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Neural correlates of phonological processing in Polish-English bilinguals: An fMRI study

Korelaty neuronalne w przetwarzaniu fonologicznym u polskich użytkowników języka angielskiego: Studium fMRI.

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Introduction

Speech is a carrier of language. Even though it might be executed by us automatically in everyday life, our minds must have some sort of representation of it to be able to encode it and decode it. This representation is in fact finely structured in the brain, and comprises a finite set of features that are able to yield all possible sounds. Even though linguistics have a name for this system, i.e. phonology, its structure has been mostly constrained to theoretical models. With the development of modern experimental methods, researchers have found the connection between brain structures and their functions, allowing for mapping of linguistic processes in our brains. However, it seems that this is not a straightforward task, and as the research shows, phonological system requires different processes to be involved, and that these processes vary considerably across languages and people.

What is more, the presence of more than one language in the brain further complicates the phonological representation in the mind, and it is not exactly known how the brain copes with managing these multiple representations, while maintaining the ability to access all of them when required. That is why, present thesis sets out to describe the model of phonological processing in the brain, with special focus on the processing of second language phonology in bilingual people by the means of experimental methods described in subsequent chapters.

The first chapter, a theoretical one, will describe classical and contemporary models of phonological representation in the mind of monolingual and bilingual people. The involvement of the brain structures and functions in these representations will also be discussed in detail, with plenty of studies reviewed for support. In the second chapter, a detailed description of the experimental methods, along with a rationale for

these methods, will be presented. In the third chapter, a step-by-step methodology of data analysis will be discussed in detail. The fourth, and final, chapter will describe the results of the experiment, and their implications for the final model of phonological processing.

As such, this work is an effort to demonstrate the benefits of interdisciplinary research, which helps develop our understanding of basic human capacity for perceiving and producing language. At the center of this work is a hypothesis, developed on the basis of linguistic ideas, which is evaluated against recent advances in neuroscience, using various neuroscientific tools.

Chapter 1: Literature review

1.1. Introduction

In this chapter, first the representation of phonological system in the mind will be described; then, a number of native and second language speech perception models will be discussed. Next, the representation of language in the brain will be explained, and neural models of speech processing will be presented. Finally, a representation of two languages in the brain will be discussed and the number of relevant neuroimaging studies presented.

1.2. Phonology in the mind

In order to map phonology in the brain, it is of great importance to first establish how the phonological system is represented in the mind. In order to do that, two cases will be taken into consideration. The first one assumes that there is a specialized system for phonological patterning, in which we are biologically equipped, and the second one assumes that phonological talents, such as recognizing phonological patterns in the structure of language and creating new phonological systems, are the result of different systems that are not specialized for phonological patterning.

In the first case, it is assumed that there is a specialized system dedicated to the computation of phonological patterns, and that at the heart of this system, there is a set of constraints that favor certain structures over others (Berent 2013). These constraints are highly productive and systematic, and are shared across different languages, thus

creating *the phonological grammar* (Berent 2013), which is acquired automatically by humans, when they learn their first language instinctively. The productivity of phonological patterns suggests that the phonological grammar is an algebraic system, and the universality suggests that it is a core knowledge system that is partly innate. Thus, we can assume that the phonological grammar is an algebraic system of core knowledge.

In the second case, we can alternatively hypothesize that phonological patterning is the outcome of several nonlinguistic systems, such as auditory perception, motor control, and general intelligence, that are not neither algebraic nor specialized for phonological computing (Berent 2013). Because of the similar linguistic experience of different speakers, and generic aspects of human perception and cognition, phonological systems happen to share some properties, but it is not reflective of a specialized system.

1.2.1. Phonology as an algebraic system of core knowledge

Phonological knowledge lets the speaker recognize and generate novel patterns of linguistic elements that are meaningless on their own (Berent 2013). Even when the speakers hear new words, they can easily asses whether the words rhyme, brake them into syllables, or adjust proper voicing agreement, which suggests that the patterns are generalized by the speakers. This generalization is mediated by algebraic properties of the phonological system, which assumes that phonological representations are discrete and combinatorial in nature. These representations differentiate between an instance of a category and a category, but treats all the instances of a category alike, because they are represented by their forms, thus ignoring their differences. Such an algebraic property, called an *equivalence class*, allows for generalizations that can be applied to existing and potential members of a category (Berent et al., 2013). What is more, phonological system operates on variables, and thus it can encode abstract relations among categories. Variables are also a property of an algebraic system (Marcus, 2001).

Algebraic properties alone, however, cannot account for another important feature of phonological patterning, which is universality across languages. As the design of phonological patterns created by humans are not found in nonhuman communication or in general aural patterns such as music, this would suggest that there must be a

specialized system responsible for producing these patterns (Berent 2013). It is important to note however, that in the literature, there have been plenty of ill-formed models of specialized mental systems, and by a specialized system Berent (2013) does not mean "an encapsulated processor whose operations is blind to any contextually relevant information" (Berent 2003: 45), nor does she treat it as "neural hermit – brain substrate sharing none of their components with any other cognitive mechanisms" (Berent 2003: 45). As there is plenty of evidence that no cognitive systems are fully encapsulated, and that all inherited traits are sensitive to variations (Balaban, 2006), this specialized phonological system could rather manifest itself as a system of core knowledge. As core knowledge systems have been documented in other areas of cognition, such as physics, numbers or biology (for references see Berent 2003), universal and idiosyncratic nature of phonology could be also innate, which is supported by the early onset of phonological patterning in infants. As the phonological core knowledge system serves a specific function, it reflects an adaptive design, controlled by evolution and genes.

1.2.2. Non-algebraic and domain-general alternatives

Even though there might be some evidence in favor of specialized algebraic computational system serving phonological generalizations, the idea faces two major challenges, which are the continuity between the phonological system and the non-algebraic component, and the success of non-algebraic connectionist systems in describing phonological patterns (Berent 2013). It has been shown in the literature, that many phonological alternations reflect natural phonetic processes (Blevins 2004). Phonetic processes, on the other hand, reflect phonological knowledge, as they are shaped by rules that vary across languages (Zsiga 2000). This phonetic-phonological continuum suggests that these two cannot be really put into separate domains, which would be inconsistent with the model of algebraic phonological grammar.

What is more, a computational model proposed by Rummelhart and McClelland (1986) argues that linguistic knowledge does not require a separate grammatical component, independent of the lexicon, structural rules, or syntactically complex representations. Thus, generalizations must follow only from the associations between

unstructured representations, acquired from linguistic experience, making the algebraic phonological grammar obsolete (Berent 2013). What follows from this associative model is that phonological system might not be a specialized system at all. To date, the arguments for specialized grammar system included the universal design of linguistic systems, the role of universal principles in language acquisition, and the domain-specificity (Berent 2013). These arguments will now be discussed in the light of the body of counterarguments.

Typological universals, which is the first argument, are said to be regular cross-linguistic patterns that are a product of principles represented in the language faculty of all speakers. However, it has been shown in the literature, that these universals are not laws that cannot be violated, but rather statistical trends that reflect favoring of simple structures over more complex ones (Berent 2013). These universals are byproducts of cultural evolution, as it is easier to transmit certain types of structures to other speakers. Thus, these universals are shaped by the phonetic channel and historical change, rather than some universal grammatical system (Blevins 2004; Bybee 2008; Evans and Levinson 2009). This notion is supported by the framework of Natural Phonology (Donegan and Stampe 1979), according to which phonological processes are phonetically motivated.

As far as the role of universal principles in language acquisition is concerned, it has been proposed by Chomsky (1965) that the impoverished linguistic experience available to the child is not sufficient for the proper acquisition of language, thus there must be some kind of innate set of universal principles, *Universal Grammar*; that they can rely on – stored in a specialized language acquisition device. However, the success of simple associative systems in learning complex syntactic structures challenges this assumption (Berent 2013). It has been shown that in the linguistic experience available to a child, there is everything he or she needs to extract the relevant structure (Reali and Christiansen 2005). As there is no poverty of stimulus in the structure of words children hear and are expected to produce, the universal grammar does not include phonology (MacNeilage 2008). And if the linguistic experience is enough to learn syntax, there is no need for a specialized machine just for acquisition of phonology (Berent 2013).

As for the role of domain-specific nature of phonological system, it has been shown in the literature that the acquisition and processing of phonology rely on mechanisms that are shared with nonlinguistic domains (Berent 2013). What is more,

the acquisition of phonology might be nothing more than learning of statistical phonological patterns, and it is known that statistical learning is not exclusive to phonological ability. It has been shown that categorical perception is not unique to speech, and certainly not to humans alone, as there are studies in which cotton-top tamarin monkeys are able to distinguish between languages, even though they rely on different sources of information than humans (Saffran et al. 2008; Tincoff et al. 2005, Ramus et al. 2000).

1.3. Psycholinguistic models of native speech perception

In order to account for the processes by which the speech sounds are heard, interpreted, and understood, many models have been proposed in the literature. It is important to discuss the most well-known psycholinguistic models before going into the neuroscientific evidence, in order to understand the most basic concepts, their evolution over time, and relevance to modern assumptions.

One of the earliest models of speech perception, the motor theory, was proposed by Liberman and colleagues in the 1960s (Liberman et al. 1967). In this model, the basic assumption was that humans are able to perceive speech by identifying vocal tract gestures used in pronunciation, rather than the sound patterns in the speech itself. This established a link between perception and production in a way that it assumed that the same processes are used in production (encoding), and perception (decoding). Later, a refined version of the model was proposed (Mattingly and Liberman 1970), that abandoned the physical movements in favor of the neural commands to the articulators, and led to an even later model (Liberman et al. 1985), in which it was the intended articulatory gestures that were perceived by the listener. However, the model faced criticism for the inability of explaining the exact processes, by which the acoustic signals might be translated into intended gestures (Hayward 2000). What is more, if the model was correct, then the production abilities of infants would predict their perceptual skills, which we know is not true (Tsao et al. 2004), and any speech-related impairments would affect perception, which we also know to be false (McNeilage et al. 1967). Also, the model does not account for any extra-linguistic information included in the speech,

such as the identity of the talker, and thus is not sufficient in explaining the whole context of speech perception.

A later model of speech perception, known as TRACE, developed by McClelland and Elman (1986), assumed that speech signal is complex and often ambiguous, and thus different units, such as words and phonemes, should be processed in isolated layers, which can transfer the information to one another, creating an interactive activation model. There are three layers in the model, namely word, phoneme, and feature layer, equipped with special detectors that help recognize relevant information. The input, which is a series of phonemes, is converted into multi-dimensional vector that represents an approximation of acoustic spectra over time. As the input is presented, it changes the activations of the layers, as features activate phoneme units, and phonemes activate word units, however there is no specific mechanisms that determines when a word or a phoneme has been recognized. Apart from inter-layer connections, there are also within-layer inhibitory connections, which help inhibit the information that does not match the input. TRACE is a bi-directional model, which means that it allows for either words or phonemes to be derived from speech. By segmenting individual sounds, it can determine the phonemes, and by combining the phonemes, it can create words and let them be perceived by the listeners. Because of this, it is one of the few models that advocate two-way processing for perception (top-down from words to phonemes, and bottom-up from phonemes to words). Even though TRACE does not fully explain the process of speech perception, in a recent review McClelland et al. (2014) show neurophysiological evidence that models based on interactive activation continue to be relevant to investigating the process of perception.

Another model of speech perception developed in the 1980s, *the cohort model*, was proposed by Marslen-Wilson (1987), and describes how the auditory (and visual) input is mapped onto a listener's lexicon. According to the model, when a listener hears the first phonemes of a word, the whole group (cohort) of words starting with that phonemes are activated. As there are more phonemes entering the brain over time, the list of possible words is getting smaller, and irrelevant cohorts are being deactivated. This process, called *the access stage*, lasts until finally only one word is left to choose from, and it is when *the selection stage* takes over. When the word is chosen in this bottom-up process, there is a need for *the integration stage*, in which the chosen word is tested against the presented word, integrating syntactic and semantic properties (Gaskell

et al. 1997). In statistical simulations performed in order to show how well the model could represent a number of competing lexical items at different cohort sizes, it has been shown that in large cohorts, members could not be distinguished effectively from the mismatched words (Gaskell and Marslen-Wilson 1998), suggesting better performance with smaller cohorts. Even though it has been shown in recent behavioral studies (McQueen 2007; Dahan and Magnuson 2006) that there is in fact a multiple activation and rapid deactivation of candidates during perception, it has been also shown that there is an effect of long-lasting processing of cohort neighbors (Friedrich et al. 2013), suggesting that there exists a parallel system of tracking unfavored candidates, for which the classical cohort model does not account.

Next model, the exemplar theory, has been based on the same premise as the cohort theory, which is the previous experience with words (Goldinger 1996). It is assumed, according to this theory, that the listeners store the memory of acoustic episodes linked to particular talkers. Thus, when a listener hears a word, it is recognized better if uttered by the same speaker as before, with the same properties (e.g. speaking rate). What is more, when recognizing a talker, all the traces of utterances linked to the talker are activated, allowing for the talker's identification. It has been shown experimentally that humans in fact identify signals better when they are familiar with the talker, or when the gender of the talker is known (Johnson 2005). As for encoding novel words, it is assumed that when they enter the memory, their imprint is compared with that of already known words (Goldinger 1998). The main problem with this model lies in the possible capacity of human memory. If a human could remember all the utterances made by all the speakers he or she met in a lifetime, it would require great resources to be used in order to store them as exemplars and recall them when needed (Johnson 2005). Alternatively, it has been shown that even the novel stimuli can be recognized more easily if they are presented by the familiar voice (Nygaard et al. 1994). That would suggest that these exemplars are more related to the properties of the speech, rather than to the content.

1.4. Nonnative and second-language perception

It has been shown in the literature that language learning may influence the perception of phonological information. The experience with more than one language and the course of development can shape the way people perceive speech and make monolinguals and bilinguals differ in their perception of the same language. It has been suggested that bilinguals will never perceive L2 or L1 speech in exactly the same way as native monolinguals of each language (Best and Tyler 2007). That is why in this section, theoretical models of second-language speech perception will be discussed in detail, and perception of speech as a function of linguistic experience will be explored.

It has been long established that the speech environment factors play a vital role in language acquisition, with factors being the length of residence, relative usage of L1/L2 (Flege 1999, 2002; Flege and MacKay 2004), and relative quantity and quality of input from native L2 speakers (for reference see Flege and Liu 2001; Jia and Aaronson 2003; Jia et al. 2006). What is more, phonetic properties of the language directed at learners interact with their developmental level and L2 learning status. Best and Tyler (2007) show a number of studies showing that factors such as vowel hyper-articulation in speech directed to children and foreigners reflect a didactic function of language learner's speech properties. Knowing that the linguistic environment is responsive to the developmental and linguistic status of the listener, the important issue is how the listener's status influence their perception of second language speech. In order to address this issue, there is a need of dividing the listeners into two groups, i.e. naive nonnative listeners, and L2-learning listeners.

The pattern of second-language speech perception is said to be well established for adults with no experience with L2. Functional monolinguals have difficulties in categorizing and discrimination of phonetic contrasts from the languages they do not know, and which are not used to distinguish lexical items in their native language (Strange al. 2001; Polka 1992; Werker and Lalonde 1988). However, it has been also shown that not all nonnative contrasts are of equal difficulty, as some are discriminated moderately, while others almost at native levels (Kochetov 2004; Bohn and Steinlen 2003; Best et al. 2003a; Best et al. 2001). What is more, the level of difficulty seems to vary according to the native language of the listener (Best et al. 2003b; Best and Steinlen 2003). This variety is believed to reflect the perceived similarities and

dissimilarities between phonetic properties of the second language stimuli and the native phonology. (Best and Tyler 2007). In addition, native phonetic biases, coarticulatory patterns, and other phonetic variations may influence monolingual adult's perception of second language speech (Halle et al. 2003; Bohn and Steinlen 2003; Harnsberger 2001). However, it has been shown that monolinguals might also be sensitive to non-contrastive phonetic variation in nonnative language, suggesting that this sensitivity might also reflect universal rather than experienced-based biases (Polka and Bohn 2003).

As far as a L2-learning listeners are concerned, they are categorized as being somewhere along in the process of becoming speakers of language, other than their native one (Best and Tyler 2007). It has been suggested that the phonological systems of L1 and L2 do not reside in complete separation, but are rather situated in an encompassing interlanguage. This might suggest a case, in which L2-learning related perceptual changes influence L1 speech perception, implying that a local change may influence the whole system. It has been suggested that the perception in L2 might be affected by a larger number of factors as compared to monolinguals, such as L2 experience, learning contexts, phonetic contrasts, and specific L1 and L2. Thus, the issue is how perceptual learning of L2 phonological and phonetic properties occurs.

To resolve this issue, two contexts of L2 learning have to be distinguished. The first one is second language acquisition (SLA), which is the acquisition of language in a natural environment, in which the target language is more predominant, and the variety of phonological structures is greater. The second one is classroom foreign language acquisition (FLA), which is more constrained and with the less usage of the target language, often with instructions based in L1 and uttered by an L1-accented teachers. Thus, it is important not to mix the results of SLA with FLA, as it has been shown that even the differences that are dialect-related can influence the perception even for native listeners of L2 (Bundgaard-Nielsen and Bohn 2004). For SLA in adulthood, it has been shown that initially the perception of L2 consonant contrasts that do not occur in the listeners' L1 is poor, which is similar to the case of monolingual listeners with no L2 experience (Brannen 2002). What is more, L2 learners' perception of L2 contrasts may be influenced by L1 phonotactic, allophonic, and coarticulatory patterning (Flege 1989). As for vowels, it has been shown that different L1 might influence the way L2-learning listeners perceive the same L2 vowel contrasts (Escudero and Boersma 2004). What is

the most important aspect, however, is that there is a case of perceptual learning of L2 contrasts that are initially difficult to discriminate, and that is it the experience with L2 that affects the process the most (Best and Tyler 2007). It has been shown that more experienced listeners categorize some nonnative contrasts significantly better than less experienced listeners, but not as well as native L2 speakers (Best and Strange 1992; Flege 1984). However, L2 contrasts that are not so difficult to discriminate for monolinguals are not strongly affected by the level of experience. What is more, perceptual skill level is positively correlated with accuracy in L2 production (Bohn and Flege 1990) and with the ratio of L1/L2 usage (Flege and MacKay 2004). It is important to note, however, that the notion of "experienced" vs. "inexperienced" listener is not clearly established in terms of the duration of L2 immersion. A time-span used in the studies to indicate experienced listeners may vary from as little as 6 months of L2 experience to as much as 10 years (for reference see Best and Taylor 2007). However, it has been suggested that the "experienced" cut off should be set around 6 to 12 months, as significant perceptual learning has been observed in late learners as little as 6-12 months of immersion, and little learning has been observed past that initial period (Flege and Liu 2001). Also, no significant differences have been found between adults with 6-12 months of experience and those with 1.5 years of experience (Aoyama et al. 2004; Jia et al. 2005; Tsukada et al. 2005). Thus, we might assume that the most important part of perceptual learning occurs early in late-onset SLA, which is believed to be intuitive, as the later acquisition of lexicon and higher-order linguistic structure help establish the language-specific relationship between phonetic details and phonological structure (Best and Tyler 2007).

1.4.1. Theoretical models of L1 and L2 speech perception

There are two major theoretical models of speech perception that are cited in the literature. The first one, Perceptual Assimilation Model (henceforth PAM; Best 1995), accounts for nonnative speech perception by naive listeners. The second one, Speech Learning Model (henceforth SLM; Flege 1995) was developed to explain the L2 perception by L2 learners. Thus, these two models will be explained in the following paragraphs, while their commonalities and complementaries will be discussed.

The first model, PAM, assumes that a when naive listeners encounter a nonnative phone, they are likely to perceptually assimilate this phone to the most articulatory-similar native phoneme, which is due to their native-only language experience. This assimilation might have three outcomes. The first possible outcome is that a non-native phone will be heard as a good or a poor exemplar of a native phonological segment, which means that it will categorized. The second outcome is that a non-native phone will be heard as unlike any single native phoneme, which will result in it being uncategorized. The last possible outcome is that a non-native phone will be treated as a non-linguistic nonpeech sound, which will result in it being non-assimilated. It is assumed that naive listeners are unaware of phonetic distinctions that constitute phonological differences, and that is why they are unable to distinguish between phonetic and phonological levels in nonnative stimuli (Best and Tyler 2007). What they can do, is to recognize phonological distinctions in their native language, and possible deviations of nonnative stimuli from their L1 phonemes. For naive listeners the phonological and phonetic levels are only related in L1, in which perceived differences at the phonetic level became related to the functional linguistic categories of a phonological system (Best and Tyler 2007). It is believed, however, that the phonological level is central to perception of L2 by L2 learners; thus, the important issue to discuss is how and when the L1 and L2 phonetic and phonological levels interact and help learn to perceive L2 speech as distinct from L1.

In order to account for this issue, the second perceptual model, SLM, will be discussed in the following paragraph. There are four main postulates of the model proposed by Flege (1995). The first one assumes that the processes and mechanisms that we use in learning the L1 sound system persist over one's life span, and can be used in L2 learning. Of course, this does not mean that throughout a life span there will be no changes accompanied by perceptual learning of higher-order invariants, for example during environmental changes, like contact with a new L1 dialect. These changes, however will result in refining of L1 perceptual processes, and as such L2 perceptual learning will be an extension of these processes. Even though it suggests that the same basic perceptual abilities are available to children learning L1, and adults learning L2, it does not entail that L2 learners acquire new speech information in L1 or L2 in the same way as children acquire it in L1, because of ever-going evolution of an individual's perceptual history and experience. The second SLM postulate assumes that language-

specific aspects of speech sounds are stored in phonetic categories in long-term memory. This is an interesting approach, as it contradicts the dynamic nature of attunement to perceptual invariants proposed by PAM, and instead proposes a set of abstract categories that serve the perceptual processes. What is more, it assumes that it is the phonetic level that is critical to perception of speech, and not the cooperation of processes at the phonetic and phonological levels. The third postulate is an extension of the second one, and assumes that the phonetic categories established in childhood for L1 sounds change over time to account for the properties of all L1 and L2 phones. This again is contradictory to PAM and its assumption that L1 and L2 sounds might be phonologically assimilated, but not necessarily be perceived as identical at the phonetic level. The last SLM postulate claims that bilinguals try to keep the contrast between L1 and L2 phonetic categories, which are stored in a common phonological space.

As it is evident that PAM and SLM are not entirely compatible, Best and Tyler (2007) proposed a model of PAM for L2 (PAM-L2), as a response to the lack of interactions between L1 and L2 phonological levels in SLM. PAM-L2 generally assumes that L2 learner begins acquiring L2 as a functional monolingual, who had developed an L1 phonological system and L1-specific phonetic attunement through monolingual language acquisition. The first contact with an unfamiliar L2 system is described in terms of assimilation processes of original PAM. From that point on, the L2 learner's goal is to learn higher-order invariants of the L2, which results in the common L1-L2 system that incorporates phonetic and phonological levels. In order to show the course of L2 development PAM-L2 proposes four cases of successful L2 perceptual learning (Best and Tyler 2007). The first case assumes that only one L2 phonological category is perceptually assimilated to a given L1 phonological category. This suggests that the learners perceive the L2 sound to behave in the same way as L1 sound at the phonological level, but they can also notice the phonetic difference between them, forming a second phonetic category within under the common phonological category. The second case assumes that both L2 phonological categories are perceived as equivalent to the same L1 phonological category, with one being perceived as being more deviant than the other. This, on the other hand, suggests that a new category for a deviant L2 phone will be created on both phonological and phonetic levels. Initially, the L2 phone will be perceptually learned as a new L2 phonetic variant of the L1 phonological category, but then with greater exposure, the learner will develop a new

phonological category for the phonetically deviant phone. The third case posits that both L2 phonological categories are perceived as equivalent to the same L1 phonological category, but as representing either good or bad instances of this category. It would suggest that initially, the learner will have troubles discriminating between singlecategory contrasts, merging both L2 phones to a single L1 category. However, with a developing adaptation to detecting single-category minimal contrasts, a new phonological category could be established. The last case assumes that if contrasting L2 phones are not assimilated to any L1 phonological category, but are rather uncategorized, then one or two new L2 phonological categories are easily learned perceptually. What is important here, according to Best and Tyler (2007), is the fact that it is not only the phonetic similarity that is key to perceptual learning, but also the comparative relationships within the interlanguage phonology. This means that if the L2 phones are distant from one another within L1 phonological space, the perception of relevant L2 lexical-functional differences should be easy to the learner. However, if the L2 phones are similar within L1 phonological space, then it might be hard for the listener to perceive relevant functional differences, and thus categories would be created differently from the former case. Over the course of L2 learning, these categories should theoretically change to foster the perception, but they may as well stay intact.

Concluding, all three models contribute greatly to a picture of L1 and L2 perception development. It is clearly visible that naive listeners and bilinguals will differ in their perceptual processes, and that experience with other languages is a key factor to these differences. What is more, there is a clear connection between phonetic and phonological levels, and it seems that cooperation between the two is contributing to successful perceptual learning. An overall view that can be derived from these models shows also that an interplay between L1 and L2 is initially important in order to create relevant categories for L2 speech in an interlanguage system, but it diminishes over the course of L2 learning when relevant categories have been already established.

1.5. Chaos and the acquisition of second language phonology

When talking about the process of second language speech perception, there is one important factor that has not yet been discussed. It is the fact that the acquisition of the

second language is an ongoing process that is never finished. In the models discussed earlier, there is an initial state, when a person is a functional monolingual. Then, through gradual acquisition he or she becomes more and more proficient in the second language, finally becoming a bilingual with native-like skills. However, we must realize that because of the high complex nature of language, it is not possible to measure if the process of approximation is ever completed. Even though we can measure the level of proficiency in the second language, we do so by using a set of arbitrary features that reflect a certain level in the acquisitional chain. The issue here is that because of the productive factor of language and ongoing evolution of dialects and accents, these arbitrary features might be easily altered, and thus the goal might never be attained. Thus, the representations of phonological elements, however these are constructed, might be easily susceptible to alteration, and the processes governing these representations might not be at all stable. This might partly explain the differences seen in different models of speech perception and production over the course of a last few decades.

More importantly, however, we have to realize that the process of second language acquisition is not at all linear, and that the initial stage is not equal for all the speakers, which might result in different final products (representations). According to chaos theory, small differences in initial states in dynamical systems might render the outcome unpredictable, even though the systems are deterministic in nature (Kellert 1993). If we take into consideration that the process of second language acquisition is such a dynamical system, in a way that we can predict the outcome of learning a specific element (e.g. learning how to pronounce a phoneme will result in its successful production), and we account for all the individual differences between speakers and their influence on the process of SLA, we might assume that it is in fact the initial stage that drives the differential representation of second language phonology. It is nothing new that individual differences mentioned in the SLA literature, such as age, sex, aptitude, motivation, learning styles and strategies, and personality traits influence the effectiveness of SLA (Zafar and Meenakshi 2012). However, what is different here, is the assumption that attending to all these differences in the process might not lead to the exact same result (which classically is the native-like proficiency). Thus, even though we might perceive highly proficient bilinguals to be similar in terms of language use, the processes and representations that govern beneath might be entirely different. Of course that does not render the speech perception modeling inconclusive, but rather stresses the importance of including all the possible factors, and comparing similarities and differences across the models to get the whole picture.

Apart from individual differences between the learners, the differences between the phonology of a first and second language are also important to focus on. The differences come from general characteristics of second language, such as speech rate and interaction between the first and second language prosody. It has been shown in the literature that the speech rate in L2 is slower than in native speech (Aoyama and Guion 2007; Guion et al. 2000; Derwing and Munro 1997, 1995). This might be primarily caused by the difference in durations of vowels and sonorant consonants between the languages. As for the interaction between the prosody of L1 and L2, such factors as pitch perception (Beckman 1986; Aoyama and Guion 2007), stress placement (Archibald 1995, 1998a, 1998b; Flege and Bohn 1989; Archibald 1997), syllable structure (Broselow and Park 1995; Broselow 1988; Eckman 1991), and tone (Sereno and Wang 2007; Guion and Pederson 2007) come into play. This also stresses the importance of cross-linguistic studies on speech perception and production, as each language pair might influence these processes.

1.6. Representation of language in the brain

In order to discuss the models of speech processing at the neural level, the overall representation of language in the brain must be discussed. Since the brain is split into two distinct cerebral hemispheres, it has been assumed that each hemisphere has different functions, in spite of the fact that both hemispheres resemble each other and the structure of each is generally mirrored by the other side (Toga and Thompson 2003). It is well established that language is generally lateralized to the left hemisphere, since almost 95% of right-handed people have left hemisphere dominance for language, whereas the right hemisphere is dominant for language in only 18% of left-handers (Taylor and Taylor 1990).

According to the classical model known since the 19th century, there are two main areas for language production and perception, namely Broca's and Wernicke's areas (Friedenberg and Silverman 2005). Broca's area, which refers to pars opercularis

and pars triangularis of the inferior frontal gyrus represented in Brodmann's cytoarchitectonic map (henceforth BA) as areas 44 and 45, has been linked to the production of language, as people suffering from lesions in this area generally lose their ability of productive speech. Wernicke's area, on the other hand, which refers to the posterior section of the superior temporal gyrus represented in Brodmann's map as posterior part of the area 22, has been linked to the perception of language, as patients suffering from lesions in this part of the brain lose their ability to understand spoken language.

Even though Broca's and Wernicke's areas are still considered to be relevant to speech production and perception, it is believed that there are more areas which are involved in language processing and that those two areas have slightly different functions than indicated in the traditional model. Amunts (2008: 33) suggests that Broca's area has more functions than just speech production. She claims that Broca's area is also used for language perception, as the dorsal part of BA 45 seems to be involved in semantic aspect of language processing (Amunts 2008). The view is also supported by Poeppel et al. (2008) who claims that many processes connected to language perception, which are ascribed to Wernicke's area are in fact taking place in Broca's area. Even though Broca's area has been long known to be involved in language processing (Sahin et al. 2009), there is an ongoing debate about its exact function (Grodzinsky et al. 2008, Hagoort 2005; 2008; Rogalsky and Hickok 2011). There are different levels mentioned in the literature, on which Broca's area is involved in language processing. The first level is action observation and execution related to motor-speech production and comprehension processes (Pulvelmuller et al. 2010; Rizzolatti et al. 1998). The next level is working memory, which is supported by Broca's region, which is visible in the activations of Broca's in the processing of syntactically complex sentences (Rogalsky et al. 2008; Caplan and Waters 1999). On the linguistic level, there exist also further divisions of Broca's area into regions which are domainspecific. These are BA 44, supporting syntactic structure building, BA 44/45 supporting thematic-role assignment and BA 45/47 supporting semantic processes (Friederici 2002). On the other hand, there is a view that all these regions (BA 44/45/47) are supporting the unification of different aspects of language (Hagoort 2005).

Binder et al. (1997) also suggest that Wernicke's area, although important for auditory processing, is not the main location in which language comprehension takes

place. They claim that language comprehension involves several left temporoparietal regions outside Wernicke's area, as well as the left frontal lobe and the frontal areas, which extend beyond traditional Broca's region, including much of the lateral and medial preftrontal cortex. Binder et al. (1997) claim that isolated damage to Wernicke's area does not produce multimodal comprehension deficits, but rather problems with decoding complex acoustic signals in speech, as the comprehension of language at the semantic level is preserved. It is also suggested that Wernicke's area is not at all the center of oral language understanding, but only an important conduit to language comprehension (Tanner 2007). Binder et al. (2007) also list the angular gyrus, middle temporal gyrus, inferior temporal gyrus, and fusiform gyrus, which are approximately BA 39, 21, 20, 37, and 36, as parts involved in the language comprehension at the linguistic-semantic level.

Furthermore, Amunts (2008) notes that it has been hypothesized that primary motor cortex and premotor cortex, which are BA 4 and 6, are also involved in language processing. The pathway from Broca's area to premotor cortex is of primary importance during early language acquisition, as the auditory-motor integration tunes the system towards the target language (Hickock and Poeppel 2007). The projection from Broca's area to premotor cortex could subserve top-down processes drawing prediction about the incoming information, thus easing its integration (Rauscheckere et al. 2011).

According to Dronkers et al. (2004), results of lesion studies indicate that middle temporal gyrus may be involved in word-level comprehension, the anterior portion of BA 22 may be critical for the comprehension of simple sentences, and superior temporal sulcus and angular gyrus may relate to working memory functions that assist complex sentence comprehension. In addition, Friederici (2006) claims that such subcortical nuclei as basal ganglia and thalamus also play an important role in language processing.

As far as the link between the areas responsible for speech production and speech perception is concerned, Skipper et al. (2005) suggest that integrating the observation of facial movements into speech perception process involves the regions that are associated with speech production, and that these areas contribute less to speech perception when only auditory signals are present. Skipper et al. (2005) observe that these areas, which include the posterior part of the superior temporal gyrus and sulcus, the pars opercularis, premotor cortex, adjacent primary motor cortex, somatosensory cortex, and the cerebellum, may participate in recognition processing by interpreting

visual information about mouth movements as phonetic information based on motor commands that could have generated those movements.

Paradis (2002) also claims that phonology is a part of implicit knowledge, and is stored in procedural memory which relies on the integrity of the cerebellum, the striatum and other basal ganglia, and on circumscribed areas of the left perisylvian cortical region. Binder and Price (2001) support the view claiming that the brain activates the regions responsible for implicit knowledge when is presented with stimuli that have phonological associations and occurs outside the conscious awareness of the subject. Explicit knowledge, on the other hand, according to Paradis (2002) is stored in the declarative memory, which relies on the integrity of the hippocampal system, the medial temporal lobes, and large areas of tertiary cortex, bilaterally.

Fabbro (1999) claims that patients suffering from pure amnesic syndrome, which affects only declarative memory, are still able to learn the second language because their procedural memory is intact, whereas the patients suffering from Parkinson's disease, which affects basal ganglia responsible for procedural memory, are not able to learn the second language, even though their explicit memory is intact.

A recent study (Arsenault et al. 2015) on the representation of phonological features in the brain has shown the activity in bilateral anterior superior temporal gyrus and supratemporal plane while listening to phonemes. What is more, the features of voicing, place and manner of articulation activated the bilateral primary, secondary, and association areas of the superior temporal cortex, but not motor cortex. Even tough there was a bilateral activation, the effect was stronger in the left hemisphere for place, but not manner of articulation.

