



Contents lists available at ScienceDirect

International Journal of Psychophysiology

journal homepage: www.elsevier.com/locate/ijpsycho

An investigation of prototypical and atypical within-category vowels and non-speech analogues on cortical auditory evoked related potentials (AERPs) in 9 year old children

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ARTICLE INFO

Article history:

Received 16 February 2010

Received in revised form 4 August 2010

Accepted 19 September 2010

Available online xxx

Keywords:

Auditory

ERP

P1

Vowel

Prototypical

Language

Children

Perceptual magnet effect

ABSTRACT

The present study examined cortical auditory evoked related potentials (AERPs) for the P1–N250 and MMN components in children 9 years of age. The first goal was to investigate whether AERPs respond differentially to vowels and complex tones, and the second goal was to explore how prototypical language formant structures might be reflected in these early auditory processing stages. Stimuli were two synthetic within-category vowels (/y/), one of which was preferred by adult German listeners ("prototypical-vowel"), and analogous complex tones. P1 strongly distinguished vowels from tones, revealing larger amplitudes for the more difficult to discriminate but phonetically richer vowel stimuli. Prototypical language phoneme status did not reliably affect AERPs; however P1 amplitudes elicited by the prototypical-vowel correlated robustly with the ability to correctly identify two prototypical-vowels presented in succession as "same" ($r = -0.70$) and word reading fluency ($r = -0.63$). These negative correlations suggest that smaller P1 amplitudes elicited by the prototypical-vowel predict enhanced accuracy when judging prototypical-vowel "sameness" and increased word reading speed. N250 and MMN did not differentiate between vowels and tones and showed no correlations to behavioural measures.

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1. Introduction

Humans possess a seemingly automatic ability to quickly and easily decipher complex streams of language. However, how even the simplest speech signal – a phoneme – is decoded, extracted, mapped and categorized by the cortical auditory system is not well understood.

All the sounds that inundate our auditory system undergo extensive processing via the brainstem and thalamus before reaching the primary auditory cortex. This initial processing is thought to be largely identical for all sounds regardless of whether they represent speech or other signals (Scott and Johnsrude, 2003). Therefore, the first point at which speech sounds might be differentially processed in comparison to non-speech sounds is most likely the primary and secondary auditory cortices.

Anatomically, it is generally accepted that the primary auditory cortex lies within the lateral Sylvian fissure on the transverse gyrus of

Heschl (Brodmann's area 41) (Brodmann, 1909). The secondary auditory cortex, or association cortex, surrounds the primary auditory cortex anatomically in regions of the superior temporal gyrus (Brodmann's areas 21, 22, 42, and 52) (Brodmann, 1909; Cellesia, 1976; Woods and Alain, 2009). The primary and secondary auditory cortices receive direct projections from distinct brain areas and are cytoarchitecturally distinct. The primary auditory cortex is directly inundated by the ventral nucleus of the medial geniculate body and has a similar cell structure to sensory cortex, whereas the secondary auditory cortex receives input from the dorsal medial geniculate body and its cells resemble those of association cortex (Kaas et al., 1999; Pandya, 1995; Woods and Alain, 2009).

Understanding audition at the cortical level, its maturation and response characteristics in humans poses an ongoing challenge in general, and for speech sounds in particular (reviewed by Young, 2008). For example, the anatomy of the auditory cortex, lying deep within the Sylvian fissure, increases difficulties to precisely record cellular activity. Furthermore, although studies reveal that the primary auditory cortex is tonotopically organized (Recanzone and Sutter, 2008), where neurons are tuned to particular frequencies in a highly structured manner, both animal and human studies on cortical

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auditory neurons have shown unexpected differential responses for a tonotopically organized system when presented with behaviourally relevant stimuli (see Young, 2008; Woods and Alain, 2009 for reviews). Here, evidence stems from investigations of vocalizations in a variety of animals (e.g. Cousillas et al., 2005; Grace et al., 2003; Nelken, 2004; Wang and Kadia, 2001) as well as in humans (Belin et al., 2000; Obleser et al., 2006). It has also been shown that these behaviourally relevant cortical responses are dynamic and can be manipulated by changing task demands and stimulus relevance (Fritz et al., 2003; Ulanovsky et al., 2003). Thus, even at early processing stages, sound relevance – which can change dynamically according to the situation an organism finds itself in – has a direct effect on cortical responses, presumably due to the behavioural relevance of the stimulus. Despite this knowledge, we are far from understanding to what extent sound relevance, for example whether sounds are familiar speech or familiar environmental sounds vs. novel sounds, affects our auditory system and how these responses might be modulated by our daily activities and behaviours.

The present study focuses on language sounds in comparison to non-speech sounds. In particular, we examine how vowel sounds, both prototypical (as reflected by long term exposure beginning at birth to sounds particular for a native language) and atypical (belonging to the same category but not considered to be best exemplars of a phoneme of a particular native language), are processed during the early acoustic cortical stages of analysis in comparison to analogous complex tones in school-aged children.

Prior studies have used brain electroencephalography (EEG) based event-related potential (ERP) methods to investigate the response characteristics of neuronal networks in the auditory cortices by measuring exogenous cortical auditory evoked related potentials (AERPs) (Ponton et al., 2002; Pool et al., 1989; Takeshita et al., 2002). Exogenous AERPs, which include the components P1, N1, P2 and N2/N250 are obligatorily elicited by exposure to simple sounds, such as tones and phonemes, regardless of attention or cognitive load (Näätänen, 1992; Näätänen and Picton, 1987). The exact AERP pattern recorded is confounded however by the very long maturational trajectory that characterizes the development of the auditory system, which extends well into adolescence, as well as the rate of stimulus presentation (Ponton et al., 2002; Ponton et al., 2000; Sussman et al., 2008). For example, P1 decreases in amplitude and latency with age. N1 on the other hand is not readily observed in children, especially if presentation times are rapid, with increasing age however N1 increases in amplitude and decreases in latency. In contrast, the P2 component increases in latency and decreases in amplitude with age. Finally, N250, a prominent AERP in childhood decreases in latency and amplitude with age and is larger in children when presentation times are short (Karhu et al., 1997). The distinct maturational trajectories of these components indicate that these peaks result from different pathways and neural generators.

In healthy school-aged children (e.g. 9 years of age), incoming sounds elicit a positivity at about 100 ms (P1) and a negativity at about 250 ms (N250) post stimulus with relatively short interstimulus intervals (ISIs), typically shorter than 1 s (Čeponienė et al., 2005, 1998, 2001, 2008; Korpilahti and Lang, 1994; Näätänen, 1992; Näätänen and Picton, 1987; Paetau et al., 1995; Ponton et al., 2002).

In comparison, under similar conditions the most prominent adult component is a negative deflection at about 100 ms (N1). The N250 is greatly diminished and is recorded only at shorter latencies (referred to as N2) (e.g. Karhu et al., 1997). In children, N1 is only observed to stimuli occurring with ISIs longer than 1 s (Čeponienė et al., 1998; Karhu et al., 1997; Kraus et al., 1993; Wunderlich and Cone-Wesson, 2006). It is not clear how differences in the adult and child N1 might reflect functional differences (Bruneau et al., 1997) or maturational aspects of the underlying neural systems (Albrecht et al., 2000; Ponton et al., 2002; Takeshita et al., 2002). Therefore, insight obtained about auditory system function in adults cannot directly be applied to children (for a

review on adult AERPs see Näätänen and Picton, 1987; for review on children AERPs see Wunderlich and Cone-Wesson, 2006).

Because adult and child AERPs are not readily comparable and because language plays such a critical role in a child's development it is arguably important to enhance the current understanding of speech processing in the auditory system of children. Furthermore, obtaining a better understanding of child AERPs might also prove beneficial to the study of these components in children with developmental disorders such as dyslexia. Children with dyslexia are characterized by language related deficits, such as very poor reading and spelling skills, and evidence exists for atypical AERPs in this population (Hämäläinen et al., 2007; Leppänen and Lyytinen, 1997; Lyytinen et al., 2005; van Herten et al., 2008).

