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Phonological and Lexical Motor Facilitation during Speech Listening: A Transcranial Magnetic Stimulation Study.

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Abstract

In the present study we used transcranial magnetic stimulation (TMS) to investigate the influence of phonological and lexical properties of verbal items on the excitability of the tongue's cortical motor representation during passive listening. In particular, we aimed to clarify if the difference in tongue motor excitability found during listening to words and pseudo-words (Fadiga et al. 2002) is due to lexical frequency or to the presence of a meaning *per se*. In order to do this, we investigated the time-course of tongue motor-evoked potentials (MEPs) during listening to frequent words, rare words, and pseudo-words embedded with a double consonant requiring relevant tongue movements for its pronunciation. Results showed that at the later stimulation intervals (200 and 300 ms from the double consonant) listening to rare words evoked much larger MEPs than listening to frequent words. **Moreover, by comparing pseudo-words embedded with a double consonant requiring much or less tongue movements, we found that a pure phonological motor resonance was present only 100 ms after the double consonant.** Thus, while the phonological motor resonance appears very early, the lexical-dependent motor facilitation takes more time to appear and depends on the frequency of the stimuli.

The present results indicate that the motor system responsible for phonoarticulatory movements during speech production is also involved during speech listening in a strictly specific way. This motor facilitation reflects both the difference in the phonoarticulatory characteristics and the difference in familiarity of the verbal material.

Keywords: motor resonance, tongue MEPs, words listening

1. Introduction

The precise neural mechanisms underlying speech perception are still largely unknown. The most accepted view is that speech perception depends on auditory-cognitive mechanisms specifically devoted to the analysis of sounds conveying words (Kuhl & Miller, 1975; Klatt, 1979; Sussman, 1989; Massaro & Cohen, 1990). An alternative hypothesis, the motor theory of speech perception, considers that what is fundamental for speech perception, are not the sounds, but the articulatory (motor) gestures generating those sounds (Liberman & Mattingly, 1985; Liberman & Wahlen, 2000). A direct prediction of this theory is, therefore, that to achieve verbal communication, phonologically relevant motor representations become active at the same time, in both the speaker's brain (to talk) and the listener's brain (to understand).

Recently, a series of studies involving Transcranial Magnetic Stimulation (TMS), have provided converging evidence that the human motor system selectively resonates in response to speech sounds. Fadiga et al. (2002) recorded motor evoked potentials (MEPs) from the tongue muscles in normal volunteers instructed to carefully listen to acoustically presented words and regular pseudo-words. In the middle of the verbal stimuli there was either a double "f" or a double "r". "F" is a labio-dental fricative consonant that, when pronounced, requires virtually no tongue movements, whereas "r" is a linguo-palatal fricative consonant that, in contrast, requires marked tongue muscle involvement to be pronounced. During verbal item presentation, the left motor cortex of the participants was stimulated with single-pulse TMS administered over the area corresponding to the tongue motor representation. The results showed that listening to verbal stimuli containing the double "r" induced a significant facilitation of tongue MEPs compared to listening to verbal stimuli containing the double "f" (phonological resonance effect). In addition to this effect, the authors reported that listening to words induced higher MEPs than listening to pseudo-words, irrespective of the importance of tongue movements (lexical resonance effect). Results congruent with those of Fadiga et al. (2002) were obtained by Watkins et al. (2003). Using the single-pulse TMS technique, they recorded MEPs from a lip muscle (*orbicularis oris*) and a hand muscle (first dorsal *interosseus*) in four conditions: listening to continuous prose, viewing speech-related lip movements, listening to non-verbal sounds, and viewing eye and brow movements. Compared to viewing eye and brow movements, listening to and viewing speech enhanced the MEP amplitude recorded from the *orbicularis oris* muscle, while the size of MEPs elicited in the first dorsal *interosseus* muscle did not differ in any condition.

