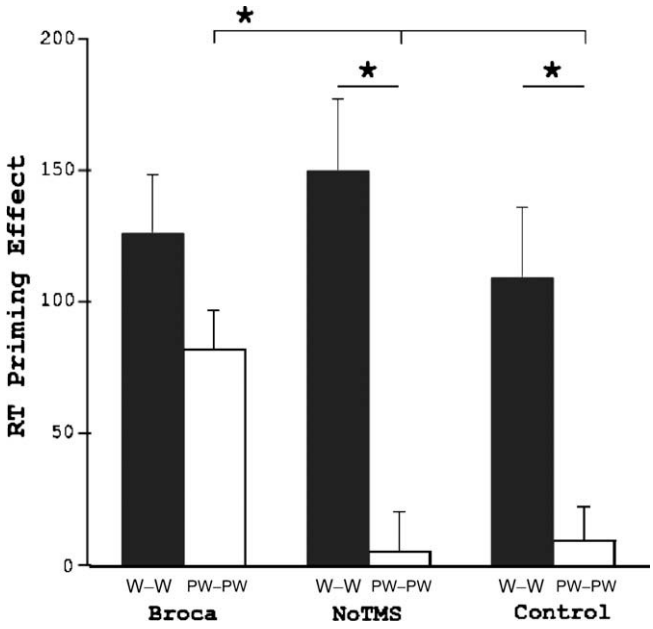


Fig. 2. TMS effects on the phonological facilitation for the W–W and PW–PW pairs. Reaction times (RTs ± SEM in milliseconds) for the TMS experiment during lexical decision with interference to Broca's area, a control site, and no TMS. Bars represent the difference in facilitation between the rhyming and non-rhyming conditions for the W–W and PW–PW pairs. Asterisks indicate the presence ($p < 0.05$, paired t-test with Bonferroni correction) of a significant difference in the phonological priming effect between W–W and PW–PW. PW–PW priming effects were larger when Broca's area was stimulated compared to the control site and no TMS conditions.

5.1.2. Stimuli and procedure

The experimental stimuli were similar to those used in the behavioral experiment except for the language (German, see Table 3 for a list of the pairs). The paradigm was kept constant and included four prime–target pair types (W–W, PW–W, W–PW, PW–PW), 20 of each type in a rhyming and 20 in a non-rhyming condition. Stimuli were recorded using a male and a female native speaker of standard German. Participants performed a lexical decision task by pressing one of two buttons on an fMRI-compatible response pad.

A total of 320 experimental trials plus 40 null events were presented, with each trial lasting 6 s. Three functional scans per trial (TR, 2 s) were acquired (total, $360 * 3 = 1080$ volumes). The onset of the auditory stimulation with respect to the beginning of each trial was randomly varied (0, 500, 1000, 1500 ms) during the experiment, and the mean duration of the audio files presented (prime–target pair) was 0.54 s. Sampling was continuous, but the HRF model was tied to the onset of auditory stimulation. The maximum response time was 1200 ms. Incorrect responses were not included in the data analysis.

5.1.3. fMRI data acquisition

The experiment was carried out on a 3T scanner (Bruker MedSpec, Germany). For functional imaging, 18 axial slices parallel to the AC-PC plane and covering almost the whole brain were acquired using a gradient-echo, echo-planar (EPI) $T2^*$-weighted sequence with a TE of 30 ms, a flip angle of 90°, a TR of 2 s, and an acquisition bandwidth of 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. The slice thickness was 4 mm with an interslice gap of 1 mm. Prior to the functional runs, 18 T1-weighted MDEFT (Ugurbil et al., 1993) images (data matrix 256×256, TR 1.3 s, TE 7.4 ms) were obtained with a non slice-selective inversion pulse followed by a single excitation of each slice (Norris, 2000).

5.1.4. fMRI data analysis

Data processing was performed with the software package LIPSIA (Lohmann et al., 2001). Functional data were corrected for motion using a matching metric based on linear correlation. Three images at the start of each session were discarded to allow the EPI signal to reach equilibrium. To correct for the temporal offset between the slices acquired in one scan, a cubic-spline interpolation was applied. A temporal high-pass filter with a cutoff frequency of 1/80 Hz was used for baseline correction of the signal, and a spatial Gaussian filter (5.65 mm FWHM) was applied.

