

A double-dissociation of English past-tense production revealed by event-related potentials and low-resolution electromagnetic tomography (LORETA)

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Abstract

Objectives: Evidence of systematic double-dissociations of neural activity associated with the generation of regular and irregular past tense in healthy individuals may prove decisive in distinguishing between single- and dual-route models of morphological processing, because the former (connectionist models of morphological processing) have only been able to simulate double-dissociations of past-tense morphology as low-probability phenomena.

Methods: Twenty-eight channel event-related potentials (ERPs) were recorded in response to past-tense production and subsequently analyzed using a 3-stage strategy.

Results: A data-driven algorithm temporally segmented the ERPs into 16 distinct epochs of stable field configuration (microstates). A space-oriented brain electric field analysis determined that one of those epochs, 288–321 ms after the verb stem presentation, showed significant differences between the regular and irregular verb conditions. As a further test of these results, a novel source localization technique that computes 3-dimensional distribution of cortical current density in the Talairach brain atlas – low-resolution electromagnetic tomography – found in the above microstate more activity for regulars in the right prefrontal and right temporal areas and for irregulars in the left temporal areas and the anterior cingulate cortex, which can be taken as evidence of systematic double-dissociation.

Conclusions: The present results achieved with a source localization technique provide evidence of a two-way compartmentalization of neural activity corresponding to regular and irregular past tense, thus corroborating the dual-mechanism character of verb morphology. © 2001 Elsevier Science Ireland Ltd. All rights reserved.

Keywords: Past-tense production; Single/dual route; Event-related potentials; Low-resolution electromagnetic tomography; Microstate analysis; Source localization

1. Introduction

Brain-mapping techniques are able to provide evidence for resolving contentious issues in cognitive science. Where competing frameworks claim equal success in accounting for behavioral data, yet are based on fundamentally different cognitive architecture, reliable and systematic mapping of associated neural activity can validate/invalidate the various claims of respective models. An example of a contentious issue in cognitive theory is past-tense morphology, which

has been viewed as a test case for theories that have attempted to explain how the brain processes patterns that differ in their regularity. Two competing frameworks have claimed equal success in accounting for behavioral data. The dual-route model proposes that the differences between regular and irregular verbs in reaction time (Prasada et al., 1990), priming (Marslen-Wilson et al., 1993), frequency effects (Prasada et al., 1990; Ullman, 1999), generalization to novel items (Kim et al., 1991) indicate distinct processing pathways for the two types of verbs. The most influential dual-route theory proposes that the regular past tense is said to be generated by a ‘default’ suffixation of the stem (*call-called*), whereas the irregular past tense (*steal-stole*) is assumed to be stored in an associative manner (Pinker, 1991). Other dual-mechanism models have also implemen-

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ted considerable computational differentiation between the processing of regulars and irregulars, but without assuming rule-based/symbolic/combinatorial processing for regular items. In these models dual computational differentiation is either built in (Westermann and Goebel, 1995; Goebel and Indefrey, 2000) or emergent (Westermann et al., 1999).

Parallel distributed processing (PDP) connectionist models of past-tense processing challenged the dual-route perspective by proposing a default-free computationally undifferentiated single system performing direct phonological mapping from the stem onto the past tense, irrespective of the regularity status of the verb. These models have been implemented as either homogeneous networks based on one type of representation (phonological) (Rumelhart and McClelland, 1986; MacWhinney and Leinbach, 1991; Plunkett and Marchman, 1991), or, more recently, as non-homogeneous networks including distinct groups of units for different types of representations (phonological and semantic),¹ (Joanisse and Seidenberg, 1999). Importantly, it has been claimed that even homogeneous networks were able to simulate the above-listed one-way dissociations between regulars and irregulars (however, see Marcus, 1998 for a critical discussion of this claim), by exploiting certain properties of the English language. Items undergoing similar phonological mappings from the stem onto the past tense can be referred to as ‘*friends*’, as opposed to ‘*enemies*’, which display dissimilar mappings. In English, regulars are numerous and tend to have more ‘*friends*’ than ‘*enemies*’ (Seidenberg and Hoeffner, 1998), being processed rapidly and with few errors, whilst the opposite is generally true for the irregulars, which are more prone to error. Thus, regulars are, overall, more *consistent* (Daugherty and Seidenberg, 1994) in their past-tense formation.² Consequently, in homogeneous networks the regular pattern is less idiosyncratic, less dependent on individual units, and, therefore, more resistant to damage than exceptions are (Bullinaria and Chater, 1995). Thus, it is not surprising that lesions to homogeneous networks result in more disruption of the irregular items (Gonnerman et al., 1997; Juola and Plunkett, 1998).

Hence, it has been rather problematic for homogeneous models to explain evidence of disruption of regulars with preserved irregulars. For example, Ullman et al. (1997b) found such a pattern of disruption in patients with Parkinson’s disease (known to affect the frontal cortex) as well as in individuals with anterior aphasia. Marslen-Wilson and Tyler (1997, 1998) found deficits in priming with regulars but not irregulars in patients with predominantly frontal damage. These findings in conjunction with evidence of

temporo-parietal damage selectively disrupting irregulars (Ullman et al., 1997b; Marslen-Wilson and Tyler, 1997, 1998) suggested a double-dissociation of regular vs. irregular morphology in the brain (Ullman, 1999). Attempts to simulate clinical double-dissociations of regular and irregular past tense by selective lesions to non-homogeneous nets (Joanisse and Seidenberg, 1999), showed no reliable irregular over regular advantage, despite the presence of the opposite pattern. An alternative approach to clinical double-dissociations has been proposed within the homogeneous framework. Thus, although systematic double-dissociations remained outside the scope of these models, its proponents argued that clinical double-dissociations could be low-probability stochastic (i.e. non-systematic) phenomena and as such can be simulated in homogeneous networks (Gonnerman et al., 1997; Juola and Plunkett, 1998).

A number of investigators turned to brain-mapping techniques in order to gather more decisive evidence. It would seem that functional neuroimaging tools with their high spatial resolution would be suitable for probing the existence of localized neural activity associated with the generation of regular and irregular past tense. Indeed, several studies employed either functional magnetic resonance imaging (fMRI) (Ullman et al., 1997a) or positron emission tomography (PET) (Jaeger et al., 1996; Indefrey et al., 1997) for comparing the regular and irregular morphology patterns. Although all these studies found differences between the functional anatomy underlying regular and irregular items, there were some significant inconsistencies (e.g. increased vs. decreased activation in temporal regions associated with irregulars). Furthermore, methodological issues complicate the interpretation of extant neuroimaging data (Seidenberg and Hoeffner, 1998; but see Jaeger et al., 1998, for a reply). For example, it soon became evident that the low temporal resolution of these techniques (of the order of several seconds at best) was a serious limitation. Since language processing is rapid (e.g. English past-tense forms are generated in 0.5–1 s), imaging paradigms employed ‘block designs’ in which regular and irregular items were grouped separately in order to measure a reliable signal. For regular items that almost certainly leads to either priming or ad hoc inference by participants: after encountering a number of regulars and no irregulars, the tendency to respond ‘regularly’ can be strongly encouraged.

Electrophysiological recordings, with their almost unconstrained time-resolution, allow flexible designs and can easily circumvent the item blocking problem, with additional gain in temporal information. With one exception (reported in Marslen-Wilson and Tyler, 1998) ERP studies to date have invariably provided evidence of dissociation between regular and irregular morphology in English (Münte et al., 1999; Newman et al., 1999), German (Penke et al., 1997; Weyerts et al., 1997), and Italian (Gross et al., 1998). All of these investigations report differences in ERP wave-features, such as the left anterior nega-

¹ We use here the term *homogeneity* with respect to the grouping of network units. In networks referred to here as *non-homogeneous* such grouping corresponds to the type of input (phonological vs. semantic) and not to the categorical distinction between regular and irregular items.

² The applicability of the consistency argument to explaining German morphology data has been questioned (Marcus et al., 1995; Clahsen, 1999; also see Bybee, 1999, for a reply).

tivity (LAN) or the N400 component, observed in response to regular and irregular items, usually interpreted as evidence for the dual-route model (see Lavric et al. (2001), for a discussion of ERP components associated with morphological processing). However, there are two sets of limitations that are common to previous studies of morphological processing.

Firstly, these investigations did not employ production paradigms. Instead, violation or priming designs were used, the former involving the presentation of correct and incorrect inflected forms (Penke et al., 1997; Newman et al., 1999) and the latter involving stems being primed by preceding inflected forms (Marslen-Wilson and Tyler, 1998; Münte et al., 1999). While the use of such designs is beneficial when no alternatives are available, the interpretation of their outcomes can be far from straightforward (see Marslen-Wilson and Tyler, 1998). The study reported here employed a production paradigm, which mirrors the ‘natural’ generation of the inflected forms and embodies precisely the process that the competing frameworks have been modeling.

