

Neurocognitive dimensions of lexical complexity in Polish

Zanna Szlachta^a, Mirjana Bozic^{a,b}, Aleksandra Jelowicka^a, William D. Marslen-Wilson^{a,b,*}

^aMRC Cognition and Brain Sciences Unit, Cambridge, United Kingdom

^bDepartment of Experimental Psychology, University of Cambridge, United Kingdom

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ABSTRACT

Neuroimaging studies of English suggest that speech comprehension engages two interdependent systems: a bilateral fronto-temporal network responsible for general perceptual and cognitive processing, and a specialised left-lateralised network supporting specifically linguistic processing. Using fMRI we test this hypothesis in Polish, a Slavic language with rich and diverse morphology. We manipulated general perceptual complexity (presence or absence of an onset-embedded stem, e.g. *kotlet* 'cutlet' vs. *kot* 'cat') and specifically linguistic complexity (presence of an inflectional affix, e.g. *dom* 'house, Nom' vs. *dom-u* 'house, Gen'). Non-linguistic complexity activated a bilateral network, as in English, but we found no differences between inflected and uninflected nouns. Instead, all types of words activated left inferior frontal areas, suggesting that all Polish words can be considered linguistically 'complex' in processing terms. The results support a dual network hypothesis, but highlight differences between languages like English and Polish, and underline the importance of cross-linguistic comparisons.

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1. Introduction

A critical issue in the study of language as a neurocognitive system has been the role of the left hemisphere, and specifically the left inferior frontal gyrus (LIFG), in the processing of morphology and syntax. Damage to these regions usually leads to significant disruption of language function, while damage to parallel areas in the right hemisphere does not (Goodglass, Christiansen, & Gallagher, 1993). Neuroimaging evidence confirms the importance of these parts of the brain for language processing, and points to a core decompositional network centred on the LIFG (Binder et al., 1997, 2000; Embick, Marantz, Miyashita, O'Neil, & Sakai, 2000; Friederici, Rüschemeyer, Hahne, & Fiebach, 2003; Hagoort, 2005; Marslen-Wilson, & Tyler, 2007; Musso et al., 2003; Tyler et al., 2011; Vigneau et al., 2006). It is argued that this left perisylvian network handles the processing of regularly inflected words (e.g. past tense or plural in English) that can be decomposed into stems and affixes, and are not stored as full forms. However, even very extensive damage to the left hemisphere can leave patients with substantial language comprehension abilities still intact, ranging from the ability to recognise simple spoken words to good comprehension of semantically predictable full sentences (Hagoort, 1997; Longworth, Marslen-Wilson, Randall, & Tyler, 2005; Tyler, Ostrin, Cooke, & Moss, 1995; Tyler et al., 2002, 2011).

This evidence has led to the proposal that two distinct but interdependent processing networks are involved in normal language comprehension – a distributed bilateral system supporting general perceptual and cognitive processing, and a specialised left-lateralised system responsible for processing specifically linguistic features. Bozic, Tyler, Ives, Randall, and Marslen-Wilson (2010) tested this assumption by co-varying the linguistic and non-linguistic complexity of a set of spoken words in an fMRI experiment. Non-linguistic complexity, realised by stem competition between the full form word and onset-embedded stem (e.g. *claim/clay*), activated a bilateral fronto-temporal network, including left and right BA 45 and BA 47. Linguistic complexity, defined here as the presence of a potential regular inflectional morpheme (e.g., real past tense forms, such as *played*, and pseudo-regulars, such as *trade*), activated only left hemisphere inferior frontal areas, peaking in BA 45.

These claims and findings, however, are primarily based on a single language, English, where the contrast between morphologically complex and simple forms has cross-linguistically unusual properties that may have led the neurocognitive processing system to organise itself in ways that are not generally representative. English inflectional morphology is very reduced in scope (with only three regular inflectional affixes¹), and the majority of surface word forms in the language are produced as bare stems (*dog*, *eat*, *elbow*, etc.). This leads to a strong distributional contrast between words that are overtly morpho-phonologically complex (*jumped*,

* Corresponding author at: Neurolex Group, Department of Experimental Psychology, Downing Site, University of Cambridge, Cambridge CB2 3EB, United Kingdom. Fax: +44 (0) 1223 333564.

E-mail address: wdm10@cam.ac.uk (W.D. Marslen-Wilson).

¹ These are the past tense {-d}, the noun plural and verb 3rd person {-s}, and the progressive {-ing}.

eats, etc.) and those that are not. Furthermore, the complex forms typically have just one very frequent affix (such as the past tense {d}) that applies across the board to all eligible stems. This contrasts with a language such as Polish, a member of the Slavic language family, both in the prevalence of morphological complexity and in the richness and diversity of its inflectional system.