To align the functional data slices with a 3D stereotactic coordinate 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 (Norris, 2000; Ugurbil et al., 1993) slices to achieve an optimal match between these slices and the individual 3D reference data set, which was acquired for each participant during a previous scanning session. The MDEFT volume data set with 160 slices and 1 mm slice thickness was standardized to the Talairach stereotactic space (Talairach & Tournoux, 1988). This linear normalization process was improved by a subsequent processing step that performed an additional nonlinear normalization (Thirion, 1998).

The statistical evaluation was based on a least-squares estimation using the general linear model for serially autocorrelated observations (Friston, 1994, Friston, 1995, Friston et al., 1995;

Author's personal copy

Table 3
List of German stimuli.

	W–W	W–PW	PW–W	PW–PW
Rhyme	Beute – Meute	Bibel – Mibel	Baage – Waage	Berter – Nerter
	Buegel – Huegel	Bummel – Nummel	Braube – Schraube	Feisehr – Leisehr
	Faden – Laden	Degen – Begen	Fappe – Kappe	Girton – Birton
	Feige – Geige	Dichter – Michter	Fate – Pate	Guder – Muder
	Feile – Meile	Dusche – Zusche	Furke – Gurke	Huter – Buter
	Gipfel – Wipfel	Feder – Teder	Geihe – Leihe	Kande – Tande
	Haube – Laube	Fessel – Pessel	Getter – Retter	Kreibe – Preibe
	Hebel – Nebel	Fieber – Kieber	Jaken – Haken	Lobast – Bobast
	Kante – Tante	Garten – Narten	Laumen – Daumen	Merte – Zerte
	Katze – Tatze	Keller – Neller	Leife – Reife	Mure – Ture
	Kelle – Schelle	Kette – Pette	Lunke – Funke	Pachen – Kachen
	Kenner – Renner	Kissen – Zissen	Mabe – Gabe	Pase – Zase
	Kupfer – Tupfer	Lehne – Nehne	Megel – Pegel	Porkort – Forkort
	Maler – Taler	Meise – Teise	Nuster – Schuster	Prosel – Frosel
	Miete – Niete	Nudel – Kudel	Schueste – Bueste	Roda – Goda
	Nahrung – Paarung	Rabe – Dabe	Tektor – Rektor	Scharin – Parin
	Paste – Taste	Rinde – Pinde	Trise – Krise	Tauper – Fauper
	Raucher – Taucher	Schuerze – Luerze	Vame – Dame	Tinnel – Finnel
	Samen – Rahmen	Sorte – Morte	Zarren – Barren	Tinsug – Minsug
	Schaefer – Kaefer	Titel – Fitel	Zende – Lende	Wusser – Lusser
No-rhyme	Becher – Wiese	Bitte – Frister	Bolter – Senat	Basse – Polgen
	Biber – Ware	Fabel – Wuno	Brasta – Hader	Boehne – Schluse
	Bulle – Salve	Gatte – Grilbe	Bremach – Scholle	Chorbung – Pompel
	Delle – Hammer	Hafen – Stema	Daufer – Henne	Dorke – Parler
	Duese – Kegel	Handel – Purke	Fage – Pute	Faegler – Worso
	Faktor – Riese	Jammer – Kalem	Frause – Hammel	Gleissel – Kraube
	Halter – Reiher	Kuehle – Zoba	Frautsche – Lade	Jeere – Zussel
	Harfe – Gasse	Kutsche – Malbo	Glode – Biene	Jinge – Draber
	Harke – Falter	Lappen – Pausto	Greiste – Kater	Kolfer – Dukan
	Huelle – Futter	Laune – Lingel	Hammi – Ruede	Kringer – Litte
	Laenge – Butter	Liege – Voda	Krommer – Zirkel	Kritsche – Floegel
	Menge – Hummer	Mueller – Mochen	Menke – Buerde	Luerste – Nalte
	Motte – Scheide	Neige – Teisand	Migen – Hagel	Maese – Loxi
	Note – Dauer	Pappe – Schloben	Misau – Scherbe	Meder – Dilo
	Puppe – Schabe	Riegel – Banter	Nautiv – Rappe	Moche – Garste
	Suppe – Wabe	Schanze – Salpe	Nuscher – Heide	Neklag – Kitto
	Therme – Schachtel	Schenkel – Gister	Schluber – Rede	Selle – Ladan
	Waerme – Distel	Schere – Bauste	Schmeter – Moewe	Wobel – Rauge
	Zuegel – Gruppe	Urlaub – Olben	Tibel – Masche	Wosten – Binga
	Zunge – Presse	Vene – Plomin	Pechel – Rache	Zaste – Kaler