All these data suggest that when an individual listens to verbal stimuli, there is an automatic activation of those speech-related motor centers that would be involved in the production of the verbal material. This automatic motor resonance, specifically related to the phonological content of the presented stimuli (Fadiga et al., 2002), demonstrates that during verbal communication there is a co-activation of articulatory motor representations in the brains of both the speaker and the listener. Although these results do not imply that this motor resonance is necessary and sufficient to understand speech, they represent the first electrophysiological data supporting a main prediction of Liberman's motor theory of speech perception (Liberman & Mattingly, 1985; Liberman & Wahlen, 2000).

The nature of the second, lexical effect found by Fadiga et al. (2002) remains, however, incompletely elucidated. **On the one hand, it may reflect the facilitation of the motor speech centers due to the recognition that the presented stimulus as a word, on the other hand, it may be explained in terms of predictability of the ongoing stimulus.** In other words, while pseudo-words are by definition verbal stimuli never before experienced, words (particularly highly frequent ones) are experienced stimuli. Thus, words may be recognized by the listener even in the absence of a contextualizing sentence, or before hearing the whole word. To discriminate between lexical- and frequency-related effects, and to verify their different occurrence in temporal terms, here we designed an experiment to test corticobulbar excitability at different delays during the presentation of pseudo-words and words with different lexical frequency (rare vs. frequent).

In summary, the first aim of the present study was to deeply investigate the lexical resonance effect found by Fadiga et al. (2002). In particular, we wanted to verify whether the difference found during listening to words and pseudo-words is due to a facilitation induced by the presence of meaning or a difference in familiarity. To do this, we recorded tongue motor evoked potentials while subjects were listening to frequent words, rare words, and pseudo-words. Moreover, we aimed to replicate the phonological resonance effect (Fadiga et al. 2002) by comparing pseudo-words that recruits or does not recruit important tongue movements when pronounced. Finally, and most importantly, we examined the time course of the potential lexical and phonological effects on motor cortical excitability, by delivering single TMS pulses at four different time-intervals while subjects listened to the verbal stimuli.

2. Materials and methods

2.1. Subjects and general procedure

Twenty-four right-handed (Oldfield, 1971) students (12 males; 12 females) from the University of Ferrara volunteered to participate in the present study. All participants were native Italian speakers. Participants were screened for neurological and other medical problems and gave their informed consent to participate in the experiment. Experimental procedures were approved by the local Ethical Committee.

Subjects lay comfortably on a reclining armchair, their head being stabilized by a headrest, and were required to carefully listen to a list of 90 disyllabic verbal stimuli, delivered through headphones. To ensure that subjects paid attention to all verbal stimuli, in some trials (on average, one out of every four) the presentation of a beep, **played after the verbal stimulus,** instructed subjects to perform a timed lexical decision task on the last stimulus they heard, by pressing one mouse button in the case of a word and the other in the case of a pseudo-word. The beep was unpredictably presented in pseudo random order. During the presentation of auditory stimuli, TMS was delivered over the left primary motor cortex of the subject's tongue representation and tongue motor evoked potentials (MEPs) were recorded (see below).

2.2. Stimuli

The list of 90 verbal stimuli presented to each subject consisted of five different sets of stimuli (four sets of 18 experimental stimuli, with TMS administered in 16 trials, and one set of **18** distracters, see Table 1). Each stimulus on the list was created according to a CVCCV (vowel, V, and consonant, C) structure.

The four sets of experimental stimuli consisted of (1) frequent words (FWll), (2) rare words (RWll), (3) pseudo-words (PWll), in which the middle double consonant required important tongue movements when pronounced (i.e., the Italian /ll/) and (4) pseudo-words (PWbb) in which the middle double consonant required a small tongue involvement (i.e., the Italian /bb/, /mm/, /ff/, or /pp/). The set of distractors consisted of frequent **(n= 9)** and rare **(n= 9)** words in which the middle double consonant required a small tongue involvement, as in the case of PWbb. The aim of the distractors was to prevent subjects from realizing that all words contained the /ll/ as middle double consonant. Stimuli presentation was fully randomized. Word frequencies were ascertained on the basis of a preliminary judgment (frequent vs. rare) made by 40 undergraduate students. According to a frequency count from the Institute of Computational Linguistics of the Pisa CNR, (ILC, 1988), the words indicated by the students as frequent had on average 59.6 ± 18.9 occurrences per million words, whereas those indicated as rare had a mean frequency of 8 ± 3.5 occurrences per million words. This difference was statistically significant (t-test for independent samples, p = 0.014). Stimuli used in the experiment together with the results of the frequency evaluation are shown in Table 1. The sets of pseudo-words were created by slightly modifying the selected words. To avoid any potential interference, the first syllable of the pseudo-word was never the same as the first syllable of the modified word.

