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Tone-grammar association within words: Concurrent ERP and fMRI show rapid neural pre-activation and involvement of left inferior frontal gyrus in pseudoword processing

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ABSTRACT

Using a concurrent ERP/fMRI paradigm, we investigated how listeners take advantage of morphologically relevant tonal information at the beginning of words to predict and pre-activate likely word endings. More predictive, low tone word stems gave rise to a 'pre-activation negativity' (PrAN) in the ERPs, a brain potential which has previously been found to increase along with the degree of predictive certainty as regards how a word is going to end. It is suggested that more predictive, low tone stems lead to rapid access to word endings with processing subserved by the left primary auditory cortex as well as the supramarginal gyrus, while high tone stems – which are less predictive – decrease predictive certainty, leading to increased competition between activated word endings, which needs to be resolved by the left inferior frontal gyrus.

1. Introduction

In spoken language processing, listeners take advantage of information at the beginning of words to pre-activate likely word endings (Breen, Dilley, McAuley, & Sanders, 2014; Cutler & Otake, 1999; Marslen-Wilson, 1987; Roll et al., 2015; Söderström, Horne, Frid, & Roll, 2016). In Swedish, a language with tones, tonal information can be used to access lexical and grammatical information. The tones in Swedish are associated with word stems, and are used to predict and access possible continuations following the word stem. It has been suggested that this morphophonologically driven predictive mechanism is reflected in the 'pre-activation negativity' (PrAN), a fronto-temporal event-related potential (ERP) which begins at around 100 ms after onset of a predictive cue (such as a word stem with a tone). PrAN amplitude correlates inversely with the number of possible word ending types a word stem cues (Söderström et al., 2016). Thus, it is suggested that the probabilistic pre-activation of likely endings is facilitated when fewer possible continuations enter into competition when the word stem is being processed. It has previously been found that lexical access in morphologically complex words is modulated by the probability of encountering a suffix given a particular stem (Solomyak & Marantz, 2010). Furthermore, the morphological structure of words has been observed to influence auditory word recognition and aid rapid prediction of phonemes (Ettinger, Linzen, & Marantz, 2014). Thus, the processor can be claimed to take advantage of statistical regularities inherent in the association between stem tones and suffixes in Swedish, so that more predictive word stems can be assumed to create stronger expectations about and pre-activate upcoming word endings. Less predictive stems are expected to give rise to an increase in competition between different endings. However, it is still not clear whether the mechanisms indexed by PrAN are only sensitive to lexical properties of word stems, or also to the morphophonological tone-suffix association modulating the predictability of upcoming word continuations. In the present study, we attempted to isolate the abstract connection between stem tones and suffixes, aiming to determine whether PrAN would still be elicited in the absence of lexical information on the stem, and to investigate the neural underpinnings of this effect. To achieve this, we used semantically empty pseudoword stems with different tonal patterns, connected to existing singular or plural suffixes, to see whether and how different stem tones function to pre-activate possible endings when the only linguistic cue the processor has to work with is the morphophonological connection between word stem tones and possible endings. In addition to using pseudoword stems, some test words had endings masked by light coughs, allowing us to see whether participants, using only the stem tone, could predict the meaning of a suffix even when it has been replaced by a cough. In order to investigate the

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mechanisms reflected in the pre-activation negativity, we took advantage of the excellent temporal resolution of ERPs as well as the spatial resolution of functional magnetic resonance imaging (fMRI) in a concurrent experimental paradigm.

In Swedish, each word stem (such as *båt*, 'boat') is associated with either a low tone (known as 'accent 1') or a high tone ('accent 2'). The tone associated with the stem is dependent on the word's ending. For example, if the singular suffix *-en* is connected to the word stem *båt*, forming the inflected word $båt_L$*-en*, 'boat' SG DEF, the stem is pronounced with a low (L) tone, while the plural suffix *-ar* induces a high tone (H) onto the stem ($båt_H$*-ar*, 'boat' PL INDEF). Furthermore, all productive compounds have a high tone on the initial morpheme. As such, the high tone is a cue signalling that at least one more syllable will follow, such as the head of a compound of any length ($båt_H$*-hus*, 'boat house', $båt_H$*-hus-brand*, 'boat house fire', etc.). This also holds if the word stem or constituent is a loan word, such as *chatt* ('chat room'), giving rise to compound words such as $chatt_H$*-diskussion* ('chat room discussion'). Consequently, since monosyllabic stems with no ending are automatically associated with the low accent 1 tone, this tone always cues a smaller number of possible word forms while the high accent 2 tone cues more possible continuations (such as compounds). Using a lexicon database, Söderström et al. (2016) found that high stem tones cue almost 11 times as many possible continuations, the majority being compounds. Another way of putting this is in terms of *entropy*, defined as a function of the distribution of probabilities of all upcoming items (Willems, Frank, Nijhof, Hagoort, & van den Bosch, 2016). Thus, high stem tones give rise to high entropy – being associated with a larger number of possible upcoming word endings – while low stem tones are associated with lower entropy, leading to greater certainty about upcoming word endings. In Ettinger et al. (2014), it was proposed that low entropy at the onset of morphologically complex words increases neural activity in e.g. transverse temporal gyrus in primary auditory cortex, while high entropy – in the case of less predictive word stems – prompts the parser to delay predictive processes until entropy has been reduced.