Secondly, some methodological factors may also complicate the interpretation of extant ERP studies of verb morphology. For instance, visual inspection of the ERP waves has often been the only ‘segmentation’ procedure in such studies, not complemented by objective criteria. Features of the ERP wave, referred to as *components*, despite their unitary appearance, have often been shown by alternative analyses to represent concatenations of temporally distinct events (Donchin and Heffley, 1978; Lavric et al., 2000). Moreover, such events often have distinct neural origins (Knight and Grabowecy, 1995). Another issue is the functional identity of ERP waveform components observed in studies of morphological processing. Thus, LAN, claimed to be specifically associated with syntactic violations (Penke et al., 1997; Newman et al., 1999), was also observed in response to increases in working memory (WM) load (Kutas, 1997). Similarly, it is not clear whether the component, reported in Marslen-Wilson and Tyler (1998) to have similar scalp distributions in response to regular and irregular priming, is the N400 whose reduction was observed by Münte et al. (1999) in response to regular, but not irregular priming.

Therefore, cortical localization of ERP activity may provide additional benefits in the context of verb morphology. Since systematic double-dissociations have proven elusive for the single-route account, evidence of localized double-dissociative differences in neural activity, in addition to previously described ERP waveform differences, could be particularly challenging for this theoretical framework. In order to establish the presence or absence of such localized differences, the current study utilized a new tomographic source localization technique that computes the 3-dimensional distribution of cortical current density in the Talairach brain atlas (low-resolution electromagnetic tomography (LORETA); Pascual-Marqui et al., 1994, 1999; see

Section 2.9. for the physiological validity of LORETA). As prerequisites for LORETA we employed a data-driven segmentation procedure to determine the ERP time-windows to be analyzed (Lehmann, 1987; Koenig et al., 1998; Pizzagalli et al., 1999, 2000) and a space-oriented brain electric field analysis (Lehmann, 1987) to establish which of those time-windows display scalp differences between the regular and irregular conditions and, hence, should be submitted to the LORETA analysis for investigating intracerebral activity.

2. Methods

2.1. Participants

A total of 23 (7 females, 16 males) British English-speaking right-handed university students with no history of alcohol or drug abuse, neurological, and psychiatric disease provided informed written consent and were paid £3 for participating in the experiment. The mean age was 21.65, range 18–40, SD = 6.01. The results obtained from two participants (one female, one male) were discarded prior to any analyses because of excessive artifact. All participants were naive with regard to electrophysiological recordings and had no previous knowledge of the theoretical issues involved.

2.2. Apparatus

For the presentation of the verbs, an IBM compatible computer with a 17 inch SVGA monitor was used. A program written in EXPE 6 (Pallier et al., 1997) was used to display the items on the screen and simultaneously trigger the NeuroSciences Brain Imager (Series III). An elastic cap (Electro Cap International Inc., Dallas, TX, USA) was used for recording the electroencephalogram (EEG).

2.3. Verb stimuli

Two practice lists and one test list of English verb stems were prepared as follows:

1. One list corresponded to *Practice 1* and consisted of 27 stems. Although participants were only asked to read the stems in this condition (see Section 2.4 and Appendix, Table A1(a)), the relative number of regular vs. irregular items was almost equal – 14 and 13, respectively.
2. A list developed for *Practice 2* (see Appendix, Table A1(b)) included 57 (29 regular and 28 irregular) items.
3. The *past-tense generation list* contained 57 regular and 57 irregular items in random order (see Appendix, Table A2).

2.3.1. Regular past-tense patterns

All 3 allomorphs of the regular past tense were present in the past-tense list: the /t/ allomorph (*picked*) appeared 19

times, the /d/ allomorph (*filled*) 28 times, and the /ed/ allomorph (*voted*) 10 times.

2.3.2. Irregular items

Since all regulars change in their past-tense form, none of the so-called no-change irregular verbs (*set–set*, *quit–quit*) were included in the past-tense generation list. This list also did not contain irregulars whose past tense is phonologically almost indistinguishable from the regular pattern (*dwelt–dwelt*).

2.3.3. Verb frequency

Irregular vs. regular stems and past-tense forms from the past-tense generation list were matched for frequency according to the Francis and Kucera (1983) database, which is a count of the number of times each form occurred in their corpus of texts. The mean stem frequency was 72.56 (range 9–318, SD = 72.45) for regulars and 75.33 (range 8–397, SD = 85.60) for irregulars; the mean past-tense frequency was 66.21 (range 10–327, SD = 74.63) for regulars and 69.54 (range 6–302, SD = 75.22) for irregulars. A two-way analysis of variance (ANOVA), having as factors the verb form (stem vs. past tense) and the past-tense pattern (regular vs. irregular) showed no significant main effects ($F(1, 110) = 0.89$, $P > 0.5$ – for factor verb form; $F(1, 110) = 0.353$, $P > 0.5$ – for factor past-tense pattern); or interaction ($F(1, 110) = 0.001$, $P > 0.5$).

2.3.4. Word length

Regular and irregular stems in the past-tense list were matched for length. All stems were monosyllabic and the average number of letters for the two grammatical types was as follows: regular condition – mean 4.18, range 3–6, SD = 0.66; irregular condition – mean 4.26, range 3–6, SD = 0.72. A one-way ANOVA showed no significant differences between the regular and the irregular items ($F(1, 112) = 0.461$, $P > 0.5$).

2.4. Procedure

Participants sat in an electrically shielded, sound proof, dimly illuminated room. A chin-rest was used to keep the distance between the subject and the screen constant and to reduce the face and neck muscle contractions and fatigue. Stimuli in black lower case letters (20–50 mm long × 15 mm high) were presented on a light-gray background one by one on the middle of the computer screen, about 370 mm from the eyes. Stimulus eccentricity was between 1.55 and 3.8° of visual angle horizontally and 1.16° of visual angle vertically.

2.4.1. Experimental design (see Table 1)

The session consisted of 3 parts (Practice 1, Practice 2, and past-tense generation). Several features of the design served the purpose of minimizing the effects of artifact originating in eye-blinks, eye and head movements, as well as articulatory and subarticulatory activity. For example, during past-tense generation participants had to withhold the immediate verbalization and avoid blinking for certain time intervals. Therefore, Practice 1 was specifically designed to facilitate withholding responses and suppressing eye-blinks. Practice 2 served as training for the subsequent past-tense generation and the two were procedurally equivalent.

A cue (exclamation mark: '!'), displayed before each word, served as a fixation point and also as a signal for the stem appearance. In all 3 presentations '!' was followed by the presentation of a stem. In Practice 1 participants were instructed to read the stem silently. In Practice 2 and the past-tense generation participants were asked to think about the past tense corresponding to the stem, without speaking it immediately. The stem was followed by an ellipsis ('...') in Practice 1 (in which no response was required) and a question mark ('?') in Practice 2 and the past-tense generation, which prompted the subjects to respond by saying the past tense they thought of earlier. In the interval between '!' and

Table 1
Experimental design

Stimulus	Present on the screen for (ms)	Participants instructed to	ERPs (applicable only for <i>past-tense generation</i>)
!	600	Be attentive, prevent blinking, sit still	–
Blank screen	200	–	–
'Walk'	200	<i>Practice 1</i> : read silently; <i>Practice 2</i> and <i>past-tense generation</i> : read silently and think of the past tense without speaking it	Time-locked to the presentation; start of the 900 ms analysis window with a 75 ms pre-stimulus baseline
Blank screen	700	–	End of the 900 ms analysis window
(...) – <i>Practice 1</i>	2000	<i>Practice 1</i> : no response required; relax, blink, adjust posture	–
? – <i>Practice 2</i> and <i>past-tense generation</i>		<i>Practice 2</i> and <i>past-tense generation</i> : speak the past tense; relax, blink, adjust posture	
Blank screen	300	Relax, blink, adjust posture	–

‘...’ (Practice 1) or ‘!’ and ‘?’ (Practice 2 and past-tense generation) participants were instructed to sit still, avoid responding, blinking, or moving their eyes. The total duration of the experimental session was 80 min (40 min for preparations and instructions and 40 min for data collection and debriefing).

2.5. Performance data

Errors and omissions were recorded on tape for both lists requiring past-tense production (Practice 2 and past-tense generation) and subsequently grouped in accordance with the following criteria: verb type, error type, and list.