To date, only three studies have examined the functional role of AERPs to simple speech sounds and their analogous complex tones in healthy school-aged children using short ISIs (Čeponienė et al., 2001, 2005, 2008). The usage of ISIs shorter than 1 s is arguably a more ecologically valid method of studying AERPs because faster presentation times more accurately reflect the rapid rate that sounds, in particular speech, are transmitted to us on a daily basis.

Čeponienė et al.'s studies (2001, 2005, 2008) addressed the functional response characteristics of AERPs to differing stimulus complexities, namely speech vs. non-speech sounds. The term “speechness” is often used to describe sounds that are speech-like or resemble speech (vowel or consonant sounds) and is in contrast to non-speech sounds, such as sinus tones. In Čeponienė et al.'s studies, non-speech sounds were acoustically equal in their complexity to the speech sounds. Specifically, the non-speech stimuli were comprised of identical spectral characteristics, but lacked relevant speech information such as glottal excitation generated by fluctuating vocal folds. Therefore, differences in AERP amplitudes and/or latencies found between responses to speech vs. non-speech stimuli could be attributed to the “speechness” of the sounds.

Čeponienė et al.'s results show that AERPs differentiate between stimulus complexities. In the latter studies (Čeponienė et al., 2005, 2008) AERP amplitudes to consonant–vowel stimuli (e.g. /ba/, /ga/, and /da/) compared to complex tones were attenuated at P1 and enhanced at N250. The authors speculated that because complex tones are easier to discriminate than speech sounds, P1 might be preferential to sound saliency, or the ease of discriminating between two sounds, and early feature detection, whereas N250 might contribute to phoneme recognition by, for example, encoding the relevant sound content features for speech.

Based on these findings, it is striking that incongruent findings to AERPs elicited by a vowel stimulus (/ö/) were reported in children of the same age (Čeponienė et al., 2001). Here, vowels elicited greater P1 amplitudes, but were attenuated compared to tones at N250. The authors also reported greater activation over the right hemisphere for complex tones compared to the left hemisphere, whereas vowels did not show any hemispheric differences.

The primary aim of the present study was to further examine the effects of speechness at P1 and N250 in healthy children with a focus on vowels. If we are able to replicate Čeponienė et al.'s (2001) results it would indirectly suggest that vowels and consonants might be processed differently in comparison to analogous non-speech sounds by the primary and/or secondary auditory cortices.

The second goal of this study was to explore how the prototypical phonemic characteristics of a listener's native language might influence sound integration and analysis of speech sounds in the auditory system as reflected in the P1 and N250 components. To our knowledge, no studies have examined this question with regards to these components. Most ERP studies have focused on the mismatch negativity (MMN). These investigations have already illustrated in adults preferential coding (e.g. enhanced MMN) of phonemes belonging to the categorical repertoire of a speaker's own language as opposed to non-native speech sounds (Näätänen et al., 1997;

Winkler et al., 1999). Näätänen et al. (1997) also reported enhanced MMN to the native-vowel over left hemisphere leads in comparison to the non-native-vowel.

In the present study two within-category vowels (/y/) were employed as standard stimuli in separate conditions in a typical oddball paradigm. One vowel was prototypical of the children's native German (here forth: "prototypical-vowel") and the other was an atypical exemplar (here forth: "atypical-vowel", being a prototypical representative for Finnish and Hungarian listeners, see below). The deviant stimulus for both conditions was also an atypical /y/ preferred by French listeners.

Within-category vowels have been shown to be affected by the psychological phenomenon known as compression or the "perceptual magnet effect" (Altonen et al., 1997; Frieda et al., 1999; Iverson and Kuhl, 1995, 2000; Kuhl, 1991). The perceptual magnet effect describes how prototypical (e.g. native language) phonemes distort the perceptual space around them. This distortion compresses the percept of other within-category (but atypical) speech sounds towards the prototype, thus reducing the *perceived* difference between within-category sounds. Compression is in contrast to the phenomenon of expansion. Expansion applies to sounds that are no longer considered within-category and sit on phonetic boundaries. Here, sounds of equal physical distance compared to within-category sounds are *perceived* as more different and are easier to tell apart. Thus, given these principles, the within-category vowel stimuli in the present study should be affected by compression effects, rendering them particularly difficult to distinguish.

Less clear is how this phenomenon might be represented neurally (for theoretical postulations see Bauer et al., 1996; Guenther and Gjaja, 1996). In a recent effort, Salminen et al. (2009) examined the principles of compression and expansion using vowels in a computational model. The perception of expansion at phonetic boundaries was successfully modeled with a few neurons that were maximally active, i.e. steep tuning curves, for either of the vowels. In contrast the perception of compression of within-category vowels was modeled by wide neural tuning curves and an increase in neuronal recruitment. This means, that a large percentage of single neurons responded maximally to both within-category vowels surrounding the prototype as well as the actual prototype. In fact, the pattern of neuronal activity varied only slightly between within-category prototypical and atypical exemplars. Altogether more neurons were preferentially activated by native language prototypes, resulting in neural over-representation (consistent with the views of Bauer et al., 1996; Guenther and Gjaja, 1996). However, a comparably large percentage of the modeled neurons were also activated when within-category atypical-vowels were presented. These modeling results suggest that for within-category vowels the neural representations for prototypes and atypical vowels are not strongly differentiated. Such patterns of neuronal activity can account for the perceptual magnet effect, or compression, where a large population of the same neurons responds to both prototypes and atypical exemplars, leading to a decrease in *perceived* difference.

In support of these findings, ERP studies have observed enhanced activity to category prototypes (e.g. Sharma and Dorman, 1998; Tremblay and Kraus, 2002; Tremblay et al., 2001). However, mixed results have been reported from an fMRI study where enhanced hemodynamic responses to trained stimuli, but less activation to prototypical-vowel and trained categorical stimuli were found (Guenther et al., 2004). Functional imaging data however, do not offer good temporal resolution and ERP studies on prototypes have largely focused on the contribution of MMN (for between category effects, e.g. Näätänen et al., 1997). Although, in adults changes in N1 and P2 have been reported with respect to training of speech sounds (Tremblay and Kraus, 2002; Tremblay et al., 2001), until now, these components have not yet been examined in children in terms of exposure effects.

With regards to the present study, ERP and fMRI results suggest that the prototypical-vowel (standard stimulus) employed in the present study should elicit greater neural response than the atypical-vowel (standard stimulus). However, the modeling results suggest that the differences in ERP amplitude between our prototypical-vowel and our atypical-vowel might be small, with slightly more activity expected for the prototypical-vowel, due to the wide neural tuning for within-category stimuli. However, if or whether AERP components like P1 and N250 might already reflect neural activity specific to the prototypical-vowel and how this is related to developmental aspects of these components is not clear.

Therefore, our overall goals were to 1) examine effects of speechness with regards to vowels and complex tones for P1 and N250 AERPs where a greater response for vowels was expected based on previous findings and 2) to determine if prototypical language formant structure in comparison with an atypical within-category vowel is reflected in these early processing stages in children.

To achieve these goals, twelve healthy school-aged children were subjected to both ERP and behavioural measures. Our main focus was on the response to the standard stimuli, which were two within-category /y/ vowels ("prototypical-vowel" and "atypical-vowel") and two complex tones with analogous formant structures. Because the complex tones represent non-speech analogues of the vowel stimuli we refer to them as "prototypical-tone" and "atypical-tone". Children were passively exposed to the sounds in separate blocks while EEG was recorded using a typical "oddball" paradigm design (see discussion below). The children were encouraged to ignore the sounds and watched a silent film of their choice. After recording the children completed the behavioural measure which was a speeded same-different decision task with the same stimuli as in the ERP experiment.