All previous ERP studies on Swedish word tones have found greater negativities for low stem tones as compared to high stem tones. Testing the hypothesis that the predictive relationship between stem tone and possible endings should be reflected linearly in PrAN amplitude, Söderström et al. (2016) found that word stems which cue fewer possible continuations indeed elicit greater pre-activation negativities, providing strong support for the idea that the effect is sensitive to the number of possible continuations of a word stem, and that it possibly indexes some type of probabilistic pre-activation of likely word endings. In support of this account, it has been found that unexpected word endings lead to N400 (Kutas & Hillyard, 1980) and P600 (Osterhout & Holcomb, 1992) effects (Gosselke Berthelsen, Horne, Brännström, Shtyrov, & Roll, 2017; Roll, 2015; Roll, Horne, & Lindgren, 2010; Roll, Söderström, & Horne, 2013; Roll et al., 2015; Söderström, Horne, & Roll, 2017), both of which have recently been suggested to reflect decision certainty and revision processes associated with disconfirmed predictions (Droge, Fleischer, Schlesewsky, & Bornkessel-Schlesewsky, 2016; Hinaut & Dominey, 2013; Rabovsky & McRae, 2014).

In a previous ERP/fMRI study using existing words as test stimuli (Roll et al., 2015), PrAN appeared to be composed of an earlier component with temporo-parietal topography and a later part with a more frontal distribution. PrAN amplitude in the early time window correlated most strongly with blood-oxygen-level dependent (BOLD) activity in the left anterior transverse temporal area, Brodmann area (BA) 41, as well as in the superior temporal gyrus, BA22, indicating a strong connection between tones and word forms, and possibly reflecting increased neural activity to lower entropy, as proposed in Ettinger et al. (2014). In the case of existing words, it is possible that frequent combinations of stem and suffix are stored and accessed as whole-word items. However, it is not obvious how the pre-activation of word continuations occurs when there are no stored whole-word representations that can be accessed from long-term memory, i.e. when new words or pseudowords are processed. The present study aimed to isolate the pre-activation mechanism driven by the purely formal morphophonological association between stem tones and endings. In the absence of stored whole-word representations, the hypothesis was that the proposed pre-activation of word endings would be more dependent on the morphophonological structure of the words. Specifically, items with greater predictive potential as regards possible continuations (low tone stems) could be assumed to have stronger associations in memory to word endings such as suffixes. We thus hypothesised that more predictive stem tones (in this case, low (accent 1) tones) would be processed via a more direct association with suffix representations in the temporal lobes, including primary auditory cortical areas (e.g. BA41 (Ettinger et al., 2014; Jacquemot, Pallier, LeBihan, Dehaene, & Dupoux, 2003)) as well areas in the inferior parietal lobe such as the supramarginal gyrus suggested to be involved in e.g. the activation of likely upcoming word endings (Roll, Söderström, Frid, Mannfolk, & Horne, in press). On the other hand, less predictive stem tones (i.e. high (accent 2) tones) could lead to increased processing in prefrontal areas. Specifically, activation of frontal areas for high stem tones would be expected since these stems lead to greater lexical competition that needs to be suppressed and resolved before the ending can be accessed and the word can be fully processed (Blumstein, 2009; Righi, Blumstein, Mertus, & Worden, 2010; Söderström et al., 2016; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Thompson-Schill, D'Esposito, & Kan, 1999; Thompson-Schill et al., 1998).

2. Materials and methods

2.1. Stimuli

The stimuli used in the present study were recorded by a male Central Swedish speaker in an anechoic chamber. The stimuli were pseudoword stems with either a low or high tone followed by either singular or plural suffixes, or a light cough (e.g. $kvup_L$*-en*, 'kvup' SG DEF, $kvup_H$*-ar*, 'kvup' PL INDEF or *kvup-COUGH*). These words were embedded in carrier sentences such as *Rut fick kvupen/kvupar till* ***lunch*** ('Rut got the kvup/kvups for **lunch**'). Sentence focus was on the final word so that the test stimuli could be produced with non-focal word accents. Participants were asked to judge as quickly as possible whether the person in the sentence got one (singular) or many (plural) thing(s). Since low tones are associated with singular endings and high tones with plural endings, the correct response for the cough condition was "singular" for low tones followed by a cough, and "plural" for high tones, i.e., assuming that the stem tone pre-activates its suffix, we expect that even in the case of a cough ending, the correct response would be made on the basis of the tone. Response time and response accuracy data were measured from the onset of the suffix or the cough. All sentences in all conditions were identical up to the onset of the critical word as well as after offset of the suffix, meaning that the stem tone (aligned with the beginning of the stem vowel) was the first point at which participants could begin to pre-activate the suffix. There were 40 stems in a 40 × 6 condition design, for a total of 240 stimuli. In two conditions (LoValid and HiValid), the stem was associated with its appropriate suffix. In another two conditions (LoInvalid and HiInvalid), an invalid tone-suffix combination was created using cross-splicing, yielding incorrect combinations such as *$kvup_L$*-ar* with a low stem tone and plural suffix (LoInvalid) and *$kvup_H$*-en* with a high stem tone and a singular suffix (HiInvalid). In the other two conditions, the suffix was replaced with a light cough, which was identical for both conditions (LoCough ($kvup_L$*-COUGH*) and HiCough ($kvup_H$*-COUGH*)). A cough was used (as in e.g. Warren (1970)) instead of silence in order to make the stimuli slightly more natural, as well as to better approximate the acoustic properties of the suffixes (i.e. as compared to silence). For all stimuli, including the cough conditions, the task was to judge as quickly as possible whether the word was singular or plural. The stimuli were identical to those used in Söderström et al. (2017). Low and high tone pseudoword stems were very similar in mean duration (472 and 467 ms, respectively). On average, the fall in fundamental frequency during the stressed stem vowel was 2.4 semitones (ST) for low stem tones and 6.7 ST for high tones. Singular suffixes had an average duration of 300 ms (with a fundamental frequency fall of 3.8 ST) while plural suffixes were 284 ms long on average (falling 3.2 ST). There was a slight average intensity difference between low (70.4 dB) and high (71.8 dB) stem tones related to the natural relationship between pitch height and intensity (Stevens, 1935), which remained after normalisation of the stimuli. The average syllable onset duration was very similar for the two different types of stem; 216 ms for low tone stems and 220 ms for high tone stems. Behavioural measures – response time and response accuracy – were analysed using repeated-measures ANOVA with the factors Tone (low or high tone) and Validity (validly or invalidly cued suffix).