List of the stimuli used in the fMRI study. All stimuli were spoken both by a male and female speaker. Each column contains one of the four stimulus categories, half rhyming, half not.

Worsley & Friston, 1995). The design matrix was generated with a synthetic hemodynamic response function (Friston et al., 1998, Josephs, Turner, & Friston, 1997) and its first derivative. The model equation, including the observation data, the design matrix and the error term, was convolved with a Gaussian kernel of dispersion of 4 s FWHM to deal with the temporal autocorrelation (Worsley & Friston, 1995). In the following step, contrast-images (i.e., estimates of the raw-score differences between specified conditions) were generated for each participant. The single-participant contrast-images were then entered into a second-level random effects analysis for each of the contrasts (Holmes & Friston, 1998). Subsequently, *t*-values were transformed into *Z*-scores. To protect against false positive activations, only regions with *Z*-scores greater than 3.1 ($p < 0.001$, uncorrected) and with a volume greater than 270 mm^3 (10 measured voxels) were considered.

5.2. Results

An ANOVA was run on correct responses for reaction times (RTs) with the factors CONDITION (four levels: W–W, PW–W, W–PW, PW–PW) and PRIMING (two levels: Rhyme, NoRhyme). Both main effects were significant (CONDITION, $F[3, 42] = 17.08$; $p < 0.001$; PRIMING, $F[1, 14] = 208.89$; $p < 0.001$) and further qualified by a two-way interaction of the factors ($F[3, 42] = 25.74$; $p < 0.001$). Post-hoc tests (Duncan, $p < 0.05$ corrected) confirmed the previous results showing that W–W and PW–PW pairs give rise to opposite priming effects. For this reason, we analyzed the fMRI contrast between rhyming and non-rhyming conditions separately for the W–W and PW–PW pairs.

The comparison of W–W and PW–PW pairs showed an interesting dissociation between the inferior frontal gyrus (IFG) and the superior temporal gyrus (STG) (as shown in Fig. 3 and Table 4) in relation to the presence/absence of a rhyme. More specifically, listening to pairs of rhyming pseudo-words (PW–PW rhyming) significantly activated the bilateral STG, with a larger extension in the left hemisphere (left: $X = -59$, $Y = -23$, $Z = 3$; cluster size: 2160 mm^3; Mean *Z*-score: 3.58; right: $X = 40$, $Y = -38$, $Z = 9$, cluster size: 1593 mm^3; Mean *Z*-score: 3.61), a site classically involved in speech perception (Wernicke's area). Listening to pairs of rhyming words (W–W rhyming) elicited activation in the left anterior IFG ($X = -56$, $Y = 28$; $Z = 6$; cluster size: 972 mm^3; Mean *Z*-score: 3.32). Listening to pairs of non-rhyming words (W–W non-rhyming) elicited a significant increase in brain activity in the pars opercularis of the IFG. The peak activation ($X = -47$, $Y = 1$, $Z = 33$; cluster size: 1593 mm^3; Mean *Z*-score: 3.40) was located in the ventral BA6 but extended into BA44. Furthermore, significant activation was also observed in the left anterior insula ($X = -32$; $Y = 13$; $Z = 6$; cluster size: 3726 mm^3; Mean *Z*-score: 3.53).