2. Materials and methods

2.1. Participants

Fifteen normally developing children were recruited to the study from a sub-cohort of children who had participated in a previous study ca. 6 months prior involving both neuropsychological testing and an ERP experiment. Children and their parents were randomly contacted from our participation list if they were between 8 years and 6 months and 10 years of age and asked if they would like to participate in a second study. The initial ERP experiment that they had participated in partially used the same stimuli as presented here and was conducted within the framework of *NeuroDys*, a collaborative cross-linguistic study among four European universities (a part of a large scale European research programme on neurobiology of dyslexia, see www.neurodys.com; the papers on this study are currently under preparation and have not yet been published). Experimental procedures were approved by the Ethical Committee of the Faculty of Medicine at the Philipps University of Marburg, Germany and adhered to the Declaration of Helsinki. All participants and their parents provided written informed consent which was obtained prior to inclusion in the study. Participants were excluded if they were or had been diagnosed with developmental disorders (dyslexia, attention deficit disorder, and specific language impairment) or had suffered severe head injuries. An estimation of IQ was obtained using a verbal and non-verbal subtest (Similarities and Block Design) of the German version of the Wechsler Intelligence Scale for Children (WISC-IV (Wechsler, 2003; German HAWIK-IV: Petermann and Petermann, 2007)). Children who scored below average (<85 IQ points) were excluded.¹ Sufficient auditory function in both ears was

¹ An estimation of IQ can be obtained by adding the standardized scores of both similarities and block design tests and then multiplying by 5. The value obtained can then be used in the IQ tables provided. A standard score of 8 on both tests is the minimum possible for inclusion.

required and assessed with an audiometer. Children were required to hear a minimum of 20 dB on both ears for all of the following frequencies: 250, 500, 1000, 2000, and 4000 Hz. Two of the fifteen participants were excluded due to excessive artefacts in the EEG resulting in less than 40 trials in one or more conditions and one participant was excluded due to a technical error with the sound output during recording. Therefore, the following data refer to the twelve children who were included in the study.

Children's language skills were determined with measures of reading fluency (one-minute fluent reading test, Eine Minute Leseflüssigkeitstest: Salzburger Lese- und Rechtschreibtest II; Moll and Landerl, 2010) and spelling (Diagnostischer Rechtschreibtest für die 4. Klasse, DRT4, Grund et al., 2003). In order to ensure inclusion of only truly average (or above average) readers and spellers in our sample, all children were required to be above 0.85 standard deviations of the lower end of the norm scale calculated in T-values (Mean 50; SD 10; cut-off criteria was therefore set to a T-value of 41.5). Children read an average of 79.6 (5.4) total words per minute which is equivalent to a T-value of 53 (range 42–66). Spelling abilities averaged 57.5 (6.5) T-values (range 47–69). The mean age of the 12 children was 9.2 years (SD = 3.5 months; range 8.8–9.8; 5 males; 11 right-handed; 1 ambidextrous).

2.2. Stimuli

The stimulus set consisted of three within-category synthetic /y/ vowels and three complex non-speech stimuli. Praat software (Boersma and Weenink, 2006) was used for the creation of a set of 135 synthetic vowels covering the formant space for /y/ and the surrounding front high and front mid–high vowels of German, French, Finnish and Hungarian (120 designated as /y/, and 15 catch trials designated as /i/, /e/, and /oe/). First, the glottal source was created by converting the pitch and timing information to a glottal source signal (0.1% noise was added to make the signal sound more natural). The duration of the source signal was 150 ms and the pitch fell linearly from 230 Hz at the onset to 200 Hz at the offset (mean pitch 215 Hz). The source was then filtered with a vocal tract model containing information about the frequencies and bandwidths of the 10 lowest formants (i.e., vocal tract resonances). All sounds were windowed by a 10 ms linear onset and a 15 ms offset ramp using CoolEdit 96 (Syntrillium Software http://www.oldapps.com/CoolEdit.php?old_cooledit=10). Female pitch characteristics were used for all stimuli. In a second step, native speakers for each of the four languages evaluated phoneme boundaries of all 135 vowel stimuli. All stimuli identified as /y/ with 95% accuracy were further inspected for their goodness (acceptability) values by the same-native speakers. For each of the four listener groups, the vowel which received the highest goodness rating was selected for use in future discrimination and ERP experiments. The results showed that Finnish and Hungarian listeners preferred the same vowel and therefore these stimuli were combined.

The non-speech stimuli were created by synthesizing five separate sine wave tones at the frequencies corresponding to the first five formant peaks used in the vowel synthesis parameters. The amplitudes of the sine tones were matched according to values obtained by directly measuring the formant amplitudes of the selected synthesized vowels with Praat. The complex tone stimuli

were composed of five sine tones located at frequencies corresponding to the lowest five formants of the synthetic vowels, thus rendering them analogous to the vowel stimuli, however lacking speech structure.

The formant frequencies of the first five formants (identical for speech sounds and complex tones) for all stimuli are presented in Table 1 and the stimuli are depicted in Fig. 1. For vowels, five additional formants were used (F6–F10: 5500, 6500, 7500, 8500 and 9500 Hz).

2.3. Procedure

The present experiment explored how monolingual German children perceive their prototypical-vowel in comparison to atypical-vowel exemplars. German /y/ and Finnish–Hungarian /y/ speech sounds were presented in two blocks as standard stimuli (82%) in an oddball experiment, where French /y/ was the deviant stimulus (18%) in both conditions. In a separate non-speech condition the corresponding complex tones were presented analogously (two blocks prototypical–tone and atypical–tone). Because many studies examining prototypicality effects have focused on MMN, oddball paradigms have often been employed (Čeponienė et al., 2001; Näätänen et al., 1997; Winkler et al., 1999). Because the focus has been on MMN obligatory responses or AERPs reflecting basic auditory processing (as opposed to preattentive change detection) have not typically been reported in these studies (Näätänen et al., 1997; Winkler et al., 1999) despite the fact that prototypes were employed as the standard stimuli. Therefore, our analysis focuses on the auditory responses to the standard stimuli in this paper and also reports on MMN. However, our MMN results are not necessarily comparable to previous studies on prototypicality because in the present study we do not manipulate the deviant stimulus between conditions.

Stimuli were presented in separate conditions pseudo-randomly in two blocks (first non-speech, followed by speech) using E-Prime software (<http://www.pstnet.com/eprime.cfm>). A total of 702 stimuli (including deviant stimuli) were presented per block with a pseudo-random stimulus onset asynchrony (SOA) of 600–700 ms (mean: 650 ms) and with an intensity of approximately 70 dBA. At least three standard stimuli occurred between each deviant stimulus. Stimuli were administered binaurally using PX200 Sennheiser headphones and attention was diverted with an engaging silent film. Total recording time was approximately 40 min.

After ERP recording children performed a short same–different task. The children made rapid judgments between the sounds (i.e. whether or not two sounds were the same or different) used in the ERP experiment (both speech and non-speech sounds) using right and left arrow keys (correct answers counterbalanced across trials). Speech sounds and complex tones were presented in separate conditions in a balanced manner across participants. Sounds were presented in pairs of two with 310 ms between sound presentations. The beginning of each trial was initiated by the child by key press. Children were given a maximum of 4 s to answer. In a trial session children became familiar with the experimental paradigm and were provided with feedback (happy or sad faces). Feedback was not provided in the actual test session. For each stimulus type there were ten “same” pairs (e.g. German vs. German) and ten “different” pairs

Table 1
Depicts the first five formant frequencies (Hz) for the standard and deviant stimuli used in the experiment, prototypical-/y/ and atypical-/y/, and their corresponding complex tones.