For each stimulus, two audio tracks were acquired, one with a male voice, the other with a female voice. Half of the subjects (6 males, 6 females) heard the male voice, the other half the female voice. Stimuli were controlled for intensity (70 dB) and duration using GoldWave (www.goldwave.com) and Praat (www.praat.org) software and peak intensity was subsequently checked with a phonometer. The double consonant in the middle of the stimuli lasted for about 300ms.

2.3. TMS procedures and data analysis

Participants' left motor cortex was magnetically stimulated by single-pulse TMS (Magstim 200). Magnetic stimuli were delivered through an eight-shaped coil placed on the skull with the handle positioned in a medial-dorsal orientation.

The experiment was subdivided into a mapping and an experimental session. In the mapping session, TMS was administered on predetermined positions on a grid (1 cm resolution) drawn on a bathing cap wore by the participants (Figure 1A). The origin of the coordinate system was located at the Cz reference point determined according to the international 10-20 EEG system (Jasper, 1958). The cortical representation of anterior tongue muscles was mapped by moving the center of the coil in one centimeter-steps according to the grid. Stimulus intensity was adjusted in order to determine the motor threshold for the recorded muscles (the motor threshold is considered as the TMS intensity capable of evoking 50% of detectable MEPs in a sequence of 10 stimulations for more details see Fadiga et al, 2002).

The hot spot of the tongue muscles' representation was located, on average, 1 cm anterior and 8 cm lateral with respect to the Cz reference point. During the experiment, the coil was kept in a stable position over the tongue representation by means of an articulated arm and participants were requested to keep a stable, relaxed position during the whole experiment. For each subject, TMS intensity was set at 120% of the tongue motor threshold.

During acoustic stimuli presentation, single-pulse TMS was automatically delivered by home-made computer software, running under MS-DOS to allow the necessary time precision, at four different time intervals (0, 100, 200, 300 ms) from the beginning of the double consonant

(Figure1B). For each stimulus, the beginning of the double consonant part (0 ms time interval) was determined on the basis of its spectrogram using Praat software. The 300ms time interval roughly corresponded to the end of the double consonant part.

Only 16 out of the 18 verbal items within each class (RWll, FWll, PWbb, PWll) were accompanied by magnetic stimulation (4 TMS stimuli during each time interval). All MEPs were band-pass filtered (20±1000 Hz), digitized (2000 Hz) and stored on a computer for off-line analysis. Trials in which tongue muscle activity was observed before the TMS pulse were discarded from the analysis. They were very few and equally distributed among the various experimental conditions. After rectification, the area underlying the MEP was calculated for each trial and then averaged for each condition. For each subject and condition, the mean intra-subject normalized MEP area (Z-score) was submitted to a two-way ANOVA with Class (FWll, RWll, PWll, PWbb) and Time (0, 100, 200, 300 ms) as within-subject factors.