Author's personal copy

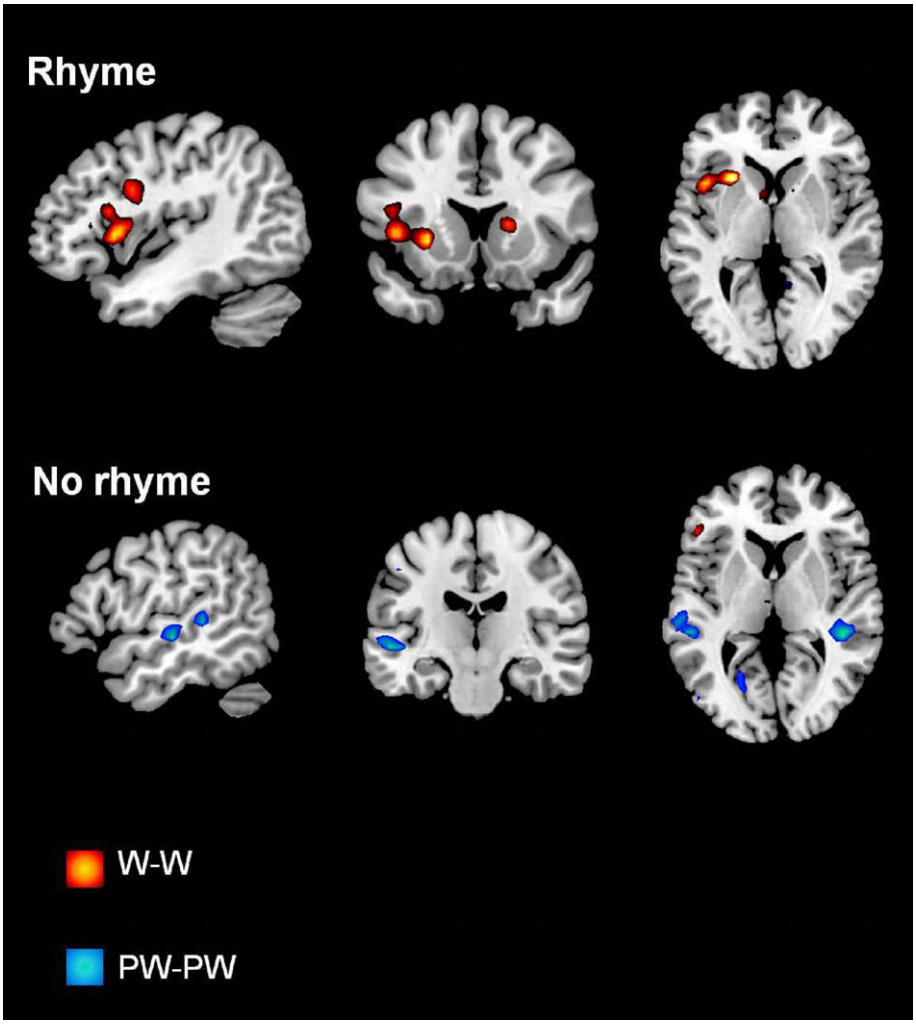


Fig. 3. Results of the fMRI study. Functional MRI results. Group statistical maps resulting from the comparison between words and pseudo-words in both non-rhyming (Panel A) and rhyming (Panel B) conditions ($p < .001$, uncorrected). Significant activity for words (W–W) and pseudo-words (PW–PW) is shown in warm and cool colors, respectively. Activation maps are superimposed on the anatomical reference image provided by the software package LIPSIA. Images are displayed in neurological convention. Coordinates of areas showing significant effects are reported in Table 4.

6. Discussion

In recent years, empirical evidence has given support to the idea originally proposed by James (1890) that the motor system plays a role beyond action planning and execution. Indeed, the finding that neurons in the monkey's frontal cortex discharge both during action execution and perception (sensorimotor neurons) suggests the existence of recurrent mechanisms bi-directionally linking the two sides of perceptuo-motor circuits (see Fadiga, Fogassi, Gallese, & Rizzolatti, 2000). These mechanisms share some similarities with the basic tenets of the motor theory of speech perception (Liberman et al., 1967). We suggest that action understanding and speech comprehension may rely on similar "motor resonant" mechanisms.

