Neural dynamics of inflectional and derivational processing in spoken word comprehension: laterality and automaticity

Caroline M. Whiting1,2 *, William D. Marslen-Wilson1,2 and Yury Shtyrov2,3,4

1 Department of Psychology, University of Cambridge, Cambridge, UK
2 MRC Cognition and Brain Sciences Unit, Cambridge, UK
3 Center of Functionally Integrative Neuroscience, Aarhus University, Aarhus, Denmark
4 Center for Languages and Literature, Lund University, Lund, Sweden

INTRODUCTION

Successful speech comprehension involves extracting linguistic information from a spoken input and accessing a unique representation from the mental lexicon. In mapping from speech to meaning, converging evidence from behavioral, neuroimaging, and neuropsychological studies indicates that the grammatical structure of a word is automatically detected and segmented – e.g., darkness is broken down into two morphemes, the stem dark and the affix -ness (Tait and Forster, 1975; Marslen-Wilson et al., 1994 see Rastle and Davis, 2008 for review). This has motivated longstanding questions about how lexical representations are organized and accessed, in particular for words containing more than one morpheme.1 Morphological complexity plays a key role in languages such as English by introducing systematic and productive elements to the language, broadening the range of possible meanings through the use of multiple morphemes within a word. A critical question in this study will be how the language system identifies and processes this linguistic complexity as the speech signal unfolds.

We examine two types of affixes in English, inflectional (-ed) and derivational (-er), both of which combine with a stem to form a morphologically complex word.2 Forms containing an inflectional suffix are semantically transparent, such that the meaning of the complex form is predictable from the meaning of the stem (e.g., jump-jumps-jumped). It has been argued that inflections create a new form but not a new lexical entry (Clahsen et al., 2003). Derivational affix function in changing the meaning and in many cases the grammatical category of the stem (e.g., farm-farmer). To date, extensive evidence from masked priming in the visual domain supports the claim for automatic morphological segmentation (Rastle et al., 2000, 2004; Longtin et al., 2003; Longtin and Meunier, 2005; Marslen-Wilson et al., 2008), where any word containing a potential stem and affix is segmented. This work has primarily focused on derived forms, but research on inflected forms – often centered on distinctions between regular and irregular past-tense processing – has also pointed to early morphological decomposition (Meunier and Marslen-Wilson, 2004; Crepaldi et al., 2010). Converging evidence for processing of inflected forms has come

1 We use here the standard linguistic definition of the morpheme as the minimal meaning-bearing linguistic unit (e.g., Matthews, 1991), distinguishing between content morphemes like the stem (dark), and grammatical morphemes like the derivational affix (-ness).

2 A third type of morphological complexity in English involves compounds words (e.g., blackboard), composed of multiple roots as opposed to a root and affix, which are not assessed in the present study (but see MacGregor and Shtyrov, 2013, for related evidence on compound processing).
from spoken word comprehension. Spoken forms ending in the
characteristic pattern of regular inflection in English—a final coro-
nal consonant (d, t, s, z) that agrees in voicing with the preceding
phone (e.g., *plays and play as opposed to vowel–consonant
voicing mismatch in plate and place)—will trigger automatic mor-
phological decomposition (Tyler et al., 2003; Post et al., 2008).
Though this appears counterproductive for words such as corner or
trade, where a decompositional reading of *corn + er or *tray + ad
has no relationship to the meaning of the whole form, it sug-
gests a tuned sensitivity of the language system to morphological
structure.

To address the neural foundations of this automatic morpho-
logical process, it is essential to use a brain imaging technique
which can provide not only spatial but also temporal preci-
sion. For this reason, we use concurrent magnetoencephalography
(MEG) and electroencephalography (EEG) recordings of brain
responses to morphologically simple and complex words. In the
visual domain, converging cross-linguistic evidence using EEG has
pointed to specific processes linked to the presence of morphologi-
cal complexity in the time window of the N400 (Münke et al.,
1999; Rodríguez-Fornells et al., 2001; Lavric et al., 2007; Lehtonen
et al., 2007), with additional studies showing earlier effects between
150 and 300 ms (Morris et al., 2008; Lehtonen et al., 2011; Lavric
et al., 2012; Morris and Stockall, 2012). Recent MEG evidence has
revealed early effects before 200 ms (Zweig and Pytkonen, 2009;
Lewis et al., 2011), as well as effects peaking at 400 ms (Vartiainen
et al., 2009). Taken as a whole, these studies provide evidence for
sensitivity to potential morphological structure, with the work on
derived forms showing that complex and pseudo-complex forms
like farmer and corner produce a similar neural pattern relative
to orthographic controls such as scandal (san + non-affix + -al; Morris
et al., 2008; Lehtonen et al., 2011; Lavric et al., 2012). These
findings have been taken as evidence for automatic morphologi-
cal segmentation independent of word meaning, confirming the
behavioral masked priming effects.

Evidence for blind morphological decomposition does not,
however, require a decompositional representation for all words
containing morphological structure—and indeed would not be
appropriate for pseudo-affixed words such as corner. Dual-route
accounts have been proposed which argue for decompositional
processes, but allow for the co-existence of whole-word and mor-
phologically decomposed representations (Caramazza et al., 1985;
Marslen-Wilson et al., 1994; Schreuder and Baayen, 1995). This
presupposes a level of processing where forms are accessed in terms
of their constituent morphemes, but does not assume all complex
words are accessed through parsing. Electrophysiological evidence
for dual-route recognition has been demonstrated through sensitiv-
ty to surface frequency and the relationship between stem and
suffix (transition probability), suggesting that both whole form
and morphological factors modulate early stages of word process-
ing (Lewis et al., 2011). Features of the affix are thought to play a
key role in determining whether a form is represented decom-
positionally or as a full form, including word formation type
(inflected vs. derived) and the productivity of the affix (Bertram
et al., 2008).

There is accumulating neuroimaging and neuropsychological evidence to suggest that the presence of an inflectional ending
engages left hemisphere fronto-temporal regions, with specific
involvement of the left inferior frontal gyrus (IFG; Laine et al.,
1999; Longworth et al., 2003; Tyler et al., 2003; Morris et al.,
2006; Bozic et al., 2010). Derivationally complex forms appear to
show a distinct neural pattern, engaging a more bilateral system
(Meinzer et al., 2009; Lehtonen et al., 2011; Bozic et al., 2013), and
suggesting that lexical access to derivations may be achieved via
the full forms. We aim to detail these putative differences in brain acti-
vation dynamics by comparing EEG/MEG activation elicited by
inflections and derivations in a tightly controlled stimulus set. We
focus in this study on the initial stages of morphological processing
involved in identifying complexity. If there is rapid morphologi-
cal segmentation, as has been argued in the visual domain (see
Rastle and Davis, 2003 for review), we would hypothesize that this
process will be triggered for both types of affixes (inflectional and
derivational) once phonological cues to the presence of the affix
are identified.

