Short communication

Cortical thickness of planum temporale and pars opercularis in native language tone processing

Andrea Schremm[a],[*], Mikael Novén[a], Merle Horne[a], Pelle Söderström[a], Danielle van Westen[b], Mikael Roll[a]

[a] Department of Linguistics and Phonetics, Lund University, Box 201, 22100 Lund, Sweden
[b] Department of Diagnostic Radiology, Clinical Sciences, Lund University, Box 201, 22100 Lund, Sweden

ABSTRACT

The present study investigated the relationship between linguistic tone processing and cortical thickness of bilateral planum temporale (PT) and pars opercularis of the inferior frontal gyrus (IFGpo). Swedish tones on word stems function as cues to upcoming endings. Correlating structural brain imaging data with participants' response time patterns for suffixes, we found that thicker cortex in the left PT was associated with greater reliance on tones to anticipate upcoming inflections on real words. On inflected pseudoword stems, however, the cortical thickness of left IFGpo was associated with tone-suffix processing. Thus cortical thickness of the left PT might play a role in processing tones as part of stored representations for familiar speech segments, most likely when inflected forms are accessed as whole words. In the absence of stored representations, listeners might need to rely on morphosyntactic rules specifying tone-suffix associations, potentially facilitated by greater cortical thickness of left IFGpo.

1. Introduction

General cognitive abilities have been found to be related to the cortical thickness in associated brain areas (Karama et al., 2009). Similarly, the structure of primary auditory regions in the left hemisphere has been observed to affect non-native lexical tone-learning ability (Wong et al., 2008). To date, however, it is not known how individual differences in brain morphology are related to word tone processing in native speakers. It is difficult to quantify the use of lexical tones in languages such as Chinese, since tones change word meaning like any other phonemes: as a word pronounced with a certain tone pattern is either identified as a specific lexical item or not, variation in tone processing performance beyond word recognition success is not straightforward to observe. In Swedish and Norwegian, however, tones on word stems are associated with suffixes (Riad, 2014). For example, the word *bil* 'car' is pronounced with accent 1 (a low tone) if it appears with the singular suffix -*en*, but with accent 2 (a high tone) if it ends in the plural suffix -*ar*. Accordingly, tones can be used to speed up suffix processing, generating an increased pre-activation negativity (PrAN) in the electrical brain potentials (Roll et al., 2015; Söderström, Horne, Mannfolk, van Westen, & Roll, 2017). PrAN has been found to increase gradually as the number of possible word completions decreased,

suggesting that it reflects predictive activation of memory traces, modulated by the certainty that an upcoming continuation will appear (Söderström, Horne, Frid, & Roll, 2016). Swedish tones are thus not associated with a categorical lexical distinction but with a graded process related to the degree of pre-activation, providing a unique opportunity to quantify the use of tones in native speech comprehension. In an experimental context, if the wrong tone-suffix association is presented, participants would be expected to take a longer time to recognize the suffix the more they rely on the tonal cue to process the ending. Thus, macrostructural differences in auditory association areas in the left planum temporale (PT) region, previously observed to be involved in processing tones on inflected Swedish word stems (Roll et al., 2015), as well as in Chinese and Thai tone processing (Xu et al., 2006), might be expected to be related to performance. Since Swedish speakers have been reported to process most inflected real words similar to monomorphemic ones, i.e. by accessing full forms in the mental lexicon (Lehtonen, Niska, Wande, Niemi, & Laine, 2006), reliance on the tonal cue might depend on the degree to which the tone is incorporated in a whole word representation. In the absence of lexical content, however, participants can be assumed to rely on morphosyntactic rules for stem tone-suffix combinations in order to optimally process inflections, since whole-word representations are unavailable.

That Swedish tones also activate areas associated with the processing of word structure was particularly obvious in a study involving pseudowords, where haemodynamic responses indicated a neural network partially distinct from that observed for real words (Roll et al., 2015), with activation centering around the pars opercularis of the left inferior frontal gyrus (IFGpo) (Söderström et al., 2017). The present study tested the relation between cortical thickness in bilateral PT and IFGpo and native speakers' use of tones for suffix pre-activation in both real words and pseudowords.