			Formant 1	Formant 2	Formant 3	Formant 4	Formant 5
Standard stimuli	German (82%)	Native-vowel and matching complex tone	250	2018	2400	3500	4500
	Finnish–Hungarian (82%)	Atypical-vowel and matching complex tone	274	1886	2400	3500	4500
Deviant stimulus	French (18%)	Atypical-vowel and matching complex tone	250	2086	2400	3500	4500

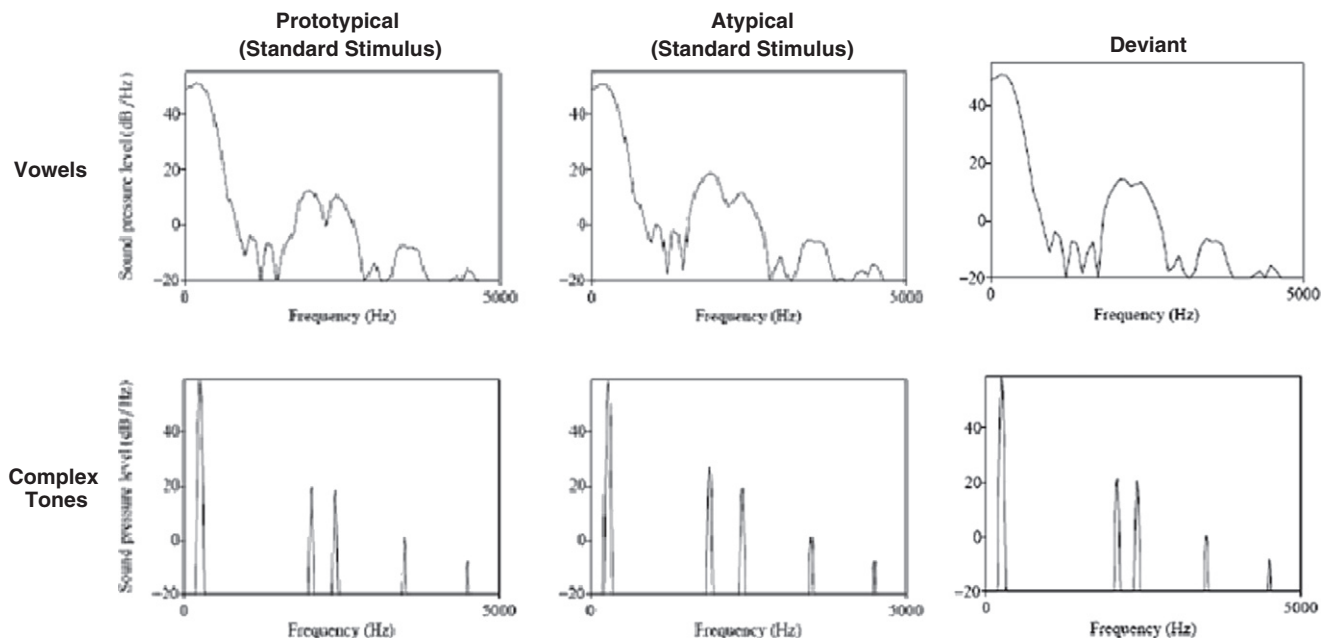


Fig. 1. The short term spectrum of the vowel stimuli (upper row) and the short term spectrum of the complex tone stimuli (bottom row) for prototypical standard (first column), atypical standard and deviant sounds (second column).

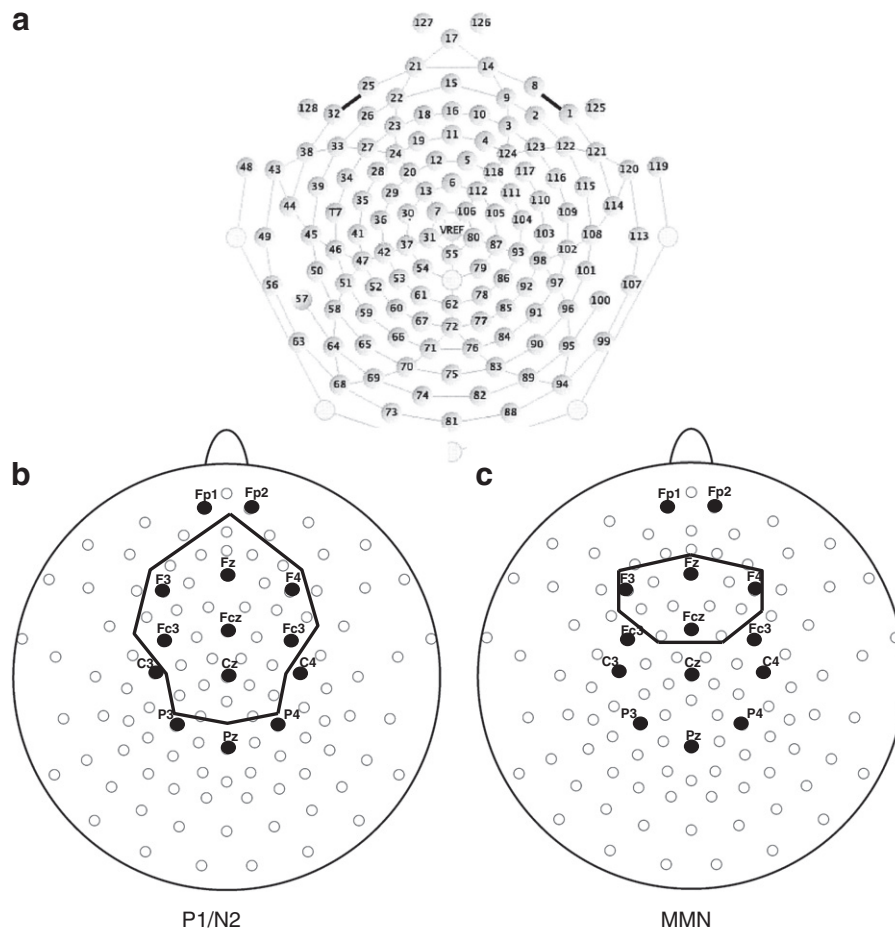


Fig. 2. (a) Illustration of the 128-channel-system and electrode position taken from *Geodesic Sensor Net Technical Manual* (2007). (b) The fronto-centrally selected area depicts the 32 electrodes chosen for examining P1 and N250. Filled black dots indicate electrodes corresponding to the 10–20 system positions (Luu and Ferree, 2000) superimposed on the Geodesic Sensor Net. (c) The selected area indicates the electrodes used for examining the mismatch negativity.

(e.g. German vs. Finnish–Hungarian) for each category (speech, non-speech), resulting in 60 total trials. For reaction times, only correct answers were analyzed, and extreme values (± 1.5 SD from the mean) were eliminated (<1% of data).

2.4. EEG recording and averaging

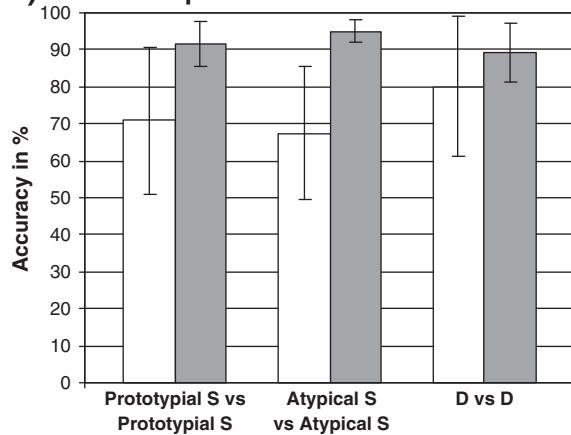
EEG was recorded continuously with an Electrical Geodesic Inc. (EGI) 128-channel-system with Cz as the reference electrode. The impedance was kept below 50 k Ω (the quality of EEG-data was monitored throughout the recording session) and sampled at 500 Hz. Further analysis steps were performed with Brainvision Analyzer. After removing all EOG-artefacts with Independent Component Analysis, exclusion of other artefacts (gradient: max 50 μ V; max-min: 150 μ V for 200 ms; amplitude: min < -150 μ V; max > 150 μ V; low activity: 0.50 μ V for 100 ms), and filtering (bandpass 0.3–30 Hz) the EEG was referenced to the average reference. ERPs were calculated by averaging epochs of 650 ms (including a prestimulus baseline of 50 ms) separately for standard and each deviant stimulus for each participant and condition. Only the responses to the standard stimuli presented before the deviant stimuli were included in the current analyses, resulting in 126 possible EEG-epochs for each of the

two standard stimulus types as well as for the deviant stimulus. A minimum of 50 usable trials was necessary for consideration for inclusion in the statistical analysis. The averages (mean (SD)) for the accepted trials for the standard stimuli were: prototypical-vowel 99.64 (19.48); atypical-vowel 97.75 (23.58); prototypical-tone 110.17 (21.83); and atypical-tone 115.73 (13.48). For the deviant stimulus an average of 110.58 (20.99) and 100.83 (20.40) trials were obtained for the prototypical-vowel and tone conditions and an average of 110.25 (11.14) and 112.83 (13.80) trials were obtained for the atypical-vowel and tone conditions.