A key prediction of the motor theory of speech perception is that Broca's area – classically considered the motor center for speech – should also be involved in speech perception. This idea has been considered very appealing by several authors, but little evidence points to Broca's area causally contributing to either phonological or word level perception (Basso et al., 1977; Moineau et al., 2005). Recent TMS work has directly studied the semantic and phonological properties of the left IFG (see Devlin & Watkins, 2007). Nixon, Lazarova, Hodinott-Hill, Gough, and Passingham (2004) found that stimulation of the caudal part of the left IFG interfered with phonological working memory. Gough et al. (2005) designed an interesting TMS experiment to test a spatial double dissociation between semantic and phonological processing in the left IFG. TMS on the rostral left IFG selectively increased response latencies when participants focused on the meaning but not when they focused on the sound pattern of words. The reverse pattern resulted from stimulation of the caudal left IFG. However, in the latter studies, phonology was studied using words (Gough et al., 2005; Nixon et al., 2004). Conversely, when phonology is investigated independent of the lexical content of the stimuli, TMS-dependent effects are found when pre-motor and motor cortices are stimulated (D'Ausilio et al., 2009; Meister, Wilson, Deblieck, Wu, & Iacoboni, 2007), but not when BA44 is (see Haggard, Craighero and Fadiga, unpublished data).

The current results suggest that lexical processing may influence phonological processing. In fact, the use of words and pseudo-words that either share the last syllable or not was specifically aimed at tackling the processing of both lexical and phonological features (Dufour, 2008; Spinelli, Segui, Radeau, 2001; Slowiaczek, Solanto, Wieting, & Bishop, 2003; Dumay et al., 2001). Our first finding is that pseudo-word/pseudo-word pairs do not lead to phonological priming. However, phonological

Author's personal copy

Table 4
Activity locations in the fMRI study.

Talairach coordinates			Mean *Z*	Volume	Region
x	*y*	*z*			
W–W_noRhyme > PW–PW_noRhyme					
−32	13	6	3.53	3726	Left insula
−11	4	9	3.51	2538	Left caudate
10	10	12	3.45	1431	Right caudate
−47	1	33	3.40	1593	Left inferior frontal gyrus
W–W_noRhyme < PW–PW_noRhyme					
34	−59	27	3.65	918	Right middle temporal gyrus
7	−56	18	3.49	3537	Right posterior cingulate
−11	−65	18	3.42	1080	Left precuneus
W–W_Rhyme > PW–PW_Rhyme					
−56	28	6	3.32	972	Left inferior frontal gyrus
34	−47	45	3.31	459	Right inferior parietal lobule
−44	−53	45	3.31	2133	Left inferior parietal lobule
−41	10	42	3.28	702	Left middle frontal gyrus
W–W_Rhyme < PW–PW_Rhyme					
40	−38	9	3.61	1593	Right superior temporal gyrus
−59	−23	3	3.58	2160	Left superior temporal gyrus
−26	−74	9	3.41	1134	Left middle occipital gyrus
−26	−59	−3	3.37	810	Left lingual gyrus

List of activations for the contrasts between W–W and PW–PW for the rhyming and non-rhyming trials. For each local maximum, Talairach coordinates, Mean *Z*-score and volume of activity (mm^3) are reported (p-value < .001, uncorrected).

priming in lexical decisions may induce a strategic bias toward answering "word" to targets that rhyme with their primes (Norris et al., 2002), and may thus not be a pre-lexical phenomenon. To address this possible criticism, we replicated the results of the lexical decision task in a vowel decision task, where such a strategic bias should not play a critical role. Indeed, the absence of a rhyming effect in the PW–PW condition is neither task (lexical or phonological decision) nor language (Italian and German) dependent.