Even though it has been mentioned that the language is mostly lateralized to the left hemisphere, comprehensive meta-analyses of language-related brain imaging studies found that at least 59 of the 128 articles also reported right sided activations during language processing tasks (Vigneau et al. 2006, 2011). It is evident from the results of various studies that the right hemisphere homologues of left language-related areas are involved in language processing (Muller and Meyer 2014).

1.7. Process-specific language-related neural networks

Spoken language comprehension requires a number of subprocesses that are able to derive the meaning from the auditory input. A comprehensive model of language processing, based on the body of previous neuroscientific research, proposed by Friederici (2011), includes acoustic-phonological, syntactic, semantic, and prosodic processes, and each of these processes will be discussed in the following subsections, based on the review by Friederici (2011), with sources cited accordingly.

1.7.1. Acoustic-phonological analysis

The process of spoken language comprehension starts with the acoustic-phonological analysis, which is supported by the neural circuits in the primary auditory cortex and adjacent areas in the brain (Rauschecker et al. 2009; Scott et al. 2003). The primary auditory cortex is located in humans on the superior surface of the temporal lobe bilaterally in Heschl's Gyrus. Adjacent areas, such as planum temporale, and planum porale, and a region extending from superior temporal gyrus to superior temporal sulcus are all involved in the acoustic analysis of speech. The cytoarchitectonic analysis indicate that the primary auditory cortex usually covers two-thirds of the anterior Heschl's gyrus (Morosan et al. 2001). The primary auditory analysis is performed in Heschl's gyrus, but the functional neuroimaging studies have shown that the areas itself is activated by any type of sound (Jonshrude et al. 2002; Mummery et al. 1999). The region extending to the superior temporal sulcus has been shown to react to acoustic features of phonetic parameters (Binder et al., 2000), but it has been also shown to react to variations in frequency and spectral information of non-speech sounds (Hall et al. 2000). Planum temporale is also active in response to speech sounds, as well as equally complex non-speech sounds (Demonet et al. 1992; Wise et al. 2001; Zatorre et al. 1992). Past studies using time-sensitive paradigm have shown that there is a difference in time between the involvement of Heschl's gyrus and planum temporale (Zaehle et al. 2004); thus, it has been suggested that Heschl's gyrus is associated with analyzing speech signals per se, and planum temporale is involved in a categorizational processes for the segregation and matching of spectrotemporal patterns, as well as sending the

information to higher-order cortical areas (Griffiths et al. 2002). The region, which was identified as the one differentiating between speech and non-speech sounds (using perception of phonemes), is the region located anterolateral to Heschl's gyrus in the superior temporal gyrus/superior temporal sulcus (Obleser et al. 2007). There is, however, another view proposed by different studies, that it is planum temporale and supramarginal gyrus that is involved in the differentiation process between speech and non-speech sounds (Dehaenne-Lambertz et al. 2005; Jacquemot et al. 2003; Meyer et al. 2005), though in contrast to Obleser et al. (2007), the latter studies involved attentiondemanding tasks, and not passive-listening tasks; thus, it might be assumed that under specific task demands, the differentiation between speech and non-speech sounds might be shifted to another processing level. As it has been mentioned earlier that right hemisphere areas also contribute to language processing, it has been shown in the literature that the left and right primary auditory cortex might have different functions. The area in the left hemisphere has been shown to react specifically to speech sounds characteristics, and the area in the right hemisphere to characteristics of tonal pitch (Zatorre et al. 2002); thus, it has been suggested that the former system might be ideal for the perception and recognition of speech sounds, while the latter for dealing with suprasegmental information.

When we talk about spoken language perception, there is an issue of intelligibility that needs to be discussed. Several functional imaging studies have shown that the anterior part of superior temporal sulcus is activated as a function of intelligibility, while the posterior part have been activated by unintelligible sounds containing phonetic information, e.g. rotated speech (Shannon et al. 1995; Scott et al. 2000). This means that the latter part is involved in the short-term representation of sequences of sounds without the stimuli being necessarily intelligible.

1.7.2. Syntactic processes

When the acoustic-phonological analysis is done, initial syntactic processes come into play when processing spoken language. It has been proposed that the simplest syntactic structure based on word category information are constructed first, and the relations are established second (Frazier 1980). This model received some support from event-related

brain potential studies (Bornkessel et al. 2006; Friederici 2002). During sentence processing, the initial stage of phrase structure building is mandatory, and it has been observed that frontal operculum cortex is activated whenever there is a sentence violation, or in the tasks which required comparing sentences to non-structured word lists or the word lists without function words (Friederici 2000). Thus, it might be assumed that local structure building is supported by frontal operculum cortex (Humphries et al. 2005, 2006; Snijders et al. 2009; Stowe et al. 1998; Vandenberghe 2002). However, it should be noted that local structure building is an automatic process in adults and it requires small resources (Hahne 1999, 2002), hence, there might be little or no activation visible in the tasks involving native adult listeners. Other studies using different processing conditions as in language development and second language learning have shown that phrase structure building violations might also involve Broca's area, which suggests that there might be a shift in the process as a function of language proficiency (Brauer et al. 2007; Ruschemeyer et al. 2005).

1.7.3. Semantic processes

When syntactic processing is done, there is time for semantic processes to follow. It is established that there are two structures involved in the process of semantic information, and these are the temporal lobe, and inferior frontal gyrus, which is Broca's area (Fedorenko et al. 2009; Grodzinsky 2010). While some of the studies found that the anterior and posterior temporal regions react specifically to semantic and syntactic processing, there are other views that regard the anterior temporal lobe or the posterior temporal lobe to be not domain-specific.

The activation in the anterior temporal lobe has been reported to change as a function of sentence-level semantic processes, but only under specific stimulus (Rogalsky and Hickok 2009) or task conditions (Vanderberghe et al. 2007). However, it has been also proposed that there are two different subregions within superior temporal gyrus/superior temporal sulcus, which react to syntactic and semantic information, with the most anterior part of superior temporal sulcus responding to syntactic manipulations, and the region posterior to it reacting to semantic manipulations (Humphries et al. 2006). Even though the anterior temporal lobe has been implicated in semantic

processing in general (Lambon et al. 2008), recent meta-analyses of functional imaging studies show that there might be no contribution of this area to semantic processing (Binder et al. 2009), or that the activation in this area might be stimulus-dependent, with greater activation when using auditory sentences (Visser et al. 2009). From the results of these studies, it seems that anterior temporal cortex might be involved in both syntactic and semantic processing, as its function is combinatorial in nature (Friederici, 2011).

As for the posterior temporal lobe, there are studies which link this area to semantic processing at the sentential level. Activation in the posterior superior temporal gyrus/superior temporal sulcus has been found in the processing of the syntactic information that integrates the relations between the verb and its arguments (Obleser et al. 2010; Friederici 2003; Bornkessel et al. 2005; Grodzinsky et al. 2006), which again suggests that semantic processing is combined with syntactic processing. Past imaging studies have shown that the poserior temporal cortex extending to the inferior parietal lobe and the middle temporal gyrus anterior to Heschl's gyrus is involved in the processing of syntactic ambiguity (Tyler et al. 2008), while the left posterior temporal cortex including the superior temporal sulcus, middle temporal gyrus, and inferior temporal gyrus is involved in the processing of semantic ambiguity (Rodd et al. 2005).

Inferior frontal gyrus, which was mentioned earlier as a part of semantic network has been shown in the literature to be the place of the final syntactic-semantic integration (Hagoort et al. 2005; Snijders et al. 2009; Kuperberg et al. 2000; Roder et al. 2002). However, it has been suggested that IFG might be subdivided into different parts, each connected to different linguistic processing, such as phonological (BA 44/6), syntactic (BA 44/45), and semantic processing (BA 45/47) (Hagoort et al. 2005). It has been also shown that the integration of syntactic and semantic information takes place in more anterior portions of Broca's area, and not BA 44 (Rodd et al. 2004; Newman et al. 2010), and thus we may assume that BA 44 is not related to semantic/syntactic processing.

1.7.4. Prosodic processes

Even though the acoustic phonological processing has been already discussed in subsection 1.7.1, it only describes the processing on a segmental level, which is the

processing of phonemes and their features. What is left is the processing of suprasegmental information, which are also needed when processing spoken language.

The brain processes involved in the processing of suprasegmental information have initially been investigated through the study of brain lesions in the left and right hemispheres. Some of the studies have shown that linguistic prosody is processed in the right hemisphere (Bradvik et al. 1991; Weintraub et al. 1980), while other studies indicated both left and right hemisphere might be involved (Bryan 1989). However, when segmental information was filtered out, leaving only suprasegmental information, it has been shown that patients with lesions in the right hemisphere show worse performance (Bryan 1989). Thus, we may assume that it is the right hemisphere that is heavily involved in the processing of suprasegmental information, as the other studies also show that with less segmental information the involvement of right hemisphere is greater (Perkins et al. 1996).

Functional neuroimaging studies support this view, as it has been shown that the processing of pitch information involves the regions in the right hemisphere (Plante et al. 2002). Detailed analyses have shown that superior frontal and fronto-opercular cortices of the right hemisphere react to the presence and absence of pitch information (Meyer et al. 2002; 2004). Right dorsolateral prefrontal cortex and right cerebellum have been also indicated in the process of prosodic segmentation during sentence processing (Strelnikov et al. 2006). One of the studies has found the bilateral activation in the anterior temporal cortex for syntactic and prosodic information, but the area in the left hemisphere was more selective for sentence structure, thus indicating the right hemisphere as the one involved in prosodic processing (Humphries et al. 2005). Concluding, the involvement of the right hemisphere in processing of intonational information (pitch) is clear, however, the localization might be modulated by the presence of concurrent segmental information (Friederici et al. 2004).

1.7.5. Summary of the neural model of spoken language processing

In order to clarify the processes described above, a concise model of spoken language processing can be inferred. In this model the first process that occurs is the acoustic-phonological processing of the incoming stimulus. Acoustic stimulation activates the

primary auditory cortex and the planum temporale. From these two regions the information is send to the anterior and the posterior superior temporal gyrus and superior temporal sulcus. The left anterior superior temporal sulcus reacts as a function of intelligibility of the stimulus, while the anterior superior temporal gyrus is involved in initial local structure building. Then, syntactic and semantic relations are processed in the left temporo-frontal networks. The syntactic network comprises the posterior superior temporal sulcus/superior temporal gyrus and BA 44 (in the frontal cortex), whereas the semantic network includes the middle and posterior middle temporal gyrus and superior temporal gyrus and BA 45 (in the frontal cortex). Then, syntactic and semantic integration takes place with the involvement of the posterior superior temporal gyrus/superior temporal sulcus, and basal ganglia. Finally, the processing of suprasegmental information takes place in the right hemisphere with the interaction of the left hemisphere. The relevant areas of the brain that are part of the model are visualized for reference in Fig. 1.

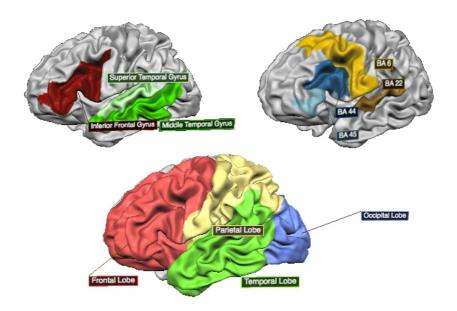


Fig. 1. Anatomical details of the left hemisphere areas that are part of the language network. BA 44/45 – Broca's area; BA 22 – Wernicke's area; BA 6 – premotor cortex.

1.8. Neurocomputational modeling of speech perception and production

Even though there are plenty of studies that pinpoint neural structures relevant to speech perception, little is known about the exact neural functioning of these structures. In order to shed some light on this matter, quantitative neurocomputational models emerged in the literature, which try to explain the exact behavior of these complex functions, combining neural simulations with neuroimaging data. Even though there are a few models prevalent in the literature (Kroger et al. 2014; Westerman and Miranda 2004; Garagnani et al. 2008; Wennekers et al. 2006; Guenther and Vladusich 2012), one of them, DIVA (Guenther and Vladusich 2012; Guenther et al. 2006), has provided a comprehensive framework for integrating neuroimaging findings with computational modeling of speech perception and production, by associating the model components with specific brain regions. Thanks to that, it is possible to compare the results of simulations to actual results found in the neuroimaging literature. The following description of the DIVA model is based on two papers describing the model by Guenther and Vladusich (2012), and Guenther et al. (2006).

DIVA in short is an adaptive neural network, which is capable of learning to control movements of a simulated vocal tracts to produce phonemes, syllables, and whole words. As an input, DIVA takes a series of speech sounds and generates time sequence of articulatory positions as an output (Guenther et al. 2006). DIVA consists of a number of neural representations, called *neural maps*, and synaptic projections that transform one representation into another. The production of a speech sound in the model starts with the activation of neurons linked to that sound in the model's speech sound map. This sound can be a phoneme, a syllable, or even a short syllable sequence, which is assumed to be the most typical unit represented by a single model neuron in the speech sound map, corresponding to a bundle of real neurons in the cortex. The activation of the speech sound map leads to motor commands that are sent to the primary motor cortex over two control subsystems, a feedforward control system, and a feedback control system. The feedforward control system is a direct projection from the speech sound map to articulatory control units in the cerebellum and primary motor cortex. The feedback control system, on the other hand, consists of two, auditory and somatosensory, subsystems that projects indirectly through sensory brain areas.

It is assumed in the model that each cell in the speech sound map corresponds to to neurons in the left ventral premotor cortex and/or Broca's area, representing a different speech sound (Guenther et al. 2006). According to the model, the speech sounds (phonemes, syllables or short utterances) that are frequently encountered in the native language are associated with the stored motor programs for their production. Less frequent sounds, however, do not have such stored programs, and are produced by activating motor programs for smaller units (e.g. phonemes) that can form a larger unit. Ventral premotor cortex is associated with the speech sound map, because of its association with mirror neurons, which are activated both during an action and while viewing the action made by others (Kohler et al. 2002). Model neurons in the speech sound map are hypothesized to reflect similar properties to mirror neurons, which is the assumption that activation during speech production drives complex articulatory movement, and activation during speech perception tunes connections between the speech sound map and sensory cortex (Guenther et al. 2006). Each time a sound is fed to the model for learning, a new cell is recruited in the speech sound map to represent that sound. After the model has learned the sound, the activation in the speech sound map leads to production of the corresponding sound through the model's feedforward and feedback systems.

According to the model, early random and reduplicated babbling generate a combination of auditory, motor, and somatosensory information that is used to tune the synaptic projections between the motor cortex and sensory error maps, using feedback control map in right ventral premotor cortex. In the later stage of imitation learning, the error maps record the difference between intended and actual sensory states, and the sensory-motor transformations learned in the babbling stage allow detected sensory errors to be mapped onto corrective motor commands (Guenther and Vladusich 2012). In the imitation stage, which corresponds to infant's learning of new native speech sounds, the detection of a novel sound leads to the activation of previously unused neurons in the speech sound map, and then to the encoding of an auditory target for this new sound in the synaptic projections from the speech sound map to the auditory error map, which includes allowable variability in the acoustic signal. The speech sound map neurons that represent the speech sound will be also used in the production, as mentioned before.

In the production stage of imitation learning process, the model attempts to produce the sound by activating the speech sound map neurons, which correspond to the sound, and leads to a readout of a feedforward command. In the initial attempts at producing a new sound, no tuned feedforward commands will exist, thus the model must employ an auditory feedback control, as the auditory errors will arise. This feedback control transforms auditory errors into corrective motor commands through the feedback control map in the right ventral premotor cortex. With each attempt at production, the feedforward commands will become refined by incorporating the commands updated by auditory feedback control. With enough practice, the feedforward system will be sufficient for producing accurate sounds, and thus with no errors, the auditory feedback control will not be evoked. At this point, when the sound is learned, a somatosensory target, as opposed to an auditory target mentioned before, is also learned, and represents the expected sensations associated with the sound, which is in turn used in somatosensory feedback control subsystem to detect somatosensory errors.

As it was mentioned before, the biggest advantage of this model is that it can be tested against the results of real neuroimaging studies, and actually Guenther and Vladusich (2012) show the results of such comparisons, focusing on feedback and feedforward control, and speech mirroring. The first component to be tested was the feedback control. As it has been discussed earlier, the auditory feedback control plays a big role in tuning the speech motor control system. According to DIVA, the auditory target region for the sound being produced is comprised of the axonal projections from the speech map neurons in the left ventral premotor cortex and posterior inferior frontal gyrus to higher-order auditory cortical areas, which represent the auditory feedback that should arise when the speakers hear themselves producing the sound (Guenther and Vladusich 2012). This target is tested against the incoming auditory information from the auditory periphery, and if the current feedback is outside of the target region, then the auditory error maps are activated in the superior temporal gyrus and planum temporale. Using the error signals, corrective motor commands are projected into the motor cortex from the auditory error maps. The auditory target projections from the sound map to the auditory cortical regions inhibit the auditory error maps, hence when the incoming feedback is within the target region, this inhibition comes into play and cancels the excitatory input from the auditory periphery. However, when the current feedback is not in the target region, this inhibition is not fully performed, thus activating

the auditory error maps. The inhibition system is assumed to be a unique functional prediction of the DIVA model in relation to mirror neurons (Guenther and Vladusich 2012). However, it was mentioned before that if the sound is learned properly, the error maps will not be activated. Thus, the only way to experimentally distort the auditory feedback is the real-time perturbation of the first formant frequency downward or upward, so that the speaker hears himself producing a wrong sound. This was hypothesized to activate auditory error maps during the perturbation, while the shift in the frequency itself would not be noticed by the speaker. The hypothesis was tested in a study (Tourville et al. 2008), in which participants were asked to produce one-syllable words, while their brain's activity was recorded by the magnetic resonance scanner. In one of the four trials, the frequency of the first formant was shifted, thus creating a perturbed trial, and allowed for the brain activation between unperturbed and perturbed trial to reflect the activation of the auditory error maps. As it was predicted by the model, there was a significant activation of the posterior superior temporal gyrus and planum temporale, with peak activation in the posterior end of the left planum temporale, which reflected the activation of the auditory error maps (Guenther and Vladusich 2012). However, the model also predicted a bilateral activity of the primary motor cortex, which should reflect the projection of corrective motor commands to the motor cortex, while the experimental results showed the right-lateralized activity in the premotor cortex. That is why, Guenther and Vladusich (2012) updated the model and introduced the feedback control map, which contains neurons responsible for coding corrective motor commands for detected sensory errors.

In order to support the sensory feedback hypothesis in the model, a second experiment was devised, using sensory perturbations. It has been long known that along the auditory information, somatosensory information is also important for speech production. In DIVA model, the somatosensory state map contains the representation of tactile and proprioceptive information from the speech articulators in primary and higher-order somatosensory cortex in the postcentral and supramarginal gyrus. According to the model, the somatosensory error map, which is located in the supramarginal gyrus, becomes activated when there is a mismatch between the feedback from the vocal tract and somatosensory target region for the sound being produced (Guenther and Vladusich 2012). Analogous to the correction from the auditory feedback, the output of somatosensory error map leads to the corrective motor

commands. In order to test this hypothesis, Tourvile et al. (2008) created an experimental somatosensory perturbation. While the participants were reading the words, like in the auditory experiment, in 1 of the 7 trials a little ballon placed behind their molars was rapidly inflated, causing the unexpected blocking of the jaw. The activations found in the brain of participants during the study have shown that in the perturbed speech the strongest activation was found in the supramarginal gyrus bilaterally, which was in accordance to the model, and in the right ventral premotor cortex, which provided support for the feedback control map mentioned earlier (Guenther and Vladusich 2012).

As for the feedforward control, in the DIVA model it is assumed that the projections from the speech sound map in left ventral premotor areas to primary motor cortex, supplemented by cerebellar projections constitute feedforward motor commands for syllable production, necessary for fluent speech (Guenther and Vladusich 2012). The location of these components are supported by the studies, which show the high interconnectivity between premotor and primary motor cortices (Krakauer and Ghez 1999; Passingham 1993), and support the idea that cerebellum receives input from premotor, higher-auditory and somatosensory areas that are required for choosing motor commands (Schmahmann and Pandya 1997). What is more, studies show that damage to the cerebellar cortex might result in a speech disorder, characterized by poorly coordinated speech (Ackermann et al. 1992), which supports the role of this region in providing feedforward commands.

Finally, as the DIVA model assumes that mirror neurons arise as a consequence of imitation learning, it predicts the link between perception and production in the form of motor programs that are acquired and associated with each speech sound. The model predicts a causal relationship, which assumes that individuals with more distinctive auditory speech representations are being able to discriminate better between similar speech sounds (Guenther and Vladusich 2012). This hypothesis in fact has been supported by several experimental studies (Villacorta et al. 2007; Perkell et al. 2004a, b).

It is clear from the above-mentioned arguments that combining interdisciplinary data to form a model might contribute to better understanding of the processes involved in such complex functions as speech perception and production. However, as long as these models will focus only on the native language systems, the simulated and

experimental results might never fully converge, as the interaction between different language systems in the brain, prevalent in the modern bilingual culture might account for the missing links.

1.9. Representation of two language systems in the brain

As far as the representation of two language systems in the brain of bilinguals is concerned, there is a number of hypotheses examined by Paradis (2004). According to the extended system hypothesis, languages are undifferentiated in their representation, and elements of the various languages are processed as allo-elements, i.e. different surface manifestations, of the same underlying concept. The dual system hypothesis states that each language is represented independently in separate systems. The tripartite system hypothesis proposed that the items, which are identical in both languages, are stored as one item in the shared system, whereas the items that are different are stored in separate systems, one for each language. There is also a variation of this hypothesis, which states that what has been acquired in the same context is stored in a common neurofunctional system, and what has been acquired in different contexts is stored in separate neurofunctional systems (Paradis 2004). According to the subset hypothesis, bilinguals have two subsets of neural connections, one for each language system, with elements from one language more strongly linked to each other than to the items from the second language.

These theories have been reviewed extensively using experimental techniques, (Abutalebi 2008; Abutalebi et al. 2001; Indefrey 2006; Stowe and Sabourin 2005) and it has been concluded that it is the level of proficiency in L2 that has the biggest impact on the representation of L1 and L2 in the brain, regardless of the age of acquisition. According to these reviews, when the level of proficiency is high, there is one common system for the processing of both languages, and when the level of proficiency is lower, there is extensive activation in the right hemisphere of the brain. It has been also shown that late language learners use the same neural substrates for L1 and L2, but the subprocesses involved in normal language processing are not utilized optimally in some aspects of L2 processing, at least for the less proficient speakers (Stowe and Sabourin 2005). A detailed review of relevant studies on the representation of L1 and L2 in the

brain, taking into consideration such variables as the difference between the languages, the age of acquisition, proficiency in language, different methods of exposure, and different cognitive techniques involved in language processing, is described in section 1.12.

1.10. Working memory and language – the case of phonological loop

Temporary storage and manipulation of information that is required for different cognitive tasks involves working memory. Baddeley and Hitch (1974) proposed a model that divides working memory into three subsystems, namely phonological loop, visuospatial sketchpad, and the central executive. As this thesis is concerned with phonological processing in the brain, only the phonological loop will be now discussed in detail, as it is concerned with verbal and acoustic information and might have possible implications for both L1 and L2 learning and processing.

The phonological loop could be divided into two subcomponents, one for holding memory traces over matter of seconds, and one for refreshing of these decaying traces (Baddeley 2003). These components incorporate subvocal rehearsal system, that leads not only to storage of information, but also to register visual information within the store, if the items can be named. This means that even though some stimuli might be presented visually to the subjects, the subjects will subvocalize them, and the retention in the memory will be dependent on the acoustic or phonological features of the stimuli. This phenomenon has been studied experimentally and shows that people are able to recall the words with phonological dissimilarity easily, while the words that are phonologically similar will be troublesome to recall (Baddeley 1966), regardless of the similarity of meaning. Further studies have also shown the effect of word length on the immediate recall of information, as the subjects were better at recalling monosyllabic items than at recalling items with at least 5 syllables (Baddeley et al. 1975). What is interesting, patients with disarthria, who lost the ability of overt articulation, are still able to perform subvocal rehearsal, which reflect the word-length effect (Baddeley and Wilson 1985). On the other hand, patients with dyspraxia, who lost control of assembling speech-motor control programs, show no sign of rehearsal (Caplan and

Waters 1995). This suggests that it is not the overt articulation, but the capacity to set up speech-motor programs that underpins phonological rehearsal.

It has been shown that the above-mentioned system might have evolved in order to facilitate language acquisition (Baddeley 2003). People with suppressed rehearsal are able to associate pairs of unrelated words in the native language, but they are unable to learn new words in L2 (Baddeley et al. 1988). What is more, there have been studies showing that people (both children and adults) with shorter memory spans have problems with learning new vocabulary and syntax in L2 (Atkins and Baddeley 1998; Gathercole et al. 1999; Service 1992). This suggests that the phonological loop might be essential in the process of learning L2.

As for the neural substrates of working memory, there have been plenty of studies that investigated this issue. It has been suggested that Broca's area is involved in working memory in general (Yang et al. 2015; Wager et al. 2003). Also, the premotor cortex have been shown to be a key part for rehearsal process (Yang et al. 2015). What is more, the inferior parietal lobule, which has been linked to phonological representation, semantic integration, and second language vocabulary learning (Della Rosa et al. 2013, Mechelli et al. 2004; Li et al. 2014) is believed to play a key role in formation and maintenance of lexical representation that is required for successful L2 acquisition (Yang et al. 2015).

1.11. Methods of brain imaging

Even though there are many different brain imaging techniques, two of them, which are magnetic resonance imaging (henceforth MRI) and positron emission tomography (henceforth PET), are commonly acknowledged as useful tools for the neurological study of the brain structure and its functions with respect to language (Obler et al. 2007). Both techniques allow researchers to record and look at the brain activity of a subject participating in a linguistic task, as they use regional cerebral blood flow, which increases in a region when there is synaptic activity, to demonstrate both location and level of activity; however, PET requires a slightly radioactive substance to be injected into subject's body, as the scanner records activity of the brain based on positive electrons which are tracked after mixing with the glucose which is the fuel of our brain,

whereas functional MRI scanners rest on magnetic properties of hemoglobin, oxygen metabolism, and blood flow, which distort magnetic field differently at different levels, revealing the parts of the brain that are active. It is important for a successful study, according to Obler et al. (2007), to get two sets of images, one during a control state and one during an experimental language task, and use a subtraction method to determine which parts are involved in a particular language task. As the spatial resolution of both types of scanners is high, activated areas may be scrutinized in great detail.

1.12. Contemporary brain imaging studies on the representation of language in bilinguals

Various studies using different brain imaging techniques show that identifying brain structures responsible for L2 system is not a straightforward process, as results of different studies vary significantly. The results also show that the difference in brain activation during language tasks may be related to various variables, namely the difference between the languages, the age of acquisition, proficiency in language, different methods of exposure, and different cognitive techniques involved in language processing. That is why, in the following subsections, the results of the most relevant studies concerning above-mentioned issues will be discussed in detail.

1.12.1. Studies on different hemispherical representations of two languages in the brain

Perani et al. (1996) show the results of a PET study conducted on nine Italian native speakers, aged between 21 and 32, who had studied English at school for at least 5 years and had not been exposed to English language before the age of 7. Subjects participated in the phonological task, which consisted of listening to stories in Italian and in English, and their brain activation during the task was recorded with PET. The results shows that during the listening to the story in the native language there was activation in both hemispheres. In the left hemisphere there was activation in the classical left perisylvian language areas, including the angular gyrus, the superior and middle temporal gyri and

the inferior frontal gyrus, and temporal pole, which are mapped by Brodmann as areas 39, 22 and 21, and 45. In the right hemisphere there was activation in the right superior and middle temporal gyri, the right temporal pole, and the posterior cingulate, which are Brodmann areas 22 and 21, 38, and 31. The right cerebellum was also significantly activated. As for the task conveyed in the second language, the set of activated areas was considerably reduced. The results show that only the left and right superior and middle temporal areas, which are BA 22 and 21, remained active and that there was a minor bilateral activation of parahippocampal gyri, which is BA 36, suggesting an increased participation of memory-related structures (Perani et al. 1996).

Dehaene et al. (1997) show the results of a functional magnetic resonance imaging (henceforth fMRI) study conducted on French learners who were moderately fluent in English, which they acquired at school after the age of 7, which indicate anatomical variability in the cortical representation of L1 as opposed to L2. Subjects listened to stories recorded in L1 and L2, and activation of their brain during these tasks was recorded by the fMRI scanner. According to the results, when listening to L1, there was remarkable consistency in the observed areas in the left hemisphere, as all subjects showed activity in the left temporal lobe all along the supierior temporal sulcus, as well as in neighboring portions of the superior and middle temporal gyri, often extending forward into the temporal pole and backward into the left angular gyrus (Dehaene et al. 1997). Although similar activity was occasionally found in the right temporal lobe, it was weaker and highly variable from subject to subject, and never extended to the right angular gyrus. Listening to L2, however, showed greater subject variability. According to the results, no single area was found active in more than 6 out of 8 subjects. There was activation in the left temporal lobe, including superior temporal sulcus, superior and medium temporal gyri, but no activation was found in the left temporal pole or angular gyrus. Two of the subjects showed a striking absence of any activation in left temporal region while listening to L2, as only right temporal lobe was active during the task. Variable activation during the L2 task was also shown in cerebral regions outside the temporal lobe. Even when subjects showed the activity in left temporal lobe while listening to L2, its volume was always smaller than while listening to L1, and always activated additional small subregions in the right temporal lobe. Dehaene et al. (1997) claim that the highly reproducible left temporal activations during the listening task in L1 confirms the assumption that it is a dedicated network of left hemispheric cerebral

areas which underlines the native speech, and that the results of the study indicate that in late and moderately proficient learners of L2 this network fails to be recruited for second language comprehension. The inferior frontal activation in L2 may suggest the use of the strategy of internal rehearsing the English words using the phonological loop to maintain L2 sentences in the working memory while processing them. (Dehaene et al. 1997).

Callan et al. (2004) show the results of an fMRI study conducted on both native and second language speakers of English, which indicate the activation of different areas of the brain in native and second language speakers during the same task of phoneme identification in English. The subject group, consisting of twenty two native speakers of English, and twenty two native speakers of Japanese who had learned English for at least 6 years in a school environment, participated in a phoneme identification task, in which they were presented with the speech stimuli consisting of English syllables beginning with r or l with nine different following English vowel contexts, and their task was to identify whether the stimuli started with r, l, or a vowel by pressing the relevant button with their left thumb, and the activity in their brains during the task was recorded by the fMRI scanner. According to Callan et al. (2004), the results support the hypothesis that second language speakers utilize articulatoryauditory and articulatory-orosensory based internal models instantiated in the cerebellum as well as in recurrent connections between cortical regions involved with speech production planning, which are Broca's area, anterior insula, and premotor cortex, auditory-articulatory mapping, which is posterior superior temporal gyrus, and orosensory-articulatory mapping, which is supramarginal gyrus, for perceptual identification of a difficult second language phonetic contrast to a greater extent than native speakers of that language. What is more, the results show that native speakers use auditory phonetic representations, localized in anterior superior temporal gyrus/sulcus for phoneme perceptual identification to a greater extent than second language speakers. Although the activation in both native and second language speakers of English was bilateral, there was considerably more activation in the left hemisphere.

Leonard et al. (2010) conducted a study on single word processing of L1 and L2 in adult bilinguals. Eleven subjects, aged 18-29, whose L1 was Spanish and L2 was English, were presented visually with names of different objects in L1 and L2, while their brain activation was recorded by MEG and fMRI, and were asked to assess

whether the object would fit into a shoebox. The results show that words in L1 evoked a typical left-lateralized sequence of activity, first in ventral occipitotemporal cortex, associated with visual word-form encoding, and then in ventral frontotemporal regions, associated with lexico-semantic processing, whereas words in L2 evoked greater activity in the right ventral occipitotemporal cortex in the early stage, with this activity receding with words becoming familiar through repetition. In general, L2 responses were later and more bilateral than L1 responses, which suggests that acquiring a language involves a recruitment of right hemisphere and posterior visual areas that are no longer necessary when the fluency is attained.

1.12.2. Studies on different levels of proficiency and the age of acquisition

Perani et al. (1998) show the results of a study conducted on nine Italian-English bilinguals who learned English at school and showed low proficiency in their L2, and nine Italian-English bilinguals who acquired English after the age of ten and showed high proficiency in that language, which indicate that the age of acquisition does not affect cortical representation of the two languages in the brain. The subjects in the study were instructed to listen to four stories in their L1 and then to listen to four stories in their L2, and the activation of their brains was recorded with the PET scanner. The results revealed that there was a similar pattern of activation in both groups of subjects while listening to the stories in L1, i.e. activation foci in the left hemisphere in the temporal pole, the superior temporal sulcus, middle temporal gyrus, and hippocampal structures. However, listening to the stories in L2 involved different activation patterns in both groups. In the subjects who were highly proficient in English the activation pattern was similar to that showed during listening to the stories in L1, whereas in the subjects who were not proficient in English there was no activation for L2 in the temporal poles, or in the left anterior and posterior parts of the middle temporal gyrus. Perani et al. (1998) claim that the results suggest that the level of proficiency have an effect on cortical activity of the brain, whereas the age of acquisition does not affect the cortical activation, as both groups were late learners of English.

Chee et al. (2005) conducted a study on the activation of different brain areas in two groups of Mandarin-English bilinguals depending on their level of proficiency in the second language. Both groups, one less proficient in English and one proficient in English, were instructed to decide which pair of words is closely related in meaning to the reference word, and the activation of their brains during the study was recorded by the fMRI scanner. The results reveal that the task in the language in which the subjects were proficient involved the same brain areas in the subjects from both groups, namely left prefrontal, midline frontal, left mid and posterior temporal, inferior temporal and left parietal, which are BA 7, regions (Chee et al. 2005). However, the task in the less proficient language showed greater left prefrontal activation. What is more, a group of less proficient L2 speakers showed additional bilateral opercular activation during the task in their L2. Chee et al. (2005) suggest that the greater left prefrontal activation may be related to the greater effort the less proficient L2 subjects had to put to retrieve the semantic information about words in their L2, since the neurons in the prefrontal cortex respond differently to familiar and unfamiliar items.