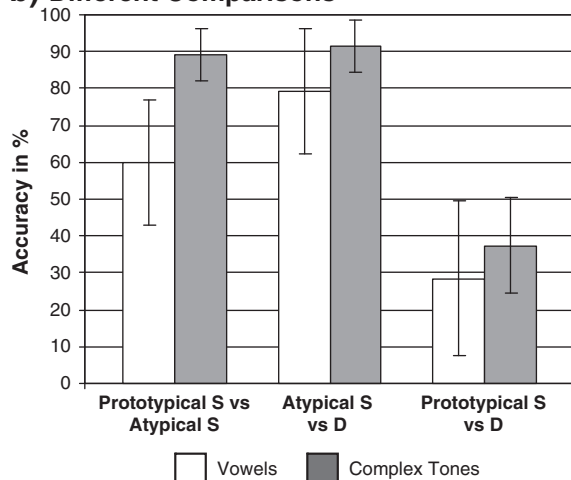
2.5. Data measurement and analysis

The children showed a robust P1–N250 peak morphology over frontal electrodes for both speech and complex tone stimuli. Windows of significant activity above zero for each electrode were determined by 2-tailed paired t-tests against zero on the grand averages. Based on these results the following peak search windows were determined for speech sounds (P1 at 60–124 ms and N250 at 208–364 ms) and for complex tones (P1 at 60–124 ms and N250 at 180–356 ms). For P1 and N250, peaks were determined over 32 fronto-central electrodes

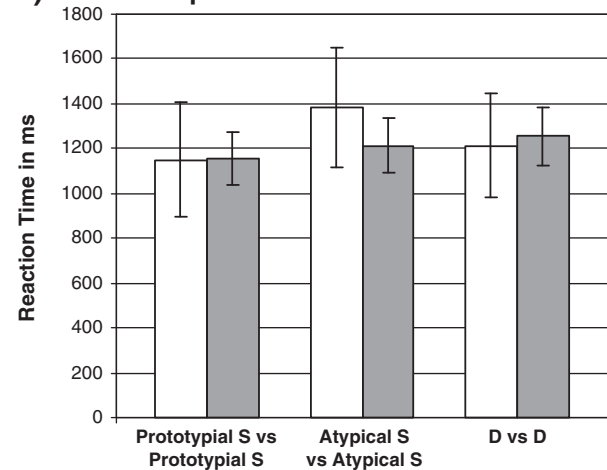
a) Same Comparisons



b) Different Comparisons



a) Same Comparisons



b) Different Comparisons

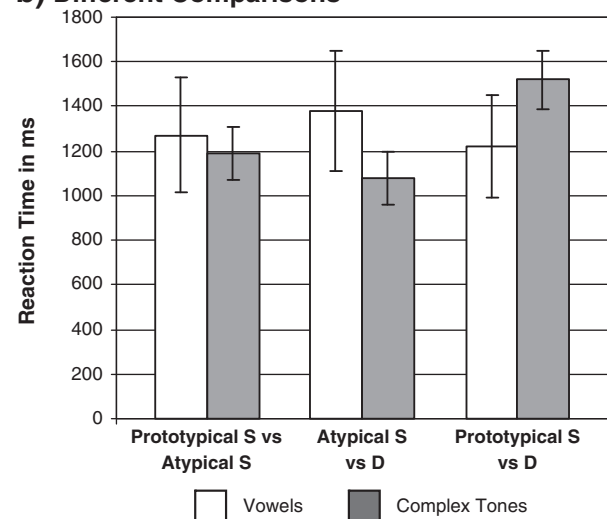


Fig. 3. (a) Depicts accuracy to “same” comparisons for vowels and complex tones; whereas (b) depicts accuracy to “different” comparisons for vowels and complex tones. S = Standard stimulus; D = Deviant stimulus. Bars indicate standard error.

Fig. 4. (a) Illustrates reaction times for “same” comparisons; whereas (b) illustrates reaction times for “different” comparisons. S = Standard stimulus; D = Deviant stimulus. Bars indicate standard error.

that showed significant activity above zero over the entire peak search windows (Fig. 2a and b).

MMN was estimated statistically by subtracting the ERPs to the standard stimulus from those to the deviant stimulus at the frontal electrodes for both speech and complex tone stimuli. The MMN was very small in all conditions reflecting the acoustic similarity of the standard and deviant stimuli. Visibly, the most distinct MMN occurred in the prototypical-vowel condition. Based on this, a window of a significant MMN response displaying negative amplitude was determined using sample-by-sample t-tests against zero on the grand average waveforms at each electrode. This analysis resulted in a time and spatial region of interest with significant activity at 124–252 ms over 12 fronto-central electrodes (Fig. 2a and c) which was applied to all conditions and was also used for group comparisons. Because distinct peaks were not evident for all MMN windows, mean peak amplitudes were calculated for each of the 12 electrodes for each condition separately.

Repeated measures analyses of variance (ANOVAs) were performed on the behavioural and ERP data. For the behavioural data, separate ANOVAs were run over accuracy and reaction time with factors *speechness* (vowels/complex tones) \times *typicality* (prototypical/atypical) and *condition* (same/different). ANOVAs for the ERP results (P1, N250 and MMN separately) were conducted with the within subject factors of *speechness* (vowels/complex tones) \times *typicality* (prototypical/atypical) \times *electrode* (all 32 electrodes for P1 and N250 and all 12 electrodes for MMN). Separate ANOVAs were conducted for the within subject factor of *hemisphere* (*speechness* (vowels/complex tones) \times *typicality* (prototypical/atypical) \times *hemisphere* (left/right) \times *electrode* (26 electrodes as midline electrodes for P1 and N250 (excluded were: 15, 16, 11/Fz, 6/Fcz, 129/Cz, and 55, see Fig. 2a and b) and 10 electrodes for MMN (exclusion of 11/Fz and 6/Fcz). Amplitude and latency were analyzed separately. Post hoc

Pearson correlations (r) were planned between the ERP components for average amplitude taken from all 32 electrodes and the same-different task results (accuracy and reaction time). The alpha level for all analyses was 0.05. Greenhouse–Geisser and Bonferroni corrections were applied when appropriate.

3. Results

3.1. Behavioural results

3.1.1. Same-different task: Accuracy

Overall, higher accuracies to complex tone stimuli revealed that they were easier to discriminate than vowels ($F(1,11) = 23.55$, $p < 0.001$). Regardless of vowel or complex tone status “same” judgments were more accurate than “different” judgments ($F(1,11) = 31.64$, $p < 0.001$ (Fig. 3a and b).

3.1.2. Same-different task: Reaction time

There were no significant differences in reaction times between or within tasks (Fig. 4a and b).

3.2. ERP results

All sounds elicited robust P1–N250 peaks (Fig. 5).

P1: A highly significant main effect for *speechness* revealed greater amplitudes to vowels (mean = 3.26 μ V (1.60)) compared to complex tones (2.65 μ V (1.03), ($F(1,11) = 14.38$, $p = 0.003$)). Peak latencies did not differentiate vowels from complex tones. Prototypical-vowel status did not have any significant effect on P1 amplitude or latency. For neither peak amplitudes nor latencies were any interactions with *hemisphere* found.