3. Results

The ANOVA revealed a significant main effect for Class ($F_{(3,69)} = 13.82$, $p < .0001$), and a significant Class x Time interaction ($F_{(9,207)} = 2.69$, $p < .005$) that was further explored with Newman–Keuls post-hoc tests. At the first time interval (0 ms), when TMS was applied synchronously with the very beginning of the double consonant, no differential effect was found in the motor cortical excitability as a function of the different classes of stimuli. In contrast, at the second time interval (100 ms) the pattern changed significantly between the two classes of pseudo-words (see Fig. 2). In particular, pseudo-words embedded with a consonant requiring important tongue movements (PWll) were characterized by MEPs (mean ± SEM, 0.2817 ± 0.15) larger than those evoked by pseudo-words requiring minor tongue movements (PWbb: -0,637 ± 0.13; **p = .009**). No other significant differences were observed at this time interval. The pattern changed again significantly (see Fig.2) at the later time interval (200 ms), when MEPs evoked by the two classes of pseudo-words no longer differed, whereas a significant difference appeared between the Rare and the Frequent words. In particular, listening to Rare words (RWll) evoked much larger MEPs (0.691 ± 0.2) than listening to Frequent words (FWll= -0.460 ± 0.11, **p = .0002**). The very same pattern of results persisted at the latest time interval (300ms): Rare words (RWll: 0.461 ± 0.23) associated with larger MEPs than Frequent words (FWll: -0.358 ± 0.17; **p = .04**). Again, no differences were found at this time interval between the two classes of pseudo-words.

4. Discussion

In a previous experiment (Fadiga et al. 2002), our group showed that passively listening to words that involve tongue mobilization induced an automatic facilitation of the listener's motor cortex, as revealed by TMS of tongue cortical motor representation (phonological resonance effect). Furthermore, listening to words induced a stronger motor facilitation than listening to pseudo-words, with no interaction with the phonological effect (lexical resonance effect).

The aim of the present study was twofold. First, we wanted to investigate if the lexical resonance effect found by Fadiga et al. (2002) is induced by the presence of the meaning or by the difference in the familiarity of the verbal material. To this purpose, we tested the time course of the excitability of tongue muscles during listening to frequent words, rare words, and pseudo-words at four different time intervals (0, 100, 200, 300 ms) from the presentation of the double consonant embedded in the presented verbal stimuli. The second aim was to replicate the presence of the specific phonological resonance effect by comparing the excitability of tongue muscles during listening to pseudo-words in which the middle double consonant required or not tongue mobilization, and to verify the presence of this effect at the different time intervals considered in the present experiment.

The present results, besides providing further evidence in favor of the active role of the motor system in coding acoustic signal into a phonetic code, considerably extend our knowledge about the possible mechanisms through which the resonance processes are assured, as well as the precise timing for their occurrence. On the basis of the present findings, and of those previously found by Fadiga et al. (2002), we suggest that the early (100 ms time interval) phonologic resonance effect might have a role in firstly categorizing verbal material according to its phonoarticulatory requirements. In contrast, the later (200 ms and 300 ms time intervals) lexical resonance effect might reflect the specific involvement of the phonoarticulatory system in the effort necessary to attribute a meaning to low frequency words, indicated by the fact that the highest MEPs were evoked by rare words, as compared to frequent words.

The current results show that the phonological resonance effect is present only at the 100 ms interval, which was roughly the time of stimulation used in our previous study[1]. At this time interval, as well as at the 0 time interval, no difference between frequent and rare words was found. On the contrary, at both the 200 and 300 ms time intervals, MEPs evoked during listening to rare words were much larger than those evoked during listening to frequent words. Listening to pseudo-words, whose pronunciation either involved or not the tongue influenced MEP amplitudes in a way

[1] The software used in the previous experiment and in the present one were different. Using a spectrogram analysis a re-examination of the stimulation applied in the 2002 paradigm revealed a time of stimulation roughly corresponding to 150 ms after the beginning of the double consonant.

which was in between MEP amplitudes recorded during listening to rare and to frequent words. Thus, it is not the presence of the meaning *per se* but, more likely, a combination between meaning and frequency (i.e. familiarity) that determines the lexical effect. The more familiar is the verbal item, the less excitable becomes the motor cortex. Moreover, this effect also depends upon the time of stimulation. While at the earliest time intervals, 0 and 100 ms, no difference between frequent words and rare words is present, at the latest ones, 200 and 300 ms, this difference becomes significant. Thus, the present results indicate that the motor system responsible for phonoarticulatory movements during speech production is involved during speech listening in a strictly specific way which reflects both the difference in the phonoarticulatory requirements and the difference in familiarity of the verbal material.