Pillai et al. (2004) show the results of a study conducted on eight subjects, aged 21 to 42 years, whose L1 is Spanish and who started learning English as their L2 after the age of 10 and attained high proficiency in the language. Subjects participated in the phonological task in which they were instructed to decide whether a pair of words rhymed or not. The task was first conveyed using Spanish words and then the same task was repeated using English words. During the whole process the activation in the brain of the subjects was recorded using the fMRI scanner. The results shown by Pillai et al. (2004) reveals greater contribution of the left cerebellar hemisphere to overall cerebellar activation in L2 than with L1, which suggests that cerebellum plays an important role in cognition, particularly second language processing. Even though the activation of cerebellum may be related to the presentation of stimulus, as the left cerebellar hemisphere is involved in visuospatial processing, the reason for greater activation during L2 tasks is unclear and calls for closer investigation (Pillai et al. 2004).

Isel et al. (2010) conducted a study on the effects of neural maturation on ultimate attainment of grammatical competence in L2 learners. A set of concrete nouns, repeated in French and German, was presented to early and late French-German bilinguals, while the activity of their brains was recorded on fMRI scanner. Early bilinguals, with the age of acquisition of 3 years showed larger repetition enhancement effects in left superior temporal gyrus, the bilateral superior frontal gyrus, and the right posterior insula, whereas late bilinguals, with the age of acquisition of 10 years, showed

greater repetition enhancement effects in the middle portion of the left insula, and the right middle frontal gyrus, which suggests that the attainment of lexical knowledge in L2 is affected by neural maturation.

Archila-Suerte et al. (2013), performed a study on English monolingual and Spanish-English bilingual children, in order to pinpoint the neural basis of non-native speech perception in bilingual children. Both monolingual and bilingual children were divided into two groups of younger (6-8 years) and older children (9-10 years). Each participant was asked to watch a silent movie, while a set of English syllable combinations was played on the headphones, and their brain activity was recorded by an fMRI scanner. The results have shown that the neural mechanisms supporting speech perception throughout development differ in monolinguals and bilinguals. Monolinguals recruited perceptual areas, i.e. superior temporal gyrus, in both early and late childhood to process native speech, while bilinguals recruited perceptual areas in early, and higherorder executive areas, i.e. bilateral middle frontal gyrus and bilateral inferior parietal lobule, in late childhood to process non-native speech. These results are interesting, as they seem to support PAM and SLM models, mentioned in previous sections. Younger bilingual children seem to recruit superior temporal gyrus exclusively, because it is in this area that the learning of L2 phonemes is facilitated by assimilating the sounds onto L1 phonology, which supports PAM. Older bilingual children, however, recruit higherorder cognitive areas to improve the discrimination of L2 sounds, which supports the idea proposed in SLM that increasing attentional resources to phonetic information help with novel L2 learning.

1.12.3. Studies on different types of exposure to language

Fabbro (1999) claims that learning a language in a school setting is apparently likely to determine a less cortical representation of L2 as opposed to L1 and that if L2 has been acquired only formally, for example at school, cortical areas involved in the comprehension of spoken L2 are activated to a lesser extent than in the comprehension of spoken L1. Fabbro (1999) also claims that learners who learned L2 in a school setting do not show activation in the right cerebellum, the structure that intervenes in the organization of procedural memory of language, during L2 comprehension tasks.

Perani et al. (2003) conducted a study on two groups of early-acquisition, highproficiency bilinguals, which indicate that the different exposure and usage of language may affect the cortical representation of highly proficient bilinguals. The subjects were six Spanish-speaking and five Catalan-speaking bilinguals who acquired their second language, Catalan and Spanish respectively, at school after the age of three, and were living in Catalonia when Catalan is used in everyday social interactions. Perani et al. (2003) conducted a lexical search and retrieval task on the subjects and used an fMRI scanner to record the activity of the brain during the task. The only difference between the two subject groups was the amount of exposure to L2 and daily usage of L2, as the exposure to L2, which was Spanish, for Catalan speakers was less than it was for Spanish native speakers. The results show that when Catalans produced Spanish words, there was more extensive activation in the left inferior, BA 44 and 47, left middle, BA 46 and 10, frontal gyrus, left premotor cortex, BA 6, and insula. What is more, brain activity was also recorded in the left inferior parietal lobule, BA 40, in the left caudate nucleus and in the right inferior frontal gyrus, BA 47. In Spanish subjects when speaking Catalan, there was a less extended pattern of brain activity in the inferior, BA 45, and middle frontal gyrus, BA 46 and 10, and in the insula. Perani et al. (2003) claim that the results suggest that the amount of exposure to language plays an important role, as it may affect the neural representation of the two languages in the brain. Perani et al. (2003) also suggest that repeated activation of the cortical representations in a language may enhance the neocortical connections so that the neural network could support lexical retrieval with a less extensive involvement of prefrontal areas.

Bloch et al. (2009) performed a study on the effect of age of exposure to L2 on brain activation elicited by narration in three different languages. They found greater variability in activation in all three languages in late learners, whereas in early multilinguals they found low variability in activation across the languages, even if one of them was learned late. There was also no difference in variance between subjects with passive and active early bilingual upbringing. The results suggest that early exposure to more than one language gives rise to a network that is activated homogeneously in early and late learned languages, whereas inhomogeneous activation in late multilinguals indicates more independent access to the multilingual resources.

Tu et al. (2015) show the results of the study on the effects of the short-term exposure on neuroplasticity in the bilingual brain. They recruited 10 Cantonese (L1)-

Mandarin (L2) speakers, who underwent the same fMRI scan twice, while performing silent narration, with the second scan occurring after 30 days of increased differential language exposure. The authors found that the interaction between language and language exposure were found in the left pars opercularis (BA 44) and marginally in the left middle frontal gyrus (BA 9), in the condition of balance language exposure in the task (L1/L2 usage percentage at 50%:50%). In the condition of L1/L2 usage percentage at 90%/10%, activations were found in bilateral BA 46 and BA 9, in the left BA 44, and marginally in the left caudate. There was also a significant negative correlation between language exposure to L2 and signal activation values in the anterior cingulate cortex. The results suggest that even a short period of exposure to a second language might influence the neuroplasticity of the brain.

Mei et al. (2015), on the other hand, conducted a study on the effects of long-time experience with Chinese language on English-Chinese speakers. In the study, they recruited three groups of participants, i.e. Chinese native speakers, English native speakers with Chinese experience, and English native speakers without Chinese experience. The participants were ordered to read aloud in their respective native language and the activity of their brains was recorded with fMRI scanner. The authors found out that when reading words aloud in the native language, Chinese speakers and English speakers without Chinese experience differed in the functional laterality of the posterior fusiform gyrus (right laterality for Chinese speakers, and left laterality for English speakers). What is more important, English speakers with Chinese experience showed more recruitment of the right posterior fusiform gyrus for words and pseudowords, which is similar to how Chinese speakers processed Chinese. These results suggest, Mei et al. (2015) argue, that long-term experience with L2 shapes the fusiform laterality of L1 and have important implications for the understanding of the cross-language influence in terms of neural organization.

1.12.4. Other imaging studies concerning bilingual subjects

Hernandez et al. (2001) show the results of a study, which was conducted to examine the neural substrate of language switching. The subjects, six Spanish-English bilinguals who learned both languages before the age of five and were enrolled in or had

completed college, participated in two tasks which consisted of switching between languages and switching within languages. In the between-language switching task the subjects were presented with the pictures of objects along with the cue, either the word "say" or "diga", and they were instructed to name the object in the language indicated by the cue word. In the within-language switching task the subjects were presented with the pictures of objects and actions, along with the cue words "the" and "to" respectively, and were instructed to either name the object or name the action. Both tasks were divided into three conditions, two blocked and one mixed. In the two blocked conditions the cues were not changing throughout the entire task, whereas in the mixed condition the cues were changing in a random manner. The results of a study reveal that naming objects led to activation in the frontal cortex, which extended from the dorsolateral prefrontal cortex to the premotor area in the left hemisphere (Hernandez et al. 2001). The pattern was similar to that obtained from the within-language switching task, and there was no difference in activation for each language, even though the naming in English was generally done faster than in Spanish. The similar pattern was also visible in the between object naming and action naming within the language. The most significant difference, according to Hernandez et al. (2001), was observed in the comparison of blocked and mixed condition results, as there was an increased activation in the right dorsolateral prefrontal cortex for switching relative to no switching in the between-language condition. What is more, there was an increased area of activation in the left inferior frontal gyrus for the blocked condition relative to the mixed condition. Hernandez et al. (2001) suggest that switching between languages in picture naming requires increased executive function as opposed to increased phonological recoding or motor planning, and that object naming and action naming involve highly overlapping neural systems.

A similar fMRI study was conducted by Klein et al. (2006), which was focused on within- and across-language adaptation for spoken words. The subject group consisted of 16 English-French bilinguals from Canada, whose native language was English and who learned their second language between 4 and 12 years of age. The subjects were instructed to listen to the sets of stimuli in 8 different conditions and the activity of their brains was recorded by the fMRI scanner. The sets of stimuli in each condition differed by the sequence of words presented. Stimuli in the first two conditions, one for each language, consisted of six words with no items varied to attain

maximal adaptation. In the remaining six conditions, three for each language, each set of stimuli consisted of six words with the five identical words and with the sixth word changed. These changes consisted of a change in meaning, change in language, change in language and meaning. The results show brain different activation in different study conditions. In the condition with no change of words, the activated areas observed were inferior frontal gyrus and superior temporal gyrus in the left hemisphere, and superior temporal gyrus in the right hemisphere. In the L1, a word change, irrespective of condition or language, resulted in extensive bilateral activations of the primary and secondary auditory areas, and the activation in the regions in posterior left inferior frontal gyrus at or near Brodmann areas 44 and 6. Klein et al. (2006) suggest that this may implicate that left inferior frontal gyrus is involved in accessing lexical information. In the L2, on the other hand, changes in meaning and both changes in meaning and language resulted in increased bilateral activity along the superior temporal gyrus and in the left inferior frontal region, but changes in language alone did not evoke any activation in the left inferior frontal gyrus. This, according to Klein et al. (2006), may suggest that either the L2 word activated the L1 equivalent automatically, or subjects were consciously translating in this condition because of their level of proficiency in L2. What is more, in the condition in which the first five words were the same words in L2 and the last word was the translation of the word in L1, there was a decrease in activation in the dorsal left inferior frontal region. Klein et al. (2006) claim, that various cognitive studies showed that in early stages of learning, L2 vocabulary items are processed primarily through association with their equivalents in L1, whereas in later stages of learning they are more strongly associated with their meanings. Hence, since the study shows that L1 and L2 vocabulary appear to access the same semantic system, the observed decrease in activation in the dorsal left inferior region may imply less release from adaptation in more proficient bilinguals. The results of the study clearly suggests that the at the lexical level the neural substrates for L1 and L2 in bilinguals are shared, and that level of proficiency plays a role in cerebral representation of language in the brain. (Klein et al. 2006).

Logie et al. (2003) conducted an fMRI study on the effect of applying a different cognitive strategy on the brain activation patterns. Six adult subjects were presented with audio stimuli consisting of sequences of single consonants, and were instructed to rehearse the letters subvocally for a period of 12 seconds, and then they were asked to

recall them orally. The task was divided into two conditions. In the first condition, the sequence consisted of letters a, b, c, d, e, presented in alphabetic order, whereas in the second condition, the sequence consisted of five random consonants. The results of a study show that the comparison between the first and the second condition revealed four clusters of activation in the left hemisphere, which were inferior parietal gyrus, BA 40, the inferior frontal gyrus, BA 8, and in the deeper white matter structures in the left frontal region. As participants could only rely on subvocal rehearsal strategy, Logie et al. (2003) suggest that these areas reflect the operation of the phonological loop, and as the activation in the left inferior and middle frontal gyri was only visible in the second condition, these regions may be involved in phonological storage. Logie et al. (2003) claim that these results differ from the results of previous studies on phonological loop, and thus, clearly show that incorporating different cognitive strategies may lead to different activation patterns in the brain.

Wang et al. (2003) conducted an fMRI study on early cortical effects of learning a tone-based second language. The subject group consisted of native American English speakers who were beginner learners of Mandarin. The subjects participated in two tone identification tasks, one prior and one after the training in Mandarin lexical tone, in which they were required to identify 40 auditory presentations of Mandarin lexical items and assign them into one of four possible tone categories. The results show that the activation during both pre-training and post-training tasks involved the areas including the left left inferior frontal gyrus, BA 44 and 45, left medial frontal gyrus, BA 6, left and right superior temporal gyrus, BA 22, and left and right middle temporal gyrus, BA 21. Wang et al. (2003) claim that cortical effects of learning Mandarin lexical tones were observed in the left superior temporal gyrus, BA 22, suggesting that the initial stages of learning these tone-based linguistic distinctions were linked to increased volume of neural processes within existing commonly believed Wernicke's area. What is more, after the training there was an emergence of activity in the neighboring left BA 42, and in the right prefrontal cortex, which is associated with pitch judgement tasks, which may suggest additional neural recruitment to perform newly acquired functions. The results of the study suggest that during the learning of a new language, areas previously specialized in the native language processing, as well as the neighboring areas, develop new specialization for nonnative language functions by enhancing an existing system (Wang et al. 2003).

Parker Jones et al. (2012) embarked on the analysis of differences in brain activation between monolinguals and bilinguals while reading aloud. 36 native English speakers and 31 non-native English speakers were asked to read aloud the words that were presented visually on the screen in English, while they underwent fMRI scanning. The results show that the activation in bilingual brains during the task was higher relative to monolingual brains in 5 left hemisphere regions, namely dorsal precentral gyrus, pars triangularis, pars opercularis, superior temporal gyrus, and planum temporale. These areas are demonstrated to be sensitive to increasing demands on speech production in monolinguals, which suggests that the advantage of being bilingual comes at the expense of increased work of brain areas that are responsible for monolingual word processing.

Morgan-Short et al. (2012) conducted an electrophysiological (ERP) study on the effects of implicit and explicit language learning on foreign language learners, using an artificial language. The results suggest that foreign language learners might rely on native-like brain mechanisms, but only if the conditions of the acquisition of the language approximated the immersion setting.

Cao et al. (2014) performed a study on the differences and similarities in brain activation and functional connectivity during first and second language reading in Chinese learners of English. Subjects were tested on English pseudoword rhyming judgment task and Chinese word rhyming judgment task. The authors found that English pseudowords reading involved a similar network as the reading of Chinese characters. Functional connectivity analysis, however, revealed different strengths of connectivity for L1 and L2. There was greater connectivity between right middle occipital gyrus and right motor cortex for L1 than L2, suggesting that the sensorimotor patterns of Chinese syllables are activated during Chinese word rhyming judgment. Greater connectivity between right middle occipital gyrus and somatosensory cortex was found for L2 rather than L1., which suggests that somatosensory feedback plays a key role in processing the foreign phonemes of English pseudowords. The authors also found a positive correlation between the accuracy and connectivity of right middle occipital gyrus, and a negative correlation between reaction time and the connectivity of aforementioned region. The results show that even though a Chinese network is involved in reading English pseudowords, the classic grapheme-phonemecorrespondence regions that are important for native English reading are involved by connecting them with the visuo-orthographic region.

Berken et al. (2015) conducted a study on neural activation in speech production and reading aloud in native and non-native languages. The participants were French-English bilinguals, who were divided into two groups, i.e. simultaneous and sequential bilinguals, who were matched for language proficiency. The activity of participants' brains was recorded with fMRI scanner, while they were reading aloud in their two languages. The results showed that similar brain regions were recruited by simultaneous bilinguals when reading aloud in L2 compared to L1. The sequential group, however, showed differences in their two languages, with greater activation in speech-motor control and ortographic-to-phonological mapping, i.e. the left inferior frontal gyrus, left premotor cortex, and left fusiform gyrus, when reading aloud in L2 compared to L1. The results support the notion of overlapping neural substrates for processing of two languages when acquired in native context from birth, and the notion of sensitive period, after which the maturation of brain regions related to speech production and phonological encoding is limited, regardless of language proficiency.

1.13. Conclusions

It is clearly visible in the above review that identifying brain structures and functions that might be associated with language processing in bilinguals is not a straightforward issue. Results might differ significantly and be highly dependent on the methods used in the study.

The number of studies presented in the review also shows that bilingualism and brain processes associated with it is not a major research topic among researchers using brain imaging techniques. Even though most of the studies come from the last decade, with the fast development of new statistical methods of analysis of brain imaging data results of these studies might be outdated and call for more investigation. It clearly stems from the theories reviewed above, though, that the brain might process linguistic information differently, depending on the organization of different languages, and the form of the stimulus.

It is important to note, that when it comes to performance in verbal and non-verbal tasks, there is no one effect of bilingualism. Research done by Bialystok (Barac and Bialystok 2013; Luk and Bialystok 2008; Bialystok et al. 2005) suggests that the effect of bilingualism may be dependent on the relation between the two languages, because of the similarity between them that varies for different pairs. That is why the following study is done on the Polish-English language pair, as to date there was no such study reported in the literature.

As it has been mentioned in the previous sections, there is substantial evidence supporting the idea that there is a common neural network shared by L1 and L2, and that aberrations from the norm stem from the variance in the level of proficiency in a given language, which manifest in the overall activation of the right hemisphere over left hemisphere homologues. Also, it has been shown that various brain areas might have different functions that can be modulated by the task and the form of the stimuli.

That is why, the present study has been designed in order to test the hypothesis that similar neural networks will be involved in the phonological processing of L1 and L2 in the participants, and that any deviations manifested in the differential activation will reflect the function of L2 proficiency. As there is also evidence supporting the idea that the phonological loop is a key factor in the successful acquisition of L2, the second hypothesis that will be tested assumes that there will be greater activations in the regions linked to phonological loop in the processing of L2.

The study will be conducted using *Magnetic Resonance Imaging* and is divided into seven experimental sessions, each investigating different aspects of language processing. The nature of each session is described in detail in the methodological chapters.

Chapter 2: Methodology of the experiment

2.1. Introduction

This chapter will describe the methodology behind the experiment. Firstly, the theoretical basis for the experimental methods will be given. Secondly, the methods and materials used in the experiment will be presented in detail. Lastly, the participants and the process of their recruitment will be discussed.

2.2. Physics of Blood-Oxygen-Level Dependence fMRI

Even though changes in blood flow and blood oxygenation in the brain have been linked to neural activity since the 1890s (James 2007: 99), only in 1990 their application to MRI studies was developed, creating a technique called Blood-Oxygen-Level Dependence functional MRI (henceforth BOLD fMRI).

BOLD technique is based on the differences in oxygen content in cerebral blood flow. Whenever neurons are active, they consume more glucose and oxygen than inactive ones. As neurons do not have their own reserve of these two, additional glucose and oxygen have to be transported through the blood stream, causing a local change of the concentration of oxyhemoglobin, i.e. oxygenated hemoglobin, and deoxyhemoglobin, i.e. deoxygenated hemoglobin, along with a change in local cerebral blood volume and blood flow (Buxton 2010: 10). Blood releases glucose to neurons at a greater rate than in inactive areas in a process called *hemodynamic response*, which results in an increase of oxyhemoglobin in the veins of the active areas, and in a

distinguishable change of the local ratio of oxyhemoglobin to deoxyhemoglobin, which is the marker of BOLD for MRI (Raichle and Snyder 2009: 86). Since oxygenation alters the magnetic susceptibility of blood, the magnetic resonance signal of blood differs depending on the level of oxygenation; thus, the MRI scanner, which is sensitive to changes in magnetic susceptibility, can assess the BOLD contrast, resulting in brighter image in areas where the level of oxygenation is higher (Smith 2004: 167).

Even though differences in BOLD signal are small, statistical methods can be used in order to determine the areas in the brain which reliably show the most of the differences. As the size of the BOLD signal increases as the square of the strength of the MRI scanner's magnetic field, the accuracy in identification of the activated brain areas depends on the scanner.

BOLD is the most widely used fMRI technique, as it allows researchers to map where activations occur in the brain, and to measure how the brain responds to different stimuli in the same brain region (Buxton 2010: 38).

2.3. MRI image structure and acquisition

Raw data from the MRI scanner is a complex recording of spatial frequencies in certain points of time. Before it is saved by the scanner, it is reconstructed to image volumes. Each volume is a collection of 2-dimensional picture slices taken according to three different reference planes which create a 3-dimensional volumetric structure. Each 2D slice is arranged according to its real spatial position, and the distance between two consecutive slices in reality is about 0.5 mm to 2mm along the axis which is described by the reference plane. The resulting 3D volume is divided into voxels, which are cubes representing 2 mm to 4 mm of tissue on each side.

The three reference planes are the basic types of planes used in anatomy, namely sagittal plane, dividing the brain into left and right portions, coronal plane, dividing the brain into posterior and anterior portions, and axial plane, dividing the brain into superior and inferior portions.

An example of representation of a 3-Dimensional volume consisting of 3 slices is shown in Fig. 2.

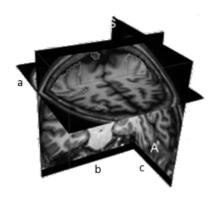


Fig. 2. 3-Dimensional representation of an MRI volume consisting of 3 slices. Reference planes: a – axial plane; b – coronal plane; c – sagittal plane.

Each volume of individual slices is collected over a period of time in intervals, called "time to repetition" (henceforth TR), which are expressed in milliseconds, and are consistent throughout the scanning session.

2.4. Experimental design

The experiment is divided into two parts, Polish (L1) and English (L2), consisting of seven scanning sessions. Four scanning sessions use task-based functional magnetic resonance imaging (fMRI), one session uses resting-state fMRI, one session uses diffusion tensor imaging (DTI), and one session uses T1-weighted structural MRI. Each of the four task-based sessions consists of different stimuli. Because the BOLD response to a sustained stimulus is weaker than predicted from the response to a brief stimulus (Buxton 2010: 37), it is important to divide the stimuli into smaller blocks which are presented to subjects during the scanning sessions. Hence, all the stimuli in this study were divided according to the relevant paradigms. The nature of each scanning sessions is described in the following subsections.

2.4.1. Passive listening task

The first session is designed to help map the activations in the brains of the subjects during the processing of spoken language. In the session, subjects listened passively to a set of recordings, mixed with recordings that were reversed. The contrast between listening to forward and reversed speech allows for dissecting brain regions that are activated by linguistic sounds from the regions activated by the sounds with no recognizable linguistic content. Such a paradigm has been used successfully in imaging studies, as reversed speech used as a baseline helps remove much of the speech responses in multiple cortical regions (Stoppelman et al. 2013).

For L2, the recordings were adopted from the study done by Vannest et al. (2009), and consisted of various stories read by a native English speaker. The stories were designed by a speech-language pathologist and consisted of complex syntactic structures in order to increase the relative processing load during the comprehension task. The recordings lasted for a total length of 150 seconds.

For L1, a recording of "Two brothers" folk tale by Brothers Grimm was made by a Polish native speaker in order to match the complexity of the English recordings. The recording lasted for a total of 150 seconds.

The recordings were split into 30-second blocks, and were put into a periodic 30s on-off block design. In the on (active) period, one block of the recording was played on the headphones of the participant, while a fixation point was being displayed. In the off (control) period, one block of the recording was played backwards on the headphones, while a fixation point was being displayed. One active and one control period constituted a trial. A scanning session consisted of 5 trials, and was conducted separately for each language. During the scanning sessions, TR of the scanner was set to 2000 milliseconds, which resulted in 150 brain volumes of data for each participant. A diagram of the experiment is presented in Fig. 3.

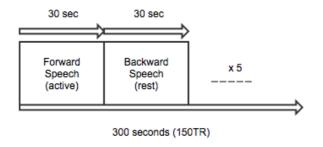


Fig. 3. Structure of the experiment in passive listening task

2.4.2. Sternberg Working Memory Task

In the second scanning session, subjects underwent a customized version of *Sternberg Working Memory Task* (henceforth SWMT, Sternberg 1969), which tests their *phonological Working Memory* (henceforth pWM). The pWM is claimed to be a key region involved in phonological processing (McGettigan 2011), thus testing it helps pinpoint the underlying brain structures and their relation to both first and second language phonology. The design of the session was adopted from a recent study done by Maher et al. (2014), which was successful in localizing phonological storage.

In contrast to the previous task, this one was not divided into simple block design, but was designed to be event-related, in order to test all four different cognitive skills involved in the original Sternberg test. Subjects had to encode the acoustically presented set of digits (encoding phase). Then, encoding was paralleled by storage processes (late encoding phase; Leung et al. 2004; Postle 2006). In the maintenance phase, which followed the late encoding phase, meaning was elaborated and implemented to the semantic network (Craik et al. 2000). In the fourth phase (retrieval phase), subjects had to retrieve the memorized verbal information from phonological storage (Rypma and D'Esposito 1999).

The scanning sessions were divided into 7 stages. Firstly, there was a cue block, with only a fixation point displayed. Then, during the encoding phase, a recording of a set of digits (in Polish for the L1 task, and in English for the L2 task) was played on the headphones, while the fixation point was displayed. During the late encoding and

maintenance phases, there was only a fixation point displayed on the screen. Finally, during the retrieval phase, a recording of one digit was played on the headphones, and a fixation point was displayed. Following the retrieval phase, there was a question mark displayed, and subjects had to decide whether the digit appeared on the recording during the encoding phase by pressing one of the two buttons on the response pad (yes/no, with an index and middle finger, respectively). All of the above stages were followed by a break block (inter-stimulus interval), which was just a blank white screen displayed with no task.

These 7 stages constituted a trial. There were 10 trials in the scanning session, and two scanning sessions (one for each language). During the sessions, TR of the scanner was set to 2000 milliseconds, which resulted in 110 brain volumes of data for each participant. A diagram of the experiment is presented in Fig. 4.

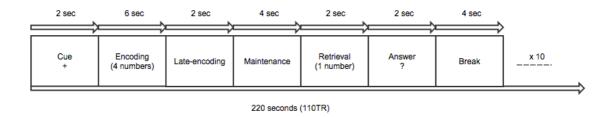


Fig. 4. Structure of the experiment in Sternberg Working Memory Task

2.4.3. Verbal Fluency Test

One of the tasks that have been used successfully in mapping language representation is verbal fluency test (Kroliczak et al. 2012). During the test, participants were asked to silently generate as many words as possible starting with the letter that is presented on the screen. It has been shown that during the test, there is an increased activation in language regions, and that is why this task was included in the present study.

The scanning session consisted of a simple block design. First, there was a single letter displayed for 30 seconds on the screen, and participants were asked to silently generate as many words starting with that letter as possible. Then, there was a fixation point displayed on the screen for the next 30 seconds, during which participants were ordered to rest. These two blocks constituted a trial, and there were three trials in

the scanning session, each with a different letter. A diagram of the experiment is presented in Fig. 5.

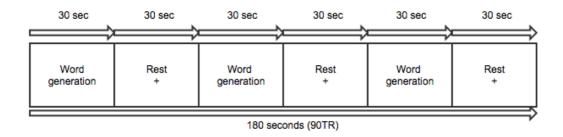


Fig. 5. Structure of the trial in passive listening task

During the scanning sessions (one for Polish and one for English), TR of the scanner was set to 2000 milliseconds, which resulted in 90 brain volumes of data for each participant.

2.4.4. Lexical Test for Advanced Learners of English

As it is shown that the familiarity of form shows substantial effects on perception (Jordan et al., 2003), present sessions were designed in order to map the brain areas involved in the processing of unfamiliar as well as familiar items of language. The test that was used to do that in English was Lexical Test for Advanced Learners of English (LexTALE, Lemhofer and Broersma 2012). This test consists of 63 trials, in which a participant must undertake a lexical decision task and decide whether presented single lexical items are real words or pseudowords (i.e. words that do not exist in the lexicon, but follow the phonotactic rules of a given language). As a quick and valid test, it not only helps assess the proficiency in the language and the knowledge of vocabulary, but also measures the performance on the psycholinguistic paradigm (Lemhofer and Broersma 2012). As LexTALE is a written test, for the purpose of this study audio recordings of the items were prepared.

The scanning session was divided into an event-related design that consisted of 3 stages. During the first one, there was a fixation point displayed on the screen for two seconds. Then, a recording of one item was played on the headphones of the participant, and the fixation point was displayed. After that, the fixation point became a question

mark, and participants had two seconds to answer whether the item was a real word by pressing one of the two buttons (yes/no, with an index and middle finger, respectively) on the response pad. Above 3 stages constituted a trial. There were 63 trials in the session. A diagram of the trial is presented in Fig. 6.

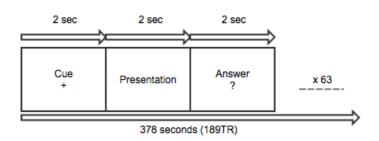


Fig. 6. Structure of the trial in passive listening task

In order to make a parallel session for Polish, a Polish version of LexTALE (Szewczyk, in preparation) was administered. The test was designed to correlate well with the English version and consisted of the same number of lexical items with the same ratio of real vs. pseudowords. The session design used for Polish was identical to that in Figure 4.

For both L1 and L2 sessions, TR of the scanner was set to 2000 milliseconds, which resulted in 189 brain volumes of data for each participant.

2.4.5. Stimulus presentation and scanning protocol for task-based sessions

All the scans were performed using Siemens Magnetom Spectra 3T. BOLD-sensitive fMRI images were acquired using echo-planar sequence (EPI). The parameters of the scan were as follows, TR/TE = 2000 ms/30ms; slice thickness = 3 mm; acquisition matrix = 64x58; number of slices = 35; Flip Angle = 90° .

During the scans, visual and audio stimuli were presented using SuperLab presentation software (Cedrus 2014). Visual stimuli were displayed on the screen, which was situated right behind the scanner. The participants were looking at the screen through a mirror that was mounted on the headpiece they were wearing. All the audio stimuli were presented through a set of noise canceling headphones. SuperLab also recorded the participants' responses and the response times through a Lumina LU-441

Thumb response pad (http://cedrus.com/lumina/). The timing of the presentation of the stimuli was synchronized with the scanner triggers using NNL SyncBox (http://www.neurodevice.pl/en/products/products-nnl/147-fmri-syncbox).

2.4.6. Resting-state fMRI

After four sessions of fMRI scanning, participants underwent a 6-minute resting-state fMRI scan, during which no tasks were administered, and the activity of the brain during rest was recorded, which allowed for further analysis of functional connections between brain areas that were found active in task-based sessions. This extends the scope of comparison of activity patterns between studied groups.

Although traditionally most of the fMRI studies focused on hypothesis-driven task-based approaches, resting-state fMRI (henceforth r-fMRI) has emerged as a powerful tool for discovery of human brain functions (Biswal et al. 2010). R-fMRI scans conducted on subjects during rest reveal large-amplitude spontaneous low frequency, less than 0.1Hz, fluctuations in fMRI signal, which are temporally correlated across functionally connected areas in the brain. These correlations are referred to as functional connectivity, and represent complex neural systems, which might be examined without the requirement of selecting a priori hypothesis. Reproducibility of such systems across subjects suggests a common functional architecture, yet each individual exhibits unique features, with stable and meaningful differences in functional patterns and strengths (Biswal et al. 2010).

All resting-state scans in the study were acquired using the same set of parameters, using echo-planar sequence (EPI) with TR/TE = 2000 ms/30ms; slice thickness = 3 mm; acquisition matrix = 64x58; number of slices = 35; Flip Angle = 90°. Participants were asked to remain still with their eyes open. The screen was blank during the whole procedure, and there was no sound being played through the headphones. A 6-minute scan yielded 180 brain volumes of data for each participant. Resting-state data was acquired to test the hypothesis that the functional connectivity between brain regions might be predictive of the results of behavioral tests administered during the study.

2.4.7. Diffusion Tensor Imaging

During the sixth scanning session, participants underwent a diffusion tensor imaging (henceforth DTI) scan, which produces whole-brain volumes of data that will be analyzed in terms of the structure of white matter tracts. During the scan participants were asked to lay still, and were not given any tasks.

DTI, as opposed to BOLD fMRI, does not depend on the blood flow, but on restricted diffusion of water molecules. It can record the rate and direction of the diffusion, which helps track the fiber tracts in the white matter of the brain. These tracts show structural connections between brain areas, and are independent of brain activity.

Even though both rs-fMRI and DTI reveal connections between brain areas, it is important to use both methods, as previous studies on functional connectivity indicate that functional connectivity between brain areas might exist in the absence of direct, monosynaptic connections detected by DTI (Greicius et al. 2008). What is more, local functional connectivity does not have to be exclusively related to the existence of structural connectivity between brain regions (Koch et al., 2002). Brain areas with high structural degree tend to form functional networks even in the absence of any direct anatomical connections between the regions (Eguiluz et al. 2005). It is also suggested that differences between results of rs-fMRI and DTI might stem from the fact that rs-fMRI shows both direct and indirect links between brain regions, whereas DTI shows only direct links, which do not involve third-party regions (van den Heuvel et al. 2009).

All the scans in the study were acquired using a single-shot echo-planar (EPI) pulse sequence, with 41 diffusion directions (b value=2000; TR=9300ms; TE=100ms; Flip Angle = 90° ; acquisition matrix = 128x128; slice thickness = 2mm; 60 slices), and one non-diffusion weighted T2 image (b = 0). DTI data was acquired to explore the structural connectivity in the language network and compare it to the results of the functional scans.

2.4.8. T1-weighted structural scan

Finally, participants underwent a structural T1-weighted MRI scan to gather a volume of high resolution structural data. Such scanning session records data, which are later used

as a reference material for transformation and visualization of functional data, which is in lower resolution.

T1-weighted MRI scan records a T1 relaxation time of tissues, and is one of the basic types of scans used to record structural data. Because fat and water have different magnetization, the resulting image shows this contrast using brighter and darker voxels for each type of tissue.

All scans in the study were acquired using a T1-weighted high resolution magnetization prepared gradient echo sequence scan (TR = 2200ms; TE = 3.39ms; acquisition matrix = 256x 240; slice thickness = 1mm; 199 slices).