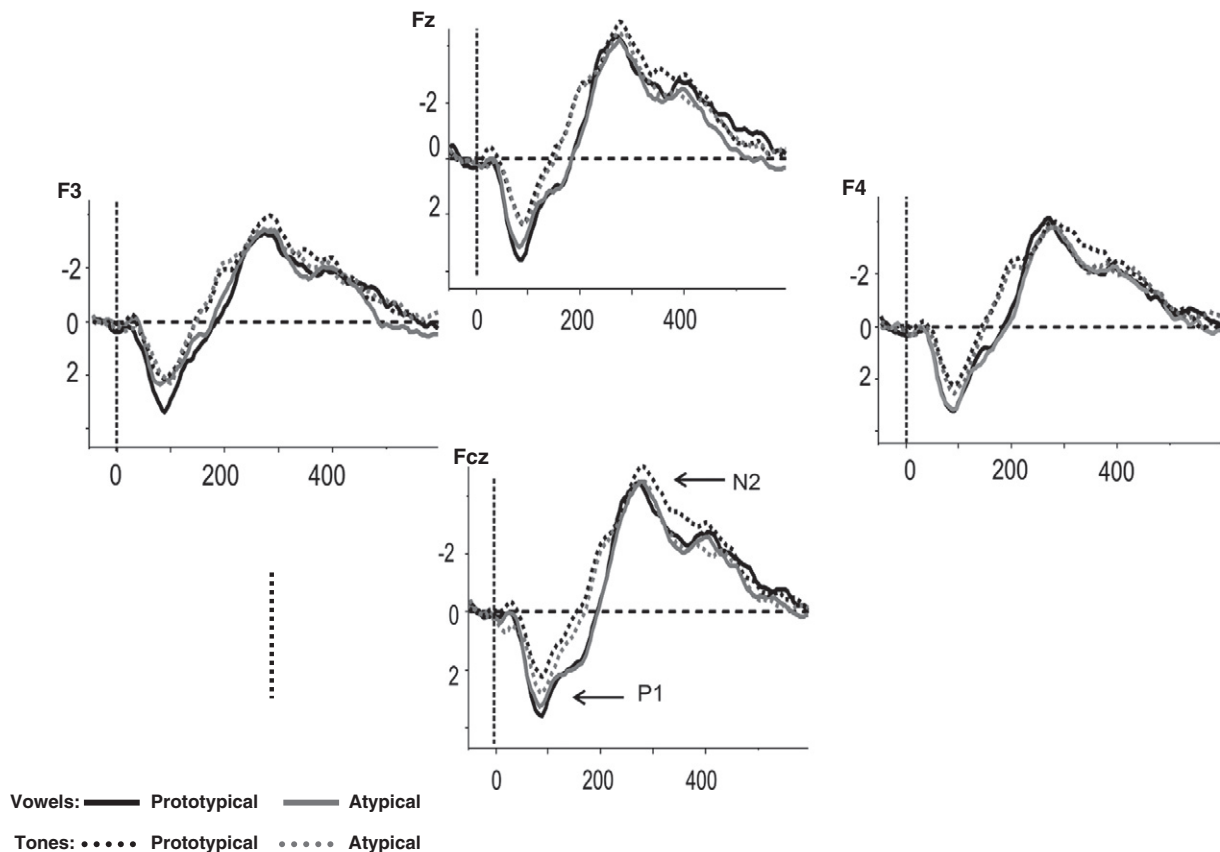


Fig. 5. AERPs for 4 selected electrodes. Refer to Fig. 2 for electrode position. Electrodes have been labelled according to international standards. For EGI users however the electrodes labelled Fz, Fcz, F3 and F4 are 11, 6, 24 and 124 according to the illustration in the technical manual (Geodesic Sensor Net Technical Manual, 2007).

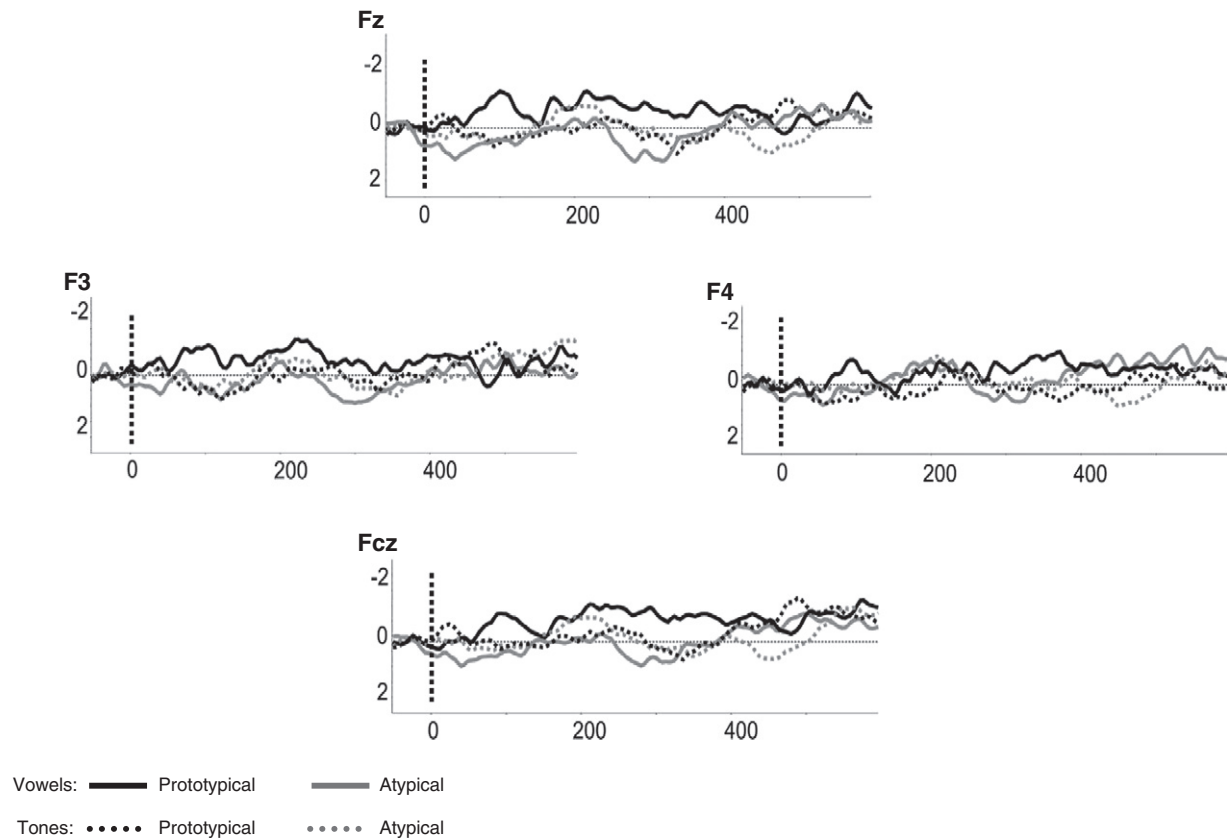


Fig. 6. Mismatch negativity curves for 4 selected electrodes. Refer to Fig. 2 for electrode position. Electrodes have been labelled according to international standards. For EGI users however the electrodes labelled Fz, Fcz, F3 and F4 are 11, 6, 24 and 124 according to the illustration in the technical manual (Geodesic Sensor Net Technical Manual, 2007).

N250: Vowels and complex tones differed neither in amplitude nor latency at N250.

MMN: Although the MMN measured was on average higher in the prototypical-vowel condition (-2.19 (1.44) compared to -1.27 (1.11) for the atypical-vowel condition and -1.06 (0.77) and -1.59 (1.27) for the prototypical and atypical-tone conditions respectively) there were no statistical differences found between MMN in either vowel or complex tone conditions. MMN is depicted for four electrodes in Fig. 6.

3.3. Correlation results

3.3.1. P1 amplitudes for vowels and vowel judgments in the same-different task

Pearson (r) correlations were performed between P1 and N250 amplitude elicited by both the prototypical-vowel and atypical-vowel in relation to the children's performance accuracy on vowel judgments in the same-different task. In order to avoid problems with multiple testing of multiple electrodes, an average of all 32

electrodes was taken for P1 and N250 amplitudes. Pearson (r) correlation coefficients between the average P1 and N250 amplitude elicited by each standard vowel type (prototypical and atypical) and for accuracy of same-different judgments (1. prototypical-vowel vs. prototypical-vowel; 2. atypical-vowel vs. atypical-vowel; 3. prototypical-vowel vs. atypical-vowel, see Fig. 3a and b, were calculated. This resulted in a total of 3 correlations per vowel type per ERP component for a total of twelve correlations. Similarly, Pearson (r) correlations were also performed between MMN amplitude averaged over 12 electrodes and accuracy measures for the deviant stimuli, resulting in a further 3 correlations (1. deviant stimulus vs. deviant stimulus; 2. atypical-vowel vs. deviant; 3. prototypical-vowel vs. deviant stimulus, see Fig. 3a and b).