Particular challenges arise when addressing morphological pro-
cessing in the auditory domain. Unlike written text, where there
are discrete letters available simultaneously to the reader, spo-
ken language is uttered in a continuous stream. The listener must
recognize linguistic units within a stream that is evolving over
time, with new information constantly arriving to the auditory
system. Models of spoken word processing state that listeners are
able to recognize words before they have finished hearing them
(Marslen-Wilson and Welsh, 1978; Groppe, 1980), where mul-
tiple candidates compete for selection until the speech input is
uniquely identifiable. The notion of simultaneous activation of all
potential candidate words is a fundamental concept in many spo-
ken word recognition models (Marslen-Wilson and Welsh, 1978;
McClelland and Elman, 1986; Norris, 1994). Thus, an important
issue is determining the point in the speech signal at which there
is sufficient information to determine its correct identity, in par-
ticular when considering the relationship between the meaning
of the stem and the meaning of the complex form (jump-jumps,
farmer-farm, corn-corner). By tracking the time course of spoken
word comprehension using time-resolved MEG/EEG, it is possi-
ble to time-lock neural responses specifically to the suffix onset and
thus investigate how the suffix triggers segmentation once it can
be identified in the speech signal.

In delineating the neural systems underlying speech compre-
ension using MEG, a bilateral fronto-temporal network has been
shown to be engaged in the processing of spoken words, includ-
ing superior and middle temporal regions which are linked to
the processing of lexical meaning (Binder et al., 2000; Scott et al.,
2006; Davis and Johnsrude, 2003; Hickok and Poeppel, 2007). A
further left-lateralized subsystem of this network has been impli-
cated in the processing of morphological complexity, comprising
left-hemisphere fronto-temporal, and parietal regions (Fründ et al.,
2003; Marslen-Wilson and Tyler, 2007; Bozic et al., 2010). Thus,
by manipulating the presence or absence of potential mor-
phological complexity, we can investigate how these bilateral and
left-lateralized networks are activated during spoken word com-
prehension. Once evidence has accumulated that a potential affix
is present in the speech signal, we would predict that processing
should automatically shift to the left-lateralized fronto-temporal
system.
To address these issues neurophysiologically, it is necessary to use brain responses that reflect automatic processing, provide accurate information on the time course of stimulus-specific processing in the brain, and that are sensitive to the linguistic properties of the stimuli. For these reasons, the present study involves the use of the mismatch negativity (MMN), a neural response component elicited by rare unexpected changes in the auditory stream. The paradigm consists of an oddball design in which a sequence of a frequent ‘standard’ stimulus is occasionally replaced by a rare ‘deviant’ stimulus (Näätänen et al., 1978). It has been argued that the MMN – typically a negative deflection peaking 100–200 ms after the onset of the change between deviant and standard – can reflect the activation of experience-dependent auditory memory traces (Näätänen et al., 1997).

Crucially for our study, the mismatch response is sensitive to linguistic sounds such as syllables and words, resulting in an increased left-lateralized response for language deviants (Näätänen et al., 1997; Shtryov et al., 2005). The amplitude of the MMN shows a specific increase for real words compared to aurally matched pseudowords (Korpipäätä et al., 2001; Pulvermüller et al., 2001). This lexical enhancement effect is explained by the existence of cortical memory traces that are automatically activated for known words in passive oddball sequences, but fail to activate for pseudowords that are not stored in the lexicon (Pulvermüller et al., 2001; Näätänen et al., 2007). Importantly, the timing of the mismatch response has been linked to behaviourally determined word-specific recognition times (Pulvermüller et al., 2006) whilst temporal patterns of local cortical activation spread show fine-tuned specificity for linguistic stimulus properties (Pulvermüller and Shtryov, 2009).

Evidence from English inflectional morphology has shown that the mismatch response is modulated by grammatical changes due to the presence of morphological structure, with effects emerging in left-lateralized perisylvian areas for affixed deviants as compared to stems (Shtryov and Pulvermüller, 2002); similar activity patterns were found for MMN responses elicited by differences in morphological structure in Arabic (Boudella et al., 2010). Our focus in this study is on the initiation of morphological segmentation of potentially complex forms, which is argued to be triggered automatically (e.g., Tyler et al., 2002; Post et al., 2008). A key advantage of the MMN paradigm is the ability to record neural responses elicited in the absence of focused attention on the auditory stream, enabling an investigation into early stages of spoken word recognition and the initiation of morphological processing before strategic effects or conscious processing of the word forms have taken place.

The MMN paradigm relies on a small set of items, implying that caution is needed in generalizing MMN results to the entire language. However, it offers a number of benefits, which make it an attractive tool for studies of spoken word recognition. It allows for ruling out acoustic confounds by incorporating the same acoustic/phonological contrast (e.g., addition of the same consonant) into different linguistic contexts which can themselves be tightly matched acoustically. By determining the time-point of standard-deviant divergence (such as addition of an affix here), neural responses can be aligned precisely allowing for a direct comparison between different morphological conditions. Finally, as mentioned above, it is an automatic response in that its elicitation does not depend on focusing attention on stimuli or engaging in a stimulus-related task.

In the present study, we include a matched set of inflected, derived and non-affixed forms. The inflectionally complex forms (bakes, beard) allow us to examine how neural activity in the language system is modulated by the presence of an affix which results in a fully transparent form. Inflectional suffixes do not modify the meaning of the stem, and it has been argued that regularly inflected forms are represented and accessed compositionally (Finkler and Ullmann, 2002; Marslen-Wilson and Tyler, 2007). We predict that inflected forms should trigger automatic decompositional processing, engaging a left-lateralized network including inferior frontal cortex compared to non-affixed forms (Tyler et al., 2005). Converging MMN findings show a left-lateralized response to inflected forms at ~150 ms (Shtryov and Pulvermüller, 2002; Shtryov et al., 2005), indicating that the mismatch response can reveal specific memory trace activations in the neural subsystems involved in morphological decomposition.

Further, such a stimulus design allows us to directly contrast the verb (bakes) and the noun (beak) in order to examine potential differences related to grammatical class (signaling agreement as opposed to nominal plural). Differential noun vs. verb processing has been suggested in previous studies, where inflected verbs have revealed an increased left-lateralized distribution compared to inflected nouns, with key involvement of left inferior frontal cortex (Shtryov and Pulvermüller, 2003; Tyler et al., 2004; Longe et al., 2007). Though both forms are morphologically complex and would require segmentation into stem and suffix, it has been argued that verbs and nouns differentially engage the neural systems involved in morphological processing when they are inflected. This has been linked to differences in grammatical function of verbs and nouns in English, where verbs can be associated with a greater range of inflections to mark number, tense and person (unlike nouns, which only mark number), thus playing a greater role in the structural interpretation of a sentence (Tyler et al., 2004). However, the automaticity of this neural distinction between word classes remains unexplored. In the present study, we hypothesise increased engagement of left fronto-temporal regions for suffixed verbs compared to nouns, in particular in left inferior frontal cortex.

Using the derivational suffix -er, we investigate a further contrast between semantically transparent and pseudo-affixed word forms (bakes vs. beaker) in order to examine whether morphological processing is indeed unaffected by the lexical appropriateness of the segmentation, as indicated by the previous behavioral investigations. Like the inflected forms, we would predict automatic segmentation of complex and pseudo-complex forms, with both derived forms patterning with the inflected forms compared to non-affixed forms. This would indicate the existence of discrete neural networks for automatic morphological processing which should be engaged for all forms containing potential complexity (e.g., Morris et al., 2008; Lehtonen et al., 2011; Lavric et al., 2012).