2.5. Participants

Twelve right-handed participants, two males and ten females, were scanned during the study. They were matched based on their age (mean: 20.8 years, SD: 2.64 years), linguistic background (Polish as a native language, English as a second language), and the level of education (first year students of English B.A. university program). As mentioned in the above subsections, the students were given four behavioral tests during the study, SWMT in Polish and English, and LexTALE in Polish and English, and their scores are presented in the results chapter (section 4.2). The study was approved by the Ethics Committee of Poznan University of Medical Sciences, and written informed consent was gathered from each participant before the scanning sessions took place.

Chapter 3: Methodology of data analysis

3.1. The analysis of behavioral tests

Even though behavioral tests were used during the experiments mainly as a tool for inducing certain types of brain activations, their results were analyzed and compared across subjects, and used in subsequent analyses of resting-state and DTI data. As the Sternberg Working Memory Task (SWMT) and LexTALE were carried out both in Polish and English, the results were also compared across languages. The tests measured both accuracy and reaction time, and these variables were used in the comparisons.

Accuracy score in SWMT was a straightforward calculation of a percentage of right answers during all ten trials. If a participant corrected the answer after giving one, only the first answer was taken into consideration, and any subsequent answers in the trial were discarded.

Accuracy score in LexTALE was calculated according to the scoring procedure of the test (Lemhofer and Broersma 2012). The LexTALE score consists of the percentage of correct responses, corrected for the unequal proportion of words (40) and pseudowords (20) in the test by averaging the percentages correct for these two item types. Again, only the first answer in each of the trials counted, and all subsequent answers in the trail were discarded.

The scores of SWMT in Polish and English were correlated, using Pearson's r correlation coefficient, in order to test whether the results in one language can be predictive of the result in the other language. Also, the means of the scores in each language were compared using Welsh's T-test in order to test whether they differer

significantly. The same measures (Pearson and Welsh) were used for LexTALE scores. SWMT and LexTALE scores were also correlated, using Pearson's r, in order to test whether the result of one test can be predictive of the other test's result.

Apart from the accuracy scores, reaction times that were recorded during the experiments were also compared across subjects and tests. Correlation analyses, using Pearson's r, were conducted on the reaction times of each test and its score, to test whether the reaction times could be predictive of the score. What is more, mean reaction times for each test were compared across tests and languages, using Welsh's T-test, in order to find significant differences.

All statistical tests performed throughout the analysis were performed in R, an open source software for statistical computing (R Foundation, 2015), unless stated otherwise.

3.2. The analysis and reconstruction of structural MRI data

After obtaining high-resolution structural MRI data, the images were used to project (register) the functional data, which is of lower resolution. This helped visualize the activations obtained during the functional scans, without the restrictions of voxel resolution, thus increasing reliability and statistical power (Reuter et al. 2012).

3.3. The analysis of functional MRI data

Functional MRI data were analyzed using FSL FEAT (Jenkinson et al. 2012) software. FEAT allows for high quality fMRI analyses, based on general linear modelling (GLM), known as multiple regression. For each of four active experiments described in the previous chapter, a model based on experimental design that fitted the data was devised and fed to FEAT. A model consists of timepoints, in which the stimuli were presented during the scanning. A good model fit indicates that the data were indeed caused by the stimuli. In order to produce the most accurate model, each timepoint was matched within a millisecond of the real onset of each stimulus, as during the scanning sessions specific times were recorded by the presentation software.

Firstly, the first-level analyses were performed, which consisted of the analysis of subjects' individual data. Then, after analyzing all the subjects individually, a higher-level analysis was performed to reveal inter-subject and inter-language effects. All the steps taken in the first and higher level analyses are described in the following subsections.

3.3.1. First-level FEAT analysis

During the first-level FEAT analysis, the first 4 timepoints (TRs) of the data were removed due to possible T1 stabilization effects, which could distort the data. Then, motion correction using Fourier interpolation was applied to the remaining timepoints, as it has been shown that motion as small as 0.1mm can systematically bias both within-and between- group effects during the analysis of fMRI data (Power et al. 2011; Satterhwaite et al. 2012; Van Dijk et al. 2012). The next step, spatial smoothing using an 8-mm FWHM Gaussian Kernel was also applied to the data, in order to increase the signal-to-noise ratio of the data. This step removes high-frequency information, which is assumed to consist mostly of noise, while preserving signals on larger spatial scales, as signals stretching across multiple voxels are most likely to reflect neuronal activity (Poldrack et al. 2011) Data were also temporally filtered, using a high-pass filter, in order to limit the longest period allowed in the timeseries.

After applying the filters, the skull was removed from the images using BET software (Smith, 2002), which deleted all non-brain tissue from the data. Finally, the images were registered to both individual and standard-space (MNI-152) high-resolution anatomical scans, using FLIRT (Jenkinson and Smith 2001).

FEAT then used a robust and accurate nonparametric estimation of time series autocorrelation to prewhiten each voxel's time series. After the calculation of statistics, Z-score maps were created with voxels that were activated during the presentation of the stimuli, and were thresholded at Z > 2.3, to reveal clusters that were statistically significant at p < 0.05.

3.3.2. Higher-level FEAT analysis

In order to analyze the inter-subjects effects like mean and variance for each paradigm and to contrast Polish vs. English language effects, contrasts of parameter estimates (COPEs) from first-level analyses were fed to FEAT. FEAT uses FMRIB's Local Analysis of Mixed Effects (FLAME) for estimating inter-subjects and inter-session random effects component of the mixed-effects variance to get an accurate estimation of the true random-effects variance and degrees of freedom at each voxel. It is a two-stage process using Bayesian modeling and estimation. Mixed-effects are used in order to ensure that inferences made from the results can be about the wider population, from which the subjects were drawn.

As there were two scanning sessions in each of the four experiments (one Polish and one English), FLAME was used to get mean activations across the whole group of subjects for each session, and to test the variance between the means for Polish and English sessions.

After the calculation of statistics, Z-score maps were created with voxels that represented the effects, and thresholded at Z > 2.3, to reveal clusters that were statistically significant at p < 0.05.

3.4. The analysis of resting-state fMRI data

After the analysis of functional MRI data from the experiments, two brain regions of interest (seed regions) were used to infer connectivity strength between them, and to model a network, which connections might be responsible for phonological processing in each language. The regions were the left and right Broca's area and the left and right premotor cortex, extracted from the Juelich histological atlas (Eickhoff et al. 2007). In order to perform such an analysis, resting-state fMRI data from each subject were analyzed in terms of functional connectivity between the seed regions by means of network centrality (NC) and voxel-mirrored homotopic connectivity (VMHC) in Configurable Pipeline for the Analysis of Connectomes (CPAC) (1000 Functional Connectomes Project 2015). Then, for each subject, network measures were calculated and used to test whether the connectivity between seed regions might be predictive of

behavioral language results (in this case SWM task and LexTALE results obtained during the experiments).

3.4.1. Preprocessing of resting-state fMRI data

Before the comparison of activations between the subjects could be done, there was a need of data preprocessing. The first step in the preprocessing was to transform individual functional and anatomical images to match a common template. This was done using an MNI-152 template, maintained by the Montreal Neurological Institute (Montreal Neurological Institute, 2009). After each subject's anatomical image was transformed to match the template, each subject's functional data was registered to their own individual anatomical image.

After the transformation and registration, CPAC automatically segmented brain images into white matter, gray matter, and cerebrospinal fluid (CSF). This was done using probability maps that contain the information on the likelihood that a given voxel belongs to a particular tissue type.

The next step in the preprocessing stage was slice timing correction. Because the images are combined from 2D slices, which are acquired sequentially, there might exist a difference in the acquisition time of different slices that could cause confounds. In order to account for the differences, CPAC interpolates the data in each slice to match the timing of a reference slice.

After slice timing was corrected, the next step, nuisance signal regression, was performed. This is a key step in preparing fMRI data for statistical analysis, as non-neural fluctuations in the signal, caused by subject motion and physiological artifacts, in the white matter and CSF might introduce temporal coherences that lead to an overestimation of functional connectivity strength (Chai et al 2012). That is why the removal of nuisance signals and noise are of great importance.

Another important step was to temporally filter the data. This increases the signal-to-noise ratio, as fMRI signal might contain low frequency fluctuations that are unrelated to the signal of interest, e.g. noise caused by cardiac and respiratory effects (Wager et al. 2007),

The last step of preprocessing stage was spatial smoothing, using a Gaussian kernel. This step was identical to the one described in section 3.3.1.

3.4.2. Network measures

Even though there are many brain areas (nodes) that constitute a whole-brain network, some nodes might be considered *central* within the network. These central nodes can be identified by applying various graph-theory based network analysis techniques which provide a measure of the *centrality* or functional importance of each node (Koschutzki et al. 2005). That is why, after preprocessing stages, *Degree Centrality (DC)* was calculated for each seed region using CPAC. *DC* is a measure of local connectivity, which identifies the most connected nodes in the network by counting the number of direct connections (edges) to all other nodes. A node with high *DC* will have direct connections to many other nodes in the network emphasizing higher order cortical associations (Zuo et al. 2012). A measure of *DC* was successfully used in order to examine node characteristics of intrinsic connectivity networks (Buckner et al. 2009; Bullmore and Sporns 2009; He et al. 2009; Wang et al. 2010; Fransson et al. 2011).

In order to calculate DC, the timeseries of each node was extracted and used to calculate temporal correlation matrix that represented the connectivity between all nodes. Then, a threshold of P-value, .001, was applied in order to create an adjacency matrix, which described all nodes that survived the thresholding. DC was then computed by counting the number of significant correlations between the timeseries of a given node and that of all other nodes in the adjacency matrix. Finally, centrality maps were generated and standardized using Z-scores for use in group analysis, from which DC values of seed regions (see Results) were correlated with behavioral measures of accuracy in SWMT and LexTALE to test whether functional connectivity of brain areas implicated in phonological processing might be predictive of behavioral results in these tasks.

3.4.3. Voxel-mirrored homotopic connectivity

In addition to the analysis of degree centrality, the strength of the connectivity between left and right hemisphere homologues was calculated and correlated with the results of SWMT and LexTALE in L1 and L2. Despite being a relatively new method of the analysis of brain connectivity, various studies have already used voxel-mirrored homotopic connectivity and shown that the results might be indicative of disturbed functional specialization of brain areas in clinical populations and of development in connectivity over a period of time in longitudinal studies (Kelly et al. 2011; Anderson et al. 2011; Gee et al. 2001; Zuo et al. 2010). What is more, the variance in the strength of homotopic connections is thought to reflect hemispheric and regional specialization in information processing (Stark et al. 2008). As it has been suggested in the literature review that subjects with lower proficiency levels in L2 might use the right hemisphere homologues of language areas to improve performance, this method may detect the areas that show this pattern of interhemispheric connectivity as a function of behavioral results.

In order to calculate the homotopic connectivity values after the preprocessing steps, CPAC transformed the anatomical images to fit the symmetric templates. This is an important step, as CPAC assumes symmetric morphology between hemispheres, which is not true for real brains. After this step, the connectivity values were computed as correlation coefficients between each pair of symmetric interehemispheric voxels and correlated with the results of SWMT and LexTALE in L1 and L2.

3.5. The analysis of DTI data

DTI data gathered during the experiment were used in two separate analyses, namely in fiber tracking and in the analysis of fractional anisotropy (henceforth FA). Both analyses are described in the subsections below, following a subsection on the preprocessing of data, which was essential, and identical for both analyses.

3.5.1. Preprocessing of DTI data

As the scanner outputs DTI data in the form of diffusion weighted images and gradient directions, there was a need to preprocess and convert the data to proper formats to conduct the above-mentioned analyses. Firstly, the data underwent eddy current correction in FDT (Behrens et al. 2007). As eddy currents in the gradient coils induce distortions (stretches and shears) for different gradient directions, eddy current correction corrects for these distortions and for simple head motion, using affine registration to a reference volume. Next, fitting of diffusion tensor model at each voxel was performed in FDT. This is a standard DTI preprocessing step that creates a set of derivative images, including maps of fractional anisotropy (FA). FA is a scalar value between zero and one that describes the degree of anisotropy of a diffusion process. A value of zero represents isotropic diffusion, which is unrestricted in all directions. A value of one represents a diffusion that occurs only along one axis and is fully restricted along all other directions. As increased FA in large fiber tracts in general indicate better performance in behavioral tasks (Konrad et al. 2009), these values were calculated in order to correlate them with the results of SWM task and LexTALE in the process, which is described in the following subsections.

3.5.2. White matter fiber tracking (probabilistic tractography)

Probabilistic tractography allows for obtaining a connectivity index along a white matter pathway that reflects fiber organization and estimates probability of a connection through the data field between any two distant points. Thus, it helps create a map of voxels that are structurally connected to the areas, from which tracking is done.

In order to run probabilistic tractography on the data, there was one more step in the preprocessing pipeline that had to be added, using BEDPOSTX (Behrens et al. 2007). BEDPOSTX runs Markov Chain Monte Carlo sampling to build up distributions on diffusion parameters at each voxel, such as local diffusion directions, to create all the files necessary for running probabilistic tractography.

Probabilistic tractography itself was performed on the data using FSL's Probtrackx (Behrens et al. 2007), which generates connectivity distributions from user-specific seeds, in order to investigate strucutral connections to the areas of interest. Probtrackx repetitively samples from the distributions on voxel-wise principal diffusion directions, calculating a streamline through these local samples to generate a probabilistic streamline or a sample from the distribution on the location of the true streamline. By taking many such samples it is able to build up the posterior distribution on the streamline location or the connectivity distribution (Behrens et al. 2007).

The seeds that were used in Probtrackx were the same seeds used in resting-state fMRI analysis, i.e. the left and right Broca's area and the left and right premotor cortex. As tractography takes place in diffusion space, the seeds were first translated into diffusion space, and then the resulting images were transformed back into seed space using non-linear forward and backward warpfields.

Resulting from probabilistic tractography were 3D images for each of the participants, containing connectivity distribution from seed regions. All 3D images were merged into a 4D volume, which underwent Threshold-Free Cluster Enhancement using FSL's Randomise to produce a group-mean image.

3.5.3. Tract-based spatial statistics (FA correlation analysis)

In order to use FA values obtained during preprocessing stages in correlation analyses, all individual FA maps have to be aligned. However, it is not a straightforward process, and the results of alignment might influence the results. That is why individual maps were first registered to a population specific template constructed in Diffusion Tensor Imaging ToolKit (Zhang et al. 2007), which is an optimized DTI spatial normalization tool (Wang et al. 2007) that has been shown to perform superior registration in comparison to scalar based registration methods (Adluru et al. 2012). The template creation was done in an unbiased way that used both average diffusion features (such as diffusivities and anisotropy) and the anatomical shape features (tract size) in the population (Zhang et al. 2007). A set of 12 diffusion tensor maps was used to create a common space template. The diffusion tensor maps were normalized to the template

with rigid, affine, and diffeomorphic alignments and interpolated to 2 x 2 x 2 mm³ voxels.

White matter alignment was performed using a diffeomorphic registration method, which preserves the topology (Zhang et al. 2007), by incrementally estimating the displacement field using a tensor-based registration formulation (Zhang et al. 2006). Tensor-based registration provides optimal alignment between subjects by taking advantage of similarity measures comparing whole tensors via explicit optimization of tensor reorientation (Alexander et al. 2001). By computing image similarity on the basis of full tensor images rather than scalar features, the algorithm incorporates local fiber orientations as features to drive the alignment of individual white matter tracts. Using full-tensor information is highly effective in spatially normalizing tract morphology and tensor orientation, and enhances sensitivity to microstructural variations (Zhang et al. 2007).

In order to perform voxel-based morphometry of DTI data, a state of the art (Bach et al. 2014) method of tract-based spatial statistics (TBSS) (Smith et al. 2006) was employed. FA has become a popular measure derived from DTI data, which allows for voxelwise statistical analysis of brain changes across a group of subjects. However, an optimal analysis is often compromised by the use of standard registration algorithms. That is why, TBSS uses carefully tuned nonlinear registration, followed by projection onto an alignment-invariant tract representation (the mean FA skeleton) in order to improve objectivity, sensitivity and interpretability of analysis of multi-subject DTI data.

FA maps were calculated in DTI-TK from all individual spatially normalized DTI maps and the population-specific DTI template (mean FA map). White matter skeleton was also created from the mean FA map using DTI-TK. All these data were then incorporated into a TBSS pipeline.

The mean FA skeleton image was thresholded, which resulted in a binary skeleton mask, which defined the set of voxels used in all subsequent processing. Next, a distance map was created from the skeleton mask and was used in the projection of FA onto the skeleton. Finally, individual FA maps were merged into a single 4D image and for each timepoint the FA data were projected onto the mean FA skeleton. This resulted in a 4D image file containing the skeletonized FA data, which was used in a voxelwise analysis.

Voxel-wise statistical analysis was done using FSL's Randomise (http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/Randomise) and general linear model design, in which SWM task and LexTALE scores were put as covariates. The resulting maps contained voxels, which account for the effects of these tasks, and were thresholded at p < .001 (both uncorrected and corrected for multiple comparisons) to reveal significant voxels.

3.6. Voxelwise brain morphometry

In order to check whether any effects found in the functional MRI analysis could be possibly caused by structural gray matter differences, a voxelwise morphometry of gray matter (GM) was also conducted. VBM allows to correlate brain regions with different variables (e.g. behavioral test results) without a priori information about the location of these regions (Douaud et al. 2007). That is why, in this study VBM was conducted in order to search for GM differences that could be correlated with individuals' results of SWMT and LexTALE.

Structural data was analyzed with FSL-VBM (Douaud et al. 2007), an optimized VBM protocol (Good et al. 2001) carried out with FSL tools (Smith et al., 2004). First, structural images were brain-extracted and grey matter-segmented before being registered to the MNI 152 standard space using non-linear registration (Andersson et al. 2007). The resulting images were averaged and flipped along the x-axis to create a left-right symmetric, study-specific grey matter template. Second, all native grey matter images were non-linearly registered to this study-specific template and "modulated" to correct for local expansion (or contraction) due to the non-linear component of the spatial transformation. The modulated grey matter images were then smoothed with an isotropic Gaussian kernel with a sigma of 8 mm. Finally, voxelwise GLM was applied using permutation-based non-parametric testing, correcting for multiple comparisons across space. Resulting were 3D maps (for each of four tasks) with voxels, in which GM difference accounted for variance in the scores.

3.7. Presentation and visualization of the results

All the brain areas presented in the tables in the Results chapter were localized using the Juelich histological atlas (Eickhoff 2007) and Harvard-Oxford cortical and subcortical structural atlases (Desikan et al. 2006). All the coordinates in the tables are presented in the standard MNI space (Montreal Neurological Institute 2009), which allows for localization of brain areas, regardless of individual differences in brain size and overall shape.

All the visualizations of the results of functional scans were done in MRIcroGL software (McCausland Center for Brain Imaging 2014), by overlaying thresholded z-stat images calculated in higher-level FEAT analyses onto a 2-mm MNI-152 brain template (Fonov et al. 2011). Each visualization was presented using a mosaic of three standard planes, i.e. axial, sagittal, and coronal planes, along with a bar presenting a scope of z-scores visible in the images.

For the visualization of DTI tracking, MedINRIA software was used (Asclepios Research Team 2008) to visualize the bundle of fibers tracked from the region of interest using the data from one of the participants.

The model of phonological processing shown in the conclusions of Chapter 5 (Fig. 16) was visualized using The Open Graph Viz Platform Gephi (Bastian et al. 2009).

Chapter 4: Results

4.1. Introduction

In this chapter, the results of the experiments described in the second chapter will be presented in detail and discussed in the light of relevant previous findings. The results of behavioral tests will be presented first, as they provide information on cognitive abilities and language proficiency of the participants, which constitute a basis for a meaningful discussion of the neuroimaging results. Then, the results of task-based fMRI experiments will be presented, as these results are the core of the present work. Finally, the results of task-independent experiments will be discussed, in order to complement the findings and gain a broader perspective on the issue of language processing.

4.2. SWMT and LexTALE results

Mean accuracy score in SWMT in Polish (0.74; SD: 0.11) and English (0.7; SD: 0.16) did not differ significantly (t = 0.971, df = 11, p-value = 0.3524). Mean reaction time in SWMT in Polish (1.730 sec; SD: 465 ms) and English (1.699 sec; SD: 444 ms) also did not differ significantly (t = 0.5591, df = 109, p-value = 0.5772). The correlation between the mean scores in Polish and English was weak (t = 0.23) and not statistically significant (at p < 0.01), thus it might be assumed that even though the means were not different, individual scores in one language were not predictive of the scores in the other language.

The difference between mean accuracy score in LexTALE in Polish (70.31; SD: 11.2) and English (55.31; SD: 4.8) was statistically significant (t = 3.8748, df = 11, p-value = 0.002586). The difference between mean reaction time in Polish (2.102 sec; SD: 510 ms) and English (2.049 sec; SD: 422ms) was statistically significant as well (t = 2.4215, df = 753, p-value = 0.01569). The correlation between the scores in Polish and English, however, was weak (r = -0.28) and not statistically significant (at p < 0.01).

The scores of participants in SWMT in Polish and English were lower than expected in comparison to other studies using the same memory load (Zakrzewska and Brzezicka 2014). LexTALE scores in English were also lower than expected for a group of advanced learners of English (Lomhofer and Broersma 2012). This fall in scores might be attributed to the fact that in this study both tasks were administered during the scanning sessions aurally. fMRI environment is known for its high noise level, and even though the stimuli were presented through a set of noise-cancelling headphones, the noise from the scanner might have contributed to the difficulty of the tasks. In case of LexTALE, which is a lexical decision task, the effect could be even higher, as it has been shown that in noisy environments, people tend to focus on word-initial phonemes when they process non-native speech (Coumans et al. 2014), thus the perception of words in LexTALE could have been distorted.

What is interesting, is the fact that the reaction times did not differ significantly between the languages in SWMT, but they did differ significantly between the languages in LexTALE. The latter case is common, as it has been thoroughly presented in the literature that reaction time is lower, whenever inhibition of other languages comes into play in bilingual people (Tse and Altarriba 2014). The same results in SWMT, however, might be explained by the fact that bilinguals show an advantage in non-verbal working memory tasks (Bialystok 2014). As the stimuli used in SWMT were digits, even though they were spoken, it might be the case that the bilingual participants in both Polish and English tasks did not rely as much on language comprehension, as on executive function involved in non-verbal reasoning. The fact that the accuracy scores in SWMT did not differ significantly between the languages might be also supporting this hypothesis. As a result, there could be an effect of other neural processes that influenced the reaction times. This is discussed in detail in the appropriate SWMT section of the results.

4.3. Passive listening task

The analysis of brain activations during listening to L1 recordings revealed two clusters of activation, which spread over a number of regions in the brain. The first cluster encompasses such areas as the right primary auditory cortex, posterior parts of the right superior temporal gyrus, angular gyrus, and planum temporale. The second cluster shows activations in the left primary auditory cortex, supramarginal gyrus, and planum temporale. All activations in the clusters are listed in Table 1 and visualized in Fig. 7.

The analysis of brain activations during listening to L2 recordings also revealed two clusters of activation. The first cluster included the left primary auditory cortex, posterior parts of STG, inferior parietal lobule, and planum temporale. The second cluster included the right primary auditory cortex, inferior parietal lobule, planum temporale, Broca's area (pars opercularis, BA 44), and premotor cortex. All activations are presented in Table 1. Inferior parietal lobule encompasses the areas of supramarginal and angular gyri. All the activated areas are visualized in Fig. 7.

Table 1. Regions in the brain activated in the passive listening task. L and R before the name of the brain region stand for left and right hemisphere, respectively.

L1 - Polish	207 1	7.0	
Brain region	MNI coordinates	Z-Score	Peak activations
L Primary auditory cortex	-52 -12 -2	4.73	4
L superior temporal gyrus	-53 -34 6	4.55	2
L Planum temporale	-42 -40 12	4.52	1
L Supramarginal gyrus	-50 -42 12	4.47	1
R Angular gyrus	56 -52 22	3.95	1
R Primary auditory cortex	42 -30 4	3.6	2
R superior temporal gyrus	52 -14 8	3.58	2
L2 - English			
Brain region	MNI coordinates	Z-Score	Peak activations
R primary auditory cortex	58 -22 10	5.32	1
R inferior parietal lobule	66 -30 20	3.51	1
R Broca's area (BA44)	48 8 0	3.35	1
R Premotor Cortex (BA6)	52 6 38	3.33	1
L Planum Temporale	-58 -20 10	5.33	1
L Primary auditory cortex	-56 -16 10	5.12	1
L Inferior parietal lobule	-50 -40 16	3.84	1

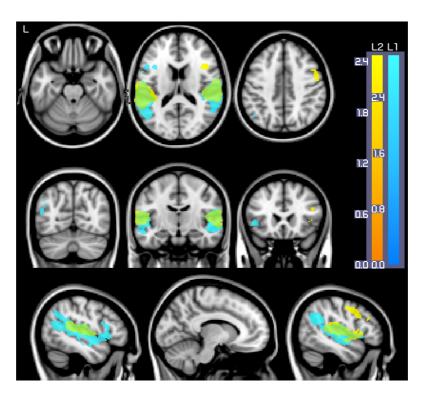


Fig. 7. Activated brain areas in the passive listening task. Z-stat > 2.3, p < 0.01. Blue-cyan clusters represent the activations in L1 task, and orange-yellow represent the activations in L2 task. Green represents the overlap of the two. Images presented in neurological convention.

Above-mentioned activations during the L1 task are typical of auditory and language processing. Activated areas in the primary auditory cortex are the first cortical structures responsible for processing of incoming auditory information (Mamah et al. 2009). Supramarginal gyrus has been shown in the literature to be heavily involved in phonological processing (Deschamps et al. 2014). It is activated during different language tasks, such as word processing (Howard et al. 1992, Newman and Joanisse 2011 and Petersen et al. 1988), nonword processing (Newman and Twieg 2001; Wise et al. 1991), syllable processing (Dehaene-Lambertz et al. 2005 and Zatorre et al. 1992), and it is also activated preferentially when people focus on the sound of the word, rather than on its meaning (Chee et al. 1999; Demonet et al. 1994; Devlin et al. 2003; McDermott et al. 2003; Price et al. 1997). Planum temporale, that was also activated, is a key anatomical component of Wernicke's area, which is connected to representation of phonetic sequences (Wise et al., 2001). Angular gyrus has been shown to cooperate with supramarginal gyrus in phonological decision tasks (Stoeckel, et al. 2009).

What is different in the activations in L2 task in comparison to the activations in the L1 task, is the activity of the right Broca's area and premotor cortex. Pars opercularis portion of Broca's area has been implicated in phonological processing, and the right

homologue contributes especially to processing of prosody (Gupta 2014). This explains the activation in English and not Polish, as English is a stress-timed language, whereas Polish is not. As stress is an important aspect in understanding English, participants' brains might be tuned to it more heavily while listening to English recordings. Premotor cortex, on the other hand, has been shown to be a part of phonological loop in Baddeley's model of working memory (Ono et al, 2013). Right premotor cortex is thought to be involved with articulatory-to-auditory mapping for feedback control (Tourville and Guenther 2011). It is established that non-native phonetic categories involve greater reliance on general articulatory-to-auditory feedback control systems, which generate auditory predictions based on articulatory planning (Callan et al. 2014), and that is why the activation in the right premotor cortex is visible only in the English task.

4.4. Sternberg Working Memory task

In the analysis of the results from the SWMT in both languages, the activations that were analyzed were broken down into three stages mentioned in the methodological section (see 2.4.2), namely encoding, retrieval, and answer. In the encoding stage, the activations reflect the activity during the aural presentation of four digits that the participants were asked to remember. In the retrieval stage, the activations reflect the activity during the aural presentation of one digit that might or might not have been presented in the encoding stage. In the last, answer, stage, the activations reflect the activity during the process of decision making, when participants decided if the digit in the retrieval stage was repeated or not by pressing a relevant button on the response pad.

The analysis of brain activations during the encoding stage in L1 yielded a number of significant voxels with peak activations in the left Heschl's gyrus, primary sematosensory cortex, putamen, thalamus, middle temporal gyrus, cerebellum, and the right planum temporale, paracingulate gyrus, superior parietal lobule and occipital fusiform gyrus. All the activated areas are listed in Table 2 and visualized in Fig. 8.

The analysis of brain activations during the encoding stage in L2 version of SWMT yielded a slightly different scope of peak activations, as there were three clusters, encompassing such areas as the left primary auditory cortex, planum

temporale, inferior parietal lobule, premotor cortex, Broca's area 44, and the right primary auditory cortex, planum temporale, inferior parietal lobule, and premotor cortex. Even though some of the activated areas might be similar, there are more peak activations in L2 than L1 in the same areas. All the areas are listed in Table 2, and visualized in Fig. 8.

Table 2. Regions in the brain activated in SWMT encoding stage. L and R before the name of the brain region stand for left and right hemisphere, respectively.

L1 - Polish			
Brain region	MNI coordinates	Z-Score	Peak activations
L Heschl's gyrus	-48 -10 4	5.32	1
L primary sematosensory	-48 -22 54	4.84	1
cortex			
L putamen	-18 0 10	4.13	1
L thalamus	-12 -22 16	4.23	1
L cerebellum	-4 -76 -12	4.34	2
L middle temporal gyrus	-52 -60 6	4.64	1
R planum temporale	58 -18 10	6.19	1
R paracingulate gyrus	4 8 50	5.32	1
R premotor cortex	46 -2 46	4.74	1
R superior parietal lobule	28 -66 42	4.84	1
R occipital fusiform gyrus	28 -62 -14	4.24	1
L2 - English			
Brain region	MNI coordinates	Z-Score	Peak activations
L primary auditory cortex	-52 -26 10	6.16	1
L inferior parietal lobule	-60 -30 18	4.07	2
L premotor cortex	-2 14 48	3.67	4
L Broca's area 44	-46 24 18	3.84	1
R primary auditory cortex	56 -12 10	5.44	1
R planum temporale	60 -18 10	5.41	2
R inferior parietal lobule	60 -50 4	3.08	1
R premotor cortex	10 18 40	3.25	2

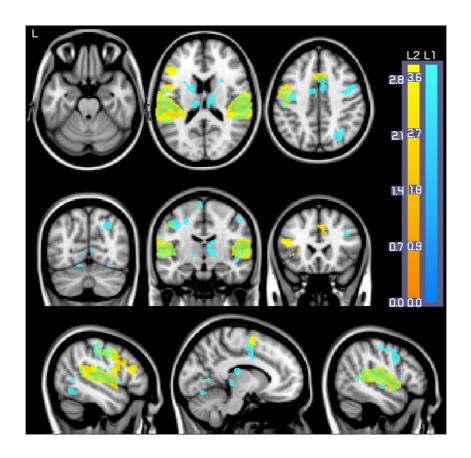


Fig. 8. Activated brain areas in the SWMT encoding stage. Z-stat > 2.3, p < 0.01. Blue-cyan clusters represent the activations in L1 task, and orange-yellow represent the activations in L2 task. Green represents the overlap of the two. Images presented in neurological convention.

As for the task in L1, the activation in the planum temporale is not surprising, as the stimuli were presented aurally. These activations are prevalent in the tasks involving listening to stimuli, and the explanation of the functions of these areas are no different in this case from the one presented in the previous subsection on passive listening. Heschl's gyrus, that was also found active in the analysis, is a part of the primary auditory cortex, and it has been linked to processing of rapid acoustic changes (Warrier et al. 2009). As such it is also not an unexpected result. Even though most of these activations are linked to the processing of speech, and are found in the passive listening to L1, five activations, in the right premotor cortex, and the left cerebellum, thalamus, putamen, and paracingulate gyrus point to the recruitment of memory and attentional resources. One of the strategies for performing verbal short-memory maintenance is phonological rehearsal by using inner speech as a conscious and attention demanding process (Herwig et al. 2003). As rehearsal has been associated with premotor cortex in the literature (Awh et al., 1996 Smith and Jonides 1999, Fiez et al. 1996; Henson et al. 2000, Herwig et al. 2003), this activation suggests that participants were consciously

using rehearsal in order to maintain the list of digits for further use in the retrieval and answer stages. The cerebellum has also been implicated in phonological storage and memory processing (Maher et al. 2014; Desmond et al. 1997; Chen and Desmond 2005), thus the activation in this task is not surprising. The same goes for putamen, which has been linked to memory processing (Packard and Knowlton 2002), and thalamus and paracingulate gyrus, which have been linked to attention and language processing, respectively (Van der Werf et al. 2003; Fornito et al. 2004).

The biggest difference in the results in L2 in comparison to L1 is visible in three areas. The premotor cortex is activated bilaterally, with as much as six peak activations instead of just one. This shows the greater effort of the participants to maintain the information in the memory. Even though there is no difference in reaction times between SWMT in L1 and L2, it is clearly visible that the brain must have involved more resources to maintain the same efficiency in the task. This is supported by the fact that the second area that was different from L1 results is the left Broca's area. This area has been also shown to be involved in rehearsal and storage processes (Trost and Gruber 2012; Gruber 2003; Paulesu et al. 1993; Jonides et al. 1998), and along with premotor cortex is believed to constitute the core articulatory rehearsal areas involved in verbal working memory (Fegen et al. 2015). The third area that was different from the L1 task is the inferior parietal lobule, that was activated bilaterally in L2. One of the functions of this area, i.e. phonological processing, has already been discussed in the previous subsection. However, inferior parietal lobule, and especially supramarginal gyrus, has been also implicated in verbal working memory (Deschamps et al. 2014). As it was not activated in L1, it supports the hypothesis of the greater effort of the brain to sustain the efficiency of verbal working memory in L2.