Almost all content words in Polish are overtly morpho-phonologically complex, realised within a rich inflectional paradigm. Nouns, which can be divided into three genders, inflect by case and number to give up to 14 possible forms (e.g. *dom* 'house, Nom', *domu* 'house, Gen', *domowi* 'house, Dat', etc.), and similarly for adjectives, numerals and pronouns. The verbal inflectional paradigm includes three tenses, with six person/number categories, as well as gender distinctions for past-tense forms (e.g. *robię* '[I] do'; *robisz* '[you, Sg] do'; *robiłem* '[I] did, Masc'; *robiłam* '[I] did, Fem'; etc.), together with affixes that express mood, voice and aspect. Additionally, verb stems undergo very common regular and irregular alternations (e.g. *złościć* 'to be/make angry': *złoszcz-* / *złości-*; or *trząść* 'to shake': *trzęse-* / *trzęsie-* / *trzęs-* / *trzęś-*; etc.), and fall into at least 9 (Grzegorzczak, Laskowski, & Wrobel, 1999) or 11 (Tokarski, 1973) major inflection classes, most divided into subclasses. Conjugation tables of Polish verbs provide 106 types of conjugational paradigms, many with subtypes (Saloni, 2007). These distributional and morphophonological properties of Polish provide an appropriate set of contrasts for exploring the cross-linguistic validity of the dual processing networks proposed for English. Using the same fMRI testing paradigms, do we see a similar bilaterally distributed system activated by general perceptual processing complexity, coupled with a left lateralised response to specifically linguistic manipulations of morphological complexity?

Polish has benefited from a number of earlier studies looking at morphological processing in adults and children (e.g. Dabrowska, 2004; Reid, Marslen-Wilson, Baayen, & Schreuder, 2003) and in aphasic populations (e.g. Jarema & Kadzielawa, 1987; Ulatowska, Sadowska, & Kadzielawa, 2001), but the most relevant research is that of Jelowicka and colleagues. In a series of studies with fluent and non-fluent Polish aphasics, using the elicitation task (Jelowicka, Bak, Seniow, Czlonkowska, & Marslen-Wilson, 2006; Jelowicka, Bak, Seniow, & Marslen-Wilson, 2007, 2008), Jelowicka showed that non-fluent aphasics – with anterior LH perisylvian damage assumed to involve inferior frontal areas – showed problems primarily with the grammatical properties of stems and inflectional affixes. In contrast, fluent aphasics – with more posterior LH temporal damage – had apparently intact grammatical function, but showed substantial problems in basic operations of stem access. This is broadly consistent with a dual system analysis where stem access is a bilateral temporal function, whereas grammatical processing is more left-lateralised and frontal. However, the studies involved did not contain contrasts directly testing the questions raised here, and they primarily use production tasks. To evaluate Polish in the context of a dual network account, it is necessary to employ contrasts that are directly comparable to those used by Bozic et al. (2010).

The aim of the current study, accordingly, is to investigate the comprehension of morphologically complex words in Polish, asking how far the framework of two interdependent subsystems could be applied to this linguistically much richer and more complex system. To do so, we need to construct, as far as the language permits, equivalent kinds of contrasts to those that allowed us to selectively tap into each subsystem in English. In the English study, specifically linguistic increases in complexity were realised by the presence or absence of a regular inflectional morpheme – for example, the past tense form *played* contrasted uninflected forms such as *learn* or *clean*. This verb-based contrast cannot be transferred exactly into Polish, since all Polish verb forms have an inflectional suffix (marking person, number, tense, etc.). However,

masculine nouns in the nominative case have no overt suffix (e.g. *dom* 'house, Nom'), even though they are suffixed for other cases and in the plural (e.g. *domu* 'house, Gen', or *domy* 'houses, Nom'). This contrast between masculine nominative and case-inflected nouns seems morpho-phonologically parallel to the contrast in English and is what we used in the experiment.

For English, the effects of increased linguistic complexity, driven by the occurrence of an inflectional affix, are strongly left lateralised (Bozic et al., 2010). The contrast between words with and without an inflectional ending produced significant effects only in LIFG, and was restricted to pars opercularis (BA 45). The strong lateralisation of this effect is consistent with a broad range of other studies using neuro-imaging and neuropsychological techniques (Embick et al., 2000; Marcus, Vouloumanos, & Sag, 2003; Marslen-Wilson & Tyler, 2007; Musso et al., 2003; Tyler et al., 2011; Vigneau et al., 2006), although there remains some dispute as to the key LIFG location supporting morphosyntactic functions. Pars triangularis (BA 44) is also implicated in many studies of these functions (e.g., Friederici et al., 2003). In the current context, we expect clear left lateralisation for the linguistic complexity manipulation, but leave open the specific locations in LIFG.

To explore the effects of general perceptual complexity, Bozic et al. (2010) used words with onset-embedded stems, such as *claim*. The conflict between the embedded stem *clay* and the whole word *claim* generated strong bilateral fronto-temporal activity, relative to words like *cream*, which have no embedded stem. In Polish it is again the masculine nominative nouns that allow us to mirror this contrast. Because these forms do not have a suffix, we can construct onset-embedded stimuli which do not additionally contain overt morpho-phonological cues to inflectional complexity – this would potentially obscure the intended contrast with linguistically complex pairs like *dom/domu*. We therefore selected masculine nouns in the nominative case which had onset-embedded stems, where these stems were also masculine nouns in a nominative case (e.g. *kotlet* 'cutlet', where *kot* 'cat', is the embedded stem). To allow possible comparisons between nouns and verbs, and to check that the results are not specific to nouns, we created a similar condition with verbs. Similarly to the nouns, these had uninflected onset-embedded stems (masculine nouns in the nominative), as in stimuli like *kwitnie* '[it] blooms', from *kwitnąć* 'to bloom', with *kwit* 'receipt' as the embedded stem.