The two affixed conditions (bakes/bake, beaks/beaker) are contrasted with non-affixed forms (bacon/beacon) that embed the same (false) stems but should not trigger any attempts at segmentation as no affix is present. These non-complex forms are likely to
engage a more bilateral cortical distribution, since morphological processes may not be engaged when no clues for morphological segmentation (such as a valid suffix) are present (Boots et al., 2016). In addition, we include a control condition aimed at assessing acoustic/phonological effects by incorporating the same deviant contrasts in a meaningless pseudoword (boke). This provides a way of assessing whether effects are due to processing of low-level acoustic changes, rather than morphological processing.

In summary, the aim of this work is to examine how the spatiotemporal dynamics of word processing are modulated once a potential affix is identified in the speech signal. We focus on pinpointing when and where morphological information is accessed, and whether this is done automatically in the absence of attention, using the fine-grained spatiotemporal resolution of combined magneto- and electroencephalography (MEG–EEG).

We address two issues of morphological processing: contrasting time.

1. We examine how the addition of a suffix modulates the spatiotemporal pattern of word recognition as the speech signal unfolds, as well as the networks that support recognition of morphologically complex forms, allowing us to rule out any acoustic confounds and concentrate on the linguistic context effects.

2. We predict increased left fronto-temporal engagement for morphologically complex forms, the latter comprising both semantically transparent and opaque derivations. We predict increased left fronto-temporal activation for all morphologically complex forms compared to simple forms, regardless of word meaning, triggered by the presence of an inflectional or derivational suffix. Furthermore, with the inflected forms we examine processing of grammatical category, contrasting noun and verb forms. Verbal -s forms should elicit more left fronto-temporal activation, in particular in IFG, compared to nominal -s forms. To assess this potential shift in left hemisphere engagement for morphologically complex forms, we incorporate a laterality analysis (Shtryov et al., 2005) to examine hemispheric differences across the complex and non-complex forms. The MMN paradigm has revealed increased left lateralization for language stimuli (Naätänen et al., 1997), and we would predict this lateralization should increase for morphologically complex forms compared to simple forms, and for verbs compared to nouns, both properties which have been shown to modulate the degree of left fronto-temporal activity. In this way we can examine how the addition of a suffix modulates the spatiotemporal pattern of word recognition as the speech signal unfolds, as well as the networks that support recognition of morphologically simple and complex spoken words.

MATERIALS AND METHODS

SUBJECTS

Fifteen subjects (13 female) took part in the experiment. All were right-handed (handedness tested according to Oldfield, 1971; range 85–100%) native British English speakers between the ages of 19–34 (mean age of 24.9) with normal hearing, normal or corrected-to-normal vision, and no history of neurological dis-

PROCEDURE

Stimuli were presented pseudo-randomly in blocks of approximately 20 min in length, with short pauses between blocks and in the middle of each block. The order of the condi-

Table 1 | Standards and deviants used in MMN study.

| Standard | *bake* | *beak* | *boke* |
|----------|--------|--------|--------|
| deviant 1 (-er) | bake | beaker | *boker* |
| deviant 2 (-e) | baker | beaker | *boker* |
| deviant 3 (-s) | bacon | beacon | *bokes* |

* indicates pseudoword.
FIGURE 1 | Waveforms of stimuli used as standards (A) and deviants (B). Deviants displayed are for the bake condition, with the three deviant endings following the same stem. The beak and boke conditions were constructed using the same endings. At 240 ms the [k] is released in each condition, marking the deviation point from the standard.

Within each block was done to ensure that at least two standards appeared between every deviant, and the order of the deviants within the blocks was completely random. Each stimulus was presented for 460 ms with a jittered inter-trial offset-to-onset interval of 460–500 ms. For each condition, 100 trials of each of the three deviants were presented in the context of 900 standards, constituting 25% deviants (8.3% of each) and 75% standards. Ten filter trials of the standard stimulus were used at the beginning of each block to build up a representation of the standard, and were not included in the average event-related field. Every standard that appeared after a deviant was also discarded, as it might produce a change detection response of its own when immediately following the deviant.

Stimuli were presented binaurally through non-magnetic earpieces attached to plastic tubes while subjects were seated in front of a screen inside a dimly lit, magnetically shielded room. Before the experiment began, subjects were given a hearing test to ensure they could hear sounds equally well in each ear. Subjects were instructed to attend to a silent video during the experiment and did not perform a task on the stimuli, which they were instructed to ignore. They were told there would be a questionnaire following the experiment on details concerning the film, and all subjects scored at least 90% on the questionnaire. The experiment was run using E-Prime 1.0 (Psychology Software Tools, Sharpsburg, PA, USA) and lasted approximately 60 min.

DATA ACQUISITION

Concurrent MEG–EEG data were acquired at a sampling rate of 1000 Hz (passband 0.10–330 Hz), with triggers placed at the onset of each stimulus. Neuromagnetic signals were recorded continuously with a 306-channel (102 magnetometers and 204 planar gradiometers) Vectorview MEG system (Elekta NeuroMag, Helsinki, Finland). Electrical activity was recorded using a 70-channel EEG cap (Easycap, Herrsching, Germany), using a reference electrode on the nose. Prior to recording, five electromagnetic coils were positioned on the head and digitized along with the EEG electrodes using the Polhemus Isotrak digital tracker system (Polhemus, Colchester, VT, USA) with respect to three standard anatomical landmarks (nasion, left and right pre-auricular points). During the recording, the position of the magnetic coils was continuously tracked using continuous head position identification (CHPI), providing information on the exact head position within the MEG dewar for later movement correction. Four electrooculogram (EOG) electrodes were placed laterally to each eye and above and below the left eye to monitor horizontal and vertical eye movements during the recording.

PRE-PROCESSING

Continuous raw data were pre-processed off-line with MaxFilter (Elekta Neuromag) implementation of signal-space separation (SSS) technique with a temporal extension (tSSS; Taal and Simola, 2006), which minimizes movement artifacts and effects of magnetic sources outside the head. Averaging was performed using the MNE Suite (Athinoulia A. Martinsen Center for Biomedical Imaging, Boston, MA, USA). Epochs containing gradiometer, magnetometer, or EEG/EOG peak-to-peak amplitudes larger than 3000 fT/cm, 6500 fT, or 200 μV, respectively, were rejected. Trials were averaged by condition with epochs generated from −50 to 500 ms from the [k] release (at 240 ms after stimulus onset), at which point the standard and deviant stimuli started to diverge. Averaged data were low-pass filtered at 45 Hz and baseline corrected using the −50 to 0 ms interval before the divergence point. This interval was selected as it falls within the closure period preceding the [k] release (a silent period of 75 ms), and the standard and all the deviants are identical up to this point, thus there should not be any differences before this time point except random noise-related variations that should be removed using
the baseline-correction procedure. The average response for the standards was subtracted from the three associated deviants to produce the MMN. For sensor-level analysis, CSS was used to transform MEG data to the head position coordinates of the subject with the median head position within the helmet, to minimize transformation distance.