2.2. Experimental paradigm

Participants ($N = 19$) gave written consent before the combined EEG-fMRI study began. All participants were speakers of Central Swedish. After being fitted with an EEG cap and after impedances were reduced, participants were placed in an MRI scanner for the main experimental run. Total experiment duration was 30 min including time for the initial structural T1 image sequence. The investigation was divided into four blocks with 60 stimuli in each block. Participants listened to stimuli through insert earphones and were asked to press a button to give a "singular" or "plural" response. A fixation cross was displayed on a screen throughout the experiment. Button order (left/right, right/left) was counterbalanced across blocks. An event-related fMRI design was used and the stimulus presentation list was generated using OptSeq2 (Dale, 1999) in order to improve deconvolution of the haemodynamic response function. The inter-stimulus interval was jittered between 2 and 8 s.

2.3. EEG/ERP

Due to technical issues related to the simultaneous acquisition of EEG and fMRI data, EEG data from 5 participants had to be excluded, leaving 14 participants for further EEG analysis (mean age 24.4 years, $SD = 4.2$, 9 female). A 32-electrode EEG system from BrainProducts (Brain Products GmbH) was used with a 5 kHz sampling rate. Impedances were kept below 5 kΩ. A frontal electrode was used as online reference, and data was re-referenced to average mastoids offline. A 0.01 Hz high-pass filter was applied online and a 30 Hz low-pass filter was applied offline. Data was resampled to 500 Hz prior to analysis. Correction of MR and cardio-ballistic artefacts was performed using BrainVision Analyzer (Brain Products GmbH). Independent component analysis (ICA) was used to reduce the impact of ocular artefacts. ERP data was analysed in 500 ms epochs following tone onset (henceforth "stem tone onset") and 800 ms epochs following suffix plosive onset ("suffix onset"). A 200 ms time window was used for baseline correction. There were thus two time points at which ERPs were measured. The first was at stem tone onset, while the second was timed to the onset of the suffix. A left fronto-temporal region of interest (ROI) (Fz, FC1, C3, CP1, P3 and CP5) was used for the stem tone ERP analysis based on the previously found topographical distribution of PrAN (Roll et al., 2015).

2.4. fMRI

Analyses of fMRI data were carried out using FSL (www.fmrib.ox.ac.uk/fsl) on 19 subjects (mean age 24.5 years, $SD = 3.9$, 11 female). An event-related fMRI design was used, with a time point at voice onset of the tone as well as a time point at suffix onset. A Siemens Prisma 3T scanner acquired structural (T1 MPRAGE) and functional data (T2* gradient-echo EPI, TR = 2100 ms, TE = 30 ms, flip angle = 75°, matrix size = 96 × 96, field of view = 192 × 192 mm^2, 25 slices, slice thickness = 4 mm). A 64-channel head coil was used. Data underwent high-pass filtering (128 s), motion correction (MCFLIRT (Jenkinson, Bannister, Brady, & Smith, 2002)), slice-timing correction and 6 mm FWHM Gaussian smoothing. Subject EPI data was co-registered with individual T1 images. An MNI template was used for normalisation to standard space. In order to isolate tone processing and to avoid any influence of the suffixes, a conjunction analysis was carried out (z-threshold = 3.2, $p = 0.001$, GRF statistics) which revealed areas activated by the word tone contrast across the three classes of endings (singular, plural and cough). Thus, for the tone contrast, a conjunction analysis (Nichols, Brett, Andersson, Wager, & Poline, 2005) of words with valid, invalid and cough suffixes was performed for low tone and high tone words, respectively, in order to isolate effects of stem tone processing. Similarly, the analysis of suffix effects used a conjunction of LoValid/HiValid and LoInvalid/HiInvalid conditions, respectively, in order to isolate areas activated by validly and invalidly cued suffixes in the absence of stem tone effects. Brodmann areas were identified using the Talairach Daemon (Lancaster et al., 1997, 2000). Anatomical ROIs (extracted using WFU Pickatlas (Maldjian, Laurienti, & Burdette, 2004; Maldjian, Laurienti, Kraft, & Burdette, 2003) as in Roll et al. (2015) were used to investigate subject variability in ERPs and BOLD data. Percent signal change (i.e. the BOLD low-high and high-low contrasts) was extracted per subject ($n = 14$) in the given ROI and correlated with subject variability in ERP amplitude (again for low-high and high-low contrasts) (Horovitz, Skudlarski, & Gore, 2002) in the two time windows in which PrAN had been found in the ERP analysis.