In both embedded stimulus sets, following the results reported by Bozic et al. (2010), we expect to see neural activity varying as a function of the degree of competition between the embedded stem and the whole word, where this is expressed as the ratio of the frequencies of the whole word and the embedded stem. For English, effects of stem competition are seen bilaterally in inferior frontal cortex and (at lower thresholds) in superior and middle temporal cortex. The inferior frontal effects were seen primarily in pars orbitalis (BA 47), extending upwards into pars opercularis (BA 45), where they overlapped, on the left, with the effects of linguistic complexity.

To isolate the lexical processing network from lower-level auditory processing, we compared words against musical rain (MR), an acoustic baseline that is closely matched to speech in terms of its temporal envelope and amount of energy, but does not produce the perception of speech (Bozic et al., 2010; Uppenkamp, Johnsrude, Norris, Marslen-Wilson, & Patterson, 2006). Finally, we required a task that engages lexical processing, but at the same time can be applied to baseline non-speech items. Therefore we used passive listening with an occasional one-back memory task. The random distribution of the task trials across the scanning session ensures sustained attention of the participants, and because it is used only on a small number of dummy trials, these can be later removed from the analysis.

2. Methods

2.1. Participants

Twenty-two right-handed (nine male) native speakers of Polish living in the Cambridge area were recruited for this study. They had normal or corrected-to-normal vision, and no hearing, language or neurological impairments. Their age range was 18–33, mean age 25.2 years, their length of stay in the UK ranged from 0 to 45 months, with mean length of stay 18.2 months. They all had at least 11 years of formal education. One participant was later removed from the imaging analyses due to a high ratio of incorrect responses (40%) in the scanner, leaving 21 participants for the analyses.

2.2. Stimuli

There were four experimental conditions, each with 60 items, divided into two pairs of conditions investigating linguistic complexity and perceptual complexity, respectively (see Table 1 for summary and examples).² The linguistic complexity contrast compared simple nouns with inflected nouns. Simple nouns were masculine nouns in the nominative case, ending with a consonant, since these possess no overt case inflection, e.g. *dom* 'house, Nom' or *sklep* 'shop, Nom'. Inflected nouns were masculine nouns in the genitive (25 items), locative (17) or instrumental (18) case (equally distributed across cases: $\chi^2(2) = 1.9, p = 0.39$), e.g. *domu* 'house, Gen' or *sklepem* 'shop, Instr'. These are the three most common cases after nominative and accusative (the accusative could not be used because its forms for masculine nouns often overlap with the nominative case).

The perceptual complexity conditions consisted of a noun set and a verb set. Embedded nouns were masculine nouns in the nominative case, with another masculine noun onset-embedded, e.g. *kotlet* 'cutlet', where *kot* 'cat' is the embedded stem. For the embedded verb condition (also 60 items) we used inflected verbs, with onset-embedded stems, where the embedded stems were masculine nouns in the nominative case, e.g. *kwitnie* '[it] blooms', from *kwitnąć* 'to bloom', where *kwit* 'receipt, Nom' is the embedded stem. In all instances the embedded stems had no semantic relationship with the full form. Items within each set varied in the degree of expected perceptual competition, as a function of the relative frequencies of the embedded stem and the whole word. This allowed the effects of embeddedness to be evaluated using the appropriate parametric modulator based on this frequency ratio.

Simple nouns and inflected nouns were matched on length (number of phonemes and syllables), form and lemma frequency and CV structure, using Match software (Van Casteren & Davis, 2007). The type of analysis used (parametric modulator, and not a subtraction) did not require the embedded conditions to be matched.

All words were recorded in a sound-proof room by a female native speaker of Polish. They were digitised at a sampling rate of 22 kHz with 16 bit conversion, and processed into separate files using CoolEdit.

As an acoustic baseline, allowing us to isolate lower-level auditory processing from lexical processing, we used Musical Rain (Uppenkamp et al., 2006). Musical rain (MR) is produced by disrupting the local spectral (formants) and temporal (pitch) constraints of normal speech. It is not perceived as speech, but is well-matched to speech in terms of its overall energy and long-term spectral and temporal characteristics of speech. The MR items we generated were matched in length to the words.

Table 1

Summary of the stimuli used in the experiment and examples.

Condition	Properties	Number of items	Examples
Simple nouns	– Masculine nouns	60	<i>dom</i> 'house, Nom'
	– Nominative case		<i>sklep</i> 'shop, Nom'
Inflected nouns	– Masculine nouns	60	<i>dom-u</i> 'house, Gen'
	– Genitive, locative or instrumental case		<i>sklep-em</i> 'shop, Instr'
Embedded nouns	– Masculine nouns	60	<i>kotlet</i> 'cutlet, Nom'
	– Nominative case		where <i>kot</i> 'cat, Nom' is the embedded stem
	– Onset-embedded stem		
Embedded verbs	– Inflected	60	<i>kwitnie</i> '[it] blooms', from <i>kwitnąć</i> 'to bloom', where <i>kwit</i> 'receipt, Nom' is the embedded stem
	– Onset-embedded stem		

2.3. Procedure

We used a passive listening paradigm with an occasional one-back memory task (same/different). Words were played every 3.4s, and for 5% of the items (about once a minute) a question appeared on the screen ("Same sound? YES NO") after which the participants answered by button press with their right hand, whether the sound they were currently hearing was the same as the previous one (same = YES, different = NO). There were four blocks of 200 items each (with 10 questions per block), and 5 dummy items at the beginning of each block. There were short breaks between the blocks. The stimuli were delivered using CAST software and NNL Electrostatic headphones. A practice session to familiarise the participants with the task was done outside the scanner prior to the experimental session, using DMDX software (<http://www.u.arizona.edu/~kforster/dmdx/dmdx.htm>).