2.6. Data acquisition and processing

The 28 channel EEG was recorded from tin electrodes – 10/20 plus 9 additional sites: FTC1, FTC2, CP1, CP2, TCP1, TCP2, PO1, PO2, Oz equidistant from F7 and C3, F8 and C4, Cz and P3, Cz and P4, C3 and T5, C4 and T6, Pz and O1, Pz and O2, O1 and O2, respectively. The EEG was referred to linked earlobes and time-locked to all verb stems in the past-tense generation list and was digitized at a sampling rate of 333 Hz for 900 ms, plus a 75 ms pre-stimulus baseline (0.1–40 Hz bandpass, impedance <5 k Ω , forehead ground). Vertical and horizontal eye movements were recorded via supra-, suborbital, and canthal sensors, respectively. EEG and electro-oculographic (EOG) epochs exceeding $\pm 60 \mu\text{V}$ were rejected on-line. All epochs were inspected off-line by one experimenter and the ones contaminated by eye-blinks, eye movements, electrode drifting, amplifier blocking, or electromyographic (EMG) activity, were rejected. The acquired epochs were averaged by verb type (regular vs. irregular) with the minimum number of artifact-free epochs per verb type set to 30. Off-line, the ERPs were re-referenced to average reference. A far infrared (FIR) filter (1.5–40 Hz) was applied to the ERPs prior to data analysis. A grandmean ERP map series was computed across subjects and conditions.

2.7. Microstate analysis

ERP data were analyzed with space-oriented brain electric field analysis (Lehmann, 1987), which was employed as a prerequisite for the subsequent tomographic analysis. An empirical observation arising during examinations of the temporal development of the brain electric field configuration is that changes in the field configuration (map landscape) occur step-wise and discontinuously (Lehmann, 1971, 1987; Koenig et al., 1998; Pizzagalli et al., 2000). Epochs of quasi-stable field configurations (referred to as ‘microstates’) are concatenated by rapid transitions in the brain electric field configurations. Accordingly, microstates index brief periods of quasi-stable spatial configurations of the active neural generators, and thus index different brain functions. Lehmann (1987) proposed that microstates represent the building blocks of a step-wise information proces-

ing in the brain, and several studies collected empirical evidence for this (e.g. Lehmann, 1987; Koenig et al., 1998; Pizzagalli et al., 1999, 2000).

From a methodological perspective, the primary goal was to identify start and end times of different field configurations (microstates). Different configurations must have been generated by at least partially different spatial configurations of the active neural generators (Fender, 1987). For this purpose, at each time frame, the field configuration was assessed by the locations of the positive and negative centroids (i.e. the location of the point of gravity of the positive and negative map areas; Wackermann et al., 1993; Fig. 1).

A data-driven segmentation procedure (Lehmann, 1987; Koenig et al., 1998; Pizzagalli et al., 1999, 2000) was employed to determine microstate start and end points.

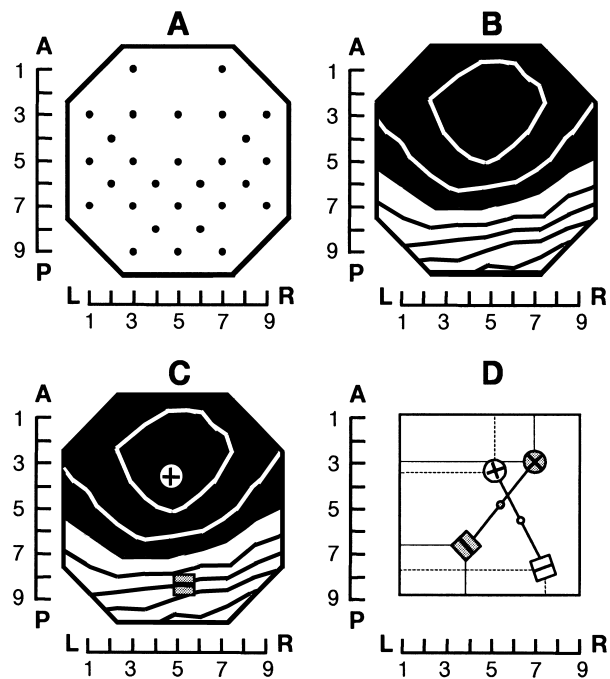


Fig. 1. Spatial feature extraction and analysis in space-oriented ERP analysis. (A) Schematic of the electrode array (28 electrodes; head see from above, left ear left). The numbers correspond to the electrode positions according to the international 10–10 system (rows: from anterior (A = 1) to posterior (P = 9), Cz = 5; columns: from left (L = 1) to right (R = 9), Cz = 5). (B) At each time point, a potential distribution map is constructed using linear interpolation between the electrodes shown in (A) (isopotential contour lines in steps of 1.0 μV). Positive area in black, negative area in white vs. the average reference. (C) At each time point, the locations of the negative (square) and positive (circle) centroids can be used to reduce and characterize the ERP field topography. (D) At each time point, the spatial configuration of a momentary map is numerically expressed by 4 coordinate values (L–R and A–P locations of the positive and negative centroid). In a last step, the L–R and A–P locations can be tested for differences between conditions (gray vs. white symbols). The small circles show the locations of the point of gravity of the absolute map voltages (mean locations between the positive and negative centroids, Pizzagalli et al., 1998) formally tested as main effect of ‘Verb’ (see Section 2.9.).

The goal of this sequential parsing procedure was to identify ERP microstate as periods in time characterized by stable field configuration by simultaneously satisfying the two contrasting goals of any segmentation procedure: stability, i.e. assignment of a maximal number of maps to a given microstate, and discrimination, i.e. detection of a maximal number of different microstates (for a detailed description of the segmentation procedure see Koenig and Lehmann, 1996). For the segmentation procedure, the locations of the negative and positive centroids of the grandmean ERP map series averaged across the two verb conditions were used. After the identification of microstate timings, locations of the positive and negative centroids was averaged for each subject between the identified microstate start and end times for the two verb conditions separately.

However, the segmentation procedure based on grandmean data does not ensure that the identified microstates are consistently present across subjects/conditions. In order to address this issue, individual segmentation for each participant and condition was run using the same strategy as for the grandmean map for microstates showing significant differences across conditions in centroid locations. For each of such microstates, 42 probability functions of microstate end points were extracted (21 subjects \times two conditions). For each participant and condition, an algorithm identified all peaks of this function within an extended time-window of the microstate length \pm two microstate lengths. This large window was chosen in order to accommodate for possible individual differences in occurrence of the microstate of interest. For each participant and condition, maps between two neighboring peaks of the probability function were averaged separately. A data-driven approach was used to identify the individual condition-dependent microstate by simultaneously fulfilling two criteria, the degree of (1) spatial and (2) temporal similarity between the grandmean map of the microstate of interest ('target map') and all maps available for a participant in the extended time-window. As in our previous research (Pizzagalli et al., 2000), the degree of spatial similarity was operationalized by computing the spatial correlation (Pearson correlation) between the target map and all available individual maps (two to 4 individual maps were typically available across subjects and conditions). If the map with the highest correlation occurred temporally closer to the target map than the map with the second highest correlation, the one with the highest correlation was considered for further analyses. If the map with the highest correlation occurred temporally farther to the target map than the map with the second highest correlation, the one with the second highest correlation was considered for further analyses, provided that it still showed a significant correlation with the target map ($r > 0.48$, $P < 0.01$).

Subsequently, for grandmean segmented microstates showing significant differences across conditions in centroid locations, centroid analyses were repeated using individually segmented data.

2.8. Brain electromagnetic tomography

For microstates showing significant differences of scalp potential distribution (configurations) between the two verb conditions, LORETA (Pascual-Marqui et al., 1994, 1999) was used to compute the 3-dimensional intracerebral distributions of current density. The algorithm solves the inverse problem assuming related orientations and strengths of neighboring neuronal sources (i.e. no assumption is made about the number of sources). Mathematically, this assumption is implemented by finding the 'smoothest' of all possible activity distributions. Generally, animal single unit recordings furnished good support for the core assumption of the algorithm (Llinas, 1988; Haalman and Vaadia, 1997). The physiological validity of this localization technique has been demonstrated in studies investigating basic visual and auditory processes (Pascual-Marqui et al., 1994), epileptic discharges (Lantz et al., 1997), and cognitive tasks tapping specific brain regions (Strik et al., 1998; Wang et al., 1999; Pizzagalli et al., 2000) as assessed independently in functional hemodynamic imaging studies. In simulations comparing 5 source localization techniques using linear solutions for the EEG inverse problem, only LORETA reliably localized sources in 3-dimensional space (Pascual-Marqui, 1999). Furthermore, recent studies from several independent groups provided important cross-modal validation for the LORETA algorithm. In a case study by Seeck et al. (1998) LORETA generators of epileptogenic discharges were confirmed by the locations of blood oxygenation level-dependent (BOLD) signal increase, as assessed by EEG-triggered fMRI, and electrocorticography from subdural electrodes. Worrell et al. (2000) obtained similar results: LORETA generators of ictal discharges were very close to MRI-identified epileptic foci. Finally, in a recent EEG study, Pizzagalli et al. (2001) found that LORETA theta activity within regions of the rostral anterior cingulate cortex was associated with treatment response in depression. The region involved was virtually the same as the one reported in previous PET studies of treatment response in depression (e.g. Mayberg et al., 1997).