3. Results

3.1. Behavioural results

3.1.1. Response time and accuracy

In a repeated-measures ANOVA with the factors Validity and Tone, a main effect of Validity showed that invalidly cued suffixes were processed more slowly as compared to validly cued suffixes ($F(1,13) = 18.196$, $p = 0.001$, $\eta^2_p = 0.583$, valid suffix $M = 891$ ms ($SD = 69$), invalid suffix $M = 977$ ms ($SD = 58$)). A repeated-measures ANOVA of response accuracy with the same factors showed that participants were more accurate in judging suffixes following low stem tones, $M = 96.6\%$ ($SD = 0.5\%$), than high stem tones, $M = 93.5\%$ ($SD = 3.6\%$) ($F(1,13) = 8.386$, $p = 0.013$, $\eta^2_p = 0.392$). In the Cough condition, response accuracy was relatively high for both stem tones, but no effect of Tone was found ($F(1,13) = 0.020$, $p = 0.890$, low tone $M = 68.5\%$ ($SD = 5.8\%$), high tone $M = 69.8\%$ ($SD = 5.8\%$)).

3.2. ERP analysis

3.2.1. Stem tone onset

The pre-activation negativity was divided into two time windows, as determined by visual inspection (see Figs. 1 and 2). The negativity for low tones as compared to high tones in the early time window at 70–170 ms ($F(1,13) = 7.714$, $p = 0.016$, $\eta^2_p = 0.372$) corresponded to a more left posterior (temporal) distribution. The later time window at 270–390 ms ($F(1,13) = 8.314$, $p = 0.013$, $\eta^2_p = 0.390$) had a more left frontal distribution (Fig. 1), similar to Roll et al. (2015).

3.2.2. Suffix onset

Two components were found after suffix onset for invalidly cued suffixes (see Fig. 2): an N400 and a frontal P600 (cf. Federmeier, Wlotko, De Ochoa-Dewald, and Kutas (2007)). A posterior ROI was used for the analysis of the N400 component (P3, Pz, P4 and POz, time window 360–400 ms) while a frontal ROI was used for the P600 (Fz, Cz, FC1, FC2, time window 580–680 ms). Main effects of Validity were

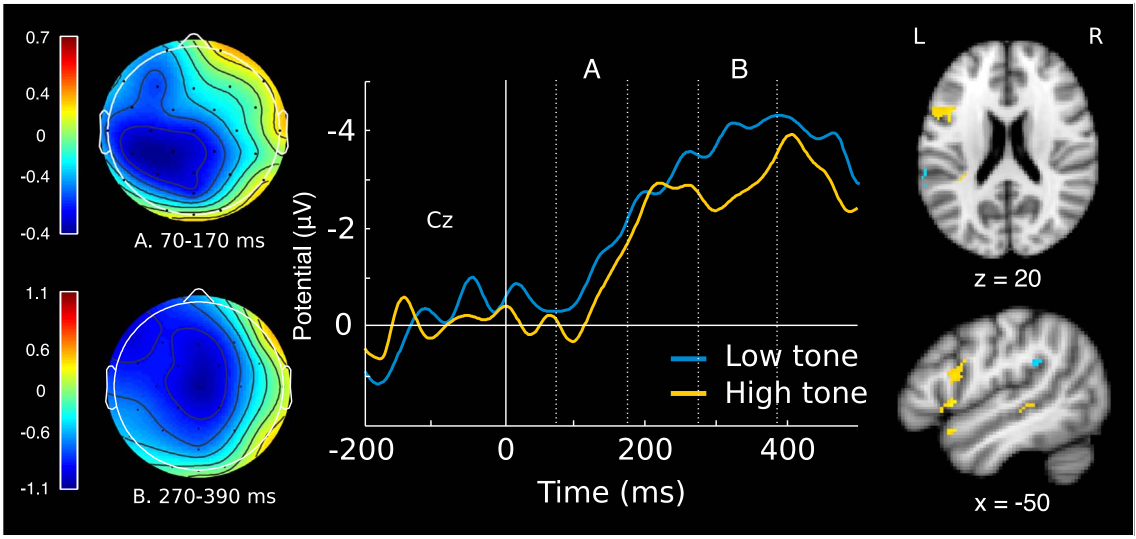

Fig. 1. Left: PrAN topography in two time windows, 70–170 ms and 270–390 ms. Centre: Low tone stems elicited greater ERP negativity. Right: Z-statistic maps (threshold = 3.2) showing activity for low tone stems (blue) and high tone stems (yellow).

found in both the N400 ($F(1,13) = 7.514$, $p = 0.017$, $\eta^2_p = 0.366$) and P600 time windows, ($F(1,13) = 6.029$, $p = 0.029$, $\eta^2_p = 0.317$).

3.3. fMRI analysis

3.3.1. Stem tone effects – fMRI

High stem tones gave rise to clusters of activation in frontal areas (see Fig. 1 and Table 1). The largest cluster for high tone stems spread from the left insula (BA13) mainly to the pars opercularis (−48, 12, −2, 196 voxels) of the left inferior frontal gyrus (BA44). Both tone contrasts revealed BOLD activity in subcortical areas, but high stem tone words in particular showed extensive activity in the dorsal striatum (bilateral putamen). A cluster in the left thalamus was found for low but not high stem tones.