2.4. Data acquisition and analysis

Scanning was performed on a 3T Trio Siemens scanner at the Medical Research Council Cognition and Brain Sciences Unit (MRC CBU), Cambridge. We utilised a fast-sparse imaging protocol to avoid scanner noise during the presentation of stimuli (fast-sparse gradient-echo EPI sequence: repetition time [TR] = 3.4 s, acquisition time [TA] = 2 s, echo delay time [TE] = 30 ms, flip angle 78°, matrix size 64 × 64, field of view [FOV] = 192 × 192 mm, 32 oblique slices 3 mm thick, 0.75 mm gap). Additionally we obtained T1-weighted structural scans for anatomical localisation.

Pre-processing and analyses of the imaging data were performed using SPM software (SPM5, <http://www.fil.ion.ucl.ac.uk/spm/>). Pre-processing was done using Automated Analysis Recipes (aa, MRC CBU, <http://www.cambridgeuroimaging.com/aa/wiki/>) and included image realignment to correct for movement, segmentation, spatial normalisation of functional images to the MNI reference brain, and smoothing using 10 mm isotropic Gaussian kernel. The data were analysed using the general linear model (GLM), with four blocks and seven event types (four word conditions, MRs, null, and fillers); or for the embeddedness analyses with four event types (embedded words, MRs, null, and fillers) and a parametric modulator for the embedded words. The neural response was modelled with the canonical haemodynamic response function (HRF)

² The experiment contained a further four verb conditions, addressing issues specifically raised by Jelowicka's earlier research. These will be reported elsewhere.

Table 2
Areas of activity for (a) speech-driven lexical processing ('All words – MR'); and (b) the effect of embeddedness (modulation of activity as a function of the degree of lexical competition). We also report significant peaks from the lower threshold ($p < 0.01$), these are marked with an asterisk. [STG – Superior temporal gyrus, MTG – middle temporal gyrus, IFG – inferior frontal gyrus].

Regions	Cluster level		z Score	Peak voxel				
	p corr	Extent		x	y	z		
<i>(a) All words – MR</i>								
L MTG (BA 21)	0.000	4988	7.22	–60	–8	–8		
L MTG (BA 21)			5.96	–62	–34	4		
L Middle Temporal Pole (BA 38)			5.93	–42	20	–28		
L Superior Temporal Pole (BA 38)			5.75	–50	10	–16		
L IFG Pars Orbitalis (BA 47)			4.95	–44	32	–8		
L STG (BA 22)			4.24	–46	–40	8		
L IFG Pars triangularis (BA 45)			4.20	–46	34	6		
R Superior Temporal Pole (BA 38)			0.000	3276	5.85	60	6	–8
R STG (BA 22)					5.78	62	–16	–2
R Superior Temporal Pole (BA 38)					5.57	52	18	–20
R MTG (BA 21)	5.39	56			–26	–2		
L Fusiform Gyrus (BA 37)	0.010	260	4.37	–30	–34	–24		
L Fusiform Gyrus (BA 37)			4.30	–48	–62	–22		
L Fusiform Gyrus (BA 37)			3.43	–38	–46	–20		
<i>(b) Embeddedness</i>								
L STG/MTG (BA 22/21)	0.017	219	4.00	–56	–4	–10		
L MTG (BA 21)			3.93	–62	–4	–8		
L IFG Pars orbitalis (BA 47)*			3.43	–38	30	–12		
L STG (BA 22)			3.35	–48	–10	–2		
L IFG Pars triangularis (BA 45)*			3.29	–44	28	2		
L MTG (BA 21)			3.26	–46	–6	–18		
R MTG/STG (BA 21/22)	0.074	129	3.86	64	–20	–6		
R IFG Pars triangularis (BA 45)*	0.369	328	3.18	58	28	12		
R IFG Pars triangularis (BA 45)*			2.99	58	26	24		
R IFG Pars opercularis (BA 44)*			2.69	62	16	18		