The LORETA version used in the present study (Pascual-Marqui et al., 1999; Pizzagalli et al., 2000, 2001) was registered to the Talairach brain atlas (Talairach and Tournoux, 1988). Based on the digitized Talairach and probability atlases (MNI305) of the Brain Imaging Centre (Montreal Neurologic Institute), computations were restricted to cortical gray matter and hippocampi. The spatial resolution of the method was 7 mm and the solution space consisted of 2394 voxels. The LORETA algorithm computed at each voxel current density as the linear weighted sum of the scalp electric potentials. For microstates with significant differences between the two verb conditions at the scalp, for each subject, the 3-dimensional intracerebral distribution of current density was computed separately for irregular and regular verbs. LORETA solutions were obtained based on grandmean segmented and individually segmented data.

In the present analyses, EEG electrode coordinates achieved using cross-registrations between spherical and realistic head geometry (Towle et al., 1993) were used. It must be acknowledged that the precision of the LORETA solution in the current implementation was limited by the lack of information on participants' individual anatomy (e.g. MRI scans for every subject) and of individualized coordinates for ERP electrodes for each participant. This being said, the studies mentioned above, despite having the same technology limitations, have reached satisfactory agreement between their LORETA results and data obtained with more precise techniques, such as fMRI or subdural recordings (Seeck et al., 1998). Furthermore, the main theoretical question asked in the current study ('Is there a double-dissociation?') was not based on specific functional-anatomical assumptions and, hence, did not rely heavily on precise localization.

2.9. Statistics

For the microstate analysis, differences between ERPs elicited by the two verb conditions were assessed using ANOVA with verb (regular vs. irregular) and centroids (positive vs. negative) as repeated measures. For every identified microstate, ANOVAs were run separately for the centroid locations along the left-right and the anterior brain axis. In cases of significant results, paired *t* tests were used in post hoc analyses. To assess the robustness of possible results, binomial statistics were used to test whether the number of subjects showing the differences as in the ANOVA analyses differed from chance. Binomial probabilities for $B(21,0.5)$ are reported.

For the LORETA analyses, voxel-by-voxel paired *t* tests were run to assess in which cortical regions the two verb conditions differed. The *t* maps were thresholded at $P < 0.05$, uncorrected for multiple comparisons. No corrections for multiple comparisons were applied because the LORETA analyses were employed as follow-up tests of the microstate analyses. Indeed, as pointed out above, reliable differences in the scalp ERP field configuration can unambiguously be interpreted as suggesting that at least partially different neuronal populations were active during the two verb conditions. LORETA assessed in which brain regions the two verb conditions differed. The Structure-Probability Maps Atlas (Lancaster et al., 1997) was used to determine which brain regions were involved in differences between conditions. Brodmann area(s) (BA) and brain regions closest to the observed locations are reported. Overall, two-tailed *P*-values are reported.

3. Results

3.1. Performance data (see Appendix, Table A3)

3.1.1. Errors

There was a total of 24 errors. Fourteen of them were

made during Practice 2 and 10 during past-tense generation. Twenty-three errors were made with irregular verbs, of which 21 were over-regularizations (e.g. *freeze-frezed*, instead of *freeze-froze*). It is difficult to categorize the only error with a regular verb (*raise-rose*), since it could be either a result of an irregularization (*raise-rose*) or stem change prior to past-tense generation (*raise-rise-rose*).

3.1.2. Omissions

There were 13 omissions in total, 5 during Practice 2 and 8 during the past-tense generation. Ten of the omitted past-tense forms were irregular and 3 were regular.

3.2. ERP data

3.2.1. Microstate analysis

Fig. 2 shows selected average-referenced waveforms of the grandmean ERPs in response to the two conditions. Sixteen microstates were identified between 87 and 816 ms. Their start and end times were (in ms): 87–123, 126–144, 147–177, 180–213, 216–258, 261–285, 288–321, 324–348, 351–411, 414–477, 480–525, 528–573, 576–603, 606–633, 636–696, 699–816 ms. Although several waveform differences are apparent between the two conditions (see Fig. 2), significant differences between irregular and regular verbs were found only in one microstate ranging between 288 and 321 ms post-stimulus. Indeed, as shown in Fig. 3, which depicts the transition of the average location of the positive and negative centroid (*electric gravity center* of the map) from microstate to microstate, the difference between the map configurations associated with the two verb types was largest in this microstate.

For the 288–321 ms microstate, the ANOVA on the centroid locations along the left-right brain axis showed a main effect of 'Verb' ($F(1, 20) = 5.02$, $P < 0.037$). Note that a main effect of Verb means that the averaged location between the positive and negative centroid (i.e. the gravity center) is located differently for the two verb conditions. The electric gravity center is the point of gravity of the absolute voltages on the head surface and is a conservative estimate of the mean location of all momentarily active, intracerebral, electric sources, projected orthogonally onto the head surface (Pizzagalli et al., 1998). Fig. 4A shows that the electric gravity center for the regular verbs (mean: 4.93; SD: 0.22) was more to the right than the one for irregular verbs (5.08 ± 0.23). This right-shift for the regular verbs was present in 17 of the 21 subjects ($P(17/21) = 0.003$). In addition, the negative centroid for regular verbs was located more to the right than the one for irregular verbs ($t(20) = 2.55$, $P < 0.020$; Table 2). This right-shift was observed in 17 of the 21 subjects ($P(17/21) = 0.003$). Overall, the microstate was characterized by a slightly lateralized potential distribution map, with the steepest positive gradients over the right posterior sites and largest negative gradients over left fronto-central sites (Fig. 4B).

The outcomes from the centroid analysis based on indi-

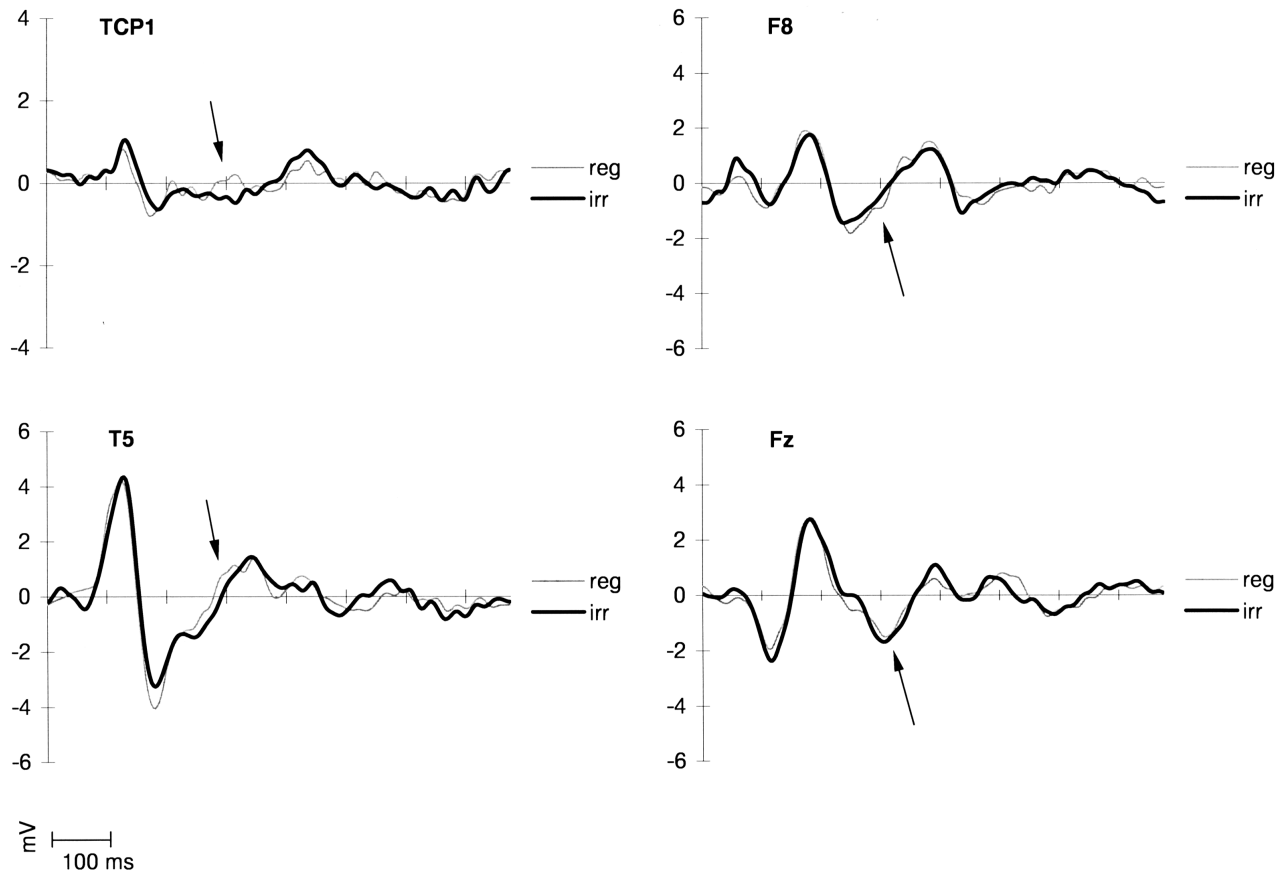


Fig. 2. Grandmean ERP waveforms (average reference) for electrodes that best circumscribe the loci of LORETA differences (see Section 3.2.2.). Two electrodes correspond to the LORETA left temporal difference locus (TCP1 and T5) and two to the right prefrontal difference locus (F8 and Fz). The selection was made according to the electrode coordinates from Towle et al. (1993). The arrows indicate the middle of the 288–321 ms microstate, in which centroid and LORETA differences were found. In this time segment, the waveform in response to irregular stems is more negative than the one in response to regular stems, while the opposite trend is present in some frontal sites.