A post-hoc analysis of the direct contrast between the areas that were active in L1 task and not L2 (L1>L2) has also revealed an activation in the left thalamus (MNI -12, -10, -2, Z-score = 4.07), and the left hippocampus (MNI -26, -34, -16, Z-score = 4.13). It has been shown in the literature that the hippocampus can be involved in working memory tasks, but that it is irrelevant to memory-based performance for phonologically codable stimuli over brief delays (Zarahn et al. 2005). This would suggest that even though the digits were presented aurally during the task in L1, the brain did not necessarily treat them as linguistic elements when encoding the information in the working memory, and that is why the hippocampus was involved in

the process leading to maintenance of the items. As there was no involvement of hippocampus in L2, it would suggest that the digits in L2 were in fact treated as phonologically codable items. The involvement of other areas than hippocampus for working memory encoding would also make sense from the point of view of network efficiency. As there are more areas activated in L2 for phonological processing and working memory encoding, the brain must sustain efficient paths leading from one area to another, in order to pass the information efficiently. It has been shown that reduced local efficiency (connections to not only one local area of the brain) and high global efficiency (short paths to different areas) lead to improved performance in working memory tasks (Yu et al. 2014). Thus, the involvement of hippocampus could distort the efficiency of information flow in L2; however, as there are lower brain requirements in L1 task, it can be used instead. As the thalamus has also been implicated in the working memory (Llano 2013), the lack of the activity of the thalamus in L2 could also be explained in the same way. Even though it is visible in Figure 8 that the activations in L1 encompassed more areas, which is supported by the bigger overall number of voxels for L1 than L2, the bigger number of important peak regions for L2 suggests the more specialized network for L2 that sustains the efficiency. Even though the number of areas might be greater for L1, the lack of specialization of these areas may distort the data flow, as already mentioned, contributing to lower efficiency. This might also explain why the reaction times and scores in SWMT in L1 and L2 were not significantly different, even though the task in L2 posited greater effort.

As for the retrieval stage, the activations found in L1 and L2 were similar. In L1, there were two activated clusters encompassing the primary auditory cortex, planum temporale, and inferior parietal lobule, all bilaterally. In L2, there were bilateral activations in the primary auditory cortex and planum temporale, and the activation in the left inferior parietal lobule. All the activations are presented in Table 3 and visualized in Fig. 9.

Table 3. Regions in the brain activated in SWMT retrieval stage. L and R before the name of the brain region stand for left and right hemisphere, respectively.

L1 - Polish			
Brain region	MNI coordinates	Z-Score	Peak activations
L primary auditory cortex	-56 18 8	4.33	2
L planum temporale	-52 -32 12	4.02	1
L inferior parietal lobule	-58 -42 12	3.41	2
R primary auditory cortex	48 -16 10	4.17	2
R inferior parietal lobule	62 -34 10	3.61	3
L2 - English			
Brain region	MNI coordinates	Z-Score	Peak activations
L primary auditory cortex	-58 -24 10	3.97	3
L planum temporale	-62 -28 12	3.4	1
R inferior parietal lobule	56 -28 12	3.12	2
R primary auditory cortex	56 -14 8	4.47	1

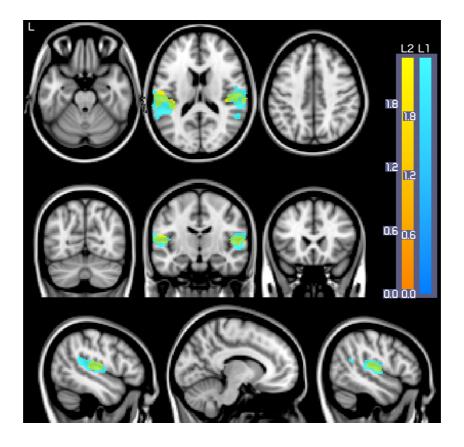


Fig. 9. Activated brain areas in the SWMT retrieval stage. Z-stat > 2.3, p < 0.01. Blue-cyan clusters represent the activations in L1 task, and orange-yellow represent the activations in L2 task. Green represents the overlap of the two. Images presented in neurological convention.

It is clear that in this stage the brain did not treat the items in L1 and L2 as significantly different, as the activations themselves did not differ significantly. It might suggest that once the items in the working memory are encoded, they are stored in the same way, independent of the source language, and that the retrieval involves the same

mechanisms, as the items are stored in the same place. As there are no differences between L1 and L2 that were visible in the encoding stage, it might mean that the stimuli upon hearing are not encoded in the usual way, but are rather prepared for the matching to the items already maintained in the phonological storage. The lack of significant differences might also be explained by the fact that it is possible to deemphasize phonological processing, if it interferes with performance (Edwards et al. 2005). During the retrieval stage the content of the item, which is a digit, is more important than its form to successful matching, and thus, phonological processing becomes irrelevant to the task. This is supported by the reaction times, which were discussed in section 4.2. There was no significant difference in reaction times in L1 and L2. It suggests that once the items are encoded, the later stages are processed on a different cognitive level, without the language being involved. It has been shown in the literature that numerical processing might involve the same network in the brain, irrespective of the language in which the numerals are encoded (Dehaene and Cohen 1995; Dehaene et al. 1999; Hubbard et al. 2005; Eger et al. 2003; Pesenti et al. 2000).

The analysis of brain activations during the last stage, i.e. the answer, revealed a varied scope of brain areas for L1 and L2. In L1, there were five clusters of activation, that encompassed such areas as the left primary somatosensory cortex, right insular cortex, and left putamen, all of which are connected to movement and the sense of touch. There was also an extensive activation in the right Broca's area, left Broca's area, left and right inferior parietal lobule, the left lingual gyrus, and the right cerebellum. All the activated areas are listed in Table 4, and visualized in Fig. 10.

In the analysis of the regions that were activated during the task in L2, five clusters with significant voxels were yielded. The regions with peak activations included the left primary motor cortex, the left and right insular cortex, the left putamen, the left inferior parietal lobule, left and right Broca's area, the left and right premotor cortex, left thalamus, the right lingual gyrus, the right cerebellum, the left and right lingual gyrus, and the right amygdala. All the activated regions are listed in Table 4, and visualized in Fig. 10.

 $\begin{tabular}{ll} Table 4. Regions in the brain activated in L1 SWMT answer stage. L and R before the name of the brain region stand for left and right hemisphere, respectively. \\ \end{tabular}$

L1 - Polish Brain region	MNI coordinates	Z-Score	Peak activations
L primary somatosensory	-40 -42 54	4.07	2
cortex	40 42 34	4.07	<u> </u>
L putamen	28 -2 0	3.09	1
L Broca's area	-46 6 4	3.96	1
L inferior parietal lobule	-42 -48 56	3.84	1
L lingual gyrus	-4 -80 -14	3.27	4
L insular cortex	-32 16 0	3.86	1
R insular cortex	28 20 6	2.99	1
R Broca's area	46 12 -2	3.97	4
R Cerebellum	4 -66 -8	3.32	1
L2 - English		5.52	-
Brain region	MNI coordinates	Z-Score	Peak activations
L primary motor cortex	-36 -30 64	3.51	1
L insular cortex	-30 18 2	4.04	1
L putamen	-26 8 12	2.79	1
L inferior parietal lobule	-50 -38 50	4.27	1
L Broca's area 44	-44 12 2	3.46	2
L premotor cortex	-24 -16 68	3.74	4
L thalamus	-14 -16 12	2.86	1
L lingual gyrus	-6 -86 -4	3.16	1
R cerebellum	4 -68 -18	3.31	3
R amygdala	26 0 -10	3.02	1
R Broca's area 44	48 14 0	3.81	2
R premotor cortex	2 20 42	4.01	1
R insular cortex	34 16 0	3.58	3
R lingual gyrus	4 - 78 - 4	4.02	1

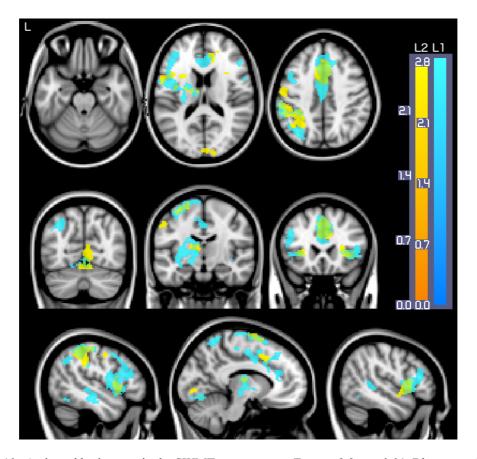


Fig. 10. Activated brain areas in the SWMT answer stage. Z-stat > 2.3, p < 0.01. Blue-cyan clusters represent the activations in L1 task, and red-yellow represent the activations in L2 task. Green represents the overlap of the two. Images presented in neurological convention.

As far as the results of the L1 answer stage are concerned, the areas connected with movement and the sense of touch were expected, as the participants had to make a decision by pressing a button with their finger. What is interesting is the extent of activation in the areas connected with memory. As mentioned before, Broca's area and the inferior parietal lobule are known to be involved in the working memory, and they were active during the encoding stage. What is new in this stage is the presence of the lingual gyrus, which was not activated in the encoding and retrieval stage. It has been shown, however, that lingual gyrus plays a role in memorization, and especially recollection in logic tasks (Leshikar et al. 2012). Also, it is suggested that there might be a potential link from the lingual gyrus to hippocampal regions of the brain (Cho et al. 2012), which would be supported by the fact that the hippocampus was active in the L1 encoding stage. The activation in the right cerebellum is also not unexpected, as the

activity in this region has been linked to working memory and phonological storage, as mentioned in the previous subsections.

The biggest difference between the activations in L1 and L2 lies in the activity in the premotor cortex in L2, which is absent in L1. It might support the hypothesis that only the items in L2 are treated as elements that need phonological processing. As the premotor cortex subserves the auditory-to-articulatory feedback control, and it is relied on more heavily in non-native contrasts, the activation shows that even in the answer stage, this feedback control might be required in order to match the items to the ones that are already encoded. It could be also the case that in this stage, the brain encodes the item that was presented in the retrieval stage, as without rehearsal, it would not be maintained long enough to match it to the already encoded information in order to make a decision. This could be supported by the lack of premotor activation in the retrieval stage. Stronger activation in the cerebellum in L2 also might suggest that a greater access to the phonological storage might be required in parallel to the regions that subserve the working memory.

It was suggested that in the retrieval stage, the brain processes the items on a deeper level without the conscious involvement of phonological processing. That is why we can assume that the processing in the retrieval stage is automatic. In the answer stage, however, as the decision is being made on the basis of conscious effort, we can see the involvement of the regions responsible for phonological processing; thus, we can assume that phonological processing occurs only when there is a conscious focus on the form of the item (which in this case is needed to match it to other items). As the activity in the cerebellum is far greater in L2 than in L1, it supports the hypothesis that the phonological processing of L2 requires more resources in the brain. However, as it has been shown in the literature, greater neural engagement (more areas activated in the brain) can be independent of reaction times (Taylor et al. 2014), and that is why there is no difference in reaction times between L1 and L2, even though different neural networks are engaged in both languages. As there was also an activation in L2 in amygdala, which is linked to processing of emotions, especially fear and sadness (Lanteaume et al. 2007), and emotional learning (Carlson 2012), it might suggest that the task in L2 was harder to the participants, and thus more stressful, inducing the activity in this part of the brain. Amygdala has been also shown to regulate memory consolidation (Blair et al. 2001). As the involvement of amygdala strengthen the

retention of information, it might have contributed to the lack of differences in the scores between L1 and L2, enhancing the performance in L2.

4.5. Verbal Fluency test

In contrast to the results from previous subsections, the analysis of verbal fluency task in L1 and L2 reflect the activation during the production, and not perception, of language. The analysis yielded similar results in both languages, with the difference on the intensity. In L1, there was only one cluster of activated voxels, which included such areas as the left primary motor cortex, the left premotor cortex, and the left Broca's area 44. In L2, there were two clusters of significant voxels that included such areas as the left premotor cortex, left Broca's area, left thalamus and insular cortex. All the activated areas are listed in Table 5, and visualized in Fig. 11.

Table 5. Regions in the brain activated in L1 and L2 verbal fluency task. L and R before the name of the brain region stand for left and right hemisphere, respectively.

L1 - Polish			
Brain region	MNI coordinates	Z-Score	Peak activations
L primary motor cortex	-38 10 36	2.93	1
L premotor cortex	-52 -44 50	4.05	3
L Broca's area 44	-52 14 38	3.31	1
L2 - English			
Brain region	MNI coordinates	Z-Score	Peak activations
L premotor cortex	-52 -2 48	4.07	6
L Broca's area 44	-38 14 12	5.06	1
L thalamus	-16 -4 14	4.38	1
L insular cortex	-26 12 12	4.75	1

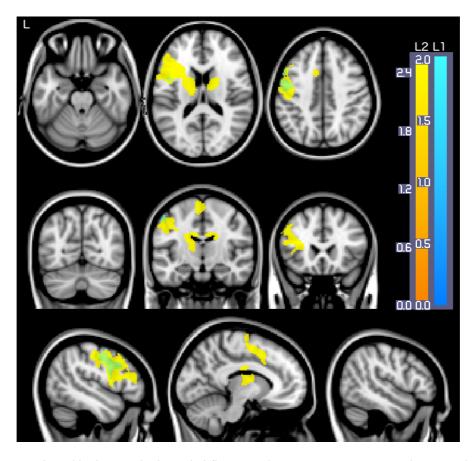


Fig. 11. Activated brain areas in the verbal fluency task. Z-stat > 2.3, p < 0.01. Blue-cyan clusters represent the activations in L1 task, and red-yellow represent the activations in L2 task. Green represents the overlap of the two. Images presented in neurological convention.

As the participants in the task were asked to silently produce words that begin with a given letter, the activation in the left Broca's area is a typical finding (Kroliczak et al. 2011). Broca's area has long been implicated in language production (Dronkers et al. 2007), and the activation in the left hemisphere is connected to the typical lateralization of language in right-handers (Knecht et al. 2000). The activation in the areas connected to the execution and planning of movement, such as premotor cortex, primary motor cortex and the insular cortex have been linked in various studies to the production of action words (Hauk et al. 2004; Lafuente and Romo 2004). As there was no control over what words were generated by the participants in the task, it might be that some of the generated words were action words, and that is why the motor areas were activated. Alternative, and more plausible, explanation might be that the motor areas were active, because during the silent articulation, the brain processes the plan of the movement of the articulators (Simmonds et al. 2011). This explanation could be supported by the fact that the activity in premotor cortex in L2 had twice as many peaks

as in L1. It has been mentioned that the premotor cortex also subserves the sensory to motor feedback, and it has been established in the literature that L2 language production is less automatic and may result in greater activity in response to sensory feedback (Simmonds et al. 2011). Even though the activated areas in both languages are similar, the extent of the activity in L2 suggests the bigger conscious effort to produce the language that approximates the phonologically accurate representations.

What is also interesting is the lack of any activation in Wernicke's area in both languages, which supports the hypothesis that it is Broca's area that is involved in language production (Dronkers et al. 2007), and that Wernicke's area is involved heavily in language comprehension (Tanner 2007), what was also visible in the previous sections. The lateralization of the processes in the left hemisphere in L2 also supports the view that the right hemisphere is not involved in L2 in highly proficient bilinguals.

4.6. LexTALE

In this experiment, the analysis was also broken down into 3 stages, namely the analysis of the activity during the presentation of a real word in L1 and L2, the presentation of a psuedoword in L1 and L2, and the decision whether the presented item belongs to either of the two categories.

The analysis of the activated areas during the presentation of a real word in L1 revealed two clusters of significant voxels, including the areas of the left and right primary auditory cortex, right planum temporale, and the left and right inferior parietal lobule. In L2, the analysis revealed 3 clusters of activated areas that included the left primary auditory cortex, the right Heschl's gyrus, the left and right inferior parietal lobule, the left planum temporale, the left premotor cortex, the right middle temporal gyrus, and posterior part of the left superior temporal gyrus. All the areas are listed in Table 6 and visualized in Fig. 12.

Table 6. Regions in the brain activated in L1 and L2 LexTALE real word condition. L and R before the name of the brain region stand for left and right hemisphere, respectively.

L1 - Polish			
Brain region	MNI coordinates	Z-Score	Peak activations
L primary auditory cortex	-44 -24 10	4.62	4
L inferior parietal lobule	-50 -44 11	4.38	2
R primary auditory cortex	54 -18 4	4.85	2
R planum temporale	56 -20 12	4.64	1
R inferior parietal lobule	56 -36 18	4.37	2
L2 - English			
Brain region	MNI coordinates	Z-Score	Peak activations
L primary auditory cortex	-48 -24 12	7.83	1
L inferior parietal lobule	-60 -44 12	3.51	1
L planum temporale	-60 -24 12	6.71	1
L premotor cortex	-4 28 62	4.23	4
R middle temporal gyrus	62 -38 8	3.03	2
R Heschl's gyrus	53 -20 21	8.95	1
R inferior parietal lobule	52 -52 -8	2.44	1
R superior temporal gyrus	60 -20 -4	3	1

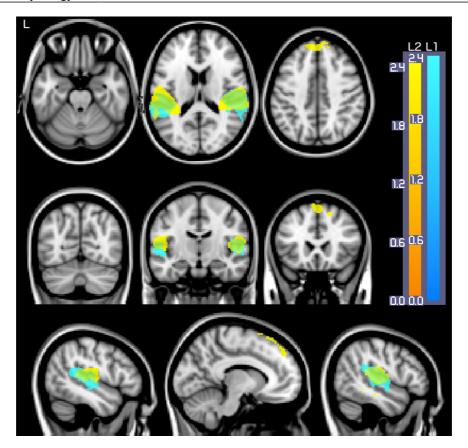


Fig. 12. Activated brain areas in the LexTALE real word condition. Z-stat > 2.3, p < 0.01. Blue-cyan clusters represent the activations in L1 task, and orange-yellow represent the activations in L2 task. Green represents the overlap of the two. Images presented in neurological convention.

It is clearly visible that the activated areas in L1 and L2 resemble these in the passive listening task. The biggest difference between the two languages is again the

activation of the premotor cortex in L2. This supports the hypothesis of the auditory-to-articulatory feedback control in L2 that was discussed earlier. Striking similarity to the activations in the passive listening task, and the lack of involvement of memory structures, also suggests that even though it is a lexical decision task, the presentation of the stimulus is not the stage in which the decision is being made, as the brain passively processes the items. Also, the lack of the activation in the premotor cortex in L1 suggests that L1 is processes automatically without the conscious focus on the form of the language.

The analysis of the activated areas during the presentation of pseudowords in L1 also revealed two clusters of significant voxels that encompassed the areas of the left and right primary auditory cortex, right planum temporale, and the left and right inferior parietal lobule. In L2, the analysis also revealed two clusters of significant voxels encompassing the left and right primary auditory cortex, the left Heschl's gyrus, the left and right inferior parietal lobule, the left planum temporale, and posterior part of the left superior temporal gyrus. All the areas are listed in Table 7 and in Fig. 13.

Table 7. Regions in the brain activated in L1 and L2 LexTALE pseudoword condition. L and R before the name of the brain region stand for left and right hemisphere, respectively.

L1 - Polish			
Brain region	MNI coordinates	Z-Score	Peak activations
L primary auditory cortex	-44 -24 10	4.75	4
L inferior parietal lobule	-52 -42 14	4.57	2
R primary auditory cortex	54 -18 4	4.98	1
R inferior parietal lobule	60 -38 14	4.83	2
R planum temporale	56 -20 12	5.08	1
L2 - English			
Brain region	MNI coordinates	Z-Score	Peak activations
L primary auditory cortex	-44 -24 10	3.76	4
L Heschl's gyrus	-46 -24 14	3.73	1
L inferior parietal lobule	-52 -42 14	3.81	2
L planum temporale	-62 -30 14	3.92	1
R inferior parietal lobule	48 -30 14	4	1
R primary auditory cortex	56 -20 10	4.5	2
R planum temporale	36 -36 16	4.18	2
R superior temporal gyrus	56 -30 0	2.84	1

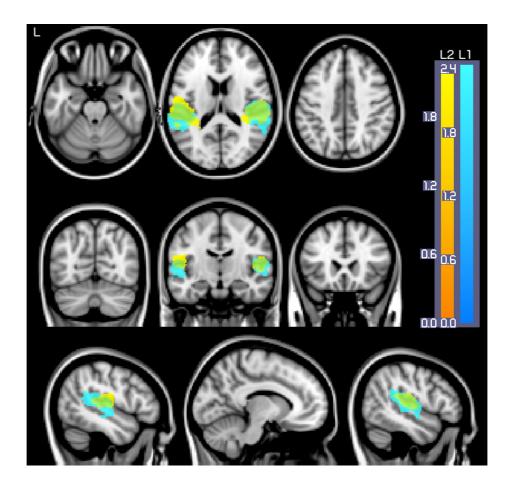


Fig. 13. Activated brain areas in the LexTALE pseudoword condition. Z-stat > 2.3, p < 0.01. Blue-cyan clusters represent the activations in L1 task, and orange-yellow represent the activations in L2 task. Green represents the overlap of the two. Images presented in neurological convention.

It seems that the areas activated during the presentation of pseudowords in L1 are no different from the areas activated during the presentation of real words in L1. However, there is a visible difference in L2, as there is no activation in the premotor cortex during the presentation of pseudowords. This is interesting, as it suggests that there was no auditory-to-articulatory feedback and that the brain automatically detected that the item did not belong to the language system. It has been shown in the literature with event-related potentials that the brain can detect lexical change in stimuli without co-occuring acoustic changes in word/pseudoword lexical decision tasks. It has been proposed that following lexical analysis of the incoming stimuli, a mental template with representations of regularity is formed, against which lexical change can be detected automatically (Muller-Grass et al. 2007). It might suggest that if this detection occurs before the auditory-to-articulatory feedback is done, the latter process becomes redundant and that is why there is no engagement of the premotor cortex.

While the processes discussed above came from the rather automatic stage of retrieving the stimuli, the following analysis revealed the brain areas activated during the conscious decision making in L1 and L2. In L1, the areas that were activated during the decision included 3 clusters of significant voxels in the left and right cingulate gyrus, the left Broca's area, the left and right lingual gyrus, the left middle temporal gyrus, the posterior part of the left superior temporal gyrus, the right paracingulate gyrus, and the left primary auditory cortex. In L2, the activated areas also included 3 clusters of significant voxels in the areas of the left secondary sematosensory cortex, the left and right Broca's area, the left premotor cortex, posterior part of the right superior temporal gyrus, the right insular cortex, and the left primary auditory cortex. All the areas are presented in Table 8 and Fig. 14.

Table 8. Regions in the brain activated in L1 and L2 LexTALE decision condition. L and R before the name of the brain region stand for left and right hemisphere, respectively.

L1 - Polish	MNI coordinates	Z-Score	Peak activations
Brain region			reak activations
L cingulate gyrus	-6 32 24	4.38	1
L Broca's area 44	-50 8 4	4	2
L lingual gyrus	-24 -58 -16	3.72	2
L middle temporal gyrus	-50 -52 6	3.21	4
L superior temporal gyrus	-48 -34 -2	3.54	1
L primary auditory cortex	-48 -20 0	2.84	1
R cingulate gyrus	6 30 24	4.13	2
R lingual gyrus	14 -54 -8	3.55	1
R paracingulate gyrus	4 30 32	4.11	1
L2 - English			
Brain region	MNI coordinates	Z-Score	Peak activations
L secondary	-52 -4 4	6.46	1
somatosensory cortex			
L Broca's area 44	-32 12 10	6.7	2
L premotor cortex	0 12 48	6.4	2
L primary auditory cortex	-52 0 2	6.45	2
R Broca's area 44	50 10 0	6.56	3
R superior temporal gyrus	52 -34 6	6.26	2
R insular cortex	32 18 0	4.66	1

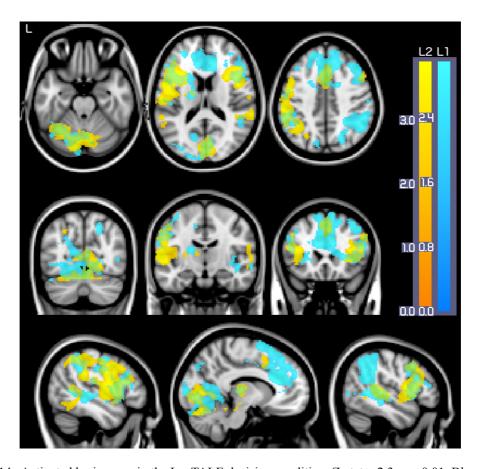


Fig. 14. Activated brain areas in the LexTALE decision condition. Z-stat > 2.3, p < 0.01. Blue-cyan clusters represent the activations in L1 task, and orange-yellow represent the activations in L2 task. Green represents the overlap of the two. Images presented in neurological convention.

The activity in the primary auditory cortex in both L1 and L2 suggests that some of the decisions must have been made before the stimuli ended playing. The first big difference in the rest of the activations is visible in the areas of cingulate and paracingulate cortex that was activated in L1 and not L2. These areas are part of the attention network in the brain, and have been linked to the processing of pseudowords (Petersen and Posner 2012), as it has been suggested that the processing of pseudowords requires substantial attentional resources (Price et al. 1996; Hagoort et al. 1999; Mechelli et al. 2000; Paulesu et al. 2000; Binder et al. 2005; Vigneau et al. 2006), and more effort (Henderson and Luke 2012, 2014; Henderson et al. 2014). It has been also suggested that there is a link between activation in cingulate cortex and subsequent performance, including the magnitude of error and reaction time (Kerns et al. 2004), which would be supported by the fact that there was no activation in cingulate cortex in L2, and error rates were higher in LexTALE in L2. Also the lower reaction times in L1

might be explained by the fact that the activation of additional attentional resources may cause a delay that manifests in the time needed for making a decision.

What is more, the middle temporal gyrus, which was activated in L1 and not L2 has been connected with semantic processing (Binder et al. 2009). Thus, it might be assumed that it is in this stage that the brain decides whether an item is a real word or not using semantic and attentional processes in L1. This would be supported by the lack of distinction between the real words and pseudowords in the automatic processing in the presentation stage. It might mean that these attentional and semantic resources are only activated when there is a conscious focus on the stimuli. In L2 there is one, as it has been shown in the previous section and in the activations of semantic regions (middle temporal gyrus) in the real word processing in the presentation stage, thus the activations in this stage differ between the languages. This could explain the lower reactions times in L2, as the semantic decision might in fact occur earlier in the brain in L2 (the presentation stage) than L1 (decision stage).

The second biggest difference in the activations is the activity in the lingual gyrus in L1, which is linked to memory consolidation. As this shows that there are more resources involved in L1 during the task, it might have an influence on the difference in the accuracy scores and the reaction times. What is more, there was a third biggest difference, which was visible in the activity of the premotor cortex in L2. This suggests that in conscious decision making, there could be a rehearsal process connected with the task difficulty, which was greater in L2, as reflected by the lower scores. It has been suggested in the literature that the premotor cortex is active in language perception only when there is a need for bigger neural effort to support speech decision tasks (Chevillet et al. 2013).

The activity of Broca's area in both L1 and L2 in the decision stage and not during the presentation stage supports the view that increased activity in this area is linked to general processes in lexical decision making (Xiao et al. 2005).

4.7. Resting-state fMRI

The analysis of degree centrality has computed the number of functional connections to the areas that were activated in the experiments described in previous sections. The voxel-wise computation has shown that there is no significant correlation between the number of overall functional connections to the areas and the accuracy scores of SWMT and LexTALE in L1 and L2. However, the analysis of voxel-mirrored homotopic connectivity has indicated that the connectivity between the left cingulate gyrus and its right homologue correlated strongly and significantly with the scores of LexTALE in L1, and that the interhemispheric connectivity between three areas in the left middle temporal gyrus and their homologues in the right hemisphere correlated strongly and significantly with the scores of LexTALE in L2. The coordinates of the areas and correlation coefficients are presented in Table 12.

Table 9. Correlation coefficients between the homotopic connectivity and accuracy scores of LexTALE

LexTALE in L1			
Brain region	MNI coordinates	Homologue coordinates	Correlation coefficient
Cingulate gyrus	-3 -33 36	3 33 36	0.938 at p < 0.0001
LexTALE in L2			
Brain region	MNI coordinates	Homologue coordinates	Correlation coefficient
Middle temporal gyrus	-48 -36 -6	60 -36 -6	0.7577 at p < 0.01
		-1 - 1 -	0.004# 0.004
Middle temporal gyrus	-54 -6 -15	54 -6 -15	0.8215 at p < 0.001

First of all, the results suggest that the overall connectivity of a brain area does not necessarily predict the performance in a cognitive task. As the degree centrality does not inform us about the destination of the connections or their distribution, the measure itself might not suffice to make correct predictions about the state of the neural network. However, the results of the voxel-mirrored homotopic connectivity analysis supports the idea, that it is the quality of interhemispheric connections between the homologues that might be predictive of the performance in a language task. This is supported by the number of studies showing the correlation (Dick et al. 2013; Northam et al. 2012).

What is more important, however, is the fact that the areas found to be correlated with the performance in LexTALE in L1 and L2 at rest, were the same areas that mediated the performance during the active task. Cingulate gyrus, which was said to be linked to attention, was active in LexTALE in L1 only during decision making. As it has been already mentioned, L1 seems to be processed more automatically, and that is why the attentional resources might need to be overtly active at rest to ensure the fast activation in the decision process. On the other hand, L2 was said to be processed with more conscious effort and attention, and that is why there is no need for cingulate gyrus to contribute to the overall attentional resources. Middle temporal gyrus that was

revealed by the homotopic connectivity analysis in L2 was linked earlier to the processing of semantic information. This makes sense, as the middle temporal gyrus was also the differential activation in L2 in the LexTALE presentation stage. This suggests that the readiness of semantic processes at rest might mediate the automation of semantic processing in L2.

The other important conclusion from these findings is that the strength of the interhemispheric connections suggest the inverted involvement of the second hemisphere in L2. It has been suggested in the literature review that the lower proficiency level subjects might rely on the right hemisphere in order to ensure the needed efficiency in linguistic processing. However, the positive correlations found in the analysis show that the more strongly connected the areas are, the more accurate the scores are in LexTALE. This case would be supported by the lack of activation in the left middle temporal gyrus in the presentation stage in LexTALE in L2. On the other hand, the scores in LexTALE in L2 were moderate (mean 55%), thus it might be assumed that the studied group was not highly proficient in L2 after all, as it was inferred from their education (English students). Hence, the right hemisphere involvement is plausible in that case. What is more, the correlation retrieved by the homotopic connectivity analysis is by no means directional. Taking this into consideration, we might assume that it could have been the right hemisphere that was involved in the low proficiency subjects in LexTALE in L2, and with higher scores, and thus proficiency, the connectivity to the left hemisphere was stronger, so the processing could be relocated to the left hemisphere. As the variance in scores in LexTALE 2 was low, the effect is only visible by the connectivity, as it was too low to actually manifest itself in the activation of the left middle temporal gyrus during the task.

4.8. Diffusion Tensor Imaging

The probtrackx analysis of white matter fibers tracked from the bilateral regions of Broca's area and premotor cortex have revealed a bundle of areas involved in the language network that are structurally interconnected. These areas in the left hemisphere included Broca's area 44 and 45, hippocampus, primary auditory cortex, primary motor cortex, primary somatosensory cortex, secondary somatosensory cortex, premotor

cortex, cingulate gyrus, planum temporale, Heschl's gyrus, insula, temporal fusiform gyrus, and cerebellum. In the right hemisphere the areas included Broca's area 44 and 45, primary motor cortex, primary and secondary somatosensory cortex, premotor cortex, and cingulate gyrus. The fibers tracked from the left Broca's area and the premotor cortex of one of the participants is visualized in Fig. 15.

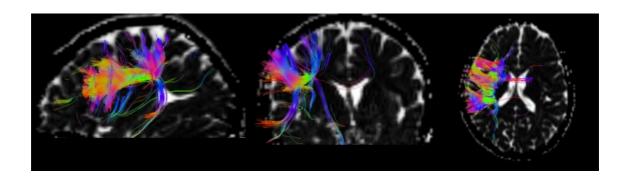


Fig. 15. White matter fiber tracts, tracked from the left Broca's and premotor cortex seeds, overlaid onto individual's diffusion weighted image. From left to right: sagittal view of the left hemisphere, coronal view of anterior brain, axial view in neurological convention.

What is important from the above results, is the difference in connection patterns between the left and the right hemisphere. In the right hemisphere there is a lack of fiber tracts connecting Broca's area or premotor cortex with the temporal lobe. On the other hand, in the left hemisphere, there is a tract encompassing both Broca's area and premotor cortex, going through the primary auditory cortex, planum temporale, Heschl's gyrus, all the way to the cerebellum. This suggests that there is a classical structural Broca's-Wernicke's connectivity, but only in the left hemisphere. From the right hemisphere there are only two tracts connecting the left temporal lobe with Broca's area and premotor cortex, which follow through the primary motor cortex or cingulate gyrus.

These findings suggest that only the left language network is heavily interconnected structurally. We may safely assume that L1 is used more often, and since earlier age, thus these connections might reflect structural changes that occur to accommodate the heavier load. Since it is suggested that the reliance on the right hemisphere in L2 diminishes with proficiency, the structural connections in the right hemisphere might not be needed. What is more, the fact that only the left temporal lobe is connected to right Broca's and premotor areas might suggest lesser efficiency in the information flow between these areas, hence the worse performance in L2 linguistic

tasks. A recent study (Garcia-Penton et al. 2014) have shown a similar pattern of greater connectivity in the left hemisphere in bilinguals in comparison to monolinguals, thus it might be hypothesized that the results visible in the left hemisphere in this analysis might reflect the bilingual effect. Of course, without a control monolingual group to compare the results to, it is impossible to to validate the effect, thus the result of this analysis should be treated only as an exploratory one.

In addition to probtrackx, tract-based spatial statistics were also computed, in order to correlate the results of SWMT and LexTALE in L1 and L2 with integrity of white matter, measured by fractional anisotropy. The analysis yielded no significant results in regard to SWMT and LexTALE, which means that fractional anisotropy in the white matter tracts could not be predictive of behavioral results on these tests. Previous studies on white matter integrity in bilinguals have shown elevated fractional anisotropy in white matter tracts in bilinguals (Mohades et al. 2012; Duffau et al. 2005; Mandonnet et al. 2007), but only in comparison to monolinguals. Schlegel et al. (2012) have shown that the effect of FA increase can be seen in bilinguals as a function of second language proficiency, but it needs a longitudinal measures using DTI. A recent study by Pilatsikas et al. (2015) found the effect of FA increase in white matter tracts in bilinguals in comparison to monolinguals, but the effect was gone when they repeated the analysis on the bilinguals alone, with the amount of immersion in months as a regressor. This supports the lack of findings in the present analysis, as there was only one group of bilinguals with a single measurement in time.