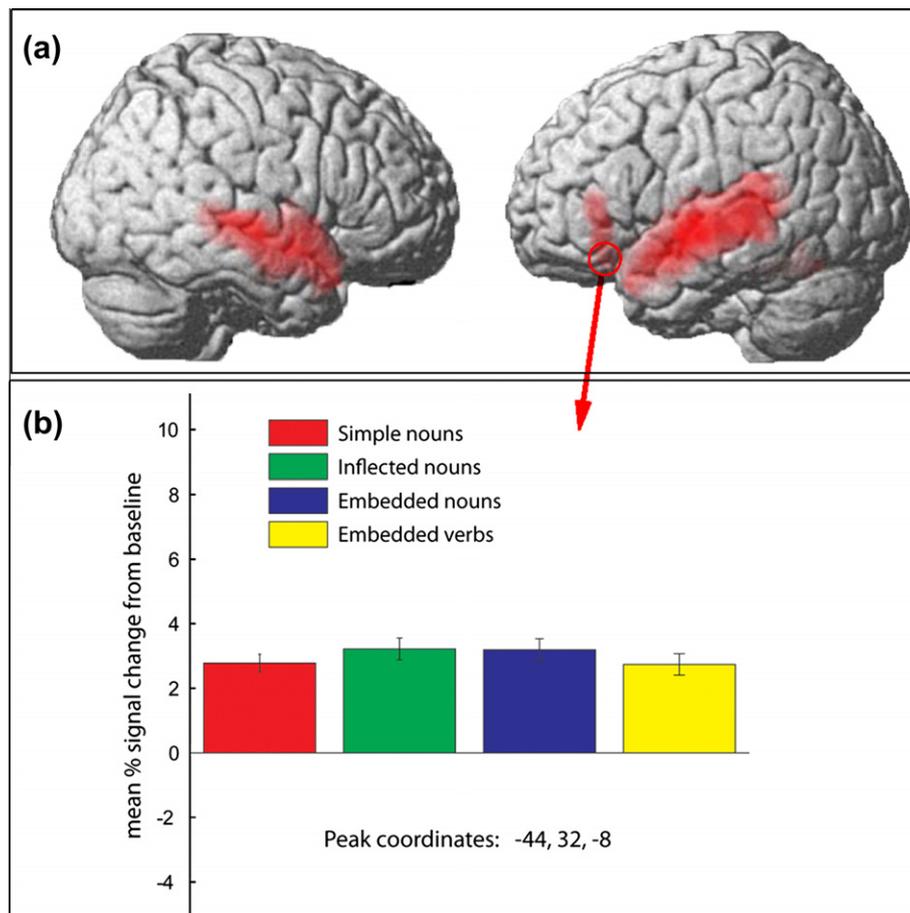


Fig. 1. (a) Significant activation for speech-driven lexical processing (All words – MR). Thresholded at $p < 0.001$ voxel level and $p < 0.05$ cluster level corrected for multiple comparison. Activation shown rendered on the surface of a canonical brain. (b) Signal plot for four word conditions (Simple nouns, Inflected nouns, Embedded nouns and Embedded verbs) in the peak LIFG activation from (a) [peak coordinates: $-44, 32, -8$].

and its temporal derivative. Motion regressors were included to code for the movement effects. A high-pass filter with a 128-s cutoff was used to remove low-frequency noise. For group random effects analysis the contrast images were combined, and the results were thresholded at voxel level $p < 0.001$ (uncorrected) and cluster level $p < 0.05$ (corrected for multiple comparisons), unless otherwise specified.

3. Results

The average ratio of correct responses in the scanner was 93.8%, with mean reaction time 1201 ms ($SD = 331$ ms).

Based on our predictions and on previous research in the field (Binder et al., 1997, 2000; Bozic et al., 2010; Tyler & Marslen-Wilson, 2008), we chose bilateral fronto-temporal areas as the

Table 3

Areas of activity for contrasts (a) 'Simple nouns – MR'; and (b) 'Inflected nouns – MR'. [STG – Superior temporal gyrus, MTG – middle temporal gyrus, IFG – inferior frontal gyrus].

Regions	Cluster level		z Score	Peak voxel		
	<i>p</i> corr	Extent		<i>x</i>	<i>y</i>	<i>z</i>
<i>(a) Simple nouns – MR</i>						
L STG (BA 22)	0.000	5060	7.01	–60	–8	–2
L MTG (BA 21)			5.96	–62	–32	6
L Superior Temporal Pole (BA 38)			5.83	–42	20	–26
L IFG Pars orbitalis (BA 47)			4.49	–36	34	–16
L IFG Pars triangularis (BA 45)			3.48	–44	34	4
R Superior Temporal Pole (BA 38)	0.000	4018	6.33	58	6	–8
R STG (BA 22)			5.86	58	–14	–4
R MTG (BA 21)	0.001	422	5.55	48	–32	2
L Fusiform Gyrus (BA 37)			4.71	–28	–34	–20
L Fusiform Gyrus (BA 37)			4.40	–46	–62	–22
L Fusiform Gyrus (BA 37)			3.83	–40	–48	–18
R Angular Gyrus (BA 39)	0.000	460	4.04	52	–62	24
R Angular Gyrus/MTG (BA 39)			3.86	36	–54	20
L Angular Gyrus/MTG (BA 39)	0.006	271	3.83	–42	–70	24
<i>(b) Inflected nouns – MR</i>						
L MTG (BA 21)	0.000	3382	7.26	–62	–6	–6
L STG (BA 22)			6.10	–62	–36	6
L MTG (BA 21)			5.29	–58	4	–14
L Superior Temp Pole (BA38)			5.20	–54	10	–18
R STG (BA 22)			0.000	2549	5.68	64
R MTG (BA 21)	5.38	60			2	–8
R Superior Temporal Pole (BA 38)	4.74	54			16	–20
R STG (BA 22)	4.73	46			–32	4
R Middle Temporal Pole (BA 38)	0.032	233	4.47	50	18	–24
L IFG Pars orbitalis (BA 47)			3.77	–34	30	–18
L IFG Pars orbitalis (BA 47)			3.75	–42	30	–12
L IFG Pars triangularis (BA 45)			3.59	–44	34	0