vidual microstate timings were consistent with the results based on grandmean segmentation. Using the segmentation method in individual participants described in Section 2.7, for all participants but 3 a microstate corresponding to the grandmean 288–321 ms microstate could be clearly and unambiguously identified. Participants' individual microstate timings were very similar for the two conditions. For the microstate start point, the mean \pm SD for regulars were 276.0 ± 17.5 ms, for irregulars 276.5 ± 14.3 ms. For the microstate end point, the mean \pm SD for regulars were 311.0 ± 19.8 ms, for irregulars 316.1 ± 12.2 ms. For the microstate duration, the mean \pm SD for regulars were 35.0 ± 9.8 ms, for irregulars 39.7 ± 9.7 ms. *t* Tests comparing the start point ($t(17) = -0.13$, $P = 0.90$), the end point ($t(17) = -1.46$, $P = 0.16$), and the duration of the microstate ($t(17) = -1.38$, $P = 0.19$) in the two conditions were not significant. The centroid analysis was performed based on the individual microstates for the 18 participants, in whom microstates corresponding to the grandmean microstate could be identified. The results were similar to those of the grandmean microstate. The electric gravity center was more to the right in regulars than in irregulars (5.07 ± 0.20

vs. 4.85 ± 0.27 , $t(17) = 2.99$, $P = 0.008$), pattern present in 16 of the 18 subjects ($P(16/18) = 0.0006$) and there was also a marginally non-significant shift to the right for the negative centroid for regular compared to irregular verbs ($t(17) = 1.99$, $P = 0.063$).

3.2.2. Brain electromagnetic tomography

The results of the microstate analyses demonstrated that significantly different neural populations were active during the microstate between 288 and 321 ms when irregular and regular verb tense were processed. The LORETA analysis clarified these differences. Thus, the LORETA solution based on grandmean segmentation showed that between 288 and 321 ms, irregular verbs were associated with more activity in the left superior and middle temporal gyri (BA 39, 22, 21), whereas regular verbs were associated with more activity in the right medial frontal gyrus (BA 10) (Fig. 5).

As with the microstate analysis, LORETA based on each participant's individually segmented microstates was also performed for the 18 participants in whom microstates corresponding to the grandmean microstate could be identi-

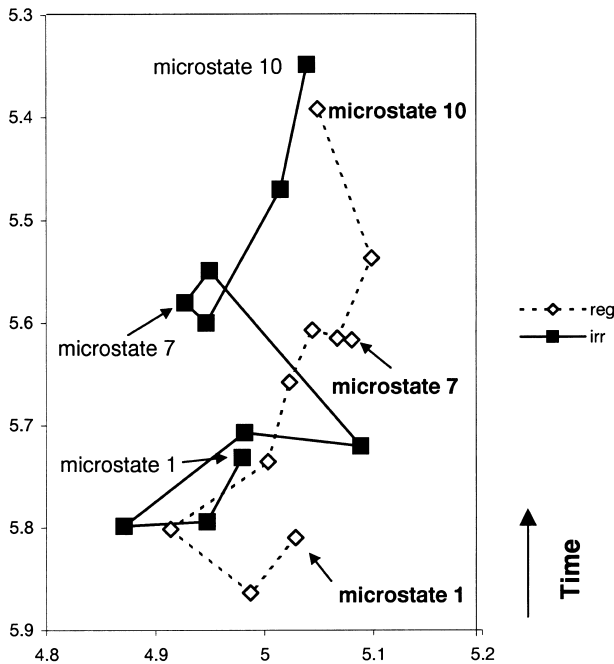


Fig. 3. The transition in the locations of the gravity center corresponding to the regular and irregular conditions for the first 10 microstates; direction of the time flow indicated by the arrow on the right of the panel. Numbers, as in Fig. 1, indicate electrode positions (e.g. 4.2 is distanced by 0.2 from electrode position 4.0 and by 0.8 from electrode position 5.0). Microstate 7 (288–321 ms after the stimulus onset) shows the greatest difference in the location of the gravity center.

fied. This analysis revealed more pronounced differences between the two conditions, compared to the LORETA based on grandmean segmentation. It was consistent with the latter in showing the right prefrontal (superior frontal gyrus, BA 10) activity predominance associated with regulars and the left temporal (superior, middle, and inferior temporal gyri, BA 22, 21, 20) activity predominance associated with irregulars. In addition, further marked differences in the electromagnetic activity associated with the two verb types emerged: regulars showed more activity than irregulars in the right superior and middle temporal gyri (BA 22, 39) and irregulars showed more activity than regulars bilaterally in the anterior cingulate (BA 24) (see Fig. 6).

4. Discussion

The novelty of the current study as compared to other ERP studies of morphological processing is two-fold. Firstly, the study employed a past-tense production paradigm, with important advantages over more intricate designs such as violation or priming designs. Past-tense production has ecological validity and it has also received most scrutiny from the proponents of the two competing frameworks (note that all computational models of verb morphology implemented past-tense production). The

outcomes from a simple design such as the present one are also relatively easy to interpret, as compared, for example, to priming paradigms (see Marslen-Wilson and Tyler, 1998, for a discussion of the latter). Secondly, microstate and brain electromagnetic tomography analyses allowed unambiguous distinction between the activities of different neural populations. Importantly, data-oriented segmentation in individual subjects was used to validate the microstate and LORETA results obtained on the basis of grandmean segmentation.

Our error data can serve as yet another indication for the overwhelming processing advantage for the regular items. However, both single- and dual-route theories can, in principle, account for this pattern of results, albeit from different perspectives. The single-route framework would invoke the advantage that regulars have in terms of consistency (see Section 1), to explain the finding that almost all errors were over-regularizations and the dual-route counterpart would explain that by the application of the default regular pattern, when irregular past-tense generation encountered difficulties.

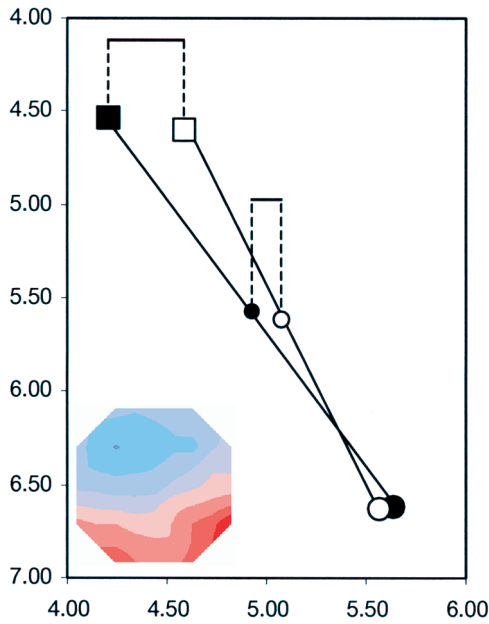
The electrophysiological results seem more conclusive. The microstate analysis revealed one microstate (288–321 ms after stimulus onset) in which the neural generators corresponding to the two verb types were at least partially non-overlapping (see Figs. 3 and 4). Importantly, virtually the same results were obtained when the microstate analysis was based on grandmean segmentation and segmentation in individual participants. Although this strongly suggests differential cortical involvement in the two past-tense patterns, it could be regarded as a one-way dissociation reflecting the recruitment of areas responsible for increased attention/effort in processing the more difficult irregulars. This would be compatible with both competing frameworks. A better theoretical test would be evidence of more activity associated with regulars in one or more cortical regions, despite their easier processing compared to processing irregulars.