Temporal and parietal activations were found for both contrasts. These activations were mostly located in the left hemisphere, but two similar activation clusters for the high minus low tone contrast were found in bilateral BA21/22. In the left temporal lobe, a cluster related to the high minus low stem tone contrast was found in superior temporal sulcus (STS). In addition, high stem tones gave rise to more activity in left planum temporale (BA22) than did the low stem tones. Conversely, the low minus high tone contrast revealed BOLD maxima in a more posterior area, left BA39 (supramarginal gyrus, max −60, −44, 24).

3.3.1.1. Subject variability in BOLD and EEG – Stem tone onset. Low stem tone words were found to elicit more negative-going ERPs as compared to high stem tones in two windows: the first was at 70–170 ms and the second was at 270–390 ms following tone onset (see Fig. 1). In the Roll et al. (2015) study on real word processing, it was found that PrAN amplitude in an early time window correlated strongly with BOLD in the left anterior transverse temporal area (BA41). While no isolated cluster of activity was found in that area in the present study involving pseudowords, results from Roll et al. (2015) were replicated as regards subject variability correlations between the low – high contrast in BA41 BOLD and ERP in the 70–170 ms time window, i.e. a strong negative correlation was found in the early time window between ERP amplitude and BOLD ($r = -0.699$, $p = 0.005$, see Fig. 3). Thus, increased BOLD activity for low stem tones in left BA41 correlated with more negative ERP amplitudes in the early PrAN time window. Conversely, an analysis of the late time window revealed a significant positive correlation between BOLD activity in left BA44 for high – low stem tones and ERP

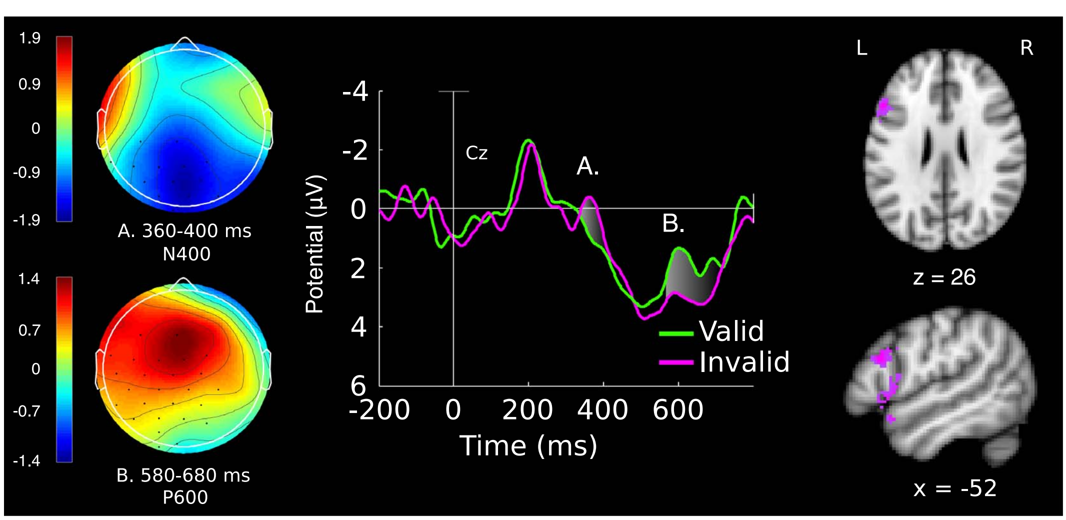

Fig. 2. Left: ERPs and ERP topography maps showing N400 and frontal P600 effects for invalidly cued word endings. Centre: ERPs revealed N400 and P600 effects for invalidly cued suffixes. Right: Z-statistic maps (threshold = 3.2) revealed activity for invalidly cued word endings in e.g. left BA44.

Table 1
Clusters found for the low – high and high – low contrasts (cluster extent threshold was 50 voxels).

Voxels	P	MAX (z-score)	MAX X (mm)	MAX Y (mm)	MAX Z (mm)	Contrast	Brodmann area	Laterality	Brain area
302	1,26E − 50	4.48	−44	8	−10	high-low	44, 13	Left	IFG Pars opercularis, insula
241	3.74E − 43	4.51	−26	2	4	high-low	–	Left	Putamen
191	1.39E − 36	4.18	48	8	−14	high-low	38	Right	Temporal Pole
170	1.17E − 33	4.43	56	−32	−4	high-low	21	Right	Middle Temporal Gyrus
145	5.21E − 30	4.35	24	4	4	high-low	–	Right	Putamen
73	4.87E − 18	3.81	−54	−26	−4	high-low	22	Left	Superior Temporal Gyrus
119	5.51E − 26	3.89	−12	−26	−4	low-high	–	Left	Thalamus
58	4.17E − 15	3.54	−60	−44	24	low-high	39	Left	Supramarginal Gyrus

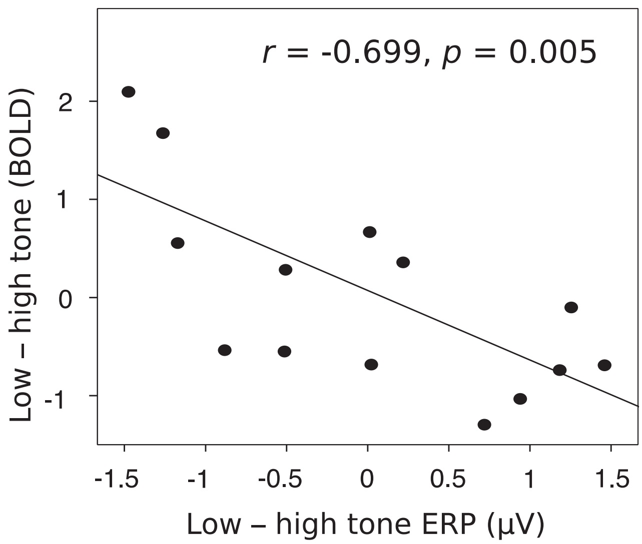

Fig. 3. Subject variability correlation (z-scores) between BOLD activity (contrast low minus high tone) in BA41 and ERP negativity amplitude (low minus high tone) in the 70–170 ms time window.