Measures of cortical thickness can be obtained by calculating the shortest distance between the white matter surface to the pial surface, constituting the border between the grey matter and the cerebrospinal fluid (Fischl & Dale, 2000). As postulated by the radial unit hypothesis (Rakic, 1988), the human cortex is characterized by a columnar organization, established during embryonic development by migration of cells along radial glial guides towards their final location. Cortical thickness can thus be related to the number and size of neurons within a column (Rakic, 1988). The number and spacing of columns affect cortical surface area instead, implicating area as a distinct feature of cortical structure (Meyer, Liem, Hirsiger, Jäncke, & Hänggi, 2014; Rakic, 1988).

Structural brain imaging data and response time values collected in two previous experiments with two different participant groups, focusing on processing Swedish tone-suffix associations in real words (Roll et al., 2015) as opposed to pseudowords (Söderström et al., 2017), were analysed. In both experiments, test items involved stimuli carrying a singular or plural suffix, which was either validly cued by its preceding associated tone or invalidly cued by a tone associated with a different suffix. A relative increase in response time from validly to invalidly cued suffixes can be assumed to reflect the degree to which the perceived ending disconfirmed the tone-induced prediction: the more the listener anticipated the validly cued number inflection based on the stem tone, the greater the expected processing cost for the invalidly cued suffix. In the present study, we investigated the association between response times and cortical thickness of bilateral PT and IFGpo. It was hypothesized that greater reliance on tonal cues on real words, when tonal patterns are incorporated into whole word representations, would be associated with variation in cortical thickness in left PT, in accordance with the central role of this area in tone processing in Swedish words (Roll et al., 2015). Pseudowords, however, do not have any existing word representations, and therefore their processing cannot rely on a tone-word form association. Since the experimental task involved a decision between singular versus plural meanings carried by inflectional suffixes but did not require interpretation of the meaning of target word stems, response times are not assumed to primarily reflect different semantic processing of real words and pseudowords due to the presence versus absence of familiar semantic content. Instead, pseudoword response time patterns would rather depend on the efficiency of tone-induced morphosyntactic rule application. Decompositional morphosyntactic processes underlying the extraction and interpretation of regular inflectional affixes seem to rely on an intact left inferior frontal gyrus (IFG) (Bozic, Fonteneau, Su, & Marslen-Wilson, 2015). Generally, the left IFG has been argued to function as a unification space, maintaining fragments of syntactic, semantic and phonological information retrieved from memory and assembling these into coherent representations. Unification processes are assumed to take place even below the phrasal level, by which word forms are composed from and decomposed into stem and affix parts (Hagoort, 2013). Previous studies indeed found areas of left IFG, specifically the pars opercularis or pars triangularis, to be crucially involved in inflectional morpheme processing (Bozic et al., 2015; Tyler, Stamatakis, Post, Randall, & Marslen-Wilson, 2005). The present study focuses on the IFGpo, the area that showed strong activation for processing inflected Swedish pseudowords (Söderström et al., 2017).

In order to develop an expectation for the direction of the relationship between tone processing and cortical structure, electrophysiological measurements obtained in Roll et al. (2015) as well as Söderström et al. (2017) were related to cortical thickness values (Supplementary material). As mentioned above, greater tone-induced suffix pre-activation was associated with an increased negativity in the electrical brain response in these studies. Electrophysiological measurements rely on synchronous firing of neurons; thus, increased electrophysiological signal might conceivably be generated by a larger number of neurons within a thicker cortex, or alternatively by more synchronized activity of neurons in a fine-tuned network of a thinner cortex (Liem, Zaehle, Burkhard, Jäncke, & Meyer, 2012). The present analysis indicated that an increased pre-activation negativity for real words tended to be associated with thicker cortex in the left PT. We therefore predicted a positive association between tone processing performance and cortical thickness in the present study. As a complementary measurement to cortical thickness, surface area of bilateral PT and IFGpo was also related to tone processing performance in a supplementary analysis (see Supplementary material).

2. Results

2.1. Real word processing

Individual participants' RT advantage for valid over invalid suffixes showed a significant positive correlation with average cortical thickness in the left PT ($r = .559$, $p = .030$), indicating that the thicker the cortex in left PT, the greater was the RT increase for invalidly cued suffixes (see Fig. 1). Cortical thickness in the left IFGpo did not correlate with RTs ($r = .134$, $p = .634$). No significant correlation was obtained between RTs and right PT ($r = .197$, $p = .481$) or right IFGpo ($r = −.097$, $p = .732$).