The involvement of the motor system in phonological perception has been corroborated by recent fMRI studies. Wilson and colleagues (Wilson et al. 2004) showed that, bilaterally, the superior part of ventral premotor cortex is constantly activated during both listening and production of meaningless syllables. More recently, Pulvermüller et al. (2006) have shown that perception of bilabial consonants (that recruited actively the lips to be pronounced) versus alveolar consonants (that, in contrast, recruited more actively the tongue) give rise to a somatotopic activation of the precentral gyrus. Taken together these results suggest that phonemes are recognized because both the speaker and the listener share the same articulatory motor repertoire. This idea is very close to Liberman's hypothesis on the mechanism at the basis of speech perception (motor theory of speech perception, Liberman et al., 1967; Liberman and Mattingly, 1985; Liberman and Wahlen, 2000). The motor theory of speech perception maintains that the ultimate constituents of speech are not sounds, but articulatory gestures that have evolved exclusively to serve language. Furthermore, speech perception and speech production processes use a common repertoire of motor primitives that, during speech production, are at the basis of articulatory gesture generation, while during speech perception, are activated in the listener as a result of an acoustically evoked motor "resonance". Consequently, the listener understands the speaker when his/her articulatory gestures' representations are activated by verbal sounds.

The present results, besides providing further evidence in favor of the active role of the motor system in coding acoustic signals into a phonetic code, extend considerably our knowledge about the possible mechanisms through which the resonance processes are assured, as well as the precise timing of their occurrence. On the basis of the present findings, and of those previously found by Fadiga et al. (2002), we suggest that the early (100 ms time interval) phonologic resonance effect might have a role in firstly categorizing verbal material according to its phonoarticulatory requirements. In contrast, the later (200 ms and 300 ms time intervals) lexical resonance effect might reflect the specific involvement of the phonoarticulatory system in the effort necessary to attribute a meaning to low frequency words, indicated by the fact that the largest MEPs were evoked by rare words, as compared to frequent words. **During speech acquisition it is plausible that frequent and rare words evoke a comparable involvement of the phonoarticulatory system, since the individual is not able to discriminate them on the basis of lexical properties. As the individual masters frequent words, these become integrated into the lexicon and their recognition is based on a multiplicity of information. Consequently, the role of motor resonance becomes less critical, and its contribution is more likely to be still required when listening to known, but rare words, as well as in ambiguous situations, such as speech listening in a noisy environment.**

This interpretation of our results is supported by a series of brain imaging studies evaluating word frequency effects on the neural response in the context of lexical decision and other semantic judgment tasks. They report greater responses within left (Chee et al, 2002; Fiebach et al, 2002) or bilateral (Nakic et al, 2006) inferior frontal cortex (BA44 and 45) to low frequency words. It is a classical finding that high frequency words are named faster than low frequency words and are also more rapidly recognized as words in lexical decision tasks (Balota and Chumbley, 1985; Forster and Chambers, 1973; Frederiksen and Kroll, 1976). Frequency effects have also been observed in tasks that overtly require semantic access (Young and Rugg, 1992). Monsell (1991) proposed that frequency effects reflect the cumulative effect of experience on the facility with which an observer identifies a word and recovers its meaning. It follows, then, that more effort is likely to be necessary when retrieving the meaning of a low frequency word, relative to a high frequency one. The results of Chee et al. (2002) are also in agreement with this interpretation. The authors found higher left prefrontal BOLD signal change when volunteers performed semantic judgments on low frequency words. This effect was not evident when volunteers only had to read these words, indicating that the locus of this effect is likely to be semantic, and that retrieval effort may modulate prefrontal activity when deliberate access to semantics is required. Similar results have been found also by Fiebach et al. (2002) in an event-related fMRI experiment in which they investigated lexical decisions to words of high and low frequency of occurrence and to pseudowords. The results showed that low frequency words and pseudowords elicited greater activations than high frequency words in the superior pars opercularis (BA 44) of the left inferior frontal gyrus (IFG) and that activation in the pars triangularis (BA 45) of the left IFG was observed only for low frequency words. Altogether these findings indicate that low frequency words require more effort to be recognized, as indicated by both the behavioral results and the stronger activation in the prefrontal cortex.