4.9. VBM

The whole-brain analysis of gray matter to white matter ratio yielded no significant correlations with the results of SWMT and LexTALE in L1 or L2. It has been shown in the previous studies that cortical thickness can be increased in bilingual individuals (Mechelli et al. 2004; Osterhout et al. 2008; Martensson et al. 2012; Klein et al. 2014), but as in the case of white matter integrity, the studies compared bilinguals to monolinguals or compared the differences in bilinguals over a period of time. As in this study the participants are only bilingual, the lack of significant findings in the analysis

may reflect the tendency, suggesting that structural changes in a homogenous group do not reflect enough variance to be predictive of L2 proficiency.

Chapter 5: Discussion

5.1. Towards a bilingual model of phonological perception and production

In this chapter, all the results will be summarized and put into relevant categories, which will help create a cohesive model of bilingual language processing in the Polish-English bilingual brain. First, the perceptual findings will be discussed in relation to passive listening, working memory encoding and retrieval, and real vs. pseudoword processing. Then, the findings on language production will be summarized. Also, the decision processes in memory vs. lexical tasks will be discussed along with the relevant findings for automatic and attentive processing of language. Finally, the structural and functional design of a resting brain and its contribution to language will be explained.

5.1.1. L1 and L2 speech perception and phonological processing

The activated regions during passive listening in L1 reflect a typical pattern of phonological processing, as described in the neural model discussed in the first chapter. Most of the regions, i.e. primary auditory cortices, inferior parietal lobules, and planum temporale, were also active in L2, however there were activations that would make the passive listening in L2 deviate from the native model. These would be the activations in the right premotor cortex, and right Broca's area in L2. As it has been discussed earlier, the premotor cortex might play multiple roles in the perception of spoken language. It has been connected to articulatory-to-auditory feedback, phonological loop component of the working memory, and rehearsal system. Even though the neurocomputational

model mentioned in the first chapter includes the premotor cortex as a part of a mirror neuron system that connects production and perception, the lack of activation in the premotor cortex in L1 in the experiment, and also in the neural model discussed earlier, would suggest that there is no need for the involvement of this area in the native speech processing. In L2, however, there is plenty of support for its role. It has been discussed in the first chapter that phonological loop might be activated in L2 to sustain the items in the memory for better processing by rehearsing. As rehearsal activates articulatory planning, the premotor cortex becomes involved. What is more, the activation of this area in the right hemisphere converges with the findings discussed in the first chapter, as it has been shown that less proficient bilinguals rely on the right hemisphere in L2 processing more than in L1 processing. Apart from the premotor cortex, the activation in the right Broca's area visible in L2 is not found in the models of native language speech perception. However, its roles in L2 have been mentioned in the first chapter. There might be two possible explanations for this activation. The first one assumes that the right Broca's area is involved in the processing of prosody. It has been mentioned that Polish and English differ in terms of prosody. Thus, the processing of L2 prosody might require an overt activation, as it deviates from the automatic processing of native prosody. The other explanation is based on the assumption, which has been made earlier, that Broca's area might be involved in the processing of syntax and morphology. We can assume that these two components are different in Polish and English, and thus there might be different areas involved in the processing in each language. It could be supported by the fact that there was an activation in the posterior superior temporal gyrus in L1, and not in L2, which has been also implicated in the processing of syntactic information. Unfortunately, there are no previous neuroimaging studies on the Polish-English bilinguals that could support the above-mentioned assumption, and we know from the first chapter that language-specific specialized processing modules are rather unlikely to exist in the brain, thus the connection of Broca's area to prosodic processing of L2 seems more plausible.

In order to account for the effect of working memory in the model of L2 perception, the differences between the findings in L1 and L2 encoding stages of SWMT have to be discussed. In the encoding stage of SWMT in L1 the activations were similar to those of passive listening task. However, there were differences related to memory usage, as there were additional activations, in comparison to passive listening,

in the right premotor cortex, hippocampus, and thalamus. The activation in the premotor cortex shows that phonological loop can be activated in L1, but only when there is a conscious effort evoked by memorization. This activation was also visible in L2. What was different between L1 and L2 was the activation in the hippocampus and thalamus in L1, and the activation of Broca's area in L2. This would suggest different patterns of memory storage and access for these two languages. Broca's area and the promotor cortex constitute a core system for rehearsal in verbal working memory. Hippocampus and thalamus, on the other hand, are a part of limbic system responsible for episodic memory. This might suggest that the items in L1 also evoke episodic memory, in addition to verbal working memory needed for the completion of the task, because of the frequency of their use in everyday life. As the items were numbers, it is intuitive that those in L1 are used more frequently than those in L2 in moderately proficient speakers. This pattern of activation might have interesting consequences, which could explain the lack of differences in the scores between the languages in SWMT. As there is a need to involve another memory components in L1, there might actually be a delay, which causes the reaction times to be not significantly different from those in L2, which intuitively should be significantly higher. It is nevertheless interesting that the activations in L2 are reflecting a typical model of verbal working memory, whereas the activations in L1 are not.

As the items in SWMT were numbers, the real words and pseudowords used in LexTALE task shed some light on the perception of isolated regular lexical items. In the processing of real words in L1 the activations reflected those of passive listening task. As such, there was no difference for the brain if the stimuli were sentences or isolated words, and whether there was a task to complete or not. In L2, however, there was a difference to L1, as there were additional activations in the premotor cortex and the part of the middle temporal gyrus responsible for semantic processing. The activation in the premotor cortex assures us that there is in fact a place for an auditory-to-articulatory feedback system in the model of L2 speech perception, as it has been visible in every L2 task that involved aural presentation of stimuli. The lack of such activation in L1 might stem from the fact that L1 lexicon is generally acquired without conscious effort and focus on the form, while the L2 vocabulary is generally consciously learned, with proper focus on the form by means of repetition, suggesting the parallel acquisition of motor plans along with the sounds. LexTALE was a lexical decision task, hence the

activation could also reflect the effort for sustaining of the item in the memory while the decision was being made for better accuracy, as in the example of SWMT encoding. The activation in the middle temporal gyrus, however, reveals the overt involvement of semantic processing. This is not at all surprising, as the participants had to decide whether the word is real or not, and as the phonotactic rules in pseudowords were observed, the meaning was the only component to rely on. However, there was no such activation in L1, thus suggesting that semantic processing is either covert and automatic or that it happens in the later stages. It has been shown in the previous sections that in fact the latter is true, but it does not exclude the former from also being the case. Nevertheless, the overt semantic involvement in L2 is interesting, as it was not manifested in L2 passive listening task. This suggests that when the listeners focus on bigger structures than words to understand what they are hearing, the syntactic/semantic integration, reflected in the activations of temporal areas that are visible in passive listening, is sufficient. When we look at the patterns of activations during pseudoword processing, it is clearly visible that L1 activations are no different from those of L1 real word processing. This suggests that the brain does not automatically categorize between real and psuedowords in the native language. However, it seems to be the case for L2. In L2 there was no activation in the premotor cortex, which deviates from our model of L2 perception. Yet, it could be a logical explanation that the brain detects the pseudoword as not being a part of the lexicon, and that is why it does not perform the rehearsal. This is an interesting finding, as it suggests that auditory-to-articulatory feedback can be suppressed, which was also shown in the neurocomputational model discussed in the first chapter. Besides, it suggests that articulatory mapping is not necessary for categorization, and that perceptual representation is sufficient.

The last issue important for our model of L2 speech perception is the deemphasis of phonological processing in SWMT retrieval stage, as there was no difference in the activation pattern for L1 and L2. It has been discussed earlier that numerals can be processed by the same network, regardless of the language in which they were coded, and that phonological processing can be de-emphasized to foster performance. This might be a similar case to pseudoword processing in L2, and suggests that the brain might have automatic processes for categorization, which in turn decide on the involvement of other processing levels, e.g. semantics, relevant to the content. There seems to be a top-down process, which transforms the aural input into abstract representation to match the items already stored in the verbal working memory, and not a bottom-up process that re-encodes the stored items phonologically to match them to the input phonological forms. What is more, the process seems to be the same, regardless of language used for input.

5.1.2. Language production in L1 and L2

Even though during the verbal fluency task the participants produced the lexical items silently, the patterns of activation were similar to that of modeled overt speech production discussed in the first chapter. In between L1 and L2 the biggest difference was in the intensity of activations, as the activated areas in both languages resembled each other. The most important finding is the activation in the area of the left Broca's area, and the lack of activation in Wernicke's area in both L1 and L2. In the classical model of language perception and production, it was assumed that the key role of Wernickes's area lies in perception, and Broca's area lies in production. It has been discussed, however, that later findings sometimes reversed these roles and added more linguistic specialization to both. This is reflected in the present findings, as no activation in Wernicke's area links the activation in Broca's to language production. Of course, the exact role of Broca's in the process cannot be easily determined. It has been suggested that together with the premotor cortex, Broca's constitute a core system for rehearsal. As there is no overt speech, we can assume that silent production is exactly that. Wernicke's area has been shown to be active in some of the studies on language production presented in the first chapter, but we can assume that it becomes active as a part of the auditory feedback control, when there are actual sounds produced by the speaker. As there are no sounds produced in the present experiment, there is no need for auditory feedback. Furthermore, the left premotor cortex was also active in both languages, which points to the fact that even silent production of language evokes articulatory planning. This supports the notion discussed in the neurocomputational model, which claims the parallel acquisition of sounds and motor commands. It seems that when it comes to silent production, the motor representation of the items produced cannot be decoupled from phonological representation.

The next interesting finding is the fact that all the activations during verbal fluency task in both languages were found only in the left hemisphere. In all other experiments discussed in the results section, the premotor cortex and Broca's area were found to be active in the right hemisphere. Thus, we might assume the involvement of the right hemisphere in perception, and not production. However, this finding is not so straight-forward to explain. One of the possible explanations could be that production requires less resources than perception, and that is why the right hemisphere is not involved, as the processing in the left hemisphere is sufficient. It has been discussed earlier that the right hemisphere involvement could be directly connected to the level of proficiency in L2. As the stimuli used in perceptual experiments were recordings of rather high complexity, we could assume that it could be a difficult task for participants to understand them as such. Production, on the other hand, was not controlled for the level of difficulty. As there was no overt production, it is not known what kind of lexical items were being produced by the participants during the task. Intuitively, however, we would assume that participants produced words that were easy for them, because it would be counter-productive to try and produce words that are difficult to pronounce. Therefore, the level of difficulty between perception and production could differ significantly, and it is reflected in the lack of activation in the right hemisphere for production. What is more, there are many different perceptual cues to process when hearing speech, e.g. prosody, which have to be processed in parallel, evoking different structures. In production, the process is simpler, as it generally comes down to executing articulatory plans. Another explanation involves the notion of assimilation discussed in the first chapter. It might be that all articulatory plans are stored together for both languages, because the sounds of L2 were assimilated to the nearest L1 equivalent during acquisition. Moderately proficient speakers might not posses the skills required for native-like pronunciation, and thus what is being produced in the task in L2 is really the approximation of L2 lexical item executed with easier L1 articulatory plans. As a consequence, there is no involvement of the right hemisphere, because it is not L2 after all that is being produced. Still, it could be problematic to support, because hypothetically with highly proficient speakers, the involvement of the right hemisphere would be lesser, or even non-existent. Thus, it could be hard to pinpoint the difference in storing articulatory plans. Nevertheless, it might be the case that when highly proficient speaker stops assimilating to L1 equivalents, and develop the plans for L2,

they are still processed in the same structure, and that is why there will be no involvement of the right hemisphere, regardless of the level of proficiency.

One more interesting issue to discuss in this section is the lack of overt activation in the structures linked to semantic processing in the temporal lobes, which was visible in the perceptual findings. One of the explanations could be that Broca's area, portion of which has been linked to semantic processing in the first chapter, is sufficient in the processing of other linguistic levels during production. However, the participants in the verbal fluency task were asked to produce any lexical items belonging to L1 or L2. This means that they did not have to focus on the meaning, but only on the form. There could be cases in which the participants used words that they associated with each language but did not understand their meaning, and that is why there is no visible activation of the semantic processes. As there was no control over semantic processing in the task, in the model of L2 production we would assume the latter case and would not pinpoint structures relevant to semantic processing.

5.1.3. Automatic processing vs. conscious effort in decision tasks

The important issue that has to be discussed in relation to the model of L2 perception is the distinction between automatic and conscious processing. It has been discussed earlier that some of the processes in the decision tasks are automatic. In the retrieval stage of SWMT in both L1 and L2 there seemed to be no conscious focus on the phonological form of the stimuli, even though it was presented aurally, as it interfered with the task at hand, distorting performance on the level of numeral processing that seems to be distinct from the language level. What is more, the findings on real words vs. pseudowords in LexTALE in L2 show the automatic categorization of these at the subconscious level. As there were also conscious decision stages in both SWMT and LexTALE, the findings of these will be now discussed, in order to segregate the functions that are automatic from those that are consciously evoked.

The findings of SWMT answer stage in L1 and L2 differed significantly, suggesting different conscious involvement in the processing. In L1 there was an activation in lingual gyrus, which has been linked to recollection in solving logic tasks, and in the cerebellum, which was connected to phonological storage. This contrast

nicely with the retrieval stage that seemed to de-emphasize phonological processing and be fairly automatic. The findings suggest that even though the brain might automatically process the information required to solve the task, the conscious decision stage seems to repeat the process at a different level, involving different structures. It would be fairly logical, as the input of the task is presented at the linguistic level, and no matter what kind of processing comes in between, the outcome would have to be feed back to the same linguistic level. This would be supported by the difference in the activation patterns for the answer stage in L1 and L2. In L2 there was additional activation in the premotor cortex and amygdala, with no activation in the cerebellum, suggesting that the processing actually takes place at the linguistic level. The activation in the premotor cortex points to the rehearsal system, as the ability to sustain the retrieved item fosters performance on the task. Again, as it was the perceptual experiment, the activation in the premotor cortex supports its role in L2 perception model. Amygdala, on the other hand, is an interesting finding in that it is linked to emotional processing, and not language per se. It could suggest the possibility of stress, related to the bigger difficulty of the task in L2. It has been discussed earlier that emotions might foster the recollection process, thus improving the performance on the task. Of course, there is no way of telling whether the effect would be visible in highly proficient bilinguals. Yet, as no previous studies has pinpointed this structure in the verbal working memory task, it would be safe not to include this structure in the model of L2 perception.

The notion of conscious processing that repeats automatic processes can be supported by the findings of LexTALE. In L2 LexTALE presentation stage, the brain seemed to automatically detect the difference between real and pseudo words, which was reflected in the lack of activation in the premotor cortex for psuedowords. However, in the answer stage, the conscious effort in decision making activated the premotor cortex. This suggests the involvement of the rehearsal system, as the item might be repeated in order to foster the recognition. What is interesting, is the fact that the automatic recognition of real vs. psueodowords in the presentation stage in the brain might not at all influence the decision, as shown by the magnitude of errors in LexTALE in L2. The only influence that is visible is in the significantly lower reaction times in L2. Thus, we may assume that the automatic detection speeds up the decision, but the outcome of this decision is made during the conscious processing in the answer stage. It has been already mentioned that the automatic detection during the presentation

stage in L2 was determined by the lack of involvement of the premotor cortex and semantic-related regions in the middle temporal gyrus in the presentation of pseudowords, as opposed to the activation of these regions in the presentation of real words. However, in L1 there was no such difference between real and psuedoword processing, thus we assume that this automatic detection does not occur in L1. This might be supported by the overt activation of the middle temporal gyrus in the answer stage in L1, which suggests that it is only in the conscious process that the meaning of the word is derived in the native language. The activation of the cingulate gyrus, which has been linked to attentional processes, seems to support the notion of conscious processing in the decision making.

The most interesting aspect of the findings mentioned above is the fact that automatic processing of L2 in decision tasks might in fact stem from the conscious effort that was involved in the acquisition. L2 is generally learned consciously with the focus on the form, as it has been mentioned before, and thus the active integration of perception and production processes might help tune the brain to detecting differences that would be impossible in the native language. As the native language is acquired without the conscious effort, the processes that are automatic might not be susceptible to such attunement, as there is no constant feedback occurring. In fact, this might be supported by the activation of the right hemisphere as a function of L2 proficiency in perceptual processing. As processes involved in passive listening in L1 seem fairly automatic in comparison to L2, they might stay the same during one's lifetime, as there will be no dramatic changes in proficiency over the course of adulthood. We might safely assume, that the conscious processing of L1 is not necessary in everyday life in most cases, and that is why the processes in lexical decision making have to be overtly conscious, as the brain is not attuned to them. In L2, however, the process is reversed. We start the L2 acquisition with conscious processing, and with more and more attunement, due to feedback, some of the processes become automatic, which is reflected in the automatic detection in LexTALE. Yet, it is important to note that this might only concern the overt linguistic tasks. It would be logical to think that the latebilingual person would be more accustomed to such tasks, as they are part of the learning process, but only in L2, as the native language acquisition does not involve them. That is why there is a reversed activation pattern in passive listening to that of LexTALE. Of course, as it has been mentioned earlier, this automatization does not

ensure better performance. The reaction times in L2 were lower than in L1, and as such better, but it was not reflected in the scores, which were significantly lower than in L1. This would support the notion of disrupted connection between automatic and conscious processes mentioned earlier. Even though the brain was able to detect the difference between pseudo and real words in L2, it did not influence the final decision. But, it might be the case that with higher proficiency, the bridge between the automatic and the conscious get stronger foundations, and the influence could be visible in the outcome of the decision. If we again take into consideration the idea of the involvement of the right hemisphere in L2 perception which decreases with proficiency, it could be assumed that this bridge is in fact reflected by the local connections in the left hemisphere, which are at first substituted with global connections to the right hemisphere. With higher proficiency, the connections in the left hemisphere are strengthened, and the connections to the right hemisphere become obsolete.

What stems from the above-mentioned arguments is that in the model of L2 perception, there is a need for two different levels, *the automatic*, and *the conscious*, and the idea that they exist in parallel and can be bridged. L1 starts at the automatic level, as reflected in perceptual experiments, and with a conscious effort can reach the conscious processes. L2, on the other hand, starts at the conscious level, and with higher exposure, and thus feedback and attunement, can reach the automatic processes. In the course of these transitions, the tasks that need the conscious or the automatic will be processed as such only if the level of this transition is met.

5.1.4. Involvement of the brain with no task in the modeling of L2 perception.

The findings of the resting-state and DTI analyses nicely add to the findings that have been already discussed, supporting the ideas mentioned in the earlier sections. The strength of the connections between the left and right brain homologue areas in L1 and L2 again point to the automatic and conscious levels of processing that are connected to linguistic proficiency. In L1, the strength of the connection between the left and right cingulate gyrus, linked to attentional processes, correlates with LexTALE scores. This suggests that with the shift in attentional resources, the score on lexical decision tasks can be better. As the method of voxel-mirrored homotopic connectivity does not show

the directionality of the connections, we cannot be certain which hemisphere might contribute to better results. There are, however, three possibilities. The first one, in accordance with the model of the contribution of the right hemisphere as a function of proficiency, assumes that it is the shift from the right to the left hemisphere that occurs with higher proficiency. The second one, in accordance to the conscious vs. automatic notion mentioned earlier, assumes the reversed situation, in which the automatic processes that the brain begins with in L1 occur in the left hemisphere, and with more attunement to conscious tasks, there is a shift towards the right hemisphere. The third possibility assumes that it is the activation of both homologues at once that predict better performance in lexical tasks, as the involvement of more resources account for the conscious effort that is required for the task. In L2, on the other hand, it is the strength of the connection between the left and right homologue of the middle temporal gyrus areas, connected to semantic processing, that correlates with LexTALE scores. This could suggest that the shift in the activation of semantic processing could be predictive of better performance. It again supports the notion mentioned in the previous subsection, as semantic processing was the one that differentiated between L1 and L2 in the LexTALE presentation stage. As in the case of L1, there could be three identical possibilities of the directionality of this shift, but it would be safe to assume that the shift from the right to the left hemisphere seems the most plausible, in the light of previous findings on L2 processing.

Apart from resting-state fMRI, the findings of DTI fiber tracking point to the connectivity as a function of proficiency. The left hemisphere reflected dense connectivity between the frontal and temporal lobes, and the cerebellum, while in the right hemisphere the connectivity was visible only between the Broca's area and the premotor cortex. As one might expect, both hemispheres were also connected structurally, which would support the hypothesis of the shift. It is interesting, though, that this structural interhemispheric bridge exists, even if it might be abandoned with higher proficiency, as there might be no functional connectivity in the later stages. It cannot be determined, however, by the course of the present study whether this structural connectivity between language networks in the left and right hemisphere is established by the processes of the second language acquisition, or whether it is available to monolinguals, who are simply not using them functionally. It has been discussed earlier that recent findings show a similar trend of denser connectivity in the

left hemisphere in bilinguals, but there are no findings concerning the right hemisphere. Yet, as the findings fit the hypothesis of the right hemisphere use as a function of L2 proficiency, the present model of L2 perception will consider these structural connections as a part of it. Still, it would be of interest in future tracking studies to investigate at which stage of acquisition the structural white matter connections of such patterns arise.

5.1.5. Conclusions and the model of L2 phonological perception and production.

In the previous sections, a model of processing of phonological information during perception and production of L2 has been extensively discussed and summarized. As it touches upon a theoretical notion of two-directional shift that is directly connected to the shift in the language proficiency, there is a need to devise a simpler version that describes the processing at the stage investigated in the present dissertation. Such a model consists of four modules, which have been derived from the active experiments performed for this dissertation, i.e. passive listening, verbal working memory, verbal fluency, and lexical decision. Each of these modules is connected to a number of brain areas, which have been activated in the relevant experiments. Thus, it easily shows which brain structures are involved in different kinds of processing of phonological information. The advantage of this visualization is that the whole model is represented as a network, and thus we can derive network measurements, such as degree, and easily show which of the brain areas are the most involved in the processing of L2 phonological information. Also, the module which requires the use of the most resources can be easily pinpointed.

As for the brain areas that are the most involved in the model, there are eight areas that have the same biggest degree, i.e. the number of connections. These are the left Broca's area, the left and right premotor cortex, the left and right primary auditory cortex, the left and right inferior parietal lobule, and the left planum temporale. Thus, in the simpler model, we can assume that these areas constitute the core of phonological processing in L2. As for the four modules in the model, verbal working memory is the most resource-demanding, followed by lexical decision, passive listening, and verbal fluency. This supports the idea mentioned earlier that L2 production might actually be

easier than perception, and that conscious effort in perception might evoke more resources as it is not automatic in nature.

The model nicely concludes the findings of the present dissertation, and can be easily used for reference in future studies in the form visualized in Fig. 16 With enough findings, it can be expanded into a dynamic model, taking into account the shift that was discussed before. As such, the model can be treated as a stepping stone in a series of findings needed to reach the goal of uncovering the bilingual effect in the brain.

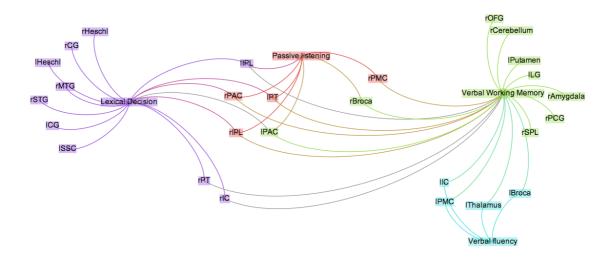


Fig. 16. A model of L2 phonological processing in perception and production. Initial lowercase l stands for the left-hemisphere, and initial lowercase r stands for the right hemisphere. The abbreviations used: PMC – premotor cortex, PAC – primary auditory cortex, LG – lingual gyrus, IPL – inferior parietal lobule, IC – insular cortex, PT – planum temporale, STG – superior temporal gyrus, MTG – middle temporal gyrus, SSC – secondary somatosensory cortex, CG – cingulate gyrus, PCG – paracingulate gyrus, SPL – superior parietal lobule, OFG – occpital fusiform gyrus. The color of a node shows to which module the node is most strongly connected.

Conclusion

The present thesis has investigated the issue of neural basis for phonological processing in Polish-English bilinguals in native and non-native speech perception and production by the means of functional Magnetic Resonance Imaging. The results of the experiment described in the thesis have shown that the brain structures and functions involved in the speech perception and production in Polish-English bilinguals might in fact differ for both languages, depending on the level of proficiency and the structure of the languages, which is in line with the body of previous research on the subject on different language pairs.

The experiment has stressed the importance of use of interdisciplinary methods in linguistic research, as the neuroscientific methods helped develop a model of phonological representation, which might help fill in the blanks left in the abstract linguistic models. Besides, the use of varied experimental methods in the present thesis has proved worthwhile, as the results of different methods being complementary to each other render the results' significance stronger.

The most important aspect of the results is that they constitute a good basis for further research on the subject. It would be worthwhile to expand the number of participants, which is limited in this study, to evaluate the findings against a bigger population. Also, testing participants with different levels of proficiency could help test whether the correlations between the activity in certain brain areas and language skills could be found in a bigger group with greater variance in scores.

Finally, the results have provided an insight into the issue of phonological processing in the Polish-English language pair, which has not been studied yet using fMRI. This is important, as the language-specific results help broaden our

understanding of how the brain processes language, and what is and what is not universal across languages and speakers around the world.

Concluding, the present thesis contributes to both fields of linguistics and neuroscience. The methods presented in the chapters help evaluate the linguistic models of speech processing, and extrapolate them to real functions of the brain. In turn, the neuroscientific methods are evaluated as to which ones can yield the best results for linguists, helping guide further research in the right direction.

SUMMARY

The present thesis investigates the issue of neural basis for phonological processing of native and non-native speech in Polish-English bilinguals. In order to pinpoint the structures and functions that are relevant to phonological processing, a set of experiments was devised on a group of moderately proficient Polish-English bilinguals. Using the method of Magnetic Resonance Imaging, and hypothesizing that there will be differences in the representation of phonological processes in the brain, dependent on the language and the level of proficiency in the language, four task-based experiments in both Polish and English, including listening to stories, Sternberg Working Memory Task, Verbal Fluency Task, and Lexical Test for Advanced Learners of English, and three task-independent experiments were conducted.

The results have shown that there might in fact be a difference in neural representation of phonological processes that is dependent on the language. They have also shown that these differences are dynamic in nature, and might be also dependent on the level of proficiency in the language. Furthermore, there were similar patterns of differences across different tasks, strengthening the effect, which was also corroborated by task-independent experiments.

The results of the thesis, along with the detailed discussion suggest a model of phonological processing in L2, which consists of different task-related modules of interacting brain networks. As such, the present thesis contributes to both fields of linguistics and neuroscience, broadening the understanding of how the brain processes language.

STRESZCZENIE

Niniejsza dysertacja bada problem neuronalnych korelatów przetwarzania fonologicznego języka ojczystego i języka obcego u polskich użytkowników języka angielskiego. W celu wskazania struktur i funkcji mózgu odpowiedzialnych za przetwarzanie fonologiczne stworzono zestaw eksperymentów, które przeprowadzono na grupie średniozaawansowanych polskich użytkowników języka angielskiego. Korzystając z metody rezonansu magnetycznego sprawdzono hipotezę zakładającą zróżnicowanie w reprezentacji procesów fonologicznych w mózgu, w zależności od przetwarzanego języka oraz stopnia zaawansowania użytkownika. Zestaw zawierał cztery eksperymenty z zadaniami w języku polskim i angielskim, takimi jak słuchanie pasywne, Test Pamięci Roboczej Sternberga, test fluencji słownej, oraz Test Leksykalny dla Zaawansowanych Uczniów Języka Angielskiego. Na eksperymenty złożyły się również trzy eksperymenty nie oparte na żadnych zadaniach.

Wyniki eksperymentów pokazały, że faktycznie mogą istnieć różnice w reprezentacji procesów fonologicznych w mózgu, które zależą od przetwarzanego języka. Wyniki wskazały również, że owe różnice są dynamiczne i mogą również zależeć od stopnia zaawansowania w danym języku. Co więcej, róznice w reprezentacjach wykazane w różnych zadaniach były podobne, co wzmacnia efekt znalezisk, które dodatkowo zostały podparte wynikami badań nie opartych na zadaniach.

Wyniki wraz z dokładną dyskusją sugerują model przetwarzania drugiego języka, który składa się z modułów związanych z zadaniami językowymi zbudowanych ze współgrających ze sobą sieci mózgowych. W związku z tym, niniejsza dysertacja

wnosi nowe odkrycia do dziedzin językoznawstwa i neuronauki, poszerzając nasze zrozumienie procesów przetwarzania języka w mózgu.

References

- 1000 Functional Connectomes Project. 2012. *The configurable pipeline for tha analysis of connectomes*. Version 0.3.3. (http://fcon_1000.projects.nitrc.org/indi/cpac/in dex.html#) (date of access: 18 Dec. 2014).
- Abutalebi, Jubin. 2008. "Neural aspects of second language representation and language control", *Acta Psychologica* 128: 466-478.
- Abutalebi, Jubin, Stefano F. Cappa and Daniela Perani. 2001. "The bilingual brain as revealed by functional neuroimaging", *Bilingualism: Language and Cognition* 4: 179-190.
- Ackermann, Hermann, Matthias Vogel, Dirk Petersen and Michael Poremba. 1992. "Speech deficits in ischaemic cerebellar lesions", *Journal of Neurology* 239: 223–227.
- Adluru, Nagesh, Hui Zhang, Andrew S. Fox, Steven E. Shelton, Chad M. Ennis, Anne M. Bartosic, Jonathan A. Oler, Do P.M. Tromp, Elizabeth Zakszewski, James C. Gee, Ned H. Kalin and Andrew L. Alexander. 2012. "A diffusion tensor brain template for rhesus macaques", *NeuroImage* 59 1: 306-318.
- Alexander, Daniel C., Carlo Pierpaoli, Peter J. Basser and James C. Gee. 2001. "Spatial transformations of diffusion tensor magnetic resonance images", *IEEE Trans Med Imaging* 20: 1131–1139.
- Amunts, Katrin. 2008. "Architectonic language research", in: Brigitte Stemmer and Harry A. Whitaker (eds.), *Handbook of neuroscience of language*. New York: Elsevier.

- Andersson, Jesper L., Mark Jenkinson and Stephen Smith. 2007. Non-linear registration, aka Spatial normalisation. FMRIB technical report TR07JA2, (http://www.fmrib.ox.ac.uk/analysis/techrep) (date of access 17 Dec 2014)
- Aoyama, Katsura and Susan G. Guion. 2007. "Prosody in second language acquisition: Acoustic analyses of duration and F0 range", in: Bohn, Ocke-Schwen and Murray J. Munro (eds.), *Language experience in second language speech learning: In honor of James Emil Flege*. Amsterdam: John Benjamins, 282-297.
- Aoyama, Katsura, James. E. Flege, Susan G. Guion, Reiko Akahane-Yamada and Tsuneo Yamada. 2004. "Perceived phonetic dissimilarity and L2 speech learning: The case of Japanese /r/ and English /l/ and /r/", *Journal of Phonetics* 32: 233- 250.
- Archibald, John. 1995. "The acquisition of stres", in: John Archibald (ed.), *Phonological acquisition and phonological theory*. Hillsdale, NJ: Lawrence Erlbaum, 81-109.
- Archibald, John. 1997. "The acquisition of English stress by speakers of tone languages: Lexical storage versus computation", *Linguistics* 35: 167-181.
- Archibald, John. 1998a. "Metrical parameters and lexical dependency: Acquiring L2 stress", in: Suzanne Flynn and Gita Martohardjono (eds.), *The generative study of second language acquisition*. Mahwah, NJ: Lawrence Erlbaum, 279-301.
- Archibald, John. 1998b. Second language phonology. Amsterdam: John Benjamins.
- Arsenault, Jessica S. and Bradley R. Buchsbaum. 2015. "Distributed Neural Representations of Phonological Features during Speech Perception", *Journal of Neuroscience* 35: 634-42.
- Asclepios Research Center. 2008. *MedINRIA*. Version 1.8.0. (http://www-sop.inria.fr/as clepios/software/MedINRIA/about.php) (date of access: 20 Mar. 2015).
- Atkins, Paul and Alan D. Baddeley. 1998. "Working memory and distributed vocabulary learning", *Applied Psycholinguistics* 19: 537-552.
- Awh, Edward, John Jonides, Edward E. Smith, Eric H. Schumacher, Robert A. Koeppe, and Stewart Katz. 1996. "Dissociation of storage and rehearsal in verbal working memory", *Psychological Science* 7: 25–31.
- Bach, Michael, Frederik B. Laun, Alexander Leemans, Chantal M. Tax, Geert J. Biessels, Bram Stielties and Klaus H. Maier-Hein. 2014. "Methodological

- considerations on tract-based spatial statistics (TBSS)", *NeuroImage* 100: 358-369.
- Baddeley, Alan D. 1966. "The influence of acoustic and semantic similarity on long-term memory for word sequences. *Quarterly Journal of Experimental Psychology* 18: 302-309.
- Baddeley, Alan D. 1975. "Word length and the structure of short-term memory", *Journal of Verbal Learning and Verbal Behavior* 14: 575-589.
- Baddeley, Alan D. 2003. "Working memory and language: An overview", *Journal of Communication Disorders* 36: 189-208.
- Baddeley, Alan D. and Barbara A. Wilson. 1985. "Phonological coding and short-term memory in patients without speech", *Journal of Memory and Language* 24: 490-502.
- Baddeley, Alan D., Susan E. Gathercole and Costanza Papagno. 1998. "The phonological loop as a language device", *Psychological Review* 105: 158-173.
- Barac, Raluca and Ellen Bialystok. 2012. "Bilingual effects on cognitive and linguistic development: Role of language, cultural background, and education", Child Development 83: 413-422
- Bastian, Mathieu, Sebastien Heymann and Mathieu Jacomy. 2009. "Gephi: an open source software for exploring and manipulating networks" (Paper presented at the International AAI Conference on Weblogs and Social Media, May 2009, San Jose, USA).
- Behrens, Tim E., Heidi Johansen-Berg, Saad Jbabdi, Matthew Rushworth and Mark Woolrich .2007. "Probabilistic diffusion tractography with multiple fibre orientations: What can we gain?", *NeuroImage* 34 1: 144-55.
- Beckman, M.E. 1986. Stress and non-stress accent. Dordrecht, Holland: Foris.
- Berent, Iris. 2013. The phonological mind. Cambridge University Press.
- Best, Catherine T. 1995. "A direct realist perspective on cross-language speech perception", in: Winifred Strange (ed.), *Speech perception and linguistic experience: Issues in cross-language research*. Timonium, MD: York Press, 171-204.
- Best, Catherine T. and Winifred Strange. 1992. "Effects of phonological and phonetic factors on cross-language perception of approximants", *Journal of Phonetics* 20: 305-330.