Our TMS study showed that interference to Broca's area eliminates the priming difference between W–W pairs and PW–PW pairs. More specifically, the virtual lesion of Broca's area led to comparable PW–PW and W–W priming effects. One possible explanation is that the TMS-induced virtual lesion of Broca's area may interfere with a top-down influence exerted on speech perception areas. Accordingly, Broca's area may not be involved in phonological analysis per se, but may rather exert modulatory influences on rhyme processing. Such modulation may be triggered by lexically rich material. In fact, when listening to words, a listener can anticipate phonological features before they actually appear (Roy et al., 2008). This may enhance phonological anticipation and, in turn, reduce reaction times when a rhyme is present. Such processes can be mediated by the bi-directional recurrent connections between the IFG and the posterior STG (Matsumoto et al., 2004). TMS may have canceled out this modulatory influence of Broca's area.

This hypothesis is further supported by our fMRI results. Rhyming stimuli activated the posterior STG when listening to pseudo-words, whereas words activated the left IFG (BA45). However, only non-rhyming word stimuli activated the posterior IFG (BA44/6). Both rhyming and non-rhyming words activated the left IFG, indicating that this area is critically involved in the processing of lexical properties. In contrast, pseudo-words activated the posterior STG only in the presence of a rhyme. This pattern of results seems to reflect the relative balance between anterior and posterior language areas when: (i) top-down lexical-driven processing is possible (W–W, rhyme and no rhyme) or (ii) stimulus-driven analysis of meaningless words is facilitated by phonological similarities (PW–PW and rhyme). A balanced interaction between anterior and posterior language areas can thus be considered the basis of both speech perception and speech production, leaving room for the acquisition of new verbal material by associating lexical meaning with a given pseudo-word.

We consider that one of the many functional roles of Broca's area is to match phonological stimuli onto a repertoire of words and not on individually meaningless "phoneme assemblies". Thus, the motor resonance of tongue representation revealed by TMS when listening to pseudo-words is probably due to a different phenomenon (Fadiga et al., 2002; Roy et al., 2008; D'Ausilio et al., 2009). Cortical regions other than area BA44 may be involved in the "acoustically evoked mirror effect", which is quite independent of the meaning of a presented stimulus. Further support for this idea comes from fMRI evidence by Wilson, Saygin, Sereno, and Iacoboni (2004) showing that the only cortical region constantly activated during both perception and production of meaningless syllables was bilaterally located in the superior part of ventral pre-motor cortex, dorsal to Broca's area. It is likely that two distinct processes act in the frontal lobe at the same time. The first, potentially located in the upper portion of the ventral pre-motor cortex, could be considered a low-level motor resonance, involved in the analysis of phonemes, a process that is meaning independent. The second, located in the pars opercularis (BA44) may be concerned with word-level analysis. This portion of Broca's area is specifically activated by meaningful words and possibly reflects a hierarchically higher level of speech analysis.

Acknowledgments

L.F. is supported by the Italian Ministry of Education, by the E.C. grants Contact, Robot-cub and Poeticon and by Fondazione Cassa di Risparmio di Ferrara. S.A.K. is supported by various grants from the German Science Foundation, and the Max-Planck-Society. We thank the MPI medical technical fMRI team for support during data acquisition and Rosie Wallis for helpful editing of the manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.bandl.2009.07.008.

Author's personal copy

References

Amunts, K., Schleicher, A., Burgel, U., Mohlberg, H., Uylings, H. B., & Zilles, K. (1999). Broca's region revisited: Cytoarchitecture and intersubject variability. *Journal of Comparative Neurology, 412*(2), 319–341.

Basso, A., Casati, G., & Vignolo, L. A. (1977). Phonemic identification defect in aphasia. *Cortex, 13*, 85–95.

D'Ausilio, A., Pulvermüller, F., Salmas, P., Bufalari, I., Begliomini, C., & Fadiga, L. (2009). The motor somatotopy of speech perception. *Current Biology, 19*(5), 381–385.

Devlin, J. T., & Watkins, K. E. (2007). Stimulating language: Insights from TMS. *Brain, 130*(Pt 3), 610–622.

di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research, 91*(1), 176–180.

Dufour, S. (2008). Phonological priming in auditory word recognition: when both controlled and automatic processes are responsible for the effects. *Canadian Journal of Experimental Psychology, 62*(1), 33–41.

Dumay, N., Benraïss, A., Barriol, B., Colin, C., Radeau, M., & Besson, M. (2001). Behavioral and electrophysiological study of phonological priming between bisyllabic spoken words. *Journal of Cognitive Neuroscience, 1*, 121–143.