In conclusion, the experimental evidence coming from this study suggests that, during speech listening, the automatic activation of the listener’s speech-related motor centers could play a role in retrieving the meaning of the word they hear. This seems to happen especially when a stronger effort in understanding is required, as in the case of low frequency words, where a stronger cortico-bulbar facilitation is revealed by TMS.

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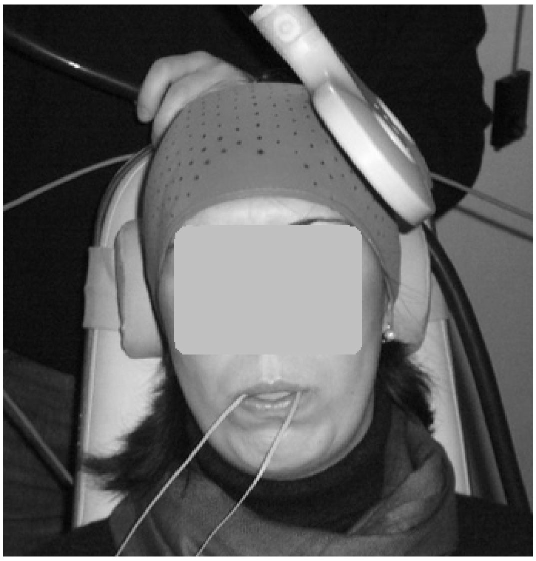
FWll	%Freq	RWll	%Freq	PWll	PWbb	Distractors
pelle	**98**	**valle**	**63**	**cillo**	**cimmo**	**mamma**
palla	**98**	**colle**	**61**	**dolla**	**dobbo**	**babbo**
bella	**98**	**cella**	**61**	**felle**	**feffo**	**tappo**
nulla	**98**	**culla**	**59**	**filla**	**fibbo**	**buffo**
mille	**95**	**bolla**	**56**	**gille**	**gippo**	**puffo**
ballo	**95**	**callo**	**44**	**gulla**	**gummo**	**gemma**
folla	**95**	**rullo**	**39**	**lullo**	**luffo**	**ceppo**
collo	**95**	**lilla**	**37**	**mello**	**meppo**	**gobba**
pollo	**90**	**zolla**	**32**	**mulle**	**mummo**	coppa
villa	**85**	**tulle**	**27**	**nallo**	**nammo**	goffo
folle	**80**	galla	15	**volla**	**vobbo**	gamma
molla	**80**	**calle**	**15**	**pille**	**piffo**	gomma
colla	**78**	**villo**	**15**	**pullo**	**pubbo**	pappa
balla	**73**	**falla**	**12**	**sallo**	**sappo**	baffo
fallo	**73**	**vallo**	**10**	**salla**	**sammo**	mappa
bollo	**68**	**calla**	**7**	**tille**	**tiffo**	muffa
gallo	66	mallo	0	tollo	toffo	sommo
sella	63	**vello**	**0**	nollo	nobbo	poppa

Table 1. The verbal stimuli used in the experiment. Single-pulse TMS was delivered only for stimuli depicted in bold. Mean word frequency, as evaluated by subjects in a preliminary experiment (see Methods) is expressed as a percentage of "frequent" judgments.