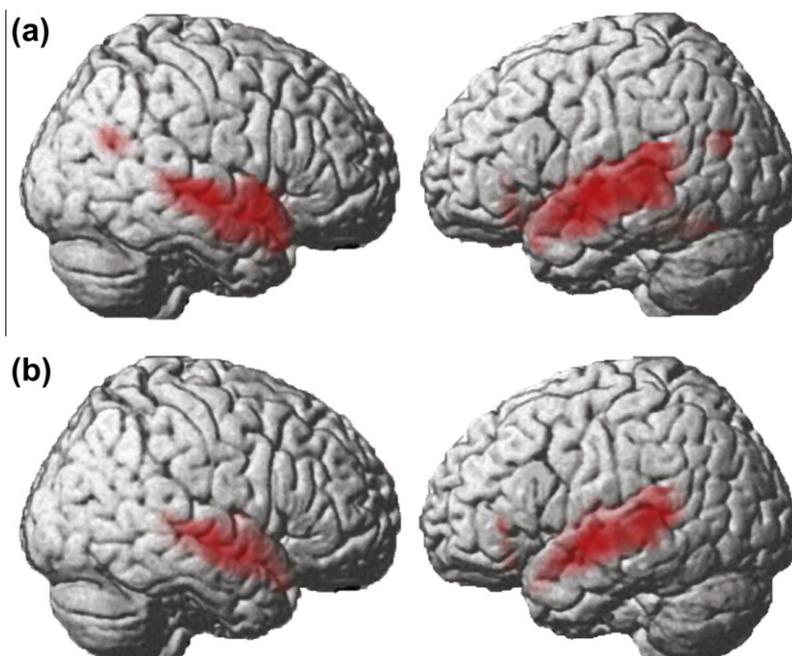


Fig. 2. Significant activations for (a) Simple nouns – MR; and (b) inflected nouns – MR. Thresholded at $p < 0.001$ voxel level and $p < 0.05$ cluster level corrected for multiple comparison. Activation shown rendered on the surface of a canonical brain.

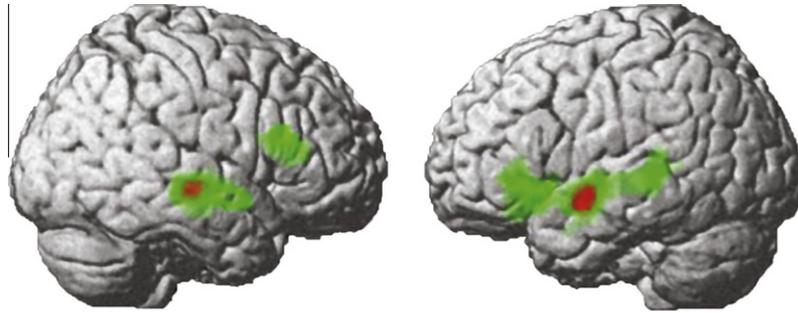


Fig. 3. Significant activations for the effect of embeddedness (modulation of activity as a function of the degree of lexical competition at 0.001 voxel level (in red); and 0.01 voxel level (in green). Activation shown rendered on the surface of a canonical brain.

regions of interest for the analyses. A mask consisting of bilateral temporal lobes (superior, middle and inferior temporal gyri, angular gyrus), inferior frontal gyri (pars orbitalis, pars opercularis, pars triangularis), insula and the anterior cingulate was constructed using WFU Pickatlas.

To establish the network that supports speech-driven lexical processing, we subtracted the MR baseline from all words. This contrast revealed a network spanning left middle and superior temporal gyri, middle and superior temporal poles and inferior frontal gyrus (pars orbitalis and triangularis); on the right middle and superior temporal gyri, and superior temporal pole; and a third cluster located in the left fusiform gyrus (see Table 2a and Fig. 1a). Plots of the activation levels for the four conditions (simple nouns, inflected nouns, embedded nouns and embedded verbs) in the LIFG peak of this analysis show that all conditions activate this area to the same extent (see Fig. 1b).

We then tested activations for simple and inflected nouns. Simple nouns (against MR baseline) activated a large network spanning temporal lobes bilaterally and LIFG (see Table 3a and Fig. 2a). The largest cluster covered left middle and superior temporal gyri, left superior temporal pole, and left inferior frontal gyrus (pars orbitalis and triangularis). The second large clusters included right middle and superior temporal gyri. Three smaller clusters included left fusiform gyrus, left angular gyrus and middle temporal gyrus, and right angular gyrus. Inflected nouns (against MR) activated a very similar network (see Table 3b and Fig. 2b). Two large clusters covered left middle and superior temporal gyri and superior temporal pole; and right middle and superior temporal gyri and middle and superior temporal poles. Additional clusters included left inferior frontal gyrus (pars orbitalis and triangularis). Direct subtraction between these two conditions showed no differences between them.

To test the effects of embeddedness, we determined whether any regions showed modulation of activity as a function of the degree of lexical competition. This was expressed as the ratio of the frequencies of the whole word and the embedded stem (as in Bozic et al., 2010), and entered as a parametric modulator. This analysis, including both embedded nouns and verbs, revealed two significant clusters spanning middle and superior temporal gyri on the left and right (see Table 2b and Fig. 3 in red) (cluster on the right with cluster level $p_{corr} = 0.07$), consistent with the claim of bilateral processing for general perceptual complexity in words with embedded stems. At lower thresholds we also see activation in bilateral inferior frontal areas, specifically pars orbitalis and triangularis on the left, and pars triangularis and opercularis on the right (see Fig. 3 in green).

4. Discussion

In this study we investigated the processing of morphologically complex Polish words, focusing on the framework of two

interdependent subsystems contributing to language comprehension. We asked whether Polish would follow the distinction showed for English (Bozic et al., 2010), where inflectional complexity dissociates from general perceptual complexity, with the two functions supported by dissociable neural systems.