Participants responded significantly faster ($t(14) = 7.348$, $p < .001$) to validly ($M = 584$ ms, $SD = 172$) as compared to invalidly ($M = 656$ ms, $SD = 174$) cued suffixes. As a follow-up analysis, participants were divided into two groups of equal size (n = 7) based on their mean cortical thickness in the left PT, resulting in a relatively thinner (2.117–2.465 mm) and a relatively thicker cortex group (2.590–2.912 mm). An independent-samples t-test conducted on average RT speed for validly cued suffixes indicated marginally faster RTs ($t(12) = 1.813$, $p = .054$) for the thicker PT cortex group ($M = 504$ ms, $SD = 89$) as compared to the thinner PT cortex group ($M = 664$ ms, $SD = 215$).

2.2. Pseudoword processing

There was a significant positive correlation between RT advantage for validly versus invalidly cued suffixes and average cortical thickness of the left IFGpo ($r = .492$, $p = .045$) (see Fig. 2). No significant correlation was obtained between RTs and left PT ($r = .071$, $p = .787$). There was no significant correlation between RTs and cortical thickness in right PT ($r = .135$, $p = .606$) or right IFGpo ($r = .303$, $p = .237$).

RTs were significantly faster ($t(16) = 6.497$, $p < .001$) to validly cued suffixes ($M = 888$ ms, $SD = 258$) than to invalidly cued suffixes ($M = 979$ ms, $SD = 232$). Subsequently, a relatively thinner cortex group (2.426–2.742 mm, n = 8) and a relatively thicker cortex group (2.758–2.992 mm, n = 8) were created based on participants' average cortical thickness in the left IFGpo. Results of an independent-samples t-test showed significantly faster RTs to validly cued suffixes ($t(14) = 1.926$, $p = .039$) in the thicker cortex group ($M = 763$ ms, $SD = 288$) relative to the thinner cortex group ($M = 997$ ms, $SD = 188$).