- Best, Catherine T. and Michael D. Tyler. 2007. "Nonnative and second-language speech perception: Commonalities and complementarities", in: Murray J. Munro and Ocke-Schwen Bohn (eds.), Second Language speech learning: The role of language experience in speech perception and production, Amsterdam: John Benjamins, 13-34.
- Best, Catherine T., P.A. Hallé, Ocke-Schwen Bohn and Alice Faber. 2003b. "Cross-language perception of nonnative vowels: Phonological and phonetic effects of listeners' native languages", in: Maria-Josep Solé, Daniel Recasens and Jesus Romero (eds.), *Proceedings of the 15th International Congress of Phonetic Sciences*, Barcelona: Causal Productions, 2889-2892.
- Best, Catherine T., Gerald W. McRoberts and Elizabeth. Goodell. 2001. "American listeners' perception of nonnative consonant contrasts varying in perceptual assimilation to English phonology", *Journal of the Acoustical Society of America* 109: 775-794.
- Best, Catherine T., Anthony Traill, Allyson Carter, David K. Harrison and Alice Faber. 2003a. "!Xóõ click perception by English, Isizulu, and Sesotho listeners", in: Maria-Josep Solé, Daniel. Recasens and Jesus Romero (eds.), *Proceedings of the 15th International Congress of Phonetic Sciences*. Barcelona: Causal Productions, 853-856.
- Bialystok, Ellen, Fergus I. M. Craik, Cheryl Grady, Wilkin Chau, Ryouhei Ishii, Atsuko Gunji and Christo Pantev. 2005. "Effect of bilingualism on cognitive control in the Simon task: evidence from MEG", *NeuroImage* 24: 40-49.
- Bialystok, Ellen, Gregory Poarch, Lin Luo and Craik Fergus. 2014. "Effects of bilin gualism and agings on executive function and working memory", *Psychology and Aging*, 29: 696-705.
- Binder, Jeffrey R., Julie A. Frost, Thomas A. Hammeke, Robert W. Cox, Stephen M. Rao and Thomas Prieto. 1997. "Human brain language areas identified by functional MRI". *Journal of Neuroscience* 17, 353 362.
- Binder Jeffrey R., Julie A. Frost, Thomas A. Hammeke, Patrick S. Bellgowan, Jane A. Springer, Jackie N. Kaufman and Edward T. Possing. 2000. "Human temporal lobe activation by speech and nonspeech sounds", *Cerebral Cortex* 10: 512–528.

- Binder Jeffrey and Cathy J. Price. 2001. "Functional neuroimaging of language", in: Cabeza Roberto and Alan Kingstone (eds.). *Handbook of functional neuroimaging of cognition*. Cambridge: MIT Press, 187–251.
- Binder Jeffrey R., David A. Medler, Rutvik Desai, Lisa Conant and Einat Liebenthal. 2005. "Some neurophysiological constraints on models of word naming", *Neuroimage* 27: 677–693.
- Binder Jeffrey R., Rutvik H. Desai, William W. Graves and Lisa L. Conant. 2009. "Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies", *Cerebral Cortex* 19: 2767–2796.
- Biswal, Bharat B., Maarten Mennes, Xi-Nian Zuo, Suril Gohel, Clare Kelly, Steve M. Smith, Christian F. Beckmann, Jonathan S. Adelstein, Randy L. Buckner and Sandtan Colcombe. 2010. "Toward discovery science of human brain function", *Preceedings of the National Academy of Sciences* 107:1-6.
- Blair, Hugh T., Glenn E. Schafe, Elizabeth P. Bauer, Sarina M. Rodrigues and Joseph E.LeDoux. 2001. "Synaptic Plasticity in the Lateral Amygdala: A Cellular Hypothesis of Fear Conditioning". *Learning and Memory* 8: 229-242.
- Blevins, Juliette. 2004. *Evolutionary phonology: the emergence of sound patterns*. Cambridge University Press.
- Bohn, Ocke-Schwen, and James E. Flege. 1990. "Interlingual identification and the role of foreign language experience in L2 vowel perception", *Applied Psycholinguistics* 11: 303-328.
- Bohn, Ocke-Schwen and Anja K. Steinlen. 2003. "Consonantal context affects cross-language perception of vowels", In: Maria-Josep Solé, Daniel Recasens and Jesus Romero (eds.), *Proceedings of the 15th International Congress of Phonetic Sciences*, Barcelona: Causal Productions, 2289-2292.
- Bornkessel, Ina and Matthias Schlesewsky. 2006. "The extended Argument Dependency Model: A neurocognitive approach to sentence comprehension across languages", *Psychological Review* 113: 787–821.
- Bradvik, Bjorn., Christina Dravins, Stig Holtas, Ingmar Rosen, Erik Ryding, and David Ingvar. 1991. "Disturbances of speech prosody following right hemisphere infarcts", *Acta Neurologica Scandinavica* 84: 114–126.
- Brannen, Kathleen. 2002. "The role of perception in differential substitution", *The Canadian Journal of Linguistics/La Revue Canadienne de Linguistique* 47: 1-46.

- Brauer, Jens., Angela D. Friederici. 2007. "Functional neural networks of semantic and syntactic processes in the developing brain", *Journal of Cognitive Neuroscience* 19: 1609–1623.
- Broselow, Ellen, and Hye-Bae Park. 1995. "Mora conservation in second language prosody", In: John Archibald (ed.), *Phonological acquisition and phonological theory*. Hillsdale, NJ: Lawrence Erlbaum, 81-109
- Bryan Karen L. 1989. "Language prosody and the right hemisphere", *Aphasiology* 3: 285–299.
- Buckner, Randy L., Jorge Sepulcre, Tanveer Talukdar, Fenna M. Krienen, Hesheng Liu, Trey Hedden, Jessica R. Andrews-Hanna, Reisa A. Sperling and Keith A. Johnson. 2009. "Cortical hubs revealed by intrinsic functional connectivity: mapping, assessment of stability, and relation to Alzheimer's disease", *Journal of Neuroscience* 29: 1860–1873.
- Bullmore, Ed and Olaf Sporns. 2009. "Complex brain networks: graph theoretical analysis of structural and functional systems", *Nature Reviews Neuroscience* 10: 186–198.
- Bundgaard-Nielsen, Rikke L., and Ocke.-Schwen Bohn. 2004. "Exploring the intelligibility of foreign-accented English vowels when "English" is ill-defined", *Journal of Acoustical Society of America* 115: 2605.
- Buxton, Richard B. 2010. Hemodynamics and fMRI signals. (Lecture given at the Advanced Neuroimaging Summer School, Los Angeles, 13 July 2010.).
- Bybee, Joan. 2008. "Formal universals as emergent phenomena: The origins of structure preservation", in: Jeff Good (ed.), *Linguistic universals and language change*. Oxford: Oxford Univ. Press, 108-121.
- Callan, Daniel E., Jeffery A. Jones, Akiko M. Callan and Reiko Akahane-Yamadaa. 2004. "Phonetic perceptual identification by native- and second-language speakers differentially activates brain regions involved with acoustic phonetic processing and those involved with articulatory—auditory/orosensory internal models", *NeuroImage* 22: 1182-1194.
- Callan, Daniel, Callan Akiko, and Jeffrey A. Jones. 2014. "Speech motor brain regions are differentially recruited during perception of native and foreign-accented phonemes for first and second language listeners", *Frontiers in Neuroscience 8:* 275.

- Caplan, David. and Gloria S. Waters. 1999. "Verbal working memory and sentence comprehension", *Behavioral Brain Science* 22: 77–94.
- Cao, Fan, Say Young Kim, Yanni Liu and Li Liu. 2014. "Similarities and differences in brain activation and functional connectivity in first and second language reading: evidence from Chinese learners of English", *Neuropsychologia 63:* 275-284.
- Carlson, Neil. 2012. Physiology of behavior. Pearson.
- Cedrus. 2014. *SuperLab*. Version 4.5. (http://www.superlab.com/) (date of access: 20 Mar. 2015)
- Chai Xiaoqian J., Alfonso N. Castanon, Dost Ongur and Susan Whitfield-Gabrieli, 2012. "Anticorrelations in resting state networks without global signal regression", *Neuroimage* 59: 1420-1428.
- Chee, Michael, Chun Siong Soon and Hwee Ling Lee. 2005. "The Influence of Language Experience on Cortical Activation in Bilinguals", in: *Proceedings of the 4th International Symposium on Bilingualism*, Somerville: Cascadilla Press, 522-526.
- Chee, Michael W., Kathleen M. O'Craven, Ruth Bergida, Bruce R. Rosen and Robert L. Savoy. 1999. "Auditory and visual word processing studied with fMRI", *Human Brain Mapping 7: 15–28*.
- Chen, Annabel S. and John E. Desmond. 2005. "Cerebrocerebellar networks during articulatory rehearsal and verbal working memory tasks", *Neuroimage* 24: 332–338.
- Chevillet, Mark A., Xiong Jiang, Josef P. Rauschecker and Maximilian Riesenhuber. 2013. "Automatic phoneme category selectivity in the dorsal auditory stream", *Journal of Neuroscience*, 33, 5208–5215.
- Chi-Shing, Tse and Jaenette Altarriba. 2014. "The relationship between language proficiency and attentional control in Cantonese-English bilingual children: evidence from Simon, Simon switching, and working memory tasks", *Frontiers in Psychology* 5:954.
- Cho, Soohyun., Arron W. Metcalfe, Christina B. Young, Srikanth Ryali, David C. Geary and Vinod Menon. 2012. "Hippocampal-Prefrontal Engagement and Dynamic Causal Interactions in the Maturation of Children's Fact Retrieval", *Journal of Cognitive Neuroscience* 24: 1849-1866.

- Chomsky, Noam. 1956. "Three models for the description of language", Proceedings of the Symposium on Information Theory, 113-123.
- Craik, Fergus I., Moshe Naveh-Benjamin, Galit Ishaik and Nicole D. Anderson. 2000. "Divided attention during encoding and retrieval: differential control effects?"

 Journal of Experimental Psychology: Learning, Memory, and Cognition 26:
 1744–1749.
- Coumans, Juul, Roeland van Hout and Odette Scharenborg. 2014. "Non-native Word Recognition in Noise: The Role of Word-initial and Word- final Information", *Proceedings of Interspeech 2014, Singapore*, 519-523.
- Dahan, Delphine and James S. Magnuson. 2006. "Spoken word recognition", in: Matthew Traxler and Morton A. Gernsbacher (eds.). *Handbook of Psycholinguistics*. Oxford: Academic Press, 249–284.
- Dehaene, Stanislas, Emmanuel Dupoux, Jacques Mehler, Laurent Cohen, Eraldo Paulesu, Daniela Perani, Pierre-Francois van de Moortele, Stéphane Lehéricy and Denis Le Bihan. 1997. "Anatomical variability in the cortical representation of first and second language", *NeuroReport* 8: 3809-3815.
- Dehaene-Lambertz, Ghislaine, Christophe Pallier, Willy Serniclaes, Liliane Sprenger-Charolles, Antoinette Jobert, and Stanislas Dehaene. 2005. "Neural correlates of switching from auditory to speech perception", *Neuroimage* 24:21–33.
- Dehaene, Stanislas and Laurent Cohen. 1995. "Towards an anatomical and functional model of number processing", *Mathematical Cognition* 1:83–120.
- Dehaene, Stanislas, Elizabeth. Spelke, Philippe Pinel, Ruxandra Stanescu and Sanna Tsivkin. 1999. "Sources of mathematical thinking: Behavioral and brainimaging evidence", *Science* 284:970–974.
- Della Rosa, Pasquale A., Gerda Videsott, Virginia M. Borsa, Matteo Canini, Brendan S. Weekes, Rita Franceschini and Jubin Abutalebi. 2013. "A neural interactive location for multilingual talent", *Cortex* 49: 605-608.
- Demonet, Jean-Francois, Cathy J. Price, Richard Wise and Richard S. Frackowiak. 1994. "Differential activation of right and left posterior sylvian regions by semantic and phonological tasks: A positron-emission tomography study in normal human subjects", *Neuroscience Letters* 182:25–28.

- Demonet Jean-Francois, Francois Chollet, Stuart Ramsay, Dominique Cardebat, Jean-Luc Nespoulous, Richard Wise, Andre Rascol and Richard Frackowiak. 1992. "The anatomy of phonological and semantic processing in normal subjects", *Brain* 115: 1753–1768.
- Derwing, Tracey M. and Murray J. Munro. 1997. "Accent, intelligibility, and comprehensibility: Evidence from four L1s", *Studies in Second Language Acquisition* 19: 1-16.
- Deschamps, Isabelle., Shari R. Baum and Vincent L. Gracco. 2014. "On the role of the supramarginal gyrus in phonological processing and verbal working memory: evidence from rTMS studies. *Neruopsychologia 53: 39-46*.
- Devlin, Joseph T., Paul M. Matthews and Matthew F. Rushworth. 2003. "Semantic processing in the left inferior prefrontal cortex: A combined functional magnetic resonance imaging and transcranial magnetic stimulation study", *Journal of Cognitive Neuroscience* 15: 71–84.
- Desikan, Rahul S., Florent Segonne, Bruce Fischl, Brian T. Quinn, Bradford C. Dickerson, Deborah Blacker, Randy L. Buckner, Anders M. Dale, Paul R. Maguire, Bradley T. Hyman, Marilyn S. Albert and Ronald J. Killiany. 2006. "An automated labeling system for subdividing the human cerebral cortex on
- MRI scans into gyral based regions of interest", NeuroImage 31:968-980.
- Desmond, John E., John D. Gabrieli, Anthony D. Wagner, Bruce L. Ginier and Gary H. Glover. 1997. "Lobular patterns of cerebellar activation in verbal working-memory and finger-tapping tasks as revealed by functional MRI", *Journal of Neuroscience* 17: 9675–9685.
- Dick, Anthony S., Anjali Raja Beharelle, Ana Solodkin and Steven L. Small. 2013. "Interhemispheric functionalconnectivity following prenatal or perinatal brain injury predicts receptive language outcome", *Journal of Neuroscience* 33: 5612-25.
- Donegan, Patricia and David Stampe. 1979. "The study of Natural Phonology", in:

 Daniel A. Dinnsen, (ed.). *Current Approaches to Phonological Theory*.

 Bloomington: IUP: 126-173.
- Douaud, Gwanaelle, Stephen Smith, Mark Jenkinson, Timothy Behrens, Heidi Johansen-Berg, John Vickers, Susan James, Natalie Voets, Kate Watkins, Paul

- M. Matthews and Anthony James. 2007. "Anatomically related grey and white matter abnormalities in adolescent-onset schizophrenia", *Brain* 130:2375-2386.
- Dronkers, Nina F., David P. Wilkins, Robert D. Van Valin Jr., Brenda B. Redfern and Jeri J. Jaeger. 2004. "Lesion analysis of the brain areas involved in language comprehension", *Cognition* 92: 145-177.
- Dronkers, Nina F., Odile Plaisant, Marie-Therese Iba-Zizen, and Emmanuel A. Cabanis. 2007. "Paul Broca's historic cases: high resolution MR imaging of the brains of Leborgne and Lelong", *Brain* 130: 1432-41.
- Duffau, Hugues., Peggy Gatignol, Emmanuel Mandonnet, Philippe Peruzzi, Nathalie Tzourio-Mazoyer and Laurent Capelle. 2005. "New insights into the anatomofunctional connectivity of the semantic system: a study using cortico-subcortical electrostimulations", *Brain* 128: 797–810.
- Edwards, Jodi D., Penny M. Pexman, Bradley G. Goodyear and Craig G. Chambers. 2005. "An fMRI investigation of strategies for word recognition", *Brain Research*. *Cognitive Brain Research* 24: 648-62.
- Eckman, Fred. 1991. "The structural conformity hypothesis and the acquisition of consonant clusters in the interlanguage of ESL learners", *Studies in Second Language Acquisition* 13: 23-41.
- Eguiluz, Victor M., Dante R. Chialvo, Guilermo A. Cecchi, Marwan Baliki and A.Vania Apkarian. 2005. "Scale-free brain functional networks", *Physical Review Letters* 94: 18102-18102.
- Eger, Evelyn, Philipp Sterzer, Michael O. Russ, Anne-Lise Giraud and Andreas Kleinschmidt. 2003. "A supramodal number representation in human intraparietal cortex", *Neuron* 37:719–725.
- Eickhoff, Simon B., Tomaus Paus, Svenja Caspers, Marie-Helene Grosbras, Alan C. Evans, Karl Zilles and Katrin Amunts.2007. "Assignment of functional activations to probabilistic cytoarchitectonic areas revisited", *NeuroImage* 36:511-521.
- Escudero, Paola and Paul Boersma. 2004. "Bridging the gap between L2 speech perception research and phonological theory". *Studies in Second Language Acquisition*, 26: 551-585.

- Evans, Nicholas and Stephen C. Levinson. 2009. "The myth of language universals: Language diversity and its importance for cognitive science", *Behavioral and Brain Sciences* 32: 429-492.
- Fabbro, Franco. 1999. *The neurolinguistics of bilingualism: An introduction.* Hove: Psychology Press.
- Fedorenko, Evelina and Nancy Kanwisher. 2009. "Neuroimaging of language: why hasn't a clearer picture emerged?", *Language and Linguistics Compass* 3: 839–865.
- Fegen, David, Bradley R. Buchsbaum and Mark. D'Esposito. 2015. "The effect of rehearsal rate and memory load on verbal working memory", *Neuroimage* 105: 120-31.
- Fiez, Julie A., Elizabeth A. Raife, David A. Balota, Jacob P. Schwarz, Marcus E. Raichle and Steven E. Petersen. 1996. "A positron emission tomography study of the shortterm maintenance of verbal information", *Journal of Neuroscience* 16: 808–822.
- Flege, James E. 1984. "The effect of linguistic experience on Arabs' perception of the English /s/ vs. /z/ contrast", *Folia Linguistica* 18: 117-138.
- Flege, James .E. 1989. "Chinese subjects' perception of the word-final English /t/-/d/contrast: Before and after training", *Journal of the Acoustical Society of America* 86: 1684-1697.
- Flege, James E. 1995. "Second language speech learning: Theory, findings, and problems", in: Winifred Strange (ed.) *Speech perception and linguistic experience: Issues in cross-language research*. Timonium, MD: York Press, 233-276.
- Flege, James E. 1999. "Age of learning and second language speech", in: David Birdsong (ed.), *Second language acquisition and the critical period hypothesis*.

 Mahwah, NJ: Lawrence Erlbaum Associates. 101-131.
- Flege, James E. 2002. "Interactions between the native and second-language phonetic systems", in: Petra Burmeister, Thorsten Piske and Andreas Rohde (eds.), *An integrated view of language development: Papers in honor of Henning Wode*. Trier, Germany: Wissenschaftlicher Verlag Trier, 217-243.
- Flege, James E. and Serena Liu. 2001. "The effect of experience on adults' acquisition of a second language", *Studies in Second Language Acquisition* 23: 527-552.

- Flege, James E. and Ian R. MacKay. 2004. "Perceiving vowels in a second language", *Studies in Second Language Acquisition* 26: 1-34.
- Flege, James E. and Ocke.-Schwen Bohn. 1989. "An instrumental study of vowel reduction and stress placement in Spanish-accented English", *Studies in Second Language Acquisition* 11: 35-62.
- Fonov, Vladimir S., Alan C. Evans, Robert C. McKinstry, Robert C. Almli and Louis D. Collins. 2009. "Unbiased nonlinear average age-appropriate brain templates from birth to adulthood", *NeuroImage* 47: 102.
- Fornito, Alexander., Murat. Yucel, Stephen. Wood, Geoffrey W. Stuart, Jo-Anne Buchanan, Tina Proffitt, Vicki Anderson, Dennis Velakoulis and Christos Pantelis. 2004. "Individual difference in anterior cingulate/paracingulate morphology are related to executive functions in healthy males", *Cereberal Cortex* 14: 424-431.
- Fransson, Peter, Ulrika Aden, Mats Blennow and Hugo Lagercrantz. 2011. "The functional architecture of the infant brain as revealed by resting-state fMRI", *Cerebral Cortex* 21: 145–154.
- Frazier, Lyn. 1987. "Theories of sentence processing", in: J. Garfield (ed.) *Modularity* in *Knowledge Representation and Natural-Language Processing*, Cambridge, MA: MIT Press, 291–307.
- Friedenberg, Jay and Gordon Silverman. 2005. *Cognitive science: An introduction to the study of mind.* New York: Sage Publications.
- Friederici, Angela D. 2006. "What's in control of language?", *Nature Neuroscience* 9: 991-992.
- Friederici, Angela D. and Stefan Frisch. 2000. "Verb-argument structure processing: the role of verb-specific and argument-specific information", *Journal of Memory and Language* 43: 476–507.
- Friederici, Angela D., Thomas C. Gunter, Anja Hahne and Kerstin Mauth. 2004. "The relative timing of syntactic and semantic processes in sentence comprehension", *NeuroReport* 15: 165–169.
- Friederici, Angela D., Shirley-Ann Rüschemeyer, Anja Hahne and Christian J. Fiebach. 2003. "The role of left inferior frontal and superior temporal cortex in sentence comprehension: localizing syntactic and semantic processes", *Cerebral Cortex* 13: 170–177.

- Friederici, Angela D. 2002. "Towards a neural basis of auditory sentence processing", *Trends in Cognitive Science* 6: 78–84.
- Friederici, Angela. 2011. "The Brain Basis of Language Processing: From Structure to Function", *Physiological Reviews* 91: 1357-1392.
- Friedrich, Claudia K., Verena Felder., Aditi Lahiri and Carsten Eulitz. 2013. "Activation of words with phonological overlap", *Frontiers in Psychology* 4: 556.
- García-Pentón Lorna, Alejandro Perez Fernandez, Yasser Iturria-Medina, Margaret Gillon-Dowens and Manuel Carreiras. 2014. "Anatomical connectivity changes in the bilingual brain", *Neuroimage* 84: 495–504.
- Garagnani Max, Thomas Wennekers and Friedemann Pulvermüller. 2008. "A neuroanatomically grounded Hebbian-learning model of attention-language interactions in the human brain", *European Journal of Neuroscience* 27: 492–513.
- Gaskell, Gareth M. and William D. Marslen-Wilson. 1998. "Mechanisms of phonological inference in speech perception", *Journal of Experimental Psychology: Human Perception and Performance* 24: 380-396.
- Gaskell, Gareth M. and William D. Marslen-Wilson. 1997. "Integrating Form and Meaning: A Distributed Model of Speech Perception", *Language and Cognitive Processes* 12: 613–656.
- Gathercole, Susan E. Elisabet Service, Graham J. Hitch, Anne-Marie Adams and Amanda J. Martin. 1999. "Phonological short-term memory and vocabulary development: Further evidence on the nature of the relationship", Applied Cognitive Psychology 13: 65-77.
- Gee, Dylan G., Bharat B. Biswal, Clare Kelly, David E. Stark, Daniel S. Margulies, Zarrar Shehzad, Lucina Q. Uddin, Donald F. Klein, Marie T. Banich, F. Xavier Castellanos and Michael P. Milham. 2011. "Low frequency fluctuations reveal integrated and segregated processing among the cerebral hemispheres", *Neuroimage*, 54: 517–527.
- Griffiths, Timothy D., and Jason D. Warren. 2002. "The planum temporale as a computational hub", *Trends in Neuroscience* 25: 348–353.
- Greicius, Michael D., Kaustubh Supekar, Vinod Menon and Robert F. Dougherty. 2009. "Resting-state functional connectivity reflects structural connectivity in the default mode network", *Cerebral Cortex* 19: 72–78.

- Grodzinsky, Yosef and Andrea Santi. 2008. "The battle for Broca's region", *Trends in Cognitive Science* 12: 474–480.
- Grodzinsky, Yosef. 2010. "The picture of the linguistic brain: how sharp can it be? Reply to Fedorenko and Kanwisher", *Language and Linguistic Compass* 4: 605–622.
- Goldinger, Stephen D. 1996. "Words and voices: episodic traces in spoken word identification and recognition memory", *Journal of Experimental Psychology: Learning, Memory and Cognition* 22: 1166-1183.
- Gruber, Oliver and Yves D. von Cramon. 2003. "The functional neuroanatomy of human working memory revisited. Evidence from 3-T fMRI studies using classical domain-specific interference tasks", *Neuroimage* 19: 797–809.
- Good, Catriona D., Ingrid S. Johnsrude, John Ashburner, Rirchard N. Henson, Karl J Friston, Richard S. Frackowiak .2001. "A voxel-based morphometric study of ageing in 465 normal adult human brains", *NeuroImage* 14: 21-36.
- Guenther, Frank H., Satrajit S. Ghosh, and Jason A. Tourville. 2006. "Neural modeling and imaging of the cortical interactions underlying syllable production", *Brain and Language* 96: 280–301.
- Guenther, Frank H. and Tony Vladusich. 2012. "A neural theory of speech acquisition and production", *Journal of Neurolinguistics* 25: 408–422.
- Guion, Susan G., and Eric Pederson. 2007. "Investigating the role of attention in phonetic learning", in: Ocke-Schwen Bohn Murray J. Munro (eds.), *Language experience in second language speech learning: In honor of James Emil Flege*. Amsterdam: John Benjamins, 57-78.
- Guion, Susan G., James E. Flege, Serena H. Liu and Grace H. Yeni-Komshian. 2000. "Age of learning effects on the duration of sentences produced in a second language", *Applied Psycholinguistics* 21: 205-228.
- Gupta, Santosh S., 2014. "fMRI for mapping language networks in neurosurgical cases", *Indian Journal of Radiology and Imaging* 24: 37-43.
- Hallé, Pierre A., Catherine T. Best and Asaf. Bachrach. 2003. "Perception of /dl/ and /tl/ clusters: A cross-linguistic perceptual study with French and Israeli listeners",
- in: Maria-Josep Solé and Jesus Romero (eds.), *Proceedings of the 15th International Congress of Phonetic Sciences*, Barcelona: Causal Productions, 2893-2896.

- Hagoort, Peter, Peter Indefrey, Colin Brown, Hans Herzog, Helmuth Steinmetz and Rudiger Seitz. 1999. "The neural circuitry involved in the reading of German words and pseudowords: a PET study", *Journal of Cognitive Neuroscience* 11: 383–398.
- Hagoort, P. 2005. "On Broca, brain, and binding: a new framework", Trends in Cognitive Science, 9:416–423.
- Hahne, Anja and Angela D. Friederici. 2002. "Differential task effects on semantic and syntactic processes as revealed by ERPs", *Cognitive Brain Research*, 13: 339–356.
- Hahne, Anja and Angela D. Friederici. 1999. "Electrophysiological evidence for two steps in syntactic analysis: early automatic and late controlled processes", Journal of Cognitive Neuroscience 11: 194–205.
- Hall, Deborah A., Ingrid S. Johnsrude, Mark P. Haggard, Alan R. Palmer, Michael A. Akeroyda and Quentin A. Summerfield. 2002. "Spectral and temporal processing in human auditory cortex", *Cerebral Cortex* 12: 140–149.
- Harnsberger, James D. 2001. "On the relationship between identification and discrimination on non-native nasal consonants", *Acoustical Society of America* 110: 489-503.
- Hauk, Olaf, Ingrid Johnsrude and Friedemann Pulvermüller. 2004. "Somatotopic representation of action words in human motor and premotor cortex", *Neuron* 41: 301–307.
- Hayward, Katrina. 2000. "Experimental Phonetics: An Introduction", Harlow: Longman.
- Hickok, Gregory and David Poeppel. 2007. "The cortical organization of speech perception", *Nature Reviews Neuroscience* 8: 393–402.
- He, Yong, Jinhui Wang, Liang Wang, Zhang J. Chen, Chaogan Yan, Hong Yang, Hehan Tang, Chaozhe Zhu, Qiyong Gong, Yufeng Zang and Alan C. Evans. 2009. "Uncovering intrinsic modular organization of spontaneous brain activity in humans", *PLoS One* 4: 5226.
- Henderson, John M. and Steven G. Luke. 2012. "Oculomotor inhibition of return in normal and mindless reading", *Psychonomic Bulletin & Review* 19: 1101–1107.
- Henderson, John M. and Steven G. Luke. 2014. "Stable individual differences in saccadic eye movements during reading, pseudo-reading, scene viewing, and

- scene search", Journal of Experimental Psychology: Human Perception and Performance 40: 1390–1400.
- Henson, Richard N., Neil Burgess and Christopher D. Frith. 2000. "Recoding, storage, rehearsal and grouping in verbal short-term memory: an fMRI study", *Neuropsychologia* 38: 426–440.
- Hernandez, Arturo E., Mirella Dapretto, John Mazziotta and Susan. Bookheimer. 2001. "Language switching and language representation in Spanish–English bilinguals: An fMRI study", *NeuroImage* 14: 510-520.
- Herwig, Uwe, Birgit Abler, Carlos Schönfeldt-Lecuona, Arthur Wunderlich, Jo Grothe, Manfred Spitzer and Henrik Walter. 2003. "Verbal storage in a premotor-parietal network: evidence from fMRI-guided magnetic stimulation" *NeuroImage* 20: 1032-41.
- Howard, David, Karalyn Patterson, Richard Wise, W. Douglas Brown, Karl Friston and Cornelius Weiller. 1992. "The cortical localization of the lexicons. Positron emission tomography evidence", *Brain* 115: 1769–1782.
- Hubbard, Edward M., Manuela Piazza, Philippe Pinel and Stanislas Dehaene. 2005. "Interactions between number and space in parietal cortex", *Nature Reviews Neuroscience* 6: 435–448.
- Humphries, Colin, Jeffrey R. Binder, David A. Medler and Einat Liebenthal. 2006. "Syntactic and semantic modulation of neural activity during auditory sentence comprehension", *Journal of Cognitive Neuroscience* 18: 665–679.
- Humphries, Colin, Tracy Love, David Swinney and Gregory Hickok. 2005. "Response of anterior temporal cortex to prosodic and syntactic manipulations during sentence processing", *Human Brain Mapping* 26: 128–138.
- Indefrey, Peter. 2006. "A meta-analysis of hemodynamic studies on first and second language processing: which suggested differences can we trust and what do they mean?", *Language Learning* 56: 279-304.
- Isel, Frederic, Annette. Baumgaertner, Johannes Thran, Jürgen M. Meisel and Christian Buchel. 2010. "Neural circuitry of the bilingual mental lexicon: Effect of age of second language acquisition", *Brain and Cognition* 72: 169-180.
- Jacquemot, Charlotte, Christophe Pallier, Denis LeBihan, Stanislas Dehaene and Emmanuel Dupoux. 2003. "Phonological grammar shapes the auditory cortex: a

- functional magnetic resonance imaging study", *Journal of Neuroscience* 23: 9541–9546.
- James, William. 2007. Principles of psychology. Vol 1. New York: Cosimo Classics.
- Jia, Gisela and Doris Aaronson. 2003. "A longitudinal study of Chinese children and adolescents learning English in the United States", *Applied Psycholinguistics*, 24: 131-161.
- Jia, Gisela, Winifred Strange, Yanhong Wu, Julissa Collado and Qi Guan. 2005. "Perception and production of English vowels by Mandarin speakers: Agerelated differences vary with amount of L2 exposure", *Journal of the Acoustical Society of America* 119: 1118:-1130.
- Jenkinson, Mark, Christian F. Beckmann, Timothy E. Behrens, MarkW. Woolrich, and Stephen M. Smith. 2012. "FSL", *NeuroImage* 62: 782-90.
- Jenkinson, Mark and Stephen M. Smith. 2001. "A global optimisation method for robust affine registration of brain images", *Medical Image Analysis* 5: 143-156.
- Jonides, John, Eric H. Schumacher, Edward E. Smith, Robert A. Koeppe, Edward Awh, Patricia A. Reuter-Lorenz, Christy Marshuetz and Christopher R. Willis. 1998. "The role of parietal cortex in verbal working memory", *Journal of Neuroscience*, 18: 5026–5034.
- Johnsrude, Ingrid S., Anne-Lise Giraud and Richard S. Frackowiak. 2002. "Functional imaging of the auditory system: the use of positron emission tomography", *Audiology and Neurootology* 7: 251–276.
- Johnson, Keith. 2005. "Speaker Normalization in speech perception", in: David B. Pisoni and Robert E. Remez (eds.), *The Handbook of Speech Perception*. Oxford: Blackwell Publishers.
- Jordan, Timothy R., Michael Redwood and Geoffrey R. Patching. 2003. "Effects of form familiarity on perception of words, pseudowords, and nonwords in the two cerebral hemispheres", *Journal of Cognitive Neuroscience* 15: 537-548.
- Knecht, Stefan, Bianca Drager, Michael Deppe, L. Bobe, Hubertus Lohmann and Agnes Floel, Bernd E. Ringelstein and Henning Henningsen. 2000. "Handedness and hemispheric language dominance in healthy humans", *Brain* 123: 2512–2518.
- Kim, Karl, Norman R. Relkin, Kyoung-Min Lee and Joy Hirsch. 1997. "Distinct cortical areas associated with native and second language", *Nature* 388: 171-174.