amplitude for high stem tones at 310–330 ms ($r = 0.573$, $p = 0.032$), a time window centered at the positive ERP peak for high stem tones. More BOLD activity in BA44 in the prefrontal cortex thus led to decreased negative ERP amplitudes for high stem tones in the late time window, lending further support for the functional division of the PrAN time window into two components driven by potentially different mechanisms. In other words, it is possible that activity in the later window is driven by an increased positivity (and increased BOLD) for high tone stems.

3.3.2. Suffix onset effects – fMRI

Clusters of BOLD activation (see Table 2) for invalid suffixes were found in striatal areas (bilateral putamen) and BA44/45 (256 voxels in left BA44 (two cluster maxima at −54, 12, 0 and −52, 20, 26, respectively) and 105 in BA45 (two maxima at −40, 28, 2 and −50, 22, 24, respectively)). The right BA44/45 activation was located ventrally in the prefrontal lateral cortex while the left BA44/45 clusters were spread both ventrally and dorsally, with one large cluster spreading from left insula to ventral areas of BA44/45.

4. Discussion

We investigated pre-activation in language processing by exploiting morphophonological tone-suffix relationships in Swedish words. Stem tones function as cues to how a word could end, although, like most sounds, they are not themselves associated with any specific semantic information. In the present study, pseudoword stems carrying either a low or a high tone were used in order to isolate effects of prosody on the pre-activation of likely word endings. This allowed us to investigate the tone-suffix association in words that the listener had never heard before, thus avoiding potential interference from activation of word meaning. Assuming the existence of a specific tone-suffix connection, the expectation was that this assumed association between tonal and grammatical information would nevertheless be activated in the processing of pseudowords. Furthermore, given that the connection between stem tones and suffixes is highly productive, it is possible that the use of pseudowords could lead to a larger set of possible continuations being activated, which would be larger still for high stem tones as compared to low stem tones.

Results from the fMRI analysis suggest that more predictive stems (i.e. those with low stem tones) with fewer possible continuations lead to activity in left inferior parietal areas (supramarginal gyrus), similar to that reported in Roll et al. (in press), where more predictive word onsets – irrespective of tone – also elicited activity in left inferior parietal cortex. High tone stems, on the other hand, gave rise to large clusters of activations in prefrontal areas. We suggest that low tone stems – which are more predictive than high tone stems – lead to a more direct pre-activation of the suffix, allowing the listener to process and activate a word more efficiently. Thus, it can be posited that more predictive stems enable more immediate access to suffixes, based on increased certainty with regard to upcoming continuations, and lower entropy. Low tone stems also gave rise to activity in the left thalamus, possibly reflecting a facilitated semantic retrieval process (Pergola et al., 2013; Wahl et al., 2008). Conversely, less predictive, high tone words appear to require more processing in left dorsolateral and ventrolateral prefrontal areas (in particular, pars opercularis of the inferior frontal gyrus, BA44), which are likely involved in the suppression of lexical candidates. In Roll et al. (2015), high stem tones did not elicit any significant activity in prefrontal areas. In light of the results in the present study, we suggest that this is due to the fact that the previous study used existing word stems rather than pseudoword stems which put heavy demands on the prefrontal areas. Thus, it is very likely that pseudoword stems lead to a greater need for the suppression of possible

Table 2
Clusters found for the invalid minus valid contrast. Cluster extent threshold was 50 voxels.

Voxels	P	MAX (z-score)	MAX X (mm)	MAX Y (mm)	MAX Z (mm)	Contrast	Brodmann area	Laterality	Brain area
559	1,58E − 77	4.99	−32	22	6	invalid-valid	44, 45, 13	Left	IFG pars opercularis, insula
142	1.47E − 29	4.83	−52	20	26	invalid-valid	44, 45	Left	IFG pars opercularis
396	3,98E − 61	4.65	22	6	−6	invalid-valid	–	Right	Putamen
217	4.60E − 40	4.42	−22	8	0	invalid-valid	–	Left	Putamen
341	5,01E − 55	4.29	54	14	2	invalid-valid	44, 45	Right	IFG pars opercularis

continuations, a state of affairs which is especially prevalent for less predictive, high tone pseudoword stems. While the low tone acts to rapidly reduce the number of possible continuations following word onset, the high tone does not lead to a similar reduction in entropy. Increased activation in prefrontal areas – as well as in the superior temporal sulcus – is also most likely tied to the fact that all productive compounds begin with a high stem tone in Swedish. Consequently, lexical competition can be expected to increase upon hearing a high tone stem, leading to a larger number of lexical candidates that need to be suppressed (Blumstein, 2009; Righi et al., 2010; Söderström et al., 2016; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Thompson-Schill, D'Esposito, & Kan, 1999; Thompson-Schill et al., 1998). In support of this interpretation of the present results, a recent study (Schremm et al., 2017) found that successful processing of the tone-suffix association was related to cortical thickness in temporal areas (left planum temporale) when real words were processed, while cortical thickness in prefrontal areas (left pars opercularis of the left inferior gyrus) correlated with processing of pseudoword stems (as in the present study). The extensive activity in frontal areas perhaps also reflects the complex activity involved in the processing of cognitively demanding pseudoword forms (Hurschler, Liem, Jancke, & Meyer, 2013; Xiao et al., 2005).