3. Discussion

Results indicated a relationship between linguistic tone processing in native speakers and cortical thickness of specific brain areas assumed to subserve these processes. Tones in Swedish are realized on word
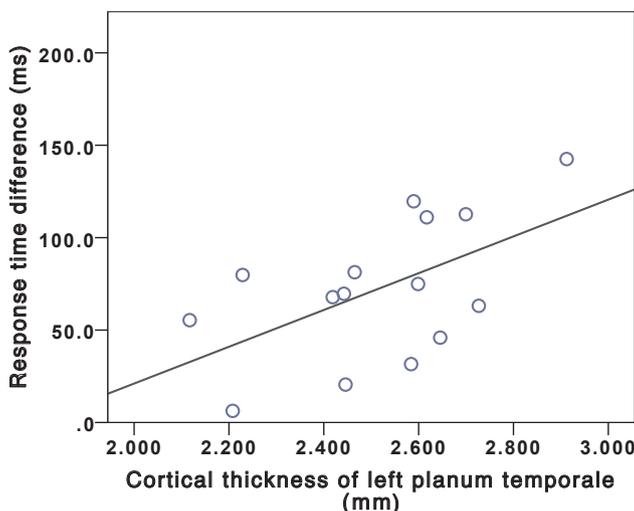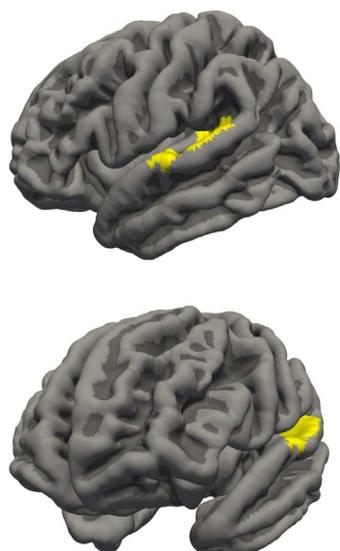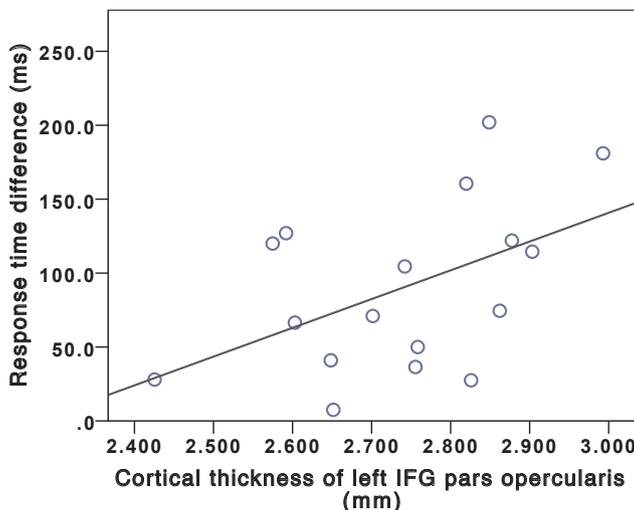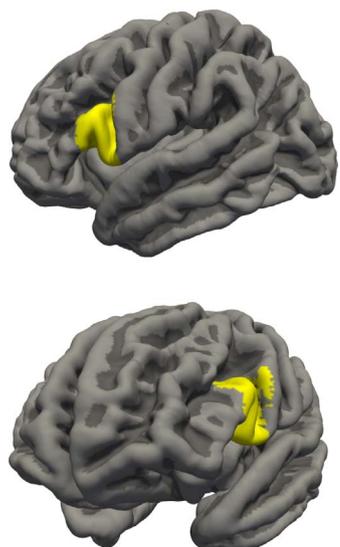
Fig. 1. Cortical thickness of left planum temporale and tone processing in real words. Left planum temporale presented on the pial surface of Freesurfer common space object fsaverage (left). Correlation between cortical thickness of left planum temporale and response time difference between suffixes invalidly vs. validly cued by the preceding tone ($r = .559$), indicating that the greater the response time increase was for invalidly cued suffixes on real word stems, the thicker the cortex was in the left planum temporale (right).

stems, and like lexical tones, are modulated by PT in the left hemisphere (Moen, 1993; Roll et al., 2015). Swedish tones function as cues to upcoming suffixes, and thus they engage left frontal cortical areas implicated in regular inflectional morpheme processing as well (Bozic et al., 2015; Tyler et al., 2005), with left IFGpo emerging as the major site of activation when tone-suffix connections were implemented on meaningless pseudowords (Söderström et al., 2017). In the present study, the degree to which listeners relied on tones to anticipate morphosyntactic structure was quantified by measuring the relative response time increase for invalid tone-suffix associations. Results showed that the thicker the cortex was in the left PT, the greater the RT increase was for invalidly cued suffixes on real words. No such correlation was found for inflected pseudowords, where larger RT increase for invalidly cued suffixes was instead associated with greater cortical thickness of left IFGpo.

These findings suggest that relatively greater cortical thickness of left PT is related to tonal cue processing, in ways specific to familiar lexical items. Furthermore, the same area showed functional activation for tone processing in the same subjects (Roll et al., 2015). Indeed, regions of the posterior superior temporal gyrus (STG) have been implicated in higher-level processes of acoustic analysis during speech perception (Chang et al., 2010; Xu et al., 2006) and left PT has been found to respond to phonemic changes in the native language

(Jacquemot, Pallier, LeBihan, Dehaene, & Dupoux, 2003). The present findings indicate that the nature of the representations involved in processing related to the cortical thickness of left PT might correspond to linguistic units larger than phonemes, since the pseudowords tested consisted of Swedish phonemes, just like real word stimuli. For instance, one might assume that listeners develop memory traces for frequently occurring patterns such as syllables, supporting rapid analysis of native language input. This would constitute an important difference between the target words of the two experiments as none of the pseudoword stem syllables used in the stimulus material appeared in any real Swedish words. Thus, cortical thickness of left PT might play a role in decoding the speech signal in terms of chunks larger than phonemes – possibly syllables – incorporating tonal information in Swedish, when linguistically relevant tone patterns are processed as part of a left-lateralized network. From this perspective, the cortical thickness of left PT might be related to the efficiency with which tonal information is accessed and, in turn, tone-associated endings are subsequently pre-activated on real words, by supporting recognition of familiar sound patterns involving tones. In line with this assumption, cortical thickness of left PT was associated not only with the degree to which listeners used tonal information to activate real words but also, for the subgroup of participants with relatively thicker left PT cortex, showed a tendency to be related to faster suffix recognition as