Emmorey, K. (1989). Auditory morphological priming in the lexicon. *Language and Cognitive Processes, 4*, 73–92.

Fadiga, L., Craighero, L., Buccino, G., & Rizzolatti, G. (2002). Speech listening specifically modulates the excitability of tongue muscles: A TMS study. *European Journal of Neuroscience, 15*(2), 399–402.

Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (2000). Visuomotor neurons: Ambiguity of the discharge or 'motor' perception? *International Journal of Psychophysiology, 35*(2–3), 165–177.

Friston, K. (1994). Statistical parametric mapping. In: R. Thatcher, M. Hallet, T. Zeffiro, E. John, & M. M. Huerta (Eds.), *Functional imaging: Technical foundations* (pp. 79–93). San Diego: Academic Press.

Friston, K. (1995). Statistical parametric maps in functional imaging: A general linear approach. *Human Brain Mapping, 2*, 189–210.

Friston, K. J., Fletcher, P., Josephs, O., Holmes, A., Rugg, M. D., & Turner, R. (1998). Event-related fMRI: Characterizing differential responses. *Neuroimage, 7*(1), 30–40.

Friston, K. J., Holmes, A. P., Poline, J. B., Grasby, P. J., Williams, S. C., Frackowiak, R. S., et al. (1995). Analysis of fMRI time-series revisited. *Neuroimage, 2*(1), 45–53.

Galantucci, B., Fowler, C. A., & Turvey, M. T. (2006). The motor theory of speech perception reviewed. *Psychonomic Bulletin & Review, 13*(3), 361–377.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain, 119*(Pt 2), 593–609.

Gold, B. T., Balota, D. A., Kirchhoff, B. A., & Buckner, R. L. (2005). Common and dissociable activation patterns associated with controlled semantic and phonological processing: Evidence from FMRI adaptation. *Cerebral Cortex, 15*, 1435–1438.

Gough, P. M., Nobre, A. C., & Devlin, J. T. (2005). Dissociating linguistic processes in the left inferior frontal cortex with transcranial magnetic stimulation. *Journal of Neuroscience, 25*, 8010–8016.

Holmes, A. P., & Friston, K. J. (1998). Generalisablity, random effects & population inference. *Neuroimage, 7*, 754.

Josephs, O., Turner, R., & Friston, K. (1997). Event-related fMRI. *Human Brain Mapping, 5*, 243–248.

Liberman, A. M., Cooper, F. S., Shankweiler, D. P., & Studdert-Kennedy, M. (1967). Perception of the speech code. *Psychological Review, 74*(6), 431–461.

Liberman, A. M., Delattre, P., & Cooper, F. S. (1952). The role of selected stimulus-variables in the perception of the unvoiced stop consonants. *American Journal of Psychology, 65*(4), 497–516.

Liberman, A. M., Delattre, P. C., Gerstman, L. J., & Cooper, F. S. (1956). Tempo of frequency change as a cue for distinguishing classes of speech sounds. *Journal of Experimental Psychology, 52*(2), 127–137.

Liberman, A. M., Harris, K. S., Hoffman, H. S., & Griffith, B. C. (1957). The discrimination of speech sounds within and across phoneme boundaries. *Journal of Experimental Psychology, 54*(5), 358–368.

Liberman, A. M., & Mattingly, I. G. (1985). The motor theory of speech perception revised. *Cognition, 21*(1), 1–36.

Liberman, A. M., & Whalen, D. H. (2000). On the relation of speech to language. *Trends in Cognitive Sciences, 4*(5), 187–196.

Lohmann, G., Muller, K., Bosch, V., Mentzel, H., Hessler, S., Chen, L., et al. (2001). LIPSIA – A new software system for the evaluation of functional magnetic resonance images of the human brain. *Computerized Medical Imaging and Graphics, 25*(6), 449–457.

Matelli, M., Luppino, G., & Rizzolatti, G. (1985). Patterns of cytochrome oxidase activity in the frontal agranular cortex of the macaque monkey. *Behavioural Brain Research, 18*(2), 125–136.