**SENSOR-LEVEL ANALYSIS**

Analyses at the sensor level were conducted on EEG, gradiometers, and magnetometers separately using the sensor-space statistical parametric mapping (SPM) SensorSPM analysis method implemented in SPM5 (www.fil.ion.ucl.ac.uk/spm/). EEG and magnetometer data were used as such, whilst for each pair of gradiometer channels, a vector sum was calculated reconstructing the field gradient from its two orthogonal components and its amplitude (computed as a square root of the sum of squared amplitudes in the two channels) was used in further analysis. For each subject and condition, a series of F-tests were performed on a three-dimensional topography (2D sensors by 1D time) image. Each contrast results in a SPM, in which clusters of contiguous supra-threshold voxels are corrected using Random Field Theory (Kiebel and Friston, 2004). The 3D images were thresholded at a voxel level of $p < 0.005$, and corrected for cluster size at $p < 0.05$. These clusters could extend in space (distributed across the topography) and in time. This made it possible to compare conditions across every sensor over time while still correcting for multiple comparisons, allowing us to investigate a wider spatiotemporal array (Shtyrov et al., 2012). This provides a conservative approach to defining significant effects, avoiding any bias inherent to conventional visual inspection.

**MRI ACQUISITION AND SOURCE ESTIMATION**

MPRAGE T1-weighted structural images with a $1\, \text{mm} \times 1\, \text{mm} \times 1\, \text{mm}$ voxel size were acquired on a 3-Tesla Trio Siemens Scanner for each subject (repetition time [TR] = 2250 ms, echo delay time [TE] = 2.99 ms, flip angle 9, field of view [FOV] = $256\, \text{mm} \times 240\, \text{mm} \times 192\, \text{mm}$), which were used for source reconstruction of the cortical surface using FreeSurfer (Athinoulia A. Martinos Center for Biomedical Imaging). The L2 minimum-norm estimation (Hämäläinen and Ilmoniemi, 1994) technique was applied for source reconstruction as implemented in the MNE Suite. A three-layer boundary element model (scalp, inner skull, outer skull) was created for each subject and was used to compute the combined MEG + EEG forward solutions. An average cortical solution was created from the fifteen subjects, to compute the combined MEG—EEG source solutions. In the presentation of the results, sensor-level results are presented separately for gradiometers, magnetometers, and EEG. Figure 2A shows the MEG responses averaged across word conditions (bake and beak) at the sensor and source level, with the MMN defined as the peak between 100 and 200 ms with a major source in posterior temporal cortex. The zero time point was placed at the release of the [k], which was equivalent across conditions. The [-s] deviant had the earliest mismatch response, peaking at approximately 135 ms, while the [-er] deviant peaked at 165 ms and the [-on] deviant at 185 ms. As expected for word deviants, all three conditions showed a left-lateralized MMN, with largest activation within left temporal sensors in MEG and fronto-central electrodes in EEG. The combined MEG—EEG source solutions, seen in Figure 2B, confirmed this left-lateralized response, which localized primarily to posterior superior temporal cortex (Figure 2C).

In the laterality analysis, a 30-ms window around the peak of each mismatch response was used in order to compare across deviant conditions with differing onset latencies. We included frontal and temporal regions bilaterally, which covers the main sources of the mismatch response across the three deviant types (see Figure 2B), and which encompasses ROIs that have previously been implicated in morphological processing (Tyler et al., 2005; Lehmann et al., 2006; Marslen-Wilson and Tyler, 2007; Bouc et al., 2010). Comparing the three deviants averaged across the two stems (bakes/beaks, baker/beaker, and bacon/beacon), there was a significant main effect of condition ($F_{0,14} = 3.62, p < 0.05$), but no effect of ROI ($F_{0,14} = 1.60, p > 0.05$) and no interaction between the two factors ($F < 1$). The effect of condition showed increased left-lateralization for the [-s] and [-er] deviants compared to [-on] ($p < 0.05$, as seen in Figure 3A). Based on the lack of a main effect of ROIs, we collapsed data across the five ROIs, which showed that the left-lateralization for the [-er] and [-s] conditions was in

**LATERALITY ANALYSIS**

Lateralization at the source level was calculated using a laterality coefficient $Q$ as previously applied in psychoacoustic research and in MEG (e.g., Shtyrov et al., 2000, 2005; Holland et al., 2012):

$$Q = \frac{(A_{l} - A_{r})}{(A_{l} + A_{r})} \times 100\%,$$

where $A_{l}$ and $A_{r}$ are the mean amplitude across vertices in the left and right hemispheres, respectively. In this way we could assess the degree of lateralization for each condition and compare across deviant types by removing any differences in absolute magnitude. Statistical analysis was carried out using repeated measures ANOVAs, with condition and ROI as within-subject factors.

**RESULTS**

In the presentation of the results, sensor-level results are presented separately for gradiometers, magnetometers, and EEG. Figure 2 shows the MMN responses averaged across word conditions (bake and beak) at the sensor and source level, with the MMN defined as the peak between 100 and 200 ms with a major source in posterior temporal cortex. The zero time point was placed at the release of the [k], which was equivalent across conditions. The [-s] deviant had the earliest mismatch response, peaking at approximately 135 ms, while the [-er] deviant peaked at 165 ms and the [-on] deviant at 185 ms. As expected for word deviants, all three conditions showed a left-lateralized MMN, with largest activation within left temporal sensors in MEG and fronto-central electrodes in EEG. The combined MEG—EEG source solutions, seen in Figure 2B, confirmed this left-lateralized response, which localized primarily to posterior superior temporal cortex (Figure 2C).
FIGURE 2 | Mismatch negativity response averaged across word conditions (bakes/beaks, baker/beaker, bacon/beacon): (A) sensor level (EEG, gradiometers and magnetometers) and (B) source level (L2 minimum norm estimate using combined MEG + EEG) for [-s] deviant (130–140 ms), [-er] deviant (160–170 ms), and [-on] deviant (180–190 ms). (C) Time course of source-level activity in left and right posterior superior temporal gyri for three deviant types.

itself significant (i.e., greater than zero; \(t(14) = 2.58, p < 0.01\) and \(t(14) = 2.59, p < 0.05\), respectively), and was not significant for the [-on] condition \(t(14) = 1.18, p > 0.05\); two-tailed).

Within individual affix types (bakes vs. beaks, baker vs. beaker, bacon vs. beacon), the inflected [-s] forms were the only words to reveal a difference in laterality, with the verbal form bakes showing a more left-lateralized response compared to the nominal form beaks (Figures 3B,C). There was no significant main effect of condition \((F < 1)\) or of ROI \((F(4,56) = 1.21, p > 0.05)\), but there was a significant interaction between condition and ROI \((F(4,56) = 2.96, p < 0.05)\) from 160 to 240 ms. We assessed this interaction statistically by carrying out a series of planned comparisons, showing greater laterality in IFG for the verb compared to the noun \((F(1,14) = 5.30, p < 0.05)\). The timing of this effect corresponds to the second half of the mismatch response for the [-s] deviants (see Figure 2B). Figure 3C demonstrates the difference in amplitude between the two hemispheres from 160 to 240 ms (LH minus RH at each vertex), with yellow/red indicating increased left hemisphere activity, and blue indicating increased right hemisphere activity. As revealed by the laterality analysis, the verb deviant showed increased left hemisphere activity in frontal and temporal areas.