Fig. 2. Cortical thickness of left inferior frontal gyrus (IFG) pars opercularis and tone processing in pseudowords. Left IFG pars opercularis presented on the pial surface of Freesurfer common space object fsaverage (left). There was a positive correlation between cortical thickness of left IFG pars opercularis and response time advantage for validly over invalidly cued suffixes on pseudoword stems ($r = .492$) (right).

compared to the subgroup with thinner left PT cortex.

Swedish word accents are realized over several segments, in terms of relative alternations in fundamental frequency, constituting slowly changing acoustic features as compared to consonant transitions. According to the AST hypothesis (Poeppel, 2003), the duration of the integration windows used to chunk the incoming speech signal in non-primary auditory areas of the left hemisphere is around 20–50 ms, underlying sensitivity to fast changing segmental information, such as consonant transitions. Slower, 150–250 ms time windows in the right hemisphere efficiently capture suprasegmental information in the speech signal, including tones and intonation. In line with this proposal, gradually decreasing the integrity of slowly changing acoustic information in the speech input was reported to shift lateralization in the PT to the right hemisphere (Liem, Hurschler, Jäncke, & Meyer, 2014).

Harasty, Seldon, Chan, Halliday, and Harding (2003) suggested that an expansion of the cortex in the left PT, possibly driven by an increase in the underlying white matter volume, could account for the well-established leftward macrostructural asymmetry of the PT. The expansion resulted in a larger surface area but thinner cortex on the left relative to smaller surface area but thicker cortex on the right (Harasty et al., 2003). Larger surface area of the left auditory-related region has been associated with the left-hemispheric advantage for rapid acoustic analysis: in the expanded cortex, the distance between neuronal columns might be greater and dendritic trees less overlapping. In such an organization, columns might be able to function more independently, performing finely differentiated processing of the incoming auditory signal (Harasty et al., 2003; Meyer et al., 2014). Conversely, greater overlap among columns in the relatively thicker right hemisphere could result in more holistic and temporally coarse-grained analysis (Harasty et al., 2003).

Thus, auditory-related regions of the right hemisphere might be fine-tuned for processing the kind of spectral information that differentiates Swedish word accents. Nevertheless, due to their strong integration in a left-lateralized morphosyntactic system, word accents appear to be processed predominantly on the left side (Roll et al., 2015). The AST hypothesis conceptualizes hemispheric differences regarding temporal resolution as a relative phenomenon, since both hemispheres are assumed to contain neuronal populations underlying different, shorter or longer, integration windows (Poeppel, 2003). Therefore, one might speculate that the prevalence of neural organization in the left PT tuned to slower acoustic cues – otherwise more typical of the right hemisphere homologue – is somewhat greater in those with thicker left PT cortex in the present study, resulting in more efficient left-hemispheric processing of tonal information, and, in turn, facilitated access to word forms with endings cued by the stem tone. Previous results reporting a positive association between cortical thickness of the right auditory areas and relative pitch task performance (Foster & Zatorre, 2010) indicate that structural variation associated with the ability to analyse slower acoustic cues might be picked up by cortical thickness measurements.

Although pseudoword stems tested in the present study could not be processed in terms of familiar syllables, tones realized on such stems still pre-activated suffixes. This was reflected in an increase in RTs for invalidly cued endings relative to validly cued continuations. Moreover, tones on pseudowords were observed to generate an increased pre-activation negativity (PrAN) in the electrical brain signal (Söderström et al., 2017). The correlation found here between tone processing and cortical thickness of left IFGpo, a region associated with morphosyntactic analysis among other functions (Bozic et al., 2015; Tyler et al., 2005), might indicate the involvement of a morphosyntactic rule underlying the pre-activation process. Haemodynamic responses of the same participants also indicated strong functional activation of left IFGpo during pseudoword processing (Söderström et al., 2017). From this perspective, cortical thickness of left IFGpo could be assumed to play a role in facilitated pre-activation of suffixes, through efficient application of the morphosyntactic rule specifying the relevant tone-