- Kelly, Clare., Xi-Nian Zuo, Kristin Gotimer, Christine L. Cox, Lauren Lynch, Dylan Brock, Davide Imperati, Hugh Garvan, John Rotrosen, F. Xavier Castellanos and Michael P. Milham.2011. "Reduced interhemispheric resting state functional connectivity in cocaine addiction", *Biological Psychiatry* 69: 684–692.
- Kellert, Stephen H. 1993. *In the wake of chaos: Unpredictable order in dynamical systems*. University of Chicago Press.
- Klein, Denise, Robert J. Zatorre, Jen-Kai Chen, Brenda Milner, Joelle Crane, Pascal Belin and Marc Bouffard. 2006. "Bilingual brain organization: A functional magnetic resonance adaptation study", *NeuroImage* 31: 366-375.
- Koch, Martin A., David G. Norris and Margret Hund-Georgiadis. 2002. "An investigation of functional and anatomical connectivity using magnetic resonance imaging", *NeuroImage* 16: 241–250.
- Kochetov, Alexei. 2004. "Processing of secondary articulation contrasts in different syllable positions: Universal and language-particular factors", *Cahiers Linguistiques d'Ottawa*, 32:24-43.
- Konrad, Andreas, Goran Vucurevic, Francesco Musso, Peter Stoeter and Georg Winterer. 2009. "Correlation of brain white matter diffusion anisotropy and mean diffusivity with reaction time in an oddball task", *Neuropsychobiology* 60: 55–66.
- Koschutzki, Dirk., Katharina A. Lehmann, Leon Peeters, Stefan Richter, Dagmar Tenfelde-Podehl and Oliver Zlotowski. 2005. "Centrality indices", in: Ulrik Brandes and Thomas Erlebach (eds.), *Network analysis: Methodological foundations*, New York: Springer-Verlag, 16–61.
- Krakauer, John and Claude Ghez. 1999. "Voluntary movement", in: Eric R. Kandel, James H. Schwartz and Thomas M. Jessell (eds.), *Principles of neural science*. *4th ed.*, McGraw Hill; New York, 756–781.
- Kroliczak, Gregory, Brian J. Piper, Scott H. Frey. 2011. "Atypical lateralization of language predicts cerebral asymmetries in parietal gesture representations", *Neuropsychologia* 49: 1698-1702.
- Kröger, Bernd J., Jim Kannampuzha and Emily Kaufmann. 2014. "Associative learning and self-organization as basic principles for simulating speech acquisition, speech production, and speech perception", *EPJ Nonlinear Biomedical Physics*, 2: 2.

- Kuperberg, Gina R., Philip K. McGuire, Edward T. Bullmore, Michael J. Brammer, Sophia Rabe-Hesketh, I.C. Wright, David J. Lythgoe, Sarah C. Williams and Anthony S. David. 2000. "Common and distinct neural substrates for pragmatic, semantic, and syntactic processing of spoken sentences: an fMRI study", *Journal of Cognitive Neuroscience* 12: 321–341.
- Lafuente, de Victor and Ranulfo Romo. 2004. "Language abilities of motor cortex", *Neuron* 41: 178–180.
- Lanteaume, Laura, Stephanie Khalfa, Jean Regis, Patrick Marquis, Patrick Chauvel and Fabrice Bartolomei. 2007. "Emotion induction after direct intracerebral stimulations of human amygdala". *Cerebral Cortex* 17: 1307–13.
- Lambon, Ralph. and Karalyn Patterson. 2008. "Generalization and differentiation in semantic memory: insights from semantic dementia" *Annals of the New York academy of sciences* 1124: 61–76.
- Lemhöfer, Kristin and Mirjam Broersma. 2012. "Introducing LexTALE: A quick and valid Lexical Test for Advanced Learners of English", *Behavior Research Methods* 44, 325-343.
- Leonard, Matthew K., Timothy T. Brown, Katherine E. Travis, Lusineh Gharapetian, Donald J. Hagler Jr, Anders M. Dale, Jeffrey L. Elman and Eric Halgren. 2010. "Spatiotemporal dynamics of bilingual word processing", *Neuroimage* 49: 3286-3294.
- Leshikar, Eric D., Audrey Duarte and Christopher Hertzog. 2012. "Task-Selective Memory Effects for Successfully Implemented Encoding Strategies", *Plos One* 7: e38160.
- Leung, Hoi-Chung, David Seelig and John. C. Gore. 2004. "The effect of memory load on cortical activity in the spatial working memory circuit", *Cognitive, Affective, & Behavioral Neuroscience* 4: 553–563.
- Li, Ping, Jennifer Legault and Kaitlyn A. Litcofsky. 2014. "Neuroplasticity as a function of second language learning: Anatomical changes in the human brain", *Cortex* 58: 301-324.
- Liberman, Alvin M., and Ignatius G. Mattingly. 1985. "The motor theory of speech perception revised", *Cognition* 21: 1-36.

- Liberman, Alvin M., Franklin S. Cooper, Donald P. Shankweiler, and Michael Studdert-Kennedy. 1967. "Perception of the speech code", *Psychological Review* 74: 431-461.
- Llano, Daniel A. 2013. "Functional imaging of the thalamus in language", *Brain and Language* 126: 62-72.
- Logie, Robert H., Annalena Venneri, Sergio Della Sala, Thomas W. Redpath and Ian Marshall. 2003. "Brain activation and the phonological loop: The impact of rehearsal", *Brain and cognition*, 53:293-296.
- Luk, Gigi and Ellen Bialystok. 2008. "Common and distinct cognitive bases for reading in English Cantonese bilinguals", *Applied Psycholinguistics* 29: 269-289.
- Macher, Katja, Andreas. Bohringer, Arno Villringer and Burkhard Pleger. 2014. "Cerebellar-parietal connections underpin phonological storage", *The Journal of Neuroscience* 34: 5029-5037.
- Mandonnet, Emmanuel, Aurelien Nouet, Peggy Gatignol, Laurent Capelle and Hugues Duffau. 2007. "Does the left inferior longitudinal fasciculus play a role in language? A brain stimulation study", *Brain* 130: 623–629.
- Mechelli, Andrea, Karl J. Friston and Cathy J. Price. 2000. "The effects of presentation rate during word and pseudoword reading: a comparison of PET and fMRI", *Journal of Cognitive Neuroscience* 12: 145–156.
- Mamah, Daniel, Deanna M. Barch and John Csernansky. 2009. "Neuromorphometric Measures as Endophenotypes of Schizophrenia Spectrum Disorders", in: Michael S. Ristner (ed.), *The Handbook of neuropsychiatric biomarkers, endophenotypes and genes*. Springer.
- McDermott, Kathleen B, Steven E. Petersen, Jason M. Watson and Jeffrey G. Ojemann. 2003. "A procedure for identifying regions preferentially activated by attention to semantic and phonological relations using functional magnetic resonance imaging", *Neuropsychologia* 41: 293–303.
- McGettigan, Carloyn., Samuel Evans, Stuart Rosen, Zarinah K. Agnew, Poonam Shah, and Sophie Scott. 2012. "An application of univariate and multivariate approaches in fMRI to quantifying the hemispheric lateralization of acoustic and linguistic processes", *Journal of Cognitive Neuroscience* 24: 636-52.
- MacNeilage, Peter .F., Thomas P. Rootes and Richard A. Chase. 1967. "Speech production and perception in a patient with severe impairment of somesthetic

- perception and motor control", *Journal of speech and hearing research* 10: 449-467.
- MacNeilage Peter. 2008. The origin of speech. Oxford University Press.
- Marcus, Gary F. 2001. *The algebraic mind: integrating connectionism and cognitive science*. Cambridge, MA: MIT Press.
- Marslen-Wilson, William. 1987. "Functional parallelism in spoken word recognition." *Cognition* 25: 71-102.
- Mattingly, Ignatius G. and Alvin M. Liberman. 1970. "The speech code and the physiology of language", in: K.N. Leibovic (ed.), *Information Processing in the Nervous System*, 97–117.
- McCausland Center for Brain Imaging. 2014. *MRIcroGL*. (http://mccauslandcenter.sc.edu/mricrogl/) (date of access: 20 Mar. 2015).
- McClelland, James L. and David E. Rumelhart. 1986. Parallel distributed processing.

 Explorations in the microstructure of cognition. Volume 2: Psychological and Biological Models. Cambridge, MA: MIT Press.
- McClelland, James L. and Jeffrey L. Elman. 1986. "The TRACE model of speech perception", *Cognitive Psychology* 18: 1-86.
- McClelland, James L., Daniel Mirman, Donald J. Bolger and Pranav Khaitan. 2014. "Interactive activation and mutual constraint satisfaction in perception and cognition", *Cognitive Science* 38: 1139-1189.
- McQueen, James M. 2007. "Eight questions about spoken word recognition", in: Gareth M. Gaskell (ed.), *The oxford handbook of psycholinguistics*, Oxford: University Press, 37–54.
- Mechelli, Andrea, Jenny T. Crinion, Uta Noppency, John O'Doherty, John Ashburner, Richard S. Frackowiak and Cathy J. Price. 2004. "Structural plasticity in the bilingual brain", *Nature* 431: 757.
- Mei, Leilei., Gui Xue, Zhong-Lin Lu, Chuansheng Chen, Miao Wei, Qinghua He and Qi Dong. 2015. "Long-term experience with Chinese language shapes the fusiform asymmetry of English reading", *Neuroimage* 110: 3-10.
- Meyer, Martin, Kai Alter, Angela D. Friederici, Gabriela Lohmann and D. Yves von Cramon. 2002. "fMRI reveals brain regions mediating slow prosodic modulations in spoken sentences", *Human Brain Mapping* 17: 73–88.

- Meyer, Martin, Karsten Steinhauer, Kai Alter, Angela D. Friederici, D. Yves von Cramon. 2004. "Brain activity varieswith modulation of dynamic pitch variance in sentence melody", *Brain and Language* 89: 277–289.
- Meyer, Patric, Axel Mecklinger, Thomas Grunwald, Juergen Fell, Christian E. Elger, and Angela D. Friederici. 2005. "Language processing within the human medial temporal lobe", *Hippocampus* 15: 451–459.
- Morgan-Short, Kara, Karsten Steinhauer, Cristina Sanz and Michael T. Ullman. 2012. "Explicit and implicit second language training differentially affect the achievement of native-like brain activation patterns", *Journal of Cognitive Neuroscience* 24: 933-947.
- Mohades, Sayede G., Esli Struys, Peter Van Schuerbeek, Katrin Mondt, Piet Van De Craen and Robert Luypaert. 2012. "DTI reveals structural differences in white matter tracts between bilingual and monolingual children", *Brain Research*, 1435: 72-80.
- Montreal Neurological Institute. 2009. MNI-ICBM 152 nonlinear brain template. (http://www.bic.mni.mcgill.ca/ServicesAtlases/HomePage) (date of access: 20 Mar. 2015).
- Morosan, Patricia, Jorg Rademacher, Axel Schleicher, Katrin Amunts, Thorsten Schormann, and Karl Zilles. 2001. "Human primary auditory cortex: cytoarchitectonic subdivisions and mapping into a spatial reference system", *NeuroImage* 13: 684–701.
- Muller, Angela M. and Martin Meyer. 2014. "Language in the brain at rest: new insights from resting state data and graph theoretical analysis", *Frontiers in Human Neuroscience* 8: 228.
- Muller-Gass, Alexandra., Margaret Macdonald, Erich Schröger, Lauren Sculthorpe, Keneth Campbell. 2007. "Evidence for the auditory P3a reflecting an automatic process: elicitation during highly focused continuous visual attention", *Brain Research* 1170: 71-78.
- Mummery, Cath J., John Ashburner, Sophie K. Scott and Richard J. S. Wise. 1999. "Functional neuroimaging of speech perception in six normal and two aphasic subjects", *Journal of Acoustical Society of America*, 106: 449–457.

- Munro, Murray J. and Tracey M. Derwing. 1995. "Processing time, accent, and comprehensibility in the perception of native and foreign-accented speech", *Language and Speech* 38: 289-306.
- Newman, Randy L. and Marc F. Joanisse. 2011. "Modulation of brain regions involved in word recognition by homophonous stimuli: An fMRI study", Brain Research, 1367: 250–264.
- Newman, Sharlene D. and Donald Twieg. 2001. "Differences in auditory processing of words and pseudowords: An fMRI study", *Human Brain Mapping* 14: 39–47.
- Newman, Sharlene D., Toshikazu Ikuta and Thomas. Burns. 2010. "The effect of semantic relatedness on syntactic analysis: an fMRI study", *Brain and Language* 113: 51–58.
- Northam, Gemma B., Frederique Liégeois, Jacques D. Tournier, Louise J. Croft, Paul N. Johns, Wui K. Chong, John S. Wyatt and Torsten Baldeweg. 2012. "Interhemispheric temporal lobe connectivity predicts language impairment in adolescents born preterm", *Brain* 135: 3781-98.
- Nygaard, Lynne C., Mitchell S. Sommers and David B. Pisoni. 1994. "Speech perception as a talker-contingent process", *Psychological Science* 5: 42–46.
- Obler, Loraine K., Jung M. Hyun, Peggy S. Conner, Barbara O'Connor and Ian Anema. 2007. "Brain organization of language in bilinugals", in: Alfredo Ardila and Eliane Ramos (eds.), *Speech and language disorders in bilinguals*. New York: Nova Science Publishers.
- Obleser, Jonas, and Sonja A. Kotz. 2010. "Expectancy constraints in degraded speech modulate the language comprehension network", *Cerebral Cortex* 20: 633–640.
- Obleser, Jonas, Jonas Zimmermann, John Van Meter and Josef P. Rauschecker. 2007. "Multiple stages of auditory speech perception reflected in event-related fMRI", *Cerebral Cortex* 17: 2251–2257.
- Ono, Yumie, Tatsuya Nanjo, Atsushi Ishiyama. 2014. "Pursuing the flow of information: connectivity between bilateral premotor cortices predicts better accuracy in the phonological working memory task", *Conference Proceedings of Engineering in Medicine and Biology Society*, 2013: 7404-7.
- Packard, Mark G. and Barbara Knowlton. 2002. "Learning and memory functions of the basal ganglia", *Annual Review of Neuroscience* 25: 563-593.

- Paradis, Michel. 2002. "Neurolinguistics of bilingualism and the teaching of language" (Paper presented at the Symposium on The Multimodality of Human Communication, Ontario, May 2002.).
- Paradis, Michel. 2006. "Implicit competence and explicit knowledge in second language acquisition and learning" (Paper presented at the Workshop on the Neurocognition of Second Language, Washington, D.C., 7 April 2006.).
- Parker-Jones, Oiwi, David W. Green, Alice Grogan, Christos Pliatsikas, Konstantinos Filippopolitis, Nilufa Ali, Hwee Ling Lee, Sue Ramsden, Karine Gazarian, Susan Prejawa, Mohamed L. Seghier and Cathy J. Price. 2012. "Where, when and why brain activation differs for bilinguals and monolinguals during picture naming and reading aloud", *Cerebral Cortex* 22: 892-902.
- Passingham, Richard E. 1993. *The frontal lobes and voluntary action*. Oxford University Press; Oxford.
- Paulesu, Eraldo, Christopher D. Frith and Richard S. Frackowiak. 1999. "The neural correlates of the verbal component of working memory", *Nature* 362: 342–345.
- Perani, Daniela, Sstanislas Dehaene, Franco Grassi, Laurent Cohen, Stefano F. Cappa, Emmanuel Dupoux, Ferruccio Fazio and Jacques Mehler. 1996. "Brain processing of native and foreign language", *NeuroReport* 7: 2439-2444.
- Perani, Daniela, Eraldo Paulesu, Nuria S. Galles, Emmanuel. Dupoux, Stanislas Dehaene, Valentino Bettinardi, Stefano F. Cappa, Feruccio Fazio, and Jacques Mehler. 1998. "The bilingual brain: Proficiency and age of acquisition of the second language", *Brain* 121:1841-1852.
- Perani, Daniela, Jubin Abutalebi, Eraldo Paulesu, Simona Brambati, Paola Scifo, Stefano F. Cappa and Feruccio Fazio. 2003. "The role of age of acquisition and language usage in early, high-proficient bilinguals: An fMRI study during verbal fluency", *Human Brain Mapping* 19: 170-182.
- Perkins, Judy M., Jane A. Baran and Jack Gandour. 1996. "Hemispheric specialization in processing intonation contours", *Aphasiology* 10: 343–362.
- Perkell, Joseph S., Frank H. Guenther, Harlan Lane, Melanie L. Matthies, Ellen Stockmann, Mark Tiede and Majid Zandipour. 2004a. "Cross-subject correlations between measures of vowel production and perception", *Journal of the Acoustical Society of America* 116: 2338–2344.

- Perkell, Joseph S., Melanie L. Matthies, Mark Tiede, Harlan Lane, Majid Zandipour, Nicole Marrone, Ellen Stockmann and Frank H. Guenther. 2004b. "The distinctness of speakers' /s-sh/ contrast is related to their auditory discrimination and use of an articulatory saturation effect", *Journal of Speech, Language, and Hearing Research* 47: 1259–1269.
- Pesenti, Mauro, Marc Thioux, Xavier Seron and Anne de Volder. 2000. "Neuroanatomical substrates of arabic number processing, numerical comparison, and simple addition: A PET study", *Journal of Cognitive Neuroscience* 12: 461–479.
- Petersen, Steven E., Peter T. Fox, Michael I. Posner, Mark Mintun and Marcus E. Raichle. 1988. "Positron emission tomographic studies of the cortical anatomy of single-word processing", *Nature* 331: 585–589.
- Petersen, Steven E. and Michael I. Posner. 2012. "The attention system of the human brain: 20 years after", *Annual Review of Neuroscience* 35: 73–89.
- Pillai, Jay J., Jerry D. Allison, Sankar Sethuraman, Julio M. Araque, Dharma Thiruvaiyaru, Claro B. Ison, David W. Loring and Thomas Lavin. 2004. "Functional MR imaging study of language related differences in bilingual cerebellar activation", *American Journal of Radiology* 25: 523-532.
- Plante, Elena, Marlena Creusere and Cynthia Sabin. 2002. "Dissociating sentential prosody from sentence processing: activation interacts with task demands", *NeuroImage* 17: 401–410.
- Pliatsikas, Christos, Elisavet Moschopoulou and James Douglas Saddy. 2015. "The effects of bilingualism on the white matter structure of the brain", *PNAS*, 112: 1334-1337.
- Poeppel, David, William J. Idsardi and Virginie van Wassenhove. 2008. "Speech perception at the interface of neurobiology and linguistics", *Philosophical transactions of the Royal Society B: Biological Science* 12: 1071-1086.
- Poldrack, Russel A., Jeanette A. Mumford and Thomas E. Nichols. 2011. "Preprocessing fMRI data", in: Russel A. Poldrack, Jeanette A. Mumford and Thomas E. Nichols (eds.), *Handbook of functional MRI data analysis*, Cambridge: Cambridge University Press.

- Polka, L. 1992. "Characterizing the influence of native experience on adult speech perception", *Perception and Psychophysics*, 52:37-52.
- Polka, Linda and Ocke-Schwen Bohn. 2003. "Asymmetries in vowel perception", Speech Communication 41: 221-231.
- Postle, Bradley R. 2006. "Working memory as an emergent property of the mind and brain", *Neuroscience* 139: 23–38.
- Power, Jonathan D., Kelly A. Barnes, Abraham Z. Snyder, Bradley L. Schlaggar and Steven E. Petersen. 2011. "Spurious but systematic correlations in functional connectivity MRI networks arise from subject motion", *NeuroImage* 59: 2142-2154.
- Price, Cathy J., Caroline J. Moore, Glyn W. Humphreys and Richards J. S. Wise. 1997. "Segregating semantic from phonological processes during reading", *Journal of Cognitive Neuroscience* 9: 727–733.
- Price Cathy J., Richard J.S. Wise and Richard S. J. Frackowiak. 1996. "Demonstrating the implicit processing of visually presented words and pseudowords", *Cerebral Cortex* 6: 62–70.
- Pulvermüller, Friedemann. and Luciano Fadiga. 2010. "Active perception: sensorimotor circuits as a cortical basis for language", *Nature Reviews Neuroscience* 11: 351–360.
- Raichle, Marcus E. and Abraham Z. Snyder. 2009. "Intrinsic brain activity and consciousness", in: Steven Laureys and Giulio Tononi (eds.), *The neurology of consciousness*. London: Elsevier.
- R Foundation. 2015. *The R project for statistical computing*. Version 3.1.2. (http://www.r-project.org/) (date of access: 30 Nov. 2014).
- Ramus, Franck, Marc D. Hauser, Corry Miller, Dylan Morris and Jacques Mehler. 2000. "Language Discrimination by Human Newborns and by Cotton-Top Tamarin Monkeys", *Science* 288: 349-351.
- Rauschecker, Josef P., Sophie K. Scott. 2009. "Maps and streams in the auditory cortex: nonhuman primates illuminate human speech processing", *Nature Neuroscience* 12: 718–724.

- Reali, Florencia and Morten H. Christiansen. 2005. "Uncovering the richness of the stimulus: Structural dependence and indirect statistical evidence", *Cognitive Science* 29: 1007-1028.
- Reuter, Martin, Nicholas J. Schmansky, H. Diana Rosas and Bruce Fischl. 2012. "Within-Subject Template Estimation for Unbiased Longitudinal Image Analysis", *Neuroimage* 61: 1402-1418.
- Rizzolatti, Giacomo and Michael A. Arbib. 1998. "Language within our grasp", *Trends in Neuroscience* 21: 188–194.
- Rodd, Jennifer M., Matthew H. Davis and Ingrid S. Johnsrude. 2005. "The neural mechanisms of speech comprehension: fMRI studies of semantic ambiguity", *Cerebral Cortex* 15: 1261–1269.
- Röder, Brigitte, Oliver Stock. Helen J. Neville, Siegfried Bien and Frank Rösler. 2002. Brain activation modulated by the comprehension of normal and pseudo-word sentences of different processing demands: a functional magnetic resonance imaging study. *NeuroImage* 15: 1003–1014.
- Rogalsky, Corianne and Gregory Hickok. 2009. "Selective attention to semantic and syntactic features modulates sentence processing networks in anterior temporal cortex", *Cerebral Cortex* 19: 786–796.
- Rogalsky, Corianne and Gregory Hickok. 2011. "The role of Broca's area in sentence comprehension", *Journal of Cognitive Neuroscience* 23: 1664–1680.
- Rogalsky, Corianne, William Matchin and Gregory Hickok. 2008. "Broca's area, sentence comprehension, and working memory: an fMRI Study", *Frontiers in Human Neuroscience* 2:14.
- Rüschemeyer, Shirley-Ann, Christian J. Fiebach, Vera Kempe and Angela D. Friederici. 2005. "Processing lexical semantic and syntactic information in first and second language: fMRI evidence from German and Russian", *Human Brain Mapping* 25: 266–286.
- Rypma, Bart and Mark D'Esposito. 1999. "The roles of prefrontal brain regions in components of working memory: effects of memory load and individual differences", *PNAS* 96:6558 6563.
- Sahin, Ned T., Steven Pinker, Sydney S. Cash, Donald Schomer and Eric Halgren. 2009. "Sequential processing of lexical, grammatical, and phonological information within Broca's area", *Science* 326: 445–449.

- Saffran, Jenny, Marc Hauser, Rebecca Seibel, Joshua Kapfhamer, Fritz Tsao and Fiery. Cushman. 2008. "Grammatical pattern learning by human infants and cotton-top tamarin monkeys", *Cognition* 107:479–500.
- Satterthwaite, Theodore D., Daniel H. Wolf, James Loughead, Kosha Ruparel, Mark A. Elliott, Hakonarson Hakon, Ruben C. Gur and Raquel E. Gur. 2012. "Impact of in-scanner head motion on multiple measures of functional connectivity: Relevance for studies of neurodevelopment in youth", *Neuroimage* 60: 623-632.
- Scott, Sophie K., Catrin C. Blank, Stuart Rosen and Richard J. S Wise. 2000. "Identification of a pathway for intelligible speech in the left temporal lobe", *Brain* 123: 2400–2406.
- Scott, Sophie K. and Ingrid S. Johnsrude. 2003. "The neuroanatomical and functional organization of speech perception", *Trends in Neuroscience* 26: 100–107.
- Schlegel, Alexander A., Justin J. Rudelson and Peter U. Tse. 2012. "White matter structure changes as adults learn a second language", *Journal of Cognitive Neuroscience* 24: 1664–1670.
- Schmahmann, Jeremy D. and Deepak N. Pandya. 1997. "The cerebrocerebellar system", International Review of Neurobiology 41: 31–60.
- Sereno, Joan A. and Yue Wang. 2007. "Behavioral and cortical effects of learning a second language: The acquisition of tone", in: Bohn, Ocke-Schwen and Murray J. Munro (eds.), *Language experience in second language speech learning: In honor of James Emil Flege*, Amsterdam: John Benjamins, 241-258.
- Service, Elisabet. 1992. "Phonology, working memory, and foreign-language learning", *Quarterly Journal of Experimental Psychology* 45A: 21-50.
- Shannon, Robert V., Fan-Gang Zeng, Vivek Kamath, John Wygonski and Michael Ekelid. 1995. "Speech recognition with primarily temporal cues", *Science* 270: 303–304.
- Simmonds, Anna J., Richard J. S. Wise and Robert Leech. 2011. "Two Tongues, One Brain: Imaging Bilingual Speech Production", *Frontiers in Psychology* 2: 166.

- Skipper, Jeremy I., Howard C. Nusbaum and Steven L. Small. 2005. "Listening to talking faces: motor cortical activation during speech perception", *NeuroImage* 25: 76-89.
- Smith, Stephen M., Yongyue Zhang, Mark Jenkinson, Jacqueline Chen, P.M. Matthews, Antonio Federico and Nicola De Stefano. 2002. "Accurate, robust and automated longitudinal and cross-sectional brain change analysis.", *NeuroImage* 17: 479-489.
- Smith, Stephen M., 2002. "Fast robust automated brain extraction", *Human Brain Mapping* 17: 143-155.
- Smith, Stephen M, Mark. Jenkinson, Heidi Johansen-Berg, Daniel Rueckert, Thomas E. Nichols, Clare E. Mackay, Kate E. Watkins, Olga Ciccarelli, M. Zaheer Cader, Paul M. Matthews and Thomas E. J. Behrens. 2006. "Tract-based spatial statistics: Voxelwise analysis of multi-subject diffusion data", *NeuroImage*, 31: 1487-1505.
- Smith, Stephen M., Mark Jenkinson, Mark W. Woolrich, Christian F. Beckmann, Timothy E. Behrens, Heidi Johansen-Berg, Peter R. Bannister, Marliena De Luca, Ivana Drobnjak, D.avid E. Flitney, Rami K. Niazy, James Saunders, John Vickers, Yongyue Zhang, Nicola De Stefano, J. Michael Brady and Paul M. Matthews. 2004. "Advances in functional and structural MR image analysis and implementation as FSL", *NeuroImage* 23: 208-219.
- Smith, Edward E. and John Jonides, 1999. "Storage and executive processes in the frontal lobes", *Science* 283: 1657–1661.
- Snijders, Tineke M., Theo Vosse, Gerard Kempen, Jos J. A. Van Berkum, Karl M. Petersson and Peter Hagoort. 2009. "Retrieval and unification of syntactic structure in sentence comprehension: an fMRI study using word-category ambiguity", *Cerebral Cortex* 19: 1493–1503.
- Stark, David E., Daniel S. Margulies, Zarrar E. Shehzad, Philip Reiss, A. M. Clare Kelly, Lucina Q. Uddin, Dylan G. Gee, Amy K. Roy, Marie T. Banich, F. Xavier Castellanos and Michael P. Milham. 2008. "Regional variation in interhemispheric coordination of intrinsic hemodynamic fluctuations", *The Journal of Neuroscience* 28: 13754–13764.
- Sternberg, Saul. 1966. "High speed scanning in human memory", Science 153: 652-654.

- Stoeckel, Cornelia, Patricia M. Gough, Kate E. Watkins and Joseph T. Devlin. 2009. "Supramarginal gyrus involvement in visual word recognition", *Cortex 45:* 1091–1096.
- Stoppelman, Nadav, Tamar Harpaz and Michal Ben-Shachar. 2013. "Do not throw out the baby with the bath water: choosing an effective baseline for a functional localizer of speech processing", *Brain and Behavior* 3: 211-222.
- Stowe, Laurie A., Cees A. J. Broere, Anne M. J. Paans, Albertus A. Wijers, Gijsbertus. Mulder, Wim Vaalburg and Frans Zwarts. 1998. "Localizing components of a complex task: sentence processing and working memory", *Neuroreport* 9: 2995– 2999.
- Stowe, Laurie A. and Laura Sabourin. 2005. "Imaging the processing of a second language: Effects of maturation and proficiency on the nerual processes involved", *IRAL* 43: 327-351.
- Strange, Winifred., Reiko Akahane-Yamada, Rieko Kubo, Sonja A. Trent and Kanae Nishi. 2001. "Effects of consonantal context on perceptual assimilation of American English vowels by Japanese listeners", *Journal of the Acoustical Society of America* 109: 1691-1704.
- Strelnikov, Kuzma N., Victor A. Vorobyev, Tatiana V. Chernigovskaya and Svyatoslav V. Medvedev. 2006. "Prosodic clues to syntactic processing: a PET and ERP study", *NeuroImage* 29: 1127–1134.
- Tanner, Dennis C. 2007. "A redefining Wernicke's area: receptive language and discourse semantics", *Journal of Allied Health* 36:63-6.
- Taylor, Insup and Martin M. Taylor. 1990. *Psycholinguistics: Learning and using language*. Englewood Cliffs: Prentice Hall.
- Taylor, J.S., Kathleen Rastle, and Matthew H. Davis. 2014. "Interpreting response time effects in functional imaging studies", *NeuroImage* 99: 419-33.
- Tincoff, Ruth, Marc Hauser, Fritz Tsao, Geertrui Spaepen, Franck Ramus and Jacques Mahler. 2005. "The role of speech rhythm in language discrimination: Further tests with a non-human primate", *Developmental Science* 8: 26 –35.
- Toga, Arthur W. and Paul M. Thompson. 2003. "Mapping brain asymmetry", *Nature Reviews Neuroscience* 4: 37-48.
- Tourville, Jason A., Kevin J. Reilly and Frank H. Guenther. 2008. "Neural mechanisms underlying auditory feedback control of speech", *NeuroImage* 39: 1429–1443.

- Tourville, Jason A. and Frank H. Guenther. 2011. "The DIVA model: A neural theory of speech acquisition and production", *Language and Cognitive Processes* 25: 952-981.
- Trost, Sarah and Oliver Gruber. 2012. "Evidence for a double dissociation of articulatory rehearsal and non-articulatory maintenance of phonological information in human verbal working memory", *Neuropsychobiology* 65: 133-40.
- Tsao, Feng-Ming, Huei-Mei Liu and Patricia K. Kuhl. 2004. "Speech perception in infancy predicts language development in the second year of life: A longitudinal study", *Child Development* 75: 1067-84.
- Tsukada, Kimiko, David Birdsong, Ellen Bialystok, Molly Mack, Hyekyung Sung and James E. Flege. 2005. "A developmental study of English vowel production and perception by native Korean adults and children", *Journal of Phonetics* 33: 263-290.
- Tu, Liu, Junjing Wang, Jubin Abutalebi, Bo Jiang, Ximin Pan, Meng Li, Wei Gao, Yuchen Yang, Bishan Liang, Zhi Lu and Ruiwang Huang. 2015. "Language exposure induced neuroplasticity in the bilingual brain: A follow-up fMRI study", *Cortex* 64: 8-19.
- Tyler, Lorraine K and William Marslen-Wilson. 2008. "Fronto-temporal brain systems supporting spoken language comprehension", *Philosophical Transactions of the Royal Society B: Biological Sciences* 363: 1037–1054.
- Van Dijk, Koene R., Mert R. Sabuncu and Randy L. Buckner. 2012. "The influence of head motion on intrinsic functional connectivity MRI", *NeuroImage* 59: 431-438.
- van den Heuvel, Martijn P., Cornelis J. Stam, Rene S. Kahn and Hilleke E. Hulshoff Pol. 2009. "Efficiency of functional brain networks and intellectual performance", *Journal of Neuroscience* 10: 7619-24.
- van den Heuvel, Martjin. P., Rene C. Mandl, Rene S. Kahn, and Hilleke.E. Hulshoff Pol. 2009. "Functionally Linked Resting-State Networks Reflect the Underlying Structural Connectivity Architecture of the Human Brain", *Human Brain Mapping* 30: 3124-3141.
- Van der Werf, Ysbrand D., Philip Scheltens, Jaap Lindeboom, Menno P. Witter, Harry B. M. Uylings, Jelle Jolles. 2003. "Deficits of memory, executive functioning

- and attention following infarction in the thalamus; a study of 22 cases with localised lesions", *Neuropsychologia* 41: 1330-1344.
- Vandenberghe, Rik., Anna C. Nobre, and Cathy J. Price. 2002. "The response of left temporal cortex to sentences", *Journal of Cognitive Neuroscience* 14: 550–560.
- Vannest, Jennifer J., Prasanna R. Karunanayaka, Mekibib Altaye, Vincent J. Schmithorst, Elena M. Plante, Kenneth J. Eaton, Jerod M. Rasmussen and Scott K. Holland. 2009. "Comparison of fMRI data from passive listening and active-response story processing tasks in children", *Journal of Magnetic Resonance Imaging* 29: 971-976.
- Vigneau Mathieu., Virginie Beaucousin, Pierre-Yves Herve, Hugues Duffau, Fabrice Crivello, Olivier Houde, Bernard Mazoyer and Natalie Tzourio-Mazoyer. 2006. "Meta-analyzing left hemisphere language areas: phonology, semantics, and sentence processing", *NeuroImage* 30: 1414–1432.
- Villacorta, Virgilio M., Joseph S. Perkell and Frank H. Guenther. 2007. "Sensorimotor adaptation to feedback perturbations of vowel acoustics and its relation to perception", *Journal of the Acoustical Society of America* 122: 2306–2319.
- Visser, Maya, Elizabaeth Jefferies and Matthew A. Lambon Ralph. 2009. "Semantic processing in the anterior temporal lobes: a meta-analysis of the functional neuroimaging literature", *Journal of Cognitive Neuroscience* 22: 1083–1094.
- Wager, Tor D., Luis Hernandes, John Jonides and Martin Lindquist. 2007. "Elements of Functional Neuroimaging", in: John T. Cacioppo, Louis G. Tassinary and Gary G. Berntson (eds.). *Handbook of Psychophysiology, Third Edition*.
- Wang, Yue., Joan A. Sereno, Allard Jongman and Joy Hirsch. 2003. "fMRI evidence for cortical modification during learning of mandarin lexical tone". *Journal of Cognitive Neuroscience* 15: 1019-1027.
- Wang, Jinhui, Xinian Zuo and Yong He. 2010. "Graph-based network analysis of resting-state functional MRI", *Frontiers in System Neuroscience* 4:16.
- Warrier, Catherine, Patrick Wong, Virginia Penhune, Robert Zatorre, Todd Parrish, Daniel Abrams and Nina Kraus. 