**WORD–PSEUDOWORD**

To test for a lexical enhancement effect (e.g., Pulvermüller et al., 2001), each deviant type ([-er], [-s], and [-on]) was analyzed...
Whiting et al. Neural dynamics of morphological processing

**FIGURE 3** Laterality analysis

(A) contrasting affixed [-s], [-er] and non-affixed [-on] deviants, showing increased left-lateralization for affixed deviants (asterisk signifies laterality significantly greater than zero at \( p < 0.05 \)); and (B) contrasting verb (bakes) and noun (beaks) deviants, showing increased left-lateralization for the verb compared to the noun from 160 to 240 ms (asterisk signifies \( p < 0.05 \)), and at right, the region-of-interest (inferior frontal gyrus) showing significant lateralization.

(C) Source activation for [-s] deviants from 160 to 240 ms, displaying the difference in amplitude between left and right hemispheres (LH minus RH at each vertex; yellow/red indicates greater left hemisphere activity; blue indicates greater right hemisphere activity).

separately contrasting the two word conditions (bake, beak) with the pseudoword (boke). The [-er] deviants elicited a significant effect in the gradiometers within left temporal sensors with a greater response to the two word conditions compared to the pseudoword condition (see Figure 4A). The cluster was significant from 150 to 185 ms with a peak at 165 ms, which corresponds to the timing and the topography of the mismatch response in the [-er] deviants. Though this predominantly gradiometer-driven effect did not reach significance in the magnetometers or EEG, the topographies in Figure 4A showed a greater response to the word conditions (more negative for EEG) compared to the pseudoword condition across the time window of the mismatch response. No other time windows were significant. Source analyses were performed on time windows from the sensor analysis where significant effects were found. Using combined MEG and EEG at the source level, the [-er] word–pseudoword contrast (baker, beaker vs. boker) localized primarily to left posterior temporal cortex (Figure 4B). Significant effects of condition \( (F_{1,14}) = 5.30, p < 0.05 \), ROI \( (F_{4,56}) = 12.61, p < 0.001 \) and the interaction of condition and ROI \( (F_{4,56}) = 2.89, p < 0.05 \) emerged in the left hemisphere from 150 to 185 ms. Planned comparisons showed increased amplitude for words compared to pseudowords...
in left posterior STG ($F_{(1,14)} = 11.35, p < 0.005$). In the right hemisphere, there was a significant effect of ROI ($F_{(4,56)} = 3.73, p < 0.01$), but no significant effect of condition ($F_{(1,14)} = 2.53, p > 0.05$) and no interaction between the two factors ($F < 1$).

Turning to the unaffixed [-on] deviants (Figure 5), these revealed a significant cluster from 175 to 200 ms within anterior right temporal gradiometers, corresponding to the timing of the [-on] mismatch response (see Figure 5A). Unlike the sensor-level analysis, no source ROIs showed a significant lexicality effect for the [-on] word–pseudoword contrast (bacon, beacon vs. bokon). In the left hemisphere, there was a significant effect of ROI ($F_{(4,56)} = 12.14, p < 0.001$) but no effect of condition ($F < 1$) or an interaction between condition and ROI ($F < 1$). In the right hemisphere, there was an effect of ROI ($F_{(4,56)} = 5.39, p < 0.001$), but no effect of condition ($F_{(1,14)} = 1.38, p > 0.05$) or an interaction between the two factors ($F < 1$).

### Derivational Transparency Contrast: Baker vs. Beaker

At the sensor level, the two word conditions were contrasted for each deviant type separately. Within the [-er] deviants (corresponding to the derivational affix), the words elicited a significant difference starting at 240 ms (see Figure 6A). In the magnetometers, the semantically opaque deviant (beaker) showed increased activity within right-hemisphere sensors compared to the transparent deviant (baker) from 240 to 270 ms. This time window corresponds to the second half of the MMN response curve, which peaks at 165 ms. The significant effect in EEG covered the time window of 240–280 ms, corresponding to distinct spatial distributions for the two conditions: a negativity for the semantically transparent deviant (baker) in posterior electrodes and a positivity for the semantically opaque deviant (beaker) in central electrodes. No significant differences were found in the gradiometers.

At the source level, an effect between the two word deviants emerged in left anterior MTG, as seen in Figure 6B. From 260
FIGURE 5 | Word–pseudoword contrast: [-on]. (A) Topographies for [-on] deviants (bacon, beacon, bokon) from 175 to 200 ms, and the location of the significant cluster from the sensor analysis. (B) Source activation for [-on] deviants from 175 to 200 ms.

to 270 ms, there was no main effect of condition ($F_{1,14} = 2.05, p > 0.05$), but a significant effect of ROI ($F_{4,56} = 3.30, p < 0.05$), and a significant condition by ROI interaction ($F_{4,56} = 3.35, p < 0.05$). Planned comparisons revealed increased activity for beaker compared to baker in left anterior MTG ($F_{1,14} = 4.94, p < 0.05$). In the right hemisphere, there was a significant effect of ROI ($F_{4,56} = 2.70, p < 0.05$), but there was no effect of condition ($F < 1$) or an interaction between the two factors ($F < 1$).

INFLATIONAL WORD CLASS CONTRAST: BAKES vs. BEAKS
In contrast to the [-er] forms, both word deviants with [-s] endings were morphologically complex and semantically transparent. At the mismatch response, peaking at 135 ms, the only difference between the [-s] deviants was linked to lateralization as described above (see Figure 3B).

MONOMORPHEMIC STIMULI WITH EMBEDDED STEMS: BACON vs. BEACON
In contrast with multiple results obtained for affixed conditions, no significant differences in the MMN response were found at the sensor level between the non-affixed monomorphemic deviant stimuli.

DISCUSSION
The aim of this study was to investigate the spatiotemporal pattern of morphological processing in the context of spoken word recognition, focusing on how neural activity within the bilateral frontal–temporal language network is modulated by the presence of a derivational or inflectional suffix. Results revealed language-specific responses that rapidly and automatically dissociated between words based on the presence of possible morphological complexity. All three conditions contained an embedded stem, and the addition of an ending that signaled either a potentially complex word or a non-affixed word resulted in distinct cortical distributions. For all conditions, the mismatch response peaked between 130 and 190 ms after the deviation point from the standard, and the source-level analysis revealed that neural activity within this time window showed a left-lateralized distribution in fronto-temporal regions. We focus on three major findings: the shift in the laterality of the brain response based on the grammatical properties of the deviants; the selectivity of the neural response for words compared to pseudowords, and the divergence between semantically transparent and opaque complex words.

LATERALIZATION
The deviants all showed a left-lateralized distribution, but there was a significant shift in the degree of lateralization which was modulated by the presence of a potential affix. Both the [-s] and [-ert] conditions showed increased left-lateralization within frontal and temporal regions compared to the [-on] condition during the mismatch response, and the lateralization for the affixed deviants was significantly greater than zero. This would suggest that the addition of a derivational or inflectional affix triggered
increased engagement of left hemisphere fronto-temporal language regions, and this process occurred automatically once the suffix was present in the speech signal. This is in line with previous fMRI findings showing increased involvement of left hemisphere perisylvian regions in morphological processing (Tyler et al., 2005; Lehtonen et al., 2006; Bozic et al., 2010), and supports the claim that the left-lateralized subsystem of the fronto-temporal network is specialized for processing of morphological complexity (e.g., Marslen-Wilson and Tyler, 2007). Importantly, unlike previous behavioral and fMRI results that could not speak to the timing of these events and were obtained using active tasks, the present study demonstrates that these fronto-temporal systems are triggered rapidly and automatically in the course of spoken word comprehension.