Such evidence was provided by the LORETA analyses of this microstate. They indicated that as early as 288 ms after the stems were displayed on the screen, distinct regions of the brain showed prevalent involvement in processing either regular or irregular past-tense production. Thus, LORETA based on grandmean segmentation found

Table 2

Mean locations (and SD; *n* = 21) of spatial descriptors (centroids) characterizing the ERP field topography evoked by irregular and regular verbs between 288 and 321 ms post-stimulus onset (locations of the positive (Cp) and negative (Cn) centroids are reported in electrode positions along the left–right (L–R) and the anterior–posterior (A–P) brain axis as described in Fig. 1A)

	Irregular verbs		Regular verbs	
	Cp	Cn	Cp	Cn
L–R	5.64 (0.71)	4.21 (0.64)	5.57 (0.69)	4.59 (0.57)
A–P	6.62 (1.19)	4.54 (1.20)	6.63 (1.22)	4.61 (1.30)



that regulars were associated with more activity in the right prefrontal cortex (PFC) and irregulars with more activity in the left temporal cortex (see Fig. 5). The LORETA solution based on segmentation in individual participants was largely consistent with the initial LORETA results: it confirmed the double-dissociative pattern of activity with right prefrontal predominance for regulars and left temporal predominance for irregulars. However, it also revealed a more pronounced difference between condi-

Fig. 4. Averaged locations of the positive (circles) and negative (squares) centroids for irregular (dark symbols) and regular (open symbols) verbs during the microstate between 288 and 321 ms post-stimulus ($n = 21$). The frame shows an area extending from electrode position 4.0–6.0 along the left–right axis (horizontal) and from 4.0 to 7.0 along the anterior–posterior axis (vertical) following the numbering introduced in Fig. 1A. In the bottom left corner: the grandmean potential distribution map between 288 and 321 ms, averaged across subjects and conditions (red colors: positive potential distribution area; blue colors: negative potential distribution area vs. the average reference).

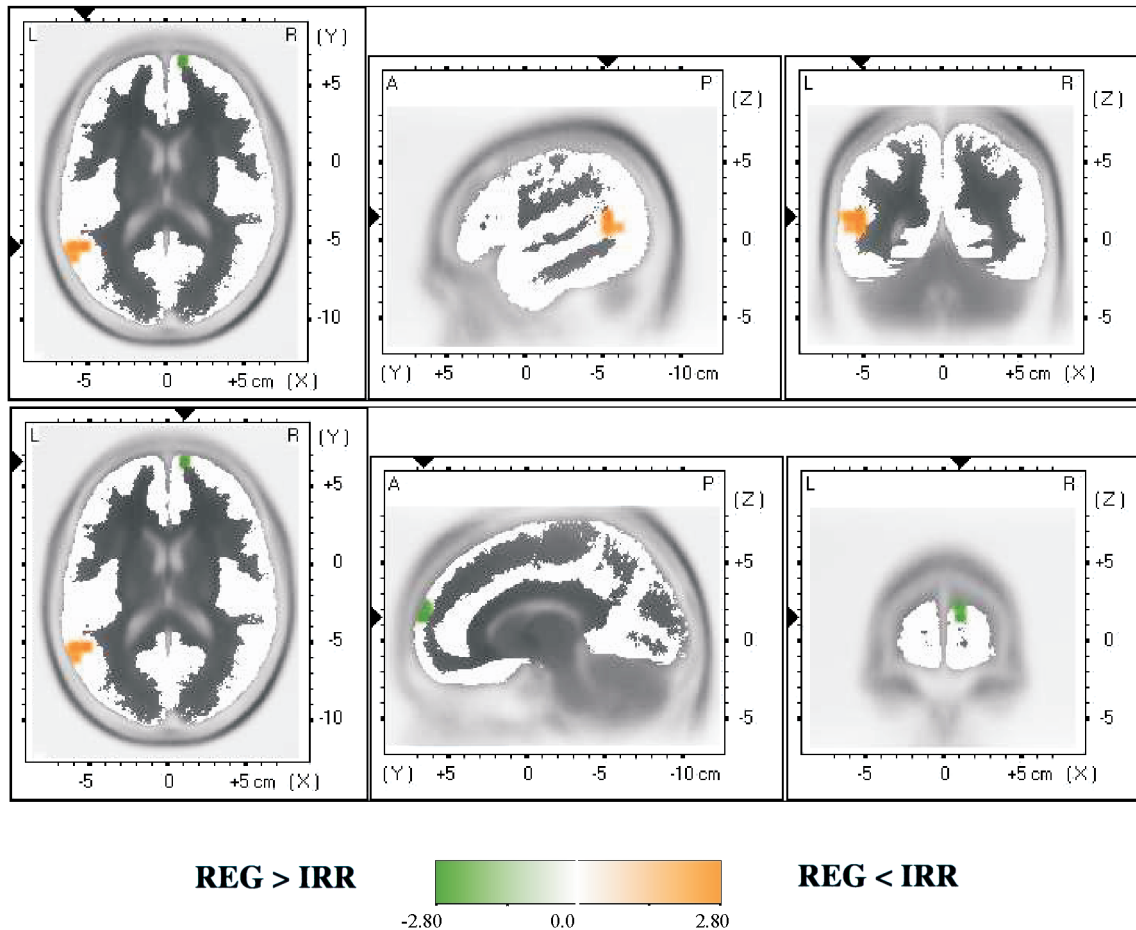


Fig. 5. LORETA results based on grandmean segmented data: images of voxel-by-voxel LORETA t tests comparing brain electric activity elicited by irregular and regular verbs during the microstate between 288 and 321 ms post-stimulus (t -values thresholded at $P < 0.05$, uncorrected for multiple comparisons, $d.f. = 20$). Axial (head seen from above, nose up, L = left, R = right), sagittal (anterior part of the head to the left), and coronal brain slices are shown to the left, middle and right part of the figure at the level of maximal differences between the two verb conditions. Black triangles show the locations of extreme t -values. LORETA's cortical solution area is shown in white. Relatively higher LORETA activity for irregular verbs is shown in orange, for regular verbs in green (see calibration). Coordinates in mm after Talairach and Tournoux (1988): origin at anterior commissure; (X) left (-) to right (+); (Y) posterior (-) to anterior (+); (Z) inferior (-) to superior (+).

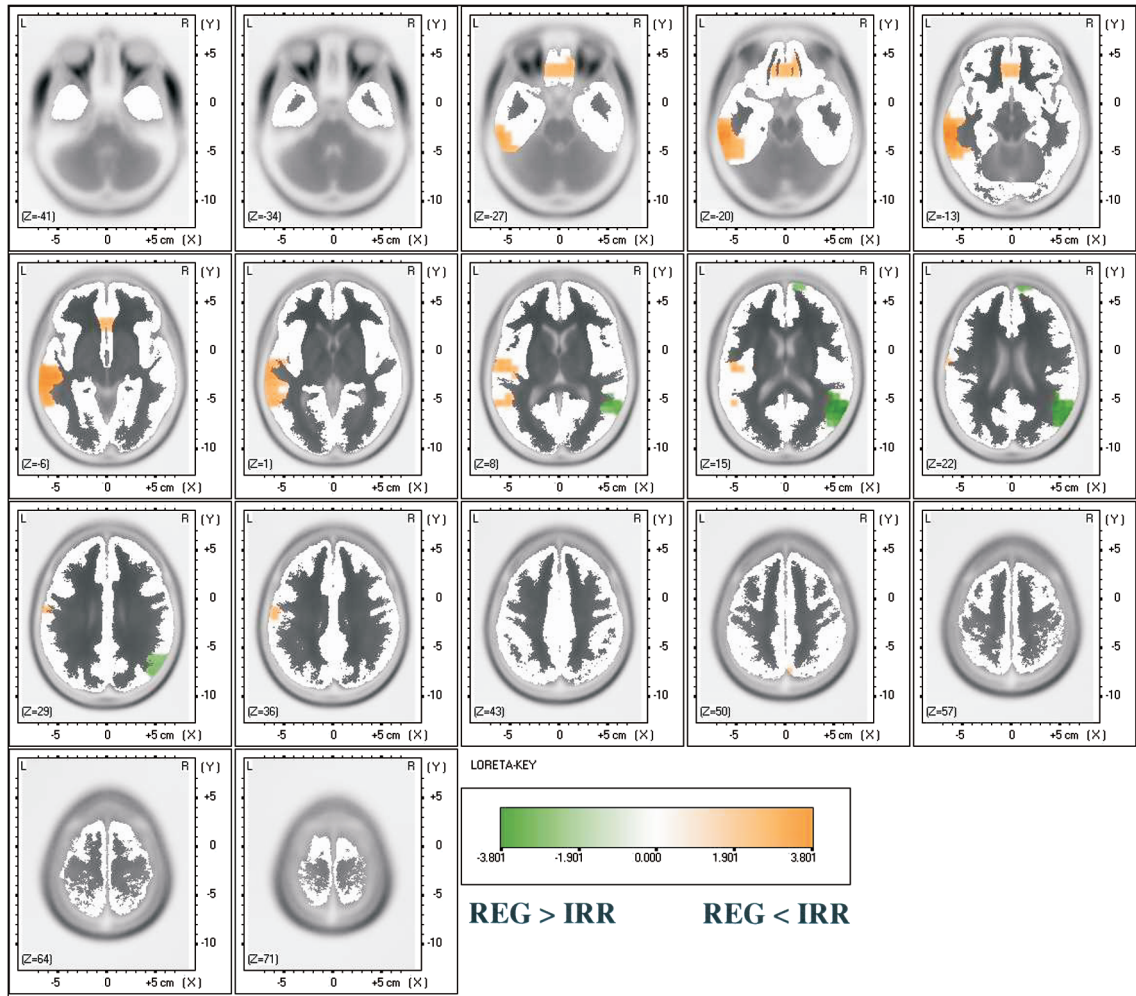


Fig. 6. LORETA results based on individually segmented data: the 17 axial brain slices shown in steps of 7 mm from the most inferior level ($Z = -41$) to the most superior level ($Z = 71$) represent the entire LORETA solution space (for additional technical details in the figure, see Fig. 5). Head seen from above, nose up, L = left, R = right.

tions: activity predominance associated with regulars was also found in the right temporal cortex and activity predominance associated with irregulars in the anterior cingulate (bilaterally) (see Fig. 6).