As in previous studies, ERP results showed a larger pre-activation negativity (PrAN) for low stem tones. The effect topography spread from temporo-parietal to frontal areas in two time windows. After suffix onset, suffixes cued by an invalid stem tone gave rise to an N400 effect and a frontal P600. These effects are most likely related to disconfirmed predictions (Droge et al., 2016; Federmeier et al., 2007; Hinaut & Dominey, 2013; Rabovsky & McRae, 2014).

Behavioural results showed that invalidly cued suffixes were processed slower as compared to validly cued suffixes. In addition to this, participants were found to be more accurate in judging the correct suffix following low tones, suggesting – as in Roll et al. (2015) – that low tones are more predictive than high stem tones.

We suggest that the early predictive mechanism – corresponding to the early time window found in Roll et al. (2015) – is sensitive to statistical regularities between stems and suffixes and driven by structures in the temporal lobe, primarily in left auditory cortices (e.g. Heschl's gyrus and adjoining areas, such as the left anterior transverse temporal area (BA41)), and possibly left supramarginal gyrus. The inferior parietal cortex has previously been found to be sensitive to entropy and predictability, and appears to be involved in the anticipation of upcoming words (Willems et al., 2016), via top-down influences on possible sentence continuations. Similar activations were found in Roll et al. (in press) for more predictive word onsets with fewer possible continuations. Thus, it is possible that activity in this area for more predictive word stems indicates that access to the word ending and the phonology-meaning association is modulated by the statistical relationship between stem and suffix, leading to facilitated access to the anticipated ending when fewer possible continuations are possible. From the point of view of predictive coding models of perception, it is assumed that the brain generally tends to strive towards minimising prediction error (Friston, 2009; Shannon & Weaver, 1949). Thus, probability densities with lower entropy – such as those found in more predictive contexts – could be claimed to facilitate processing, while less predictive contexts with unexpected outcomes lead to greater uncertainty and need for suppression of alternative candidates. Replicating the results in Roll et al. (2015), activity in left BA41 was found to correlate with the early part of PrAN, which has been proposed to reflect a process related to the pre-activation of highly likely word endings cued by the tone. Another possibility is that suggested by Ettinger et al. (2014), i.e. that increased activity in the transverse temporal gyrus reflects a facilitatory effect of lower entropy, sensitivity to greater certainty with regard to upcoming word endings, as well as to statistical regularities in general (McNealy, Mazziotta, & Dapretto, 2006; Tobia, Iacovella, Davis, & Hasson, 2012). It must be noted that since the BOLD effect has a slower time-course as compared to ERP, it is possible that the rapid, early PrAN processes are more difficult to localise using fMRI, leading to a discrepancy in the ERP signal – which is stronger for low stem tones – and BOLD signal, which was found to be greater for high stem tones in e.g. BA44. In other words, there is a possibility that transient activity in e.g. primary auditory cortex is reflected in the ERP, while the slower BOLD response reflects a later processing stage in connected brain areas. In the later PrAN time window, we suggest that areas in left frontal cortical areas (such as BA44) engage in processes related to lexical selection, combination and competition. The correlation between BOLD activity and high tone ERP amplitude in the late PrAN time window lends support to this account. Furthermore, activity in these lateral frontal cortices is modulated by inhibitory influence from striato-cortical connections (Radulescu et al., 2013). More posterior areas such as the supramarginal gyrus (BA39) have previously been found to play a part in successful lexical access and activation (Blumstein, 2009; MacGregor, Pulvermuller, van Casteren, & Shtyrov, 2012). Since words with fewer possible continuations (low stem tones) gave rise to increased activity in this area, we suggest that low stem tones lead to a more direct access to predicted word endings.

When an unexpected word ending is encountered (i.e. in the case of invalid tone-suffix combinations), bilateral BA44 activation possibly reflects a process of decision making, involving conflict resolution and the selection of an appropriate candidate among several possible representations (Badre & Wagner, 2007; Blumstein, 2009; Prabhakaran, Blumstein, Myers, Hutchison, & Britton, 2006; Righi et al., 2010; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Thompson-Schill, D'Esposito, & Kan, 1999; Thompson-Schill et al., 1998; Zhuang, Tyler, Randall, Stamatakis, & Marslen-Wilson, 2014). Together with the findings of an N400 and a P600, this is further evidence that listeners create expectations about the upcoming word ending based on the word stem tone, which are then disconfirmed and need to be updated. While it is difficult to claim with certainty exactly what is specifically being predicted based on the current paradigm, the presence of an N400 would suggest that the pre-activation of the possible word ending involves the meaning of the suffix.