This increase in left hemisphere engagement was present for both suffix types, derivational and inflectional. Previous MMN research has not focused on derivationally complex forms; however source estimation from other studies examining morphological complexity and grammatical processing have demonstrated the key role of the left perisylvian areas in early stages of spoken word recognition (Shtryov and Pulvermüller, 2002; Shtryov et al., 2003). Furthermore, we found increased left-lateralization for both semantically transparent and opaque forms (baker and beaker), suggesting that morphological processing is triggered for any form containing morphological structure, regardless of word meaning. This is consistent with evidence from the visual domain showing automatic segmentation of word forms containing a stem and an affix, both behaviourally (Longtin et al., 2003; Rastle et al., 2004), and with MEG/EEG (Lavric et al., 2007; Morris et al., 2008; Lehtonen et al., 2011; Lewis et al., 2011), as well as fMRI evidence from spoken word comprehension demonstrating automatic decomposition of a stem and suffix (Tyler et al., 2002). Our findings are also in line with a dual-route account, in which parallel access through the full form as well as the constituents is engaged from early stages of recognition (Schreuder and Baayen, 1997). Word forms containing a stem and suffix would be initially decomposed; at a later stage the acceptability of the parsed form would be assessed, and semantically opaque forms would not be consistent with the decompositional route. However, the current study cannot speak directly to falsifying or strongly supporting dual-route accounts. Our results support initial morphological processing for all forms containing a potential suffix, which does not discount representation as whole forms.

We found additional laterality effects based on differences related to word class. The inflected word deviants contained a verb (bakes) and a noun (beaks). As both forms are semantically
translucent and should be segmented into a stem and a suffix, they should not result in any differential processing due to the presence of morphological complexity. There were sustained laterality differences during the mismatch response, showing increased left-lateralization for the verb compared to the noun in frontal regions. The laterality analysis at the source level was in line with the evidence that verbs engage greater left perisylvian activity when they are inflected, which may be linked to the greater number of roles verbal affixes play in specifying number, tense and person (Tyler et al., 2004; Longe et al., 2007).

**LEXICALITY**

The mismatch response showed a sensitivity to lexicality, with an increased response to words compared to the pseudoword which was strongest for the derived forms, i.e., [-er] deviants. The effect for the [-er] deviants appeared in left temporal sensors when comparing words vs. pseudowords, and at the source level was localized to left posterior STG. This is consistent with previous MMN findings showing a lexical enhancement effect (e.g., Pulvermüller et al., 2001), and indicates that lexical processing takes place automatically and does not require focused attention on the linguistic input. The presence of robust lexicality effects within left posterior temporal cortex during the mismatch response suggests that this area is involved in signaling acoustic changes (when deviants are sufficiently different from the standard) that are language-specific and in activating long-term cortical memory traces for stored words. In fMRI, left middle and superior temporal regions have been shown to play a key role in accessing stored lexical representations (Indefrey and Levelt, 2004; Hickok and Poeppel, 2007; Turkcn and Dronkers, 2011). Left STG has been previously identified as underlying lexical MMN enhancement both in MEG (Shtryov et al., 2005) and fMRI (Shtryov et al., 2008).

The monomorphic [-on] deviants also showed a left-lateralized distribution in temporal sensors, but the difference between word and pseudoword deviants appeared in the right hemisphere, showing increased activity for words. This suggests that both hemispheres respond to spoken words, although there may be a stronger left hemisphere involvement in this response. Whereas previously reported MMN lexicality effects were focused on the left temporal cortex, the potential role of right hemisphere generators has not been ruled out; furthermore, in at least one previous study a bilateral MMN response to concrete imageable nouns was linked to semantic stimulus features that are encoded by memory circuits encompassing both hemispheres (Pulvermüller et al., 2004). This is in line with extensive evidence for the involvement of the right hemisphere in language comprehension (e.g., Federmeier et al., 2008), as well as for increased bilateral engagement for morphologically simple words (Bozic et al., 2010). As we see in the laterality analysis, the monomorphic [-on] deviants, which do not contain a potential suffix, show more bilateral fronto-temporal activity compared to the bisemorphic [-s] and [-er] forms, with the [-s] forms showing almost no right hemisphere activity at the peak of the MMN response (see Figures 2B,C). The combination of lexicality and laterality results point to the engagement of both the left and right temporal regions in lexical processing.

There was no significant lexicality effect in the inflected [-s] deviants, suggesting that the inflectional suffix was processed similarly for all forms, regardless of the meaning of the stem. This points to a specificity in the processing of the inflectional affix, which plays a grammatical role but does not alter the meaning of the stem (unlike derivational affixes, which change meaning and grammatical category). The inflectionally complex forms fokes and beaks do not require access to a separate representation from the stem, based on the argument that inflected forms are represented decompositionally (e.g., Pinker and Ullman, 2002). Thus, the same process of morphological segmentation should apply to both the words and pseudowords, suggesting that the [-s] suffix is triggering morphological processing as opposed to additional lexical processing.

**SEMANTIC TRANSPARENCY**

The [-er] word forms varying in semantic transparency (baker, beaker) showed differential processing starting at 240 ms following the deviation point. We found increased processing of the semantically opaque word (beaker) which occurred more anteriorly, engaging left middle temporal cortex. We did not find similar amplitude differences between [-s] and [-on] pairs. This supports claims from the visual domain for a processing stage following blind segmentation which is constrained by word meaning, whereby the appropriateness of the segmentation is analyzed (Domínguez et al., 2004; Lavric et al., 2012). Semantically opaque forms such as beaker would require re-analysis since a decompositional meaning is not appropriate. The involvement of left anterior MTG points to additional processing demands required in accessing the appropriate meaning after an incorrect segmentation. Left MTG has been shown to be a key region in language comprehension (Turken and Dronkers, 2011), and anterior MTG in particular has been previously implicated in lexical retrieval (Damasio et al., 1996; Martin and Chao, 2001).

**AUTOMATICITY**

In the present study, we extend the issue of automatic morphological processing to investigate how suffixed and non-suffixed forms are processed when attention is not focused on the stimuli and participants are not engaged in a stimulus-related task. Our results suggest that morphological segmentation is triggered automatically by the presence of a suffix, regardless of word meaning, activating a left-lateralized network of frontal and temporal regions. This would point to a primarily feedforward stimulus-driven process, driven by acoustic cues to morphological structure (-s or -er suffix). We report further evidence for automatic lexical processing, a finding which has been previously demonstrated when attention is not directed towards word identity (Price et al., 1996; Hinoosa et al., 2004). This does not disregard the crucial role of top-down processing, a relevant issue for understanding interactions between feedforward and feedback processes during word recognition – for instance, in examining task-relevant effects and how neural responses linked to morphological processing may be tuned by task demands (e.g., Wright et al., 2011). MEG and EEG could be beneficial in future studies in tracking neural activity across time between regions in the language network in order to investigate recurrent interactions between bottom-up...
and top-down processes during morphological and lexical processing.