It is unlikely that potential imprecision associated with the current implementation of LORETA could account for such distinct patterns of activation as the ones corresponding to the two conditions in the current study. Such imprecision (see Section 2.8) would be significantly smaller than the boundaries of the anatomical regions where differences were found, or the distance between these regions (e.g. right vs. left temporal cortex).

Further insights can be gained if one examines the processes that are implemented by the cortical regions found to be predominantly involved in processing regular and irregular past tenses. We will start with the regions present in both LORETA solutions: the right PFC and the left temporal cortex associated prevalently with regular and irregular past tenses, respectively. These double-dissocia-

tive findings are by and large consistent with preliminary evidence from a recent magnetoencephalographic study. Using a similar production paradigm, Rhee et al. (2000) found regular items associated with prefrontal and temporo-parietal activity and irregular items only with temporo-parietal activity in the same latency range as in the present study. The dual-route model processing sequence postulates that initially two processes take place in parallel: lexical retrieval of the past-tense form and the default application (suffixation). At a later stage, lexical retrieval prevails for irregular items and suffixation for the regular ones. The involvement of the left temporal regions in lexical retrieval is a well-documented finding. A large corpus of neuroimaging studies using paradigms, which required access to the lexicon, found left-lateralized activation in temporal areas (Damasio et al., 1996; Fiez et al., 1996; see also Cabeza and Nyberg, 2000, for a review). Furthermore, a recent fMRI study, which contrasted processing sentences with semantic vs. syntactic anomalies, found

that the former were associated with activation in the left temporal cortex and the latter with activation in Broca's area (Ni et al., 2000). Therefore, more left temporal cortical activity for irregulars most likely represents a stronger dependence of irregular past-tense production on lexical retrieval. Such a conclusion would be consistent with the extant evidence of impaired word comprehension (Damasio, 1992; Goodglass, 1993), as well as irregular past-tense morphology (Marslen-Wilson and Tyler, 1997, 1998; Ullman et al., 1997b; Ullman, 1999) in patients with left temporal damage.

The precise role of the right prefrontal region in regular past-tense production is less clear. Since morpho-syntactic processing has been consistently linked to the left and not right PFC (Broca's area) (Embick et al., 2000; Ni et al., 2000), it seems unlikely that the right prefrontal activity associated with the regulars reflects syntactic aspects of regular past-tense processing. Thus, the right prefrontal activity predominance for the regulars can hardly be viewed as direct evidence for rule application. However, there is substantial support for the role of the right dorso-lateral PFC in executive processes, such as the manipulation of information in WM. Thus, although bilateral PFC activation has been found in most verbal WM tasks (Nystrom et al., 2000), there is considerable evidence indicating that WM tasks with executive demands, e.g. *n*-back tasks, tend to activate more strongly the right PFC (see Braver et al., 1997; Cohen et al., 1997, for such evidence from verbal WM tasks). From a symbolic dual-route perspective, it is conceivable that there may be executive differences between processing the two types of items. Albeit highly speculative, the idea that combinatorial (rule-based) processes are more reliant than memory search on executive function has some appeal. For example, for irregular items the stem initially held in working memory would have to be replaced with a different item – its past-tense form. In contrast, the executive demands during regular past-tense generation are more complex: the stem has to be held in memory, while the suffix (*-ed*), has to be retrieved and added to the stem, thus updating the working memory contents.

Finally, it would also be interesting to examine the functional neuro-anatomy differences revealed by LORETA based on individual microstates. There is relative consensus with regard to the role of the anterior cingulate cortex in error detection and correction (Bush et al., 2000). On the other hand, it is beyond doubt that irregular past-tense generation is associated with considerably higher error rates and longer reaction times, as compared to regular past-tense generation (see present performance data and also Kim et al., 1991; Daugherty and Seidenberg, 1994). Therefore, we propose that more anterior cingulate activity in response to irregulars reflects a stronger demand for error detection and correction. The current study is not unique in finding an association between regular verb morphology and the right temporal cortex. A PET study of German past-

tense and participle production (Indefrey et al., 1997) found only one region associated with more activation for regular as compared to irregular past tenses and participles and it was in the right temporal cortex. Indefrey et al. (1997) also found a two-way laterality effect in temporal cortex (left temporal – irregulars, right temporal – regulars) similar to the one revealed in the current study. There is substantial evidence for the superior role of the right hemisphere in automatic speech production. Milner and co-workers (Milner et al., 1966; Milner, 1974) employed the Wada technique and showed that left-handed neurologically intact individuals with bilateral representation for speech production had impaired automatic speech (serial counting and reciting of the days of the week) following right-side anesthesia. However, following left-side injection subjects made errors in naming, not in automatic speech (for a review of evidence on the right hemisphere in automatic speech production see Code, 1997). The idea that regular past tense is more automatic and more closely related to speech production routines than the irregular past tense is consistent with the dual-route framework. Some of its proponents explicitly state that they view the regular pattern as part of procedural memory and provide evidence of selectively impaired regulars in patients with deficits in motor control (Ullman et al., 1997b). However, automatic speech supported primarily by the right hemisphere is believed to operate at a lexical level and the right hemisphere has been assumed to host few, if any, representations of morphology or syntax (Code, 1997). However, there are studies that appear to indicate the contrary. For example, a recent MEG study found more right than left temporal activity associated with syntactic processing at latencies longer than 250 ms after the stimulus onset (Knoesche et al., 1999). The above-mentioned fMRI study on processing semantic vs. syntactic anomalies found right-lateralized activation in a region of the parietal cortex (BA 40, adjacent to temporal areas) associated with syntactic anomalies (Ni et al., 2000). While this would suggest that the right temporal cortex may hold morpho-syntactic information, e.g. the regular suffix *-ed*, the issue of morpho-syntactic abilities of the right hemisphere remains unclear.

The disagreement between single- and dual-system models with regard to their implicit predictions of brain activity is most evident when one considers the following. In traditional (homogeneous) single-mechanism networks individual units can and, indeed, do respond more strongly to one type of item, as indicated by weight change during learning. However, the units do not group themselves according to their response in any systematic way, or do not display what is often referred to as *compartmentalization*. A newer generation of network models (non-homogeneous), also ascribed to the single-route class, attempts to simulate compartmentalization by using different types of representations (e.g. 'phonology' vs. 'semantics') being differentially relied upon by regulars and irregulars (Joanisse and Seidenberg, 1999). Apart from the obvious

question of ‘how single-route’ these models are, with their built-in differentiation, they did not manage to show reliable dissociations of the two verb types. Therefore, evidence of compartmentalization remains problematic for the single-route framework.

As with other higher-level cognitive processes, which consist of many partially overlapping constituents, the generation of regular and irregular past-tense forms has much in common, in terms of perceptual, semantic and phonological processing. Consequently, the functional anatomy associated with the examined types of past-tense production will largely overlap. Furthermore, even the most radical versions of the dual-route framework (Pinker, 1991) postulate that for all items the two mechanisms work ‘in parallel’ up to a certain time point. In addition, the same account admits that a substantial subset of (regular) items can be fully processed by both the rule and the lexicon mechanisms – regulars that are phonologically similar to frequent irregulars. Consequently, compartmentalization is unlikely to be represented by totally separate networks corresponding to the two verb types. It may instead take the form of relative predominance in activity for one or the other type in distinct anatomical locations. In other words, even a double-dissociation in relative terms, e.g. more activity for regulars in the right prefrontal and temporal cortices and more activity for irregulars in the left temporal cortex and the anterior cingulate, is inconsistent with the single-route account, as long as the patterns are statistically reliable and anatomically distinct (e.g. in left temporal vs. right temporal cortices). In contrast, compartmentalization of activity associated with regular vs. irregular past tense seems more compatible with the dual-route framework, which proposes significant differences in the computational mechanisms associated with processing regular and irregular past tenses. Nonetheless, as discussed above, the functional anatomy corresponding to regulars in the current results does not unequivocally corroborate the rule-based (symbolic) nature of the regular past tense. Therefore, our data do not distinguish between symbolic (Pinker, 1991; Clahsen, 1999) and subsymbolic (Westermann et al., 1999; Goebel and Indefrey, 2000) dual-mechanism models of morphological processing; further investigations using advanced brain-mapping tools, which combine high temporal resolution with improved spatial capabilities, are required.