Figure1

A

B



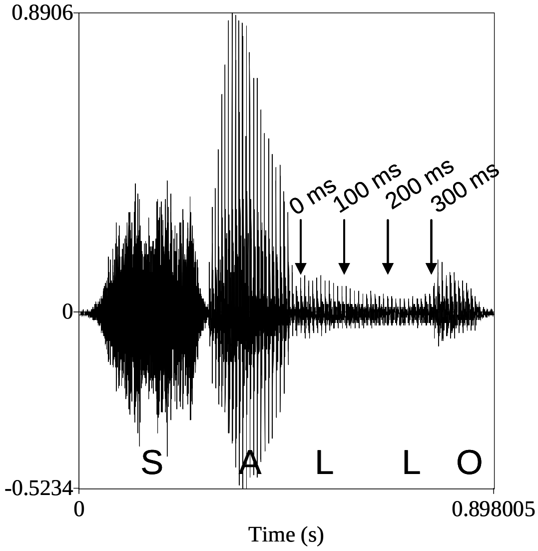


Figure 2

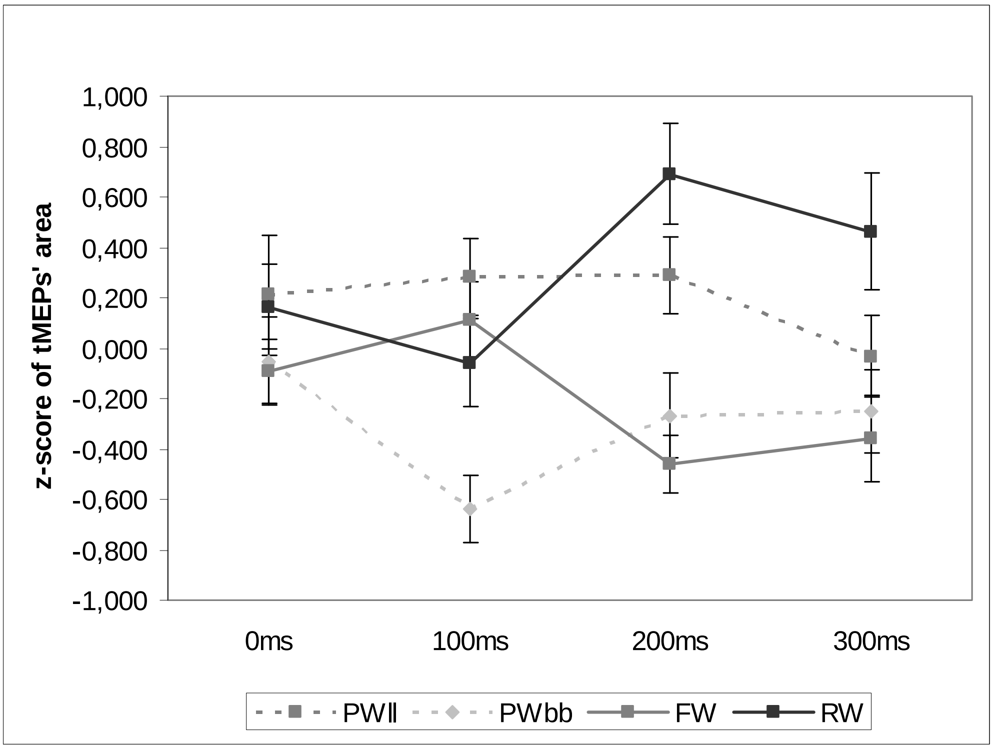


Figure captions

Figure 1

A) Each subject's left motor cortex was magnetically stimulated using single-pulse TMS. In the mapping session, the stimulation was made through a figure-of-eight coil on predetermined positions on a grid drawn on a bathing cap wore by the participants. To record MEPs from tongue muscles, each participant wore a silicon cast of his/her mouth on which four electrodes were placed on the surface contacting the tongue.

B) Schematic representation of stimulation time-course for the pseudo-word "Sallo". Single-pulse TMS was delivered at four different time intervals (0, 100, 200, 300 ms) from the beginning of the double consonant /ll/. For each verbal stimulus, the beginning of the double consonant part (0 ms time interval) was determined on the basis of its spectrogram using Praat software. The 300ms time interval roughly corresponded to the end of the double consonant part.

Figure 2

Time course of the Z-scores of the area of tongue MEPs (mean ± SEM) for the four types of verbal stimuli. Note that at the very beginning of the double consonant (0ms) there is no difference between conditions, then, at 100ms, a phonological effect emerges between pseudo-words (PWll and PWbb). Finally, at 200ms and 300ms, a lexical effect occurs, resulting in lower MEPS for frequent words (FW) than rare words (RW).