While using a limited set of stimuli, the MMN methodology offers a number of unique advantages because it (1) provides a tightly controlled method for studying neural processing of spoken words that are well-matched for acoustic and phonological similarity, (2) allows for examining language processes that occur independently of focused attention, and (3) allows for precise time-locking of brain activation to word recognition points in the spoken stimuli (Sh wyn and Pulvermüller, 2007). Variability in uniqueness point across words presents a challenge for examining large, controlled sets of stimuli in a typical event-related design. This is particularly important for suffixed words, since it makes it possible to control the point at which information about the stem and suffix is present in the speech signal across conditions. Importantly, at least in lexical and syntactic domains, initial MMN findings on rapid automatic processing could be confirmed in multi-item non-oddball designs (Hasting and Kotz, 2008; MacGregor and Shytrov, 2013) when similarly rigorous stimulus matching was applied. In this way, focused MMN results could pave the way for further studies using more ecologically valid design. Future studies are needed to confirm the current MMN findings using other paradigms, including for example multi-item stimulus sequences with uniqueness point time-locking (cf. Lemen et al., 2011).

It is therefore crucial to consider how we can extrapolate to other words, and whether we can make conclusions about derivational, inflectional, and non-affixed words more generally from this study. The effects within this paradigm were robust and showed spatiotemporal patterns consistent with previous findings using morphologically simple and complex word forms. In order to further establish these results, additional studies looking at morphology need to be performed using the MMN and other paradigms in the spoken domain. Given the limited morphological complexity of English in comparison with other languages, future studies are needed that will allow us to confirm these results using different stimuli in different languages. Using combined MEG and EEG and focusing analyses at the source level, it is possible to dissociate morphological processing from later stages involved in integration of semantic and syntactic aspects of the word, providing a more complete picture of the neural processing streams that support recognition of morphologically simple and complex words.

CONCLUSION

We recorded automatic brain responses to acoustically and psycholinguistically controlled sets of morphologically complex words, monomorphemic items, and pseudoword-control stimuli using combined MEG–EEG. In this study, we found:

- Automatic activation of lexical and morphological neural processes in response to complexity in spoken words as early as 130 ms after affix onset;
- Enhanced left lateralization of cortical activity for morphologically complex forms, which indicates involvement of left fronto-temporal cortical circuits;
- Stronger degree of left-lateralized processing for verb than noun stimuli;
- Modulation of automatic brain response to complex forms by their semantic coherence (transparency/opacity).

This study provides evidence that the spatiotemporal pattern of speech processing is modulated by the morphological status of the word ending. These results demonstrate processing of lexical and morphological features in the absence of focused attention, pointing to the key role that morphology plays in language comprehension.

ACKNOWLEDGMENTS

This research was supported by a grant to William D. Marslen-Wilson from the European Research Council (NEUROLEX 230075) and by MRC: Cognition and Brain Sciences Unit funding (William D. Marslen-Wilson: U.1055.04.002.00001.01, Yury Shytrov: U.1055.04.014.00001.01). Caroline M. Whiting was supported by funding from the Cambridge Trusts and a Howard Research Studentship from Sidney Sussex College, Cambridge.

REFERENCES

Baayen, R. H., Piepenbrock, R., and Gulikers, L. (1995). The CELEX Lexical Database (CD-ROM). Philadelphia, PA: Linguistic Data Consortium, University of Pennsylvania.

Bertram, R., Baayen, R. H., and Schreuder, R. (2000). Effects of family size for complex words. J. Ment. Lang. 42, 590–605. doi: 10.1016/s0168-3819.2000.00042.x

Borod, J. J., Frost, J. A., Hammock, T. A., Bellgowan, P. S. F., Springer, J. A., Kaufman, J. N., et al. (2010). Human temporal lobe activation by speech and nonspeech sounds. Cereb Cortex 20, 512–526. doi: 10.1093/cercor/bh1511

Bozdag, S., Pulvermüller, F., Hauk, O., Shytrov, Y., and Marslen-Wilson, W. D. (2010). Arabic morphology in the neural language system. J. Cogn. Neurosci. 22, 988–1010. doi: 10.1162/jocn.2009.21273

Bozeat, M., Tylke, L. K., Ives, D. T., Randi di, B., and Marslen-Wilson, W. D. (2010). Bihemispheric foundations for human speech comprehension. Proc. Natl Acad. Sci. U.S.A. 107, 17439–17444. doi: 10.1073/pnas.1003511107

Bouzid, S., Pulvermüller, F., Hauk, O., Shytrov, Y., and Marslen-Wilson, W. D. (2015). The cognitive-linguistic processing of affixation: the MMN revisited. Neurosci. Biobehav. Rev. 56, 196–207. doi: 10.1016/j.neubiorev.2015.02.013

Borod, J. J., Frost, J. A., Hammock, T. A., Bellgowan, P. S. F., Springer, J. A., Kaufman, J. N., et al. (2010). Human temporal lobe activation by speech and nonspeech sounds. Cereb Cortex 20, 512–526. doi: 10.1093/cercor/bh1511

Bozeat, M., Tylke, L. K., Ives, D. T., Randi di, B., and Marslen-Wilson, W. D. (2010). Bihemispheric foundations for human speech comprehension. Proc. Natl Acad. Sci. U.S.A. 107, 17439–17444. doi: 10.1073/pnas.1003511107

Caramazza, A., Me чис, G., Silver, M. C., and Laudanna, A. (1985). Reading mechanisms and the organization of the lexicon: evidence from acquired dyslexia. Cogn. Neuropsychol. 2, 85–114. doi: 10.3233/CNS1980252862

Clahsen, H., Sommerst ob, I., and Hieber, J. P. (2003). “Derivational morphology in the German mental lexicon: a dual-mechanism account,” in Morphological Structure in Language Processing, eds R. H. Baayen and R. Schreuder (Berlin: Mouton de Gruyter), 125–155.

Crupi di, D., Rostl, K., Cohnhae per, M., and Nickels, L. (2010). “Fell” primes “fall”, but does “bell” prime “ball”? Masked priming with irregularly-inflected primes. J. Ment. Lang. 45, 83–99. doi: 10.1016/j.jmentlang.2010.03.002

Danis, H., Grafovska, T. J., Trend, D., and Heicho, R. D. (1988). A neural basin for lexical retrieval. Nature 338, 499–501. doi: 10.1038/380499a0

Davis, M. H., and Johnsrude, I. S. (2003). Hierarchical processing in spoken language comprehension. J. Cogn. Neurosci. 15, 4123–4131.