A significant correlation occurred between P1 amplitudes elicited by the prototypical-vowel and the ability to correctly judge sameness between two prototypical-vowels ($r = -0.70$, $p = 0.01$) (Table 2 and Fig. 7). The negative correlation indicates a relationship between smaller P1 amplitudes to the prototypical-vowel and an enhanced ability to judge two prototypical-vowels as "same". The atypical-

Table 2

Pearson r correlations between P1 amplitudes for both vowel types (prototypical-vowel and atypical-vowel) and accuracy measures in the same-different task for speech stimuli only. "Same-atypical" refers to the presentation of two atypical-vowels, where the judgement "same" is correct. "Same-prototypical" refers to the presentation of two prototypical-vowels, where the judgement "same" is correct. "Different" refers to the presentation of a prototypical and an atypical vowel, where the judgement "different" is correct. * = $p < 0.02$

		Vowel type		Accuracy		
		P1 amplitude native-vowel	P1 amplitude atypical-vowel	Same-atypical	Same-prototypical	Different
Vowel type	P1 amplitude native-vowel	1.0				
	P1 amplitude atypical-vowel	0.31	1.0			
Accuracy	Same-atypical	0.38	0.19	1.0		
	Same-prototypical	-0.70*	-0.15	-0.13	1.0	
	Different	-0.12	0.06	-0.05	0.50	1.0

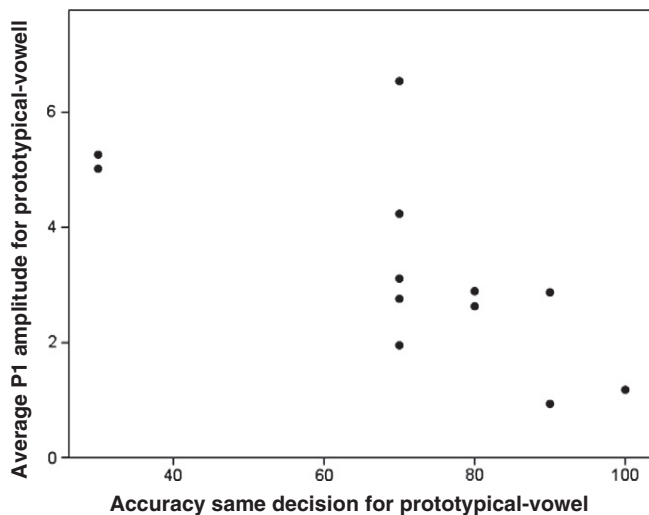


Fig. 7. The scatterplot depicts the negative correlation ($r = -0.70$) between the average P1 amplitude of the prototypical-vowel and accuracy measures to same judgements when presented with two prototypical-vowels. Children with higher accuracy scores had lower P1 amplitudes to the prototypical vowel.

vowel did not correlate with any accuracy measure. There were no significant correlations with N250 or MMN amplitudes.

3.3.2. P1 amplitude and reading and spelling scores

Because P1 amplitudes elicited by the prototypical-vowel seemed to be specific for native language processing, as suggested by the correlations with judging “sameness” of prototypical-vowels, we further explored the relationship between this amplitude and language measures. Two correlations between averaged P1 amplitudes (prototypical-vowel) and the numbers of words read per minute (*words/min*) and *spelling* were conducted. *Spelling* did not correlate with P1 amplitude. A significant correlation between P1 amplitude of the prototypical-vowel and *words/min* ($r = -0.63$, $p = 0.03$) was found (Table 3 and Fig. 8). The negative correlation indicates that smaller P1 amplitudes to prototypical-vowel sounds are related to the ability to read an increased number of words in one minute's time.

4. Discussion

This study aimed at advancing the understanding of cortical auditory sensory processing of vowels using acoustically matched complex tone control stimuli in school-aged children. A further goal was to examine possible influences of prototypical phonemes on AERPs.

The various stimuli were examined by manipulating the standard stimuli employed in a typical oddball paradigm format. The deviant stimuli were held constant for the speech and complex tone conditions. All standard stimuli elicited a robust P1–N250 pattern and small MMN curves were observed to the presence of deviant within-category stimuli. Whether standard stimuli were vowels or

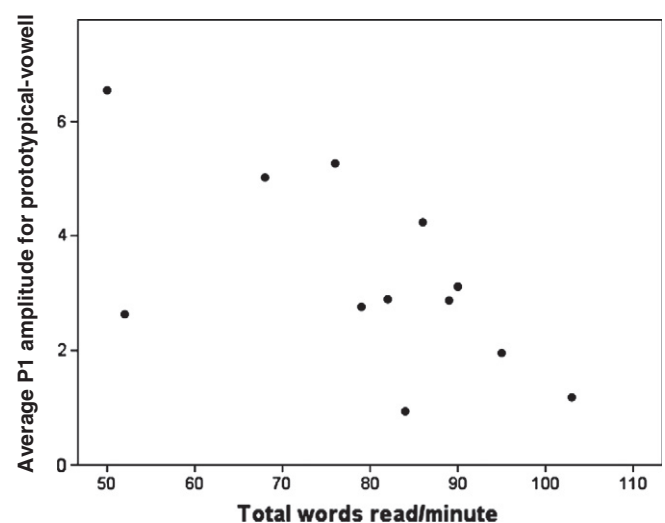


Fig. 8. The scatterplot depicts the negative correlation ($r = -0.63$) between the average P1 amplitude of the prototypical-vowel and the amount of words read in minute. Children with higher P1 amplitudes had lower word fluency scores.

complex tones was significantly reflected at P1 where peak amplitudes were enhanced for vowels compared to complex tones. Both N250 and MMN did not reflect “speechness” of the stimuli. None of the ERP components reliably discriminated between “prototypicality” of the stimuli. However, robust negative correlations demonstrated how lower amplitudes to P1 elicited by the prototypical-vowel were highly related to 1) increased accuracy to “same” judgments to prototypical-vowel pairs; and 2) a greater word reading speed.

Our finding of enhanced P1 amplitude to vowels compared to complex tones in healthy school-aged children replicates the result of a previous investigation where P1 was enhanced to a vowel stimulus in comparison to both a simple and to a complex tone (Čeponienė et al., 2001). In general, greater amplitudes to vowel stimuli in the present study support the results of earlier investigations suggesting that neuronal response reflected in basic obligatory ERPs is stronger with increasing complexity of acoustical input (Čeponienė et al., 2002; Shahin et al., 2007; Tervaniemi et al., 2000). Therefore, the present results do not support the view that these early components merely reflect perceptual saliency, or the ease of discrimination (Čeponienė et al., 2005, 2008; Näätänen and Winkler, 1999). In these studies, complex tones were found to be enhanced at P1 compared to consonant–vowel stimuli. Because consonant–vowel stimuli were more complex than the tone stimuli employed, it seemed as though P1 was sensitive to the ease of perceptual discrimination and identification. In our study, perceptual discrimination of complex tones was more accurate, as reflected in the behavioural data; however P1 was enhanced to the vowel stimuli. Presently, it is unclear why our findings and those of Čeponienė et al., 2001 find enhanced P1 to vowel sounds, whereas those of Čeponienė et al., 2005, 2008 report enhanced N250 in children to consonant–vowel sounds.

P1 in response to incoming sounds and has been described as a stage dedicated to mere sensory processing of sounds (Martin et al., 2008) and recent functional magnetic resonance imaging (fMRI) results support a “low-level” processing interpretation of primary auditory cortex function (Whalen et al., 2006). However, as Young (2008) reviews, numerous studies using finer measurements such as direct recordings from auditory cortical neurons in animals show that these neurons react to more than simply the spectro-temporal aspects of auditory stimuli if a stimulus contains relevant information for the behaviour of the organism, a finding which also received support from recent fMRI studies in humans (Staeren et al., 2009; Woods and Alain, 2009). The results of the present study suggest that, at least for vowels, the P1 component might play an especially important role for

Table 3

Pearson r correlations between P1 amplitudes for the prototypical-vowel and spelling and reading measures. Reading is measured in total words read per minute (*words/min*). * = $p < 0.05$.