suffix associations, subsequently speeding up the processing of an expected ending in the input. Also, strong pre-activation of the anticipated inflection might even support rapid morphological decomposition of pseudowords into stem and suffix parts, by providing reliable cues to stem boundaries in items for which no stored lexical representations exist. Such processes can be assumed to be essential for interpreting the pseudoword forms tested, since the task crucially depended on the ability to extract the number inflection from the otherwise meaningless string of segments. The subgroup with thicker cortex in left IFGpo was indeed generally faster at responding to validly cued suffixes than the thinner cortex group.

As is the case with PT, leftward asymmetry of IFGpo has been reported; however, its relation to functional language lateralization is far from clear (Keller, Crow, Foundas, Amunts, & Roberts, 2009), and it is difficult to speculate how thicker cortex in this area might support inflected pseudoword processing. Based on the discussion above, facilitated responses to word endings were presumably based on an abstracted connection between tone patterns and suffixes, implicating some form of higher level processing of the input. This might be related to previous results showing a positive connection between cortical thickness in association areas and performance of higher-level cognitive skills assumed to underlie general intelligence (Karama et al., 2009).

No significant relation was found between cortical thickness in the left PT and tone processing on pseudowords. Nevertheless, smaller cortical surface area in the left PT was associated with greater response time increase from validly to invalidly cued suffixes on pseudowords, suggesting increased reliance on tonal cues to anticipate upcoming endings (Supplementary material). This was the only significant correlation obtained with surface area in the present study, which might be assumed to reflect in part the contribution of left PT to the prelexical processing of linguistically relevant tones (Xu et al., 2006) since effective recognition and discrimination of tonal patterns necessarily precedes activation of the cued morphosyntactic information. This result is in line with the suggestion that a neural organization associated with a relatively smaller surface area, and in turn with greater overlap between cortical columns, might be especially adapt at decoding suprasegmental information (Harasty et al., 2003). The fact that no significant relationship was observed with surface area in the real word experiment could be taken to indicate certain differences in the specific cortical features of the left PT that are associated with facilitated tone processing on real words versus pseudowords. Based on the discussion above, this difference could be tentatively related to the presence versus absence of stored memory representations for syllables or whole words, which include the stem tone.

The fact that no correlation was found between cortical thickness of left IFGpo and tone processing on real words could be taken to indicate that morphosyntactic regularities and decompositional processing might play a smaller role in suffix pre-activation on familiar word stems. One possible explanation is that more than one route is available for the predictive processing of tones on inflected words. This would be in line with dual-system models distinguishing between two mechanisms for the production and comprehension of morphologically complex items (Pinker & Ullman, 2002): through decomposition into stem and affix parts based on the application of productive morphosyntactic rules, which combine morphemes into complex words, or by direct access to whole-word representations of inflected forms in the mental lexicon. The decompositional route is argued to be implemented in a fronto-striatal brain network whereas whole-word access has been associated with a largely temporal system (Ullman, 2004), which is consistent with the frontal versus temporal distinction found in the present study.

Since different individuals were tested in the real word and the pseudoword experiment, one cannot exclude the possibility that the present results might in fact to some degree reflect anatomical variations between the groups. Also, these findings do not enable us to determine the source of the observed variation in cortical thickness across

participants, which might reflect genetic, environmental and/or experiential influences (e.g. Chiarello, Vazquez, Felton, & McDowell, 2016; Panizzon et al., 2009), including adaption to the demands of processing linguistic tones in the native language. Longitudinal studies involving focused training in word accent processing and tracking associated changes in cortical thickness and surface area could, therefore, further clarify the role the cortical structure of PT and IFGpo plays in linguistic tone processing.

In conclusion, the present results indicate that individual differences in the cortical structure of left PT as well as left IFGpo might be related to word tone processing in native speakers. The role of these brain regions seems to be modulated by the presence versus absence of lexical content in incoming speech, suggesting that the cortical thickness of left PT might influence processing when tones are accessed as part of stored representations for familiar speech sound sequences, potentially corresponding to whole-word forms, whereas the cortical thickness of left IFGpo might play a greater role during rule-based processing of regularly inflected items.