Dong, B. S., Sng, F., Fook, B. Q., and Dijkstra, B., Blacket, D., et al. (2006). An automated labeling system for subdividing the human cerebral cortex into gyral based regions of interest. Neuroimage 31, 968–980. doi: 10.1016/j.neuroimage.2005.01.021

Dudouy, A., De Vega, M., and Barber, H. (2004). Event-related brain potentials elicited by morphological, homographic, orthographic, and semantic priming. J. Cogn. Neurosci. 16, 598–608. doi: 10.1162/089892904323057236

Federmeister, K. D., Welsos, E. W., and Meyer, A. M. (2008). “What’s right in language comprehension: event-related potentials reveal right hemisphere language capabilities.” Lang. Linguist. Compass 2, 1–17. doi: 10.1111/j.1749-8105.2007.00002.x

Frontiers in Human Neuroscience www.frontiersin.org November 2013 | Volume 7 | Article 708 | 13

“fnhum-07-00759” — 2013/11/16 — 13:43 — page 13 — #13
Frith, C., & Frith, U. (2008). The role of left inferior frontal and superior temporal cortex in sentence comprehension: linking extractive and semantic processes. Cogn. Ctr. Brain. 1, 170–177. doi: 10.1016/S1369-1096(08)70012-7

Friederici, A. D., Binschger, C. A., Haider, A., and Forbach, C. J. (2005). The role of left inferior frontal and superior temporal cortex in sentence comprehension: linking extractive and semantic processes. Cogn. Ctr. Brain. 1, 170–177. doi: 10.1016/S1369-1096(08)70012-7

Grosjean, F. (1980). Spoken word recognition processes and the gating paradigm. Psychol. Psycho. 28, 267–281. doi: 10.1016/0033-2917(80)90008-1

Hamalainen, M. S., and Ilomäki, R. J. (1994). Interpreting magnetic fields of the brain: minimum norm estimates. Med. Biol. Eng. Comput. 32, 35–42. doi: 10.1016/0025-737X(94)90008-1

Heston, A. S., and Kutas, M. A. (2006). Spooling up syntax: on the relative timing and automaticity of local phrase structure and morphosyntactic processing as reflected in event-related brain potentials. J. Cogn. Neurosci. 20, 1230–1239. doi: 10.1162/jocn.2008.2028

Hickok, G., and Poeppel, D. (2007). The cortical organization of speech processing. Front. Hum. Neurosci. 1:66. doi: 10.3389/fnhum.2007.00066

Holland, R., Brindley, L., Shtyrov, Y., Pulvermüller, F., and Patterson, K. (2012). They played with the trade: MEG investigation of the processing of past tense verbs and their phonological twins. Neurophysiol. 50, 3735–3720. doi: 10.1016/j.neuroph.2012.10.019

Indefrey, P., and Levelt, W. J. (2004). The spatial and temporal signatures of word production components. Cognition 92, 103–144. doi: 10.1016/j.cognition.2002.04.001

Kajola, S. J., and Friston, K. J. (2004). Statistical parametric mapping for event-related potentials (ERPs) in a hierarchical temporal model. Neuroimage 22, 505–520. doi: 10.1016/1053-8119(04)90013-X

Knoblich, G., Kraus, C. M., Holopainen, T., and Lang, A. H. (2001). Early and late manuscript negativity elicited by words and speech-like stimuli in children. Brain Lang. 78, 332–359. doi: 10.1006/brln.2000.2430

Kovecses, T., and Kuntschik, J. (2009). Opaque for the reader but transparent for the brain: morphological transparency in French verbal inflection. Lang. Cogn. Process. 24, 394–421. doi: 10.1080/01690960802299386

Kutas, M., and Hillyard, S. A. (1980). Event-related brain potentials: early evidence for regular past tense forms. Brain Res. 1812–1820. doi: 10.1016/0006-8993(80)90028-7

Laine, M., Vainio, S., and Hyönä, J. (1999). Lexical access routes to nouns in a morphologically rich language. J. Cogn. Neurosci. 11, 1–17. doi: 10.1162/0898929995480279

Marslen-Wilson, W. D., and Welsh, A. (1978). Processing interactions and lexical memory in the mental lexicon. J. Mem. Lang. 17, 1087–1097. doi: 10.1016/0022-2456(78)90018-X

Mattsson, P., and Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. Acta Psychol. 200, 456–463. doi: 10.1016/S1386-6573(09)80038-4

Muir, G., Daumas, T., and Millet, G. (1996). The TRACE model of speech perception. Cogn. Psychol. 32, 35–42. doi: 10.1016/0010-0285(96)00019-4

Näätänen, R., Gaillard, A. W. K., and Mäntysalo, S. (1978). Early selective-attention effect on evoked potential reinterpreted. Acta Psychol. 42, 313–329. doi: 10.1016/0001-6918(78)90029-6

Näätänen, R., Louniskoski, A., Lemos, M., Cheever, M., Huotilainen, M., Iivanainen, A., et al. (1994). Language-specific phonemes: representations revealed by electric and magnetic brain responses. Nat. Rev. Neurosci. 3, 432–436. doi: 10.1038/308524a0

Näätänen, R., Huotilainen, P., Rösing, T., and Allonen, K. (2007). The mismatch negativity (MMN) in basic research of central auditory processing: a review. Clin. Neurophysiol. 118, 2344–2399. doi: 10.1016/j.clinph.2007.04.026

Nevins, D. (1994). Shortlist: a connectionist model of continuous speech recognition. Cognition 51, 199–234. doi: 10.1016/0010-0285(94)90027-5

Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9, 97–113. doi: 10.1016/0028-3932(71)90016-7

Perfkin, S., and Lilien, M. T. (2002). The past and futures of the past tense. Trends Cogn. Sci. 6, 406–403. doi: 10.1016/S1364-6613(02)00990-5

Price, C. J., Wise, R. J. S., and Frackowiak, R. S. J. (1996). Demonstrating the implicit processing of visually presented words and pseudowords. Cereb. Cortex 6, 62–70. doi: 10.1093/cercor/6.1.62

Pulvermüller, F., Kujala, T., Hietanen, J., Rinne, T., and Alho, K. (2004). Spatiotemporal signatures of large-scale synchrony chains for speech processing as revealed by MEG. Cereb. Cortex 18, 79–88. doi: 10.1093/cercor/bhn060
Pulvermüller, F., Shtyrov, Y., Ilmoniemi, R. J., and Marslen-Wilson, W. D. (2003). The representation of grammatical categories in the brain. *Eur. J. Neurosci.* 15, 1189–1206. doi: 10.1046/j.1469-8966.2003.02918.x

Shriver, K., and Caramazza, A. (2003). The representation of grammatical categories in the brain. *Front. Cogn. Sci.* 2, 201–206. doi: 10.3738/fcog.2.1.201

Shtyrov, Y., Kujala, T., Lyytinen, H., Kujala, J., Ilmoniemi, R. J., and Näätänen, R. (2005). Determinants of dominance: an fMRI study of past tense processing. *Neuropsychologia* 43, 404–413. doi: 10.1016/j.neuropsychologia.2005.06.002

Wright, P., Randall, B., Marslen-Wilson, W. D., and Tyler, L. K. (2011). Dissociating linguistic and task related activity in the left inferior frontal gyrus. *J. Cogn. Neurosci.* 23, 404–413. doi: 10.1162/jocn.2010.21450

Zweig, E., and Pulvermüller, F. (2009). A visual M170 effect of morphological violations in Catalan. *Cereb. Cortex* 19, 29–37. doi: 10.1093/cercor/bhm028

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 10 May 2013; accepted: 22 October 2013; published online: 18 November 2013.

Citation: Whiting CM, Marslen-Wilson WD and Shtyrov Y (2013) Neural dynamics of inflectional and derivational processing in spoken word comprehension: laterality and automaticity. *Front. Hum. Neurosci.* 7:101. doi: 10.3389/fnhum.2013.00101

This article was submitted to the journal Frontiers in Human Neuroscience. Copyright © 2013 Whiting, Marslen-Wilson and Shtyrov. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) or licensor are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.