We proposed that words with embedded stems, when compared to simple words, would activate bilateral fronto-temporal areas. These areas support sound-to-meaning mapping and general perceptual complexity demands, here marked by onset-embedded stems competing with the whole words over time as the speech signal unfolds. We found that the bilateral middle temporal gyri showed modulation of activity as a function of the degree of lexical competition between the embedded stem and the whole word. This activation spread to bilateral inferior frontal areas at lower thresholds, involving BA 47 (pars orbitalis) and BA 45 (pars triangularis) on the left, and BA 45 and 44 (pars opercularis) on the right. These findings overlap substantially with those of Bozic et al. (2010), who found bilateral inferior frontal activation (BA 45 and 47) for embedded vs. simple words, extending to bilateral STG and MTG at lower thresholds.

We also predicted increased left hemisphere (especially LIFG) activation for increased linguistically-specific complexity, tested here by comparing case-inflected and simple nouns (e.g. *domu* vs. *dom*). We found no differences between activation patterns for the two types of nouns. Nevertheless, when we look more closely at the activations for both these conditions against the baseline (MR), we see consistent activation of bilateral temporal areas and of LIFG (BA 47 and 45), which is associated with inflectional complexity (see Fig. 2). This suggests that all Polish nouns are treated as inflectionally complex, whether they have an overt affix or not. This would explain why we do not see differences in LIFG activation between case-inflected and simple nouns – nor indeed between the noun conditions and the verb condition (see Fig. 1).

Nouns in English (excluding pronouns) are not morphologically inflected for case (nominative, accusative, etc), so that the lack of a case-marking affix, indicating the grammatical role of the noun in the utterance, is generally not informative about the syntactic and morphological function of the word in question. Polish nouns, in contrast, sit in a rich and productive inflectional paradigm, where the lack of an overt affix is one of many inflectional options and carries specific information about a word's grammatical role. For example, a masculine noun in the nominative (marked by the absence of an overt inflection) is most likely to be the subject of the sentence. If it was the object, or fulfilled some other case role, it would have the appropriate overt inflection. Golka (2009) makes a similar point in a study investigating cues to grammatical status in Polish, concluding that “the null morpheme in Polish is as informative as inflectional endings with respect to the syntactic categorization of nouns” (p. 2).

These considerations suggest that the comparison of simple and case-inflected nouns in Polish does not mirror the English simple

vs. complex (*play* vs. *played*) contrast we used in earlier studies. More generally, however, the finding here of LIFG activation for all conditions, nouns and verbs (see Fig. 1), suggests that Polish behaves similarly to English, with inflectionally complex forms (here all words used as stimuli; in English, only words with an inflectional affix) triggering activity in the core LH perisylvian circuit, but with no corresponding activity in RIFG.

Bozic and colleagues (2010) report left BA 45 as the peak of activity for the inflectionally complex words, while here we find BA 47 and BA 45. While this diverges in part from the Bozic et al. (2010) results, a recent study combining extensive neuropsychological and neuroimaging data (Tyler et al., 2011) also picks out left BA 45 and BA 47 as key areas supporting morphosyntactic function in English. LIFG activation for linguistic complexity has also frequently been reported for BA 44 (e.g., Caplan, Chen, & Waters, 2008; Embick et al., 2000; Friederici et al., 2003; Musso et al., 2003). It is unclear, however, how far these contrasting outcomes are due to cross-linguistic differences and how far to the many methodological differences between these studies.

In summary, this study supports previous evidence indicating a special role for the left hemisphere, and especially LIFG, in the processing of inflectionally complex words. It also agrees with the functional dissociation between bilateral and left-lateralised fronto-temporal subsystems proposed by Bozic et al. (2010). Most importantly, it provides cross-linguistic evidence from a language with a much richer morphological system than English, and without the typological features that make the English system potentially unrepresentative. It suggests that processing of Polish does not differ substantially from English, yet provides some new insights regarding morphological processes that may not operate in English.