4. Method

4.1. Participants

As the research question of the present study focused on the relationship between the degree of predictive tone processing and cortical structure, participants who did not show a response time advantage for validly cued suffixes, indicating that they did not use tones predictively during the experimental task, were excluded from the present analysis ($n = 3$ in the real word experiment and $n = 2$ in the pseudoword experiment). Thus, data obtained with 15 native speakers of Central Swedish (7 females, mean age: 25.4 years, $SD = 5.2$) participating in the real word experiment, as well as data from 17 native speakers of Central Swedish (11 females, mean age: 24.9 years, $SD = 4.0$ participating in the pseudoword experiment were analysed.

4.2. Stimuli and procedure

There were two experimental conditions, valid and invalid tone-suffix association. In the valid condition, word accents on the stem validly cued their associated suffix, i.e. accent 1 was followed by the singular suffix and accent 2 was followed by the plural suffix. In the invalid condition, the stem tone-suffix combinations were invalid, i.e. accent 2 on the stem preceded the singular suffix and accent 1 preceded the plural suffix. The word stem was always a monosyllabic Swedish word in the real word experiment (e.g. Valid: *hatt*$_{Accent\ 1}$+*en*, 'hat+sg'; Invalid: ∗*hatt*$_{Accent\ 1}$+*ar*, 'hat+pl'), and a meaningless, but phonotactically legal, pseudoword (pseudoword stem+suffix) in the pseudoword experiment (e.g. Valid: *kvut*$_{Accent\ 1}$+*en*, 'kvut+sg'; Invalid: ∗*kvut*$_{Accent\ 1}$+*ar*, 'kvut+pl'). Target words were placed in carrier sentences with identical structure, e.g. *Kurt fick [target word] till jul,* 'Kurt got [target word] for Christmas'. Stimulus material preparation involved the same recording and splicing procedures for both experiments. Sentences were presented auditorily and participants' task was to decide, as quickly as possible, if the person mentioned in the sentence received one or many things, by pressing a button. Response times were measured from suffix onset. In the real word experiment, there were 60 different target words (30 different lexical words presented once in singular, once in plural) in each of the two experimental conditions. In the pseudoword experiment, each of the experimental conditions consisted of 80 different target words (40 lexical words presented once in singular, once in plural). For more details, see Roll et al. (2015) and Söderström et al. (2017).

4.3. MRI

T1-weighted MPRAGE MRI scans were collected on Magnetom

Siemens 3T Skyra (real word experiment) and Prisma (pseudoword experiment) systems (TR/TE/TI 1900/2.54/900 ms, 1 mm³ isovoxel, 256 × 256 matrix, 176 slices, flip angle 9°). Cortical reconstruction and volumetric segmentation were performed with the Freesurfer image analysis suite (Dale, Fischl, & Sereno, 1999). Masks of PT and IFGpo were taken from the probabilistic Harvard-Oxford Cortical Structure Atlas in FMRIB Software Library thresholded at 20 and 15, respectively. The value in a point in the atlas corresponds to the probability of that point being included in the anatomical structure of interest based on expert raters in studies involving cortical parcellation (Desikan et al., 2006). Mask thresholds were chosen generously to account for individual differences in patterns of cerebral gyri (see Figs. 1 and 2). Mean cortical thickness of the PT and IFGpo masks were extracted using Freesurfer tool mri_segstats.

4.4. Response times

Correlation analyses were performed relating individual participants' mean cortical thickness values in the left PT as well as in the left IFGpo masks to their response time (RT) differences between validly versus invalidly cued suffixes. Results were statistically evaluated using one-tailed t-tests with Bonferroni-corrected p-values for multiple comparisons. Invalid minus valid RT difference was also correlated with the right PT and right IFGpo in a separate analysis.

Statement of significance

We found a relationship between the cortical thickness of specific language-related brain areas and the performance of certain associated native language processing skills. Whole word access versus decompositional processing seems to modulate involvement of the left planum temporale and IFG pars opercularis, in line with dual-route models of morphosyntactic processing.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.bandl.2017.12.001.

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