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Appendix

Table A1
Verb lists^a

Regular items		Irregular items	
No.		No.	
<i>(a) Verb list for Practice 1</i>			
1	Report	3	Think
2	Note	5	Build
4	Check	6	Cling
7	Save	8	Ring
9	Act	10	Fit
13	Decide	11	Hear
14	Form	12	Know
16	Guess	15	Spit
17	Match	18	Read
19	Care	21	Come
20	Press	22	Put
23	Push	24	Split
25	Cross	26	Bid
27	Wish		
<i>(b) Verb list for Practice 2</i>			
1	Color	2	Flee
3	Hunt	5	Steal
4	Rush	6	Freeze
7	Clean	8	Bind
9	Cite	10	Weave
12	Glance	11	Creep
14	Toss	13	Cut
15	Sense	18	Bite
16	Heave	20	Quit
17	Pack	21	Light
19	Spill	23	Set
22	Grant	25	Bleed
24	Stress	28	Wake
26	Stain	29	Get
27	Hurry	32	Dwell
30	Trust	33	Spend
31	Sweat	35	String
34	Thank	37	Make
36	Issue	39	Thrust
38	Face	42	Beat
40	File	43	Set
41	Apply	45	Kneel
44	Open	47	See
46	Lack	50	Burst
48	Solve	51	Stink
49	Add	53	Tread
52	Test	55	Sweep
54	Stop	57	Spread
56	Rest		

^a No., number in the order of presentation.

Table A2
Verb list for past-tense generation^a

Regular items					Irregular items					
No.	Stem	Freq. of stem	Freq. of past	Number of letters	No.	Stem	Freq. of stem	Past	Freq. of past	Number of letters
1	Raise	47	42	5	2	Feed	45	Fed	8	4
4	Please	47	11	6	3	Fight	43	Fought	23	5
5	Fill	49	31	4	6	Drive	46	Drove	58	5
7	Tend	43	15	4	8	Bear	43	Bore	14	4
9	Pick	49	51	4	11	Draw	46	Drew	63	4
10	End	40	41	3	13	Teach	41	Taught	19	5
12	Cause	52	39	5	15	Rise	48	Rose	60	4
14	Share	40	19	5	16	Deal	41	Dealt	8	4
17	Love	53	45	4	18	Choose	50	Chose	37	6
19	Close	39	39	5	22	Sell	39	Sold	20	4
20	Prove	53	48	5	24	Win	53	Won	45	3
21	Pull	39	54	4	25	Catch	39	Caught	54	5
23	Watch	53	68	5	27	Lose	57	Lost	49	4
26	Fail	37	52	4	29	Throw	35	Threw	46	5
28	Die	57	63	3	30	Eat	58	Ate	16	3
31	Drop	34	76	4	33	Wear	32	Wore	65	4
32	Kill	60	34	4	36	Grow	61	Grew	65	4
34	Touch	32	24	5	38	Ride	32	Rode	40	4
35	Join	63	33	4	39	Break	65	Broke	66	5
37	Plan	29	19	4	41	Sleep	31	Slept	18	5
40	Pass	64	91	4	42	Sit	66	Sat	139	3
44	Claim	28	25	5	43	Sing	27	Sang	28	4
46	Walk	66	143	4	45	Fall	66	Fell	87	4
47	Count	26	11	5	48	Shoot	26	Shot	18	5
49	Hope	68	33	4	51	Buy	68	Bought	32	3
50	Vote	26	22	4	52	Hang	26	Hung	53	4
53	Place	74	25	5	54	Seek	69	Sought	35	4
55	Point	26	48	5	56	Drink	25	Drank	19	5
57	Wait	82	68	4	59	Lead	81	Led	82	4
58	Force	24	19	5	60	Strike	22	Struck	40	6
61	Play	110	65	4	62	Stand	108	Stood	198	5
64	Gain	23	18	4	63	Hide	18	Hid	6	4
65	Talk	114	41	4	66	Write	109	Wrote	179	5
67	State	20	38	5	69	Fly	18	Flew	27	3
68	Ask	123	300	3	71	Speak	110	Spoke	86	5
70	Step	20	33	4	75	Wake	16	Woke	14	4
72	Pay	130	50	3	77	Run	126	Ran	134	3
73	Cry	18	25	3	78	Stick	16	Stuck	13	5
74	Call	134	165	4	80	Meet	141	Met	80	4
76	Mark	18	15	4	81	Shake	15	Shook	57	5
79	Turn	144	253	4	83	Hold	144	Held	125	4
82	Roll	18	34	4	86	Weep	13	Wept	7	4
84	Live	154	72	4	88	Mean	158	Meant	70	4
85	Jump	15	32	4	89	Swing	11	Swung	43	5
87	Need	160	57	4	92	Bring	158	Brought	133	5
90	Fix	13	12	3	93	Sink	11	Sank	18	4
91	Work	179	76	4	94	Leave	191	Left	157	5
95	Head	13	23	4	97	Swim	10	Swam	6	4
96	Help	211	40	4	99	Feel	201	Felt	302	4
98	Urge	13	21	4	102	Swear	10	Swore	14	5
100	Use	228	137	3	104	Keep	257	Kept	115	4
101	Smile	10	68	5	105	Tear	9	Tore	15	4
103	Seem	229	311	4	107	Tell	262	Told	286	4
106	Wash	10	10	4	109	Dig	9	Dug	7	3
108	Look	302	327	4	110	Give	387	Gave	285	4
111	Stare	9	58	5	112	Blow	8	Blew	12	4
114	Want	318	204	4	113	Find	397	Found	268	4
Mean		72.56	66.21	4.18			75.33		69.54	4.26
SD		72.45	74.63	0.66			85.60		75.22	0.72

^a No., number in the order of presentation; freq., frequency count after Francis and Kucera (1983).

Table A3
Past-tense generation errors and omissions

Stem	Form generated	Correct form	Verb type	Error type	No. of participants	List
Steal	<i>Stealed</i>	Stole	Irregular	Over-regularization	3	Practice 2
Spread	<i>Spreaded</i>	Spread	Irregular	Over-regularization	3	Practice 2
Light	<i>Lighted</i>	Lit	Irregular	Over-regularization	2	Practice 2
Spend	<i>Spended</i>	Spent	Irregular	Over-regularization	1	Practice 2
Freeze	<i>Freezed</i>	Froze	Irregular	Over-regularization	1	Practice 2
Wake	<i>Waken</i>	Woke	Irregular	Participle	1	Practice 2
Beat	<i>Beated</i>	Beat	Irregular	Over-regularization	1	Practice 2
Cut	<i>Cuted</i>	Cut	Irregular	Over-regularization	1	Practice 2
Quit	<i>Quited</i>	Quit	Irregular	Over-regularization	1	Practice 2
Burst	–	Burst	Irregular	Omission	1	Practice 2
Dwell	–	Dwelt	Irregular	Omission	1	Practice 2
Clean	–	Cleaned	Regular	Omission	1	Practice 2
Grant	–	Granted	Regular	Omission	1	Practice 2
Issue	–	Issued	Regular	Omission	1	Practice 2
Seek	<i>Seeked</i>	Sought	Irregular	Over-regularization	2	Past tense
Draw	<i>Drawed</i>	Drew	Irregular	Over-regularization	1	Past tense
Drive	<i>Drived</i>	Drove	Irregular	Over-regularization	1	Past tense
Fight	<i>Fighted</i>	Fought	Irregular	Over-regularization	1	Past tense
Fly	<i>Flided</i>	Flew	Irregular	Over-regularization	1	Past tense
Ride	<i>Rided</i>	Rode	Irregular	Over-regularization	1	Past tense
Rise	<i>Raised</i>	Rose	Irregular	Stem change	1	Past tense
Stand	<i>Standed</i>	Stood	Irregular	Over-regularization	1	Past tense
Raise	<i>Rose</i>	Raised	Regular	Irregularization or stem change	1	Past tense
Buy	–	Bought	Irregular	Omission	1	Past tense
Fly	–	Flew	Irregular	Omission	1	Past tense
Lead	–	Led	Irregular	Omission	2	Past tense
Speak	–	Spoke	Irregular	Omission	1	Past tense
Stick	–	Stuck	Irregular	Omission	1	Past tense
Run	–	Ran	Irregular	Omission	1	Past tense
Win	–	Won	Irregular	Omission	1	Past tense

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