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References

- Binder, J. R., Frost, J. A., Hammeke, T. A., Bellgowan, P. S., Springer, J. A., Kaufman, J. N., et al. (2000). Human temporal lobe activation by speech and nonspeech sounds. *Cerebral Cortex*, 10(5), 512–528.
- Binder, J. R., Frost, J. A., Hammeke, T. A., Cox, R. W., Rao, S. M., & Prieto, T. (1997). Human brain language areas identified by functional magnetic resonance imaging. *Journal of Neuroscience*, 17(1), 353–362.
- Bozic, M., Tyler, L. K., Ives, D. T., Randall, B., & Marslen-Wilson, W. D. (2010). Bihemispheric foundations for human speech comprehension. *Proceedings of the National Academy of Sciences of the United States of America*, 107(40), 17439–17444.
- Caplan, D., Chen, E., & Waters, G. (2008). Task-dependent and task-independent neurovascular responses to syntactic processing. *Cortex*, 44(3), 257–275.
- Dabrowska, E. (2004). Rules or schemas? Evidence from Polish. *Language and Cognitive Processes*, 19(2), 225–271.
- Embick, D., Marantz, A., Miyashita, Y., O'Neil, W., & Sakai, K. L. (2000). A syntactic specialization for Broca's area. *Proceedings of the National Academy of Sciences of the United States of America*, 97(11), 6150–6154.
- Friederici, A. D., Rüschemeyer, S.-A., Hahne, A., & Fiebach, C. J. (2003). The role of left inferior frontal and superior temporal cortex in sentence comprehension: Localizing syntactic and semantic processes. *Cerebral Cortex*, 13(2), 170–177.
- Golka, M. (2009). *The role of morphology in on-line speech processing*. Unpublished master's thesis, EHESS-ENS-Paris 5, France.
- Goodglass, H., Christiansen, J. A., & Gallagher, R. (1993). Comparison of morphology and syntax in free narrative and structured tests: Fluent vs. nonfluent aphasics. *Cortex*, 29(3), 377–407.
- Grzegorzczkova, R., Laskowski, R., & Wrobel, H. (Eds.). (1999). *Gramatyka wspolczesnego jezyka polskiego: Morfologia* (3rd ed. Warszawa: Wydawnictwo Naukowe PWN.
- Hagoort, P. (1997). Semantic priming in Broca's aphasics at a short SOA: No support for an automatic access deficit. *Brain and Language*, 56(2), 287–300.
- Hagoort, P. (2005). On Broca, brain, and binding: A new framework. *Trends in Cognitive Sciences*, 9(9), 416–423.
- Jarema, G., & Kadzielawa, D. (1987). Agrammatism in Polish: A case study. *Aphasiology*, 1(3), 223–234.
- Jelowicka, A., Bak, T. H., Seniow, J., Czlonkowska, A., & Marslen-Wilson, W. D. (2006, April). Elicitation, irregularity, and stem change in non-fluent aphasia: Evidence from Polish. Poster presented at the Annual Meeting of the Cognitive Neuroscience Society, San Francisco, CA.
- Jelowicka, A., Bak, T. H., Seniow, J., & Marslen-Wilson, W. D. (2007, July). Stems and affixes in complex word production: Dissociations in Polish aphasia. Poster presented at the Fifth International Workshop on Morphological Processing, Marseille, France.
- Jelowicka, A., Bak, T. H., Seniow, J., & Marslen-Wilson, W. D. (2008, September). Stem and affix processing in Polish aphasics. Poster presented at the 29th Poznan Linguistic Meeting, Poznan, Poland.
- Longworth, C. E., Marslen-Wilson, W. D., Randall, B., & Tyler, L. K. (2005). Getting to the meaning of the regular past tense: Evidence from neuropsychology. *Journal of Cognitive Neuroscience*, 17(7), 1087–1097.
- Marcus, G. F., Vouloumanos, A., & Sag, I. A. (2003). Does Broca's play by the rules? *Nature Neuroscience*, 6(7), 651–652.
- Marslen-Wilson, W. D., & Tyler, L. K. (2007). Morphology, language and the brain: The decompositional substrate for language comprehension. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1481), 823–836.
- Musso, M., Moro, A., Glauche, V., Rijntjes, M., Reichenbach, J., Büchel, C., et al. (2003). Broca's area and the language instinct. *Nature Neuroscience*, 6(7), 774–781.
- Reid, A. A., Marslen-Wilson, W. D., Baayen, R. H., & Schreuder, R. (2003). Lexical representation of morphologically complex words: Evidence from Polish. In R. H. Baayen & R. Schreuder (Eds.), *Morphological structure in language processing* (pp. 287–337). Berlin: Mouton de Gruyter.
- Saloni, Z. (2007). *Czasownik polski: Odmiana, słownik* (3rd ed.). Warszawa: Wiedza Powszechna.
- Tokarski, J. (1973). *Fleksja polska*. Warszawa: Wydawnictwo Naukowe PWN.
- Tyler, L. K., deMornay-Davies, P., Anokhina, R., Longworth, C., Randall, B., & Marslen-Wilson, W. D. (2002). Dissociations in processing past tense morphology: Neuropathology and behavioral studies. *Journal of Cognitive Neuroscience*, 14(1), 79–94.
- Tyler, L. K., & Marslen-Wilson, W. (2008). Fronto-temporal brain systems supporting spoken language comprehension. *Philosophical Transactions of the Royal Society of London: Series B, Biological Sciences*, 363(1493), 1037–1054.
- Tyler, L. K., Marslen-Wilson, W. D., Randall, B., Wright, P., Devereux, B. J., Zhuang, J., et al. (2011). Left inferior frontal cortex and syntax: Function, structure and behaviour in patients with left hemisphere damage. *Brain*, 134(2), 415–431.
- Tyler, L. K., Ostrin, R. K., Cooke, M., & Moss, H. E. (1995). Automatic access of lexical information in Broca's aphasics: Against the automaticity hypothesis. *Brain and Language*, 48(2), 131–162.
- Ulatowska, H. K., Sadowska, M., & Kadzielawa, D. (2001). A longitudinal study of agrammatism in Polish: A case study. *Journal of Neurolinguistics*, 14(2–4), 321–336.
- Uppenkamp, S., Johnsrude, I. S., Norris, D., Marslen-Wilson, W., & Patterson, R. D. (2006). Locating the initial stages of speech-sound processing in human temporal cortex. *NeuroImage*, 31(3), 1284–1296.
- Van Casteren, M., & Davis, M. H. (2007). Match: A program to assist in matching the conditions of factorial experiments. *Behavior Research Methods*, 39(4), 973–978.
- Vigneau, M., Beaucousin, V., Herve, P. Y., Duffau, H., Crivello, F., Houde, O., et al. (2006). Meta-analyzing left hemisphere language areas: Phonology, semantics, and sentence processing. *NeuroImage*, 30(4), 1414–1432.