With regard to the early onset of PrAN, predictive processing appears to begin as early as on the pseudoword stem before the ending has been heard (cf. the relatively high accuracy in judging the meaning of masked suffixes based on the word stem tone alone). We suggest that this process is reflected in the functional dissociation of PrAN into an early temporo-parietal negativity indexing the pre-activation of highly likely candidates – suggested to be related to the lower entropy of more predictive word stems – followed by a frontal effect which reflects an increased competition evaluation/resolution process (Friston, FitzGerald, Rigoli, Schwartenbeck, & Pezzulo, 2017; van der Meer, Kurth-Nelson, & Redish, 2012) when there are more possible word endings to choose from (as is the case with high tone stems). The activity in more posterior areas (supramarginal gyrus (BA39)) found for low stem tones potentially suggests facilitated pre-activation/lexical access when there are fewer competing candidates to choose from. While the present study used meaningless pseudoword stems, we are assuming that lexical competition effects will still be present, since these have been found to be triggered by inherent properties of the mental lexicon (such as the morphophonological tone-suffix association or compound prosody association in Swedish) rather than properties pertaining to specific stimuli (Peramunage, Blumstein, Myers, Goldrick, & Baese-Berk, 2011).

It must be noted that it is difficult to explain the current – and previous – results as simply reflecting the acoustic difference between low and high tones. In a study on South Swedish, in which accent 1 is a high tone and accent 2 is a low tone – the phonetic mirror image of Central Swedish – accent 1 stems still elicited an ERP negativity similar to that found in the present study (Roll, 2015). Also, a recent study (Gosselke Berthelsen et al., 2017) found that while Swedish listeners elicit pre-activation negativities in response to accent 1 word stems, German listeners do not. Instead, non-native speakers processed the word tones in a manner similar to musical tones. Also, Roll et al. (2013) used de-lexicalised stimuli in which segmental properties were removed but fundamental frequency was kept intact. In contrast to the present study, as well as previous studies, a greater ERP negativity was found for high tone stems. Thus, it appears as if the effect cannot simply be explained by the acoustic difference between low and high stem tones. Furthermore, low and high tone stems had very similar syllable onset durations, suggesting that duration differences did not drive the effect.

To summarise, we suggest that strongly predictive cues (such as low stem tones in Swedish) lead to greater pre-activation and rapid access to suffix representations (inferior parietal areas (supramarginal gyrus (BA39)) as well as temporal areas (BA41)) even before the ending of the word has been perceived. In support of the view that the neurophysiological results reflect the pre-activation of possible endings, Söderström et al. (2017) found that the amplitude of PrAN correlated with listener accuracy in restoring replaced suffixes. Furthermore, participants with greater PrAN amplitudes elicited greater P3a responses in response to replaced suffixes, potentially suggesting a stronger commitment to an anticipated word ending. Another explanation of the neurophysiological results could be – as proposed by Ettinger et al. (2014) – that what is observed is predictive mechanisms being delayed for less predictive cues (such as high tone stems in the present study). The present results could be said to be similar to the M130 and M170 found in Solomyak and Marantz (2010). The M130 is suggested to reflect the detection of statistical regularities, while the subsequent M170 appears to reflect morphological decomposition and complexity. It is possible that the two time windows of PrAN reflect something similar. Thus, word stems elicit a neurophysiological response which is related to the increased likelihood of encountering a given suffix – larger for more predictive stems – which is followed by a response driven by and reflecting the increased morphological complexity of high tone stems.

Weaker predictive cues (such as high stem tones) appear to require the inhibition of possible candidates, as well as lead to a possible increase in demands on the processor as regards the grammatical connection between stems and suffixes. The increased activity in left ventrolateral and dorsolateral prefrontal cortex (predominantly in BA44) for high stem tones could also suggest that more combinatorial/grammatical processing is required to process these stems (Bozic, Fonteneau, Su, & Marslen-Wilson, 2015; Bozic, Marslen-Wilson, Stamatakis, Davis, & Tyler, 2007; Pinker & Ullman, 2002; Tyler, Stamatakis, Post, Randall, & Marslen-Wilson, 2005; Vannest, Polk, & Lewis, 2005), and that this effect is clearer when pseudoword stems are used. High stem tones also led to increased activity in left posterior STS, an area implicated in the processing of words in high-density neighbourhoods (Okada & Hickok, 2006). Thus, less predictive word stems appear to lead to increased competition between more candidate word endings that need to be suppressed before lexical access to the ending can proceed. Furthermore, the more prefrontal activity found for high stem tones, in contrast to previous findings (Roll et al., 2015), could also suggest that when pseudowords – which lack lexical representations – are being perceived, high stem tones prompt the processor to analyse the forms combinatorially to a greater degree. This is similar to the suggestion that compound words in English are more likely to be processed as whole-word items if they are semantically opaque, high-frequency compounds (such as *clockwork*), while more transparent compounds (such as *homework*) are more likely to be decomposed and processed combinatorially, and potentially lead to an increase in attentional demands (MacGregor & Shtyrov, 2013).

5. Conclusions

Tones on word stems can be used to pre-activate likely upcoming word endings, such as suffixes. In the present study, predictive tones on semantically void word stems were shown to be used to anticipate upcoming word endings based on a morphophonological connection between word stems and suffixes. More predictive tones are suggested to lead to a more direct access to word endings, involving e.g. left supramarginal gyrus as well as areas in the primary auditory cortex sensitive to statistical regularities. Less predictive tones instead lead to more activity in the left inferior frontal gyrus, suggesting that when a word stem can have many potential endings, the left prefrontal cortex is engaged in order to suppress word endings that are contextually inappropriate.

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Statement of Significance to the Neurobiology of Language

The pre-activation of upcoming word endings is shown to be sensitive to the morphophonological connection between word stems and suffixes in Swedish. More predictive word-internal contexts rely on left inferior parietal areas, suggesting more rapid lexical access to a pre-activated word ending. In less predictive contexts, left prefrontal areas resolve competition between possible endings.

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.2017.08.004.

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