	P1 amplitude native-vowel	Words/min	Spelling
P1 amplitude native-vowel	1.00		
Words/min	−0.63*	1.00	
Spelling	−0.12	0.59*	1.00

representing speechness of sounds. According to functional neuro-anatomy data, areas within the core or centre of the primary auditory cortex are highly tonotopic in their organization and response patterns, whereas, the association auditory cortices anterior to these areas respond to behaviourally relevant sounds (Belin et al., 2000; Obleser et al., 2006; Woods and Alain, 2009). Therefore, the present findings of speech specificity at P1 might be explained by extra contributions from these cortical areas (also known as the parabelt vocalization area (PVA)).

Furthermore, our findings suggest that P1 might play an important role in the accurate recognition of speech cues and may be relevant for reading skills in children. This assumption is supported by our finding that P1 amplitude elicited by a prototypical-vowel is related to measures of language as well as accuracy of same-sound detection of speech sounds typical to a listener's native language. Thus, it would seem that even very early stages of cortical acoustic processing are involved in not only perception of the physical properties of sound, but also in speech sound representation.

4.1. Prototypicality

Attenuated MMN has been shown to distinguish native and non-native speech sounds for across category stimuli (Näätänen et al., 1997). Furthermore, MMN is sensitive to changes in vowels that are relevant for one speaker's language, such as vowel duration, but not for another speaker's language (Kirmse et al., 2008). In line with previous findings, our MMN measured to within-category stimuli was quite small (Winkler et al., 1999). Interestingly in the present study MMN did not distinguish between prototypical and non-prototypical speech sounds which is in contrast to one finding where MMN was enhanced to stimuli prototypes (Sharma and Dorman, 1998). Unlike in previous studies, in the present study we did not employ a prototype for the deviant stimulus, rather across all conditions deviance was held constant. This experimental difference might at least partially explain why MMN did not distinguish between prototypical and atypical conditions.

In the present study prototypicality was related to P1 amplitudes elicited by the prototypical-vowel stimulus. At first, the correlation results between P1 amplitude elicited by a prototypical-vowel and reading and accuracy measures might seem counter-intuitive as they suggest that a decrease in neural response to a prototypical language stimulus is related to both improved conscious perception and reading skills. As discussed in this article, the literature body suggests that prototypes enhance brain responses, but does not offer any explanations as to why we find that a down-regulation of this enhancement might be linked to better perception and reading. Furthermore, it is unclear why the strongest effects are observed when comparing P1 amplitudes and accuracy for judging two identical prototypical stimuli, and not for discrimination of different stimuli. A possible explanation for these results might be found in light of the perceptual magnet effect (Aaltonen et al., 1997; Frieda et al., 1999; Iverson and Kuhl, 1995, 2000; Kuhl, 1991) and recent computational data (Salminen et al., 2009).

As reviewed earlier in this paper, computational data suggest that the perceptual magnet effect might be attributed to a widened tuning of neural responses to prototypes of native language phonemes and within-category exemplars (Salminen et al., 2009). This is in line with previous findings stemming from neurophysiological research (Sharma and Dorman, 1998; Tremblay and Kraus, 2002; Tremblay et al., 2001). As discussed, prototypes are believed to elicit an over-representation of neural activity. This over-representation of neural activity might result in increased amplitudes, like those recorded in the present study, to prototypes. A neuronal over-representation can also be understood as imprecision in the neural tuning. This imprecise neural response at the relatively early stage of auditory processing

observed for within-category stimuli comparisons explains the difficulties in consciously deciphering two incoming within-category vowels, and might also explain the imprecision in judging the same vowels as equal.

In the present study, larger P1 amplitudes, or greater over-representation, of the prototypical-vowel consequently correlated with poor performance when comparing prototypical-vowel exemplars (i.e. the same judgments). According to the literature reviewed, an over-representation of prototypical sounds seems normal, but our results seem to suggest that too much over-representation of the prototype might actually result in lower precision in coding for that particular sound. This increased imprecision might lead to difficulties determining when two identical prototypical-vowels are actually the same, to which the P1 amplitude seems to be particularly sensitive.

Our findings are in fact quite intriguing when considering the neural representation of speech and speech discrimination. In light of Salminen et al.'s recent modeling work, it would seem that enhanced ability to judge sameness might be coded by slightly less wide (i.e. narrower) tuning curves to native language prototypes. Our findings suggest that the perceptual magnet effect for within-category stimuli (i.e. compression) might be explained partly by activity in the P1 component in the auditory system, at least for vowels presented with ISIs less than 1 s.

Recent fMRI data lend some further support to the present findings. Guenther et al. (2004) reported that when presented with a prototypical-vowel representing the centre of a category, lower levels of activity were recorded from the auditory cortex of nine adults in comparison to an atypical exemplar. Thus, analogous to the present study, it would seem that prototypes might be modeled by less activity, however in the present study there were no statistically significant findings found between the two vowel types. The authors suggested that lower levels of activity might be indicative of less neural representation for within-category vowels which would also render them more difficult to discriminate, than those sounds sitting on category boundaries. Because fMRI is characterized by a low temporal resolution, it is not clear to what extent their findings might be relevant for the components examined in the present study. Furthermore, Guenther et al. (2004) reported on data collected from adults. It could be the case that with increasing exposure to a particular language, prototypes become characterized by decreases in neural activity, but in young children neural responses to speech sounds are likely still developing.

It is interesting that in the present study the amplitude recorded between the prototypical and atypical-vowel sounds did not significantly differ suggesting that their neural response patterns were quite similar. However, no significant correlations between the atypical-vowel and behavioural data were found, whereas the amplitude of the prototypical-vowel at P1 correlated reliably with accurate discrimination of the prototypical-vowel sounds and with reading skills. Therefore, our results point toward a functional significance of early cortical acoustic analysis processes on not only speech sound representation, but also on the relevance of these processes for higher cognitive function and the relevance of native language for these processes.

Finally, because the present findings suggest that P1 amplitudes to prototypical-vowel stimuli are strongly linked to good reading skills, the P1 amplitude might be a very interesting component for the study of dyslexia, which is characterized by poor reading skills and affect about 10% of the population (Katusic et al., 2001; Shaywitz et al., 1990, 1999). To date, most ERP studies on dyslexia have focused on the MMN or later components (e.g. Bishop, 2007; Cohen-Mimran, 2006; Cunningham et al., 2001; Kraus et al., 1996; Meng et al., 2005; Schulte-Körne et al., 1998). These studies normally find abnormal (e.g. attenuated, later) ERPs to speech stimuli; however these components have not been strongly linked to reading measures, in contrast to P1 in the present study.

4.2. Summary

To date, only a few studies have examined the functional significance of AERPs in children. The present findings build on current knowledge, suggesting that differential processing of speech sounds and complex tones is reflected in exogenous auditory responses. P1 amplitudes strongly differentiated vowels from complex tones. Based on previous reports and our own findings, we suggest that P1 is partly indexing categorical responses specific to speech stimuli, especially vowels. Furthermore, we provide insight into how native language phonemes might be indexed in early stages of acoustic processing. Although the prototypical-vowel was only moderately indexed at P1, reliable negative correlations were found between P1 amplitude elicited by the prototypical-vowel and the ability to judge two prototypical-vowels as “same” as well as word reading fluency. We have interpreted our results with the help of the perceptual magnet account and recent neurobiological results and computational modeling.

Acknowledgements

We would like to acknowledge the collective work of work package 7 of the NeuroDys Consortium (Pis Paavo Leppänen and Valéria Csépe) responsible for the development of the original cross-linguistic paradigm, from which the current stimuli originate. We thank Julia Kaya for her great work in subject recruitment and testing. Finally, special thanks for all of the children and their parents who were so kind and willing to participate in this study, and who continue to take part in many important studies. This research was funded by the European Union Sixth Framework Programme #018696 “NeuroDys Dyslexia Genes and Neurobiological Pathways”. The collection and evaluation of the presented data was performed by Jennifer Bruder as part of her Ph.D. thesis (Medical Faculty, Department of Child and Adolescent Psychiatry, Psychosomatic and Psychotherapy, Ludwig-Maximilians-University, Munich).

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