Matsumoto, R., Nair, D. R., LaPresto, E., Najm, I., Bingaman, W., Shibasaki, H., et al. (2004). Functional connectivity in the human language system: A cortico-cortical evoked potential study. *Brain, 127*, 2316–2330.

Meister, I. G., Wilson, S. M., Deblieck, C., Wu, A. D., & Iacoboni, M. (2007). The essential role of premotor cortex in speech perception. *Current Biology, 17*, 1692–1696.

Moineau, S., Dronkers, N. F., & Bates, E. (2005). Exploring the processing continuum of single-word comprehension in aphasia. *Journal of Speech Language and Hearing Research, 48*, 884–896.

Nixon, P., Lazarova, J., Hodinott-Hill, I., Gough, P., & Passingham, R. (2004). The inferior frontal gyrus and phonological processing: An investigation using rTMS. *Journal of Cognitive Neuroscience, 16*, 289–300.

Norris, D. G. (2000). Reduced power multislice MDEFT imaging. *Journal of Magnetic Resonance Imaging, 11*(4), 445–451.

Norris, D. G., McQueen, J. M., & Cutler, A. (2002). Bias effects in facilitatory phonological priming. *Memory & Cognition, 30*, 399–411.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*(1), 97–113.

Petrides, M., Cadoret, G., & Mackey, S. (2005). Orofacial somatomotor responses in the macaque monkey homologue of Broca's area. *Nature, 435*(7046), 1235–1238.

Petrides, M., & Pandya, D. N. (1999). Doroslateral prefrontal cortex: Comparative cytoarchitectonic analysis in the human and the macuaque brain and cortococortical connection patterns. *European Journal of Neuroscience, 11*, 1011–1036.

Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Luppino, G., & Matelli, M. (1988). Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements. *Experimental Brain Research, 71*(3), 491–507.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience, 27*, 169–192.

Roy, A. C., Craighero, L., Fabbri-Destro, M., & Fadiga, L. (2008). Phonological and lexical motor facilitation during speech listening: a transcaranial magnetic stimulation study. *Journal of Physiology, Paris, 102*, 101–105.

Slowiaczek, L. M., Solanto, E. G., Wieting, S. J., & Bishop, K. L. (2003). An investigation of phonology and orthography in spoken word recognition. *Quarterly Journal of Experimental Psychology, A, Human Experimental Psychology, 56*, 233–262.

Spinelli, E., Segui, J., & Radeau, M. (2001). Phonological priming in spoken word recognition with bisyllabic targets. *Language and Cognitive Processes, 16*, 367–392.

Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. New York: Thieme.

Thirion, J. P. (1998). Image matching as a diffusion process: An analogy with Maxwell's demons. *Medical Image Analysis, 2*(3), 243–260.

Toni, I., de Lange, F. P., Noordzij, M. L., & Hagoort, P. (2008). Language beyond action. *Journal of Physiology – Paris, 102*(1–3), 71–79.

Turella, L., Pierno, A. C., Tubaldi, F., & Castiello, U. (2009). Mirror neurons in humans: Consisting or confounding evidence? *Brain and Language, 108*, 10–21.

Ugurbil, K., Garwood, M., Ellermann, J., Hendrich, K., Hinke, R., Hu, X., et al. (1993). Imaging at high magnetic fields: Initial experiences at 4 T. *Magnetic Resonance, 9*(4), 259–277.

Vigneau, M., Beaucousin, V., Hervé, P. Y., Duffau, H., Crivello, F., Houdé, O., et al. (2006). Meta-analyzing left hemisphere language areas: Phonology, semantics, and sentence processing. *Neuroimage, 30*, 1414–1432.

James, W. (1890). *The principles of psychology*. New York: Henry Holt and Co.

Wilson, S. M., Saygin, A. P., Sereno, M. I., & Iacoboni, M. (2004). Listening to speech activates motor areas involved in speech production. *Nature Neuroscience, 7*(7), 701–702.

Worsley, K. J., & Friston, K. J. (1995). Analysis of fMRI time-series revisited-again. *Neuroimage, 2*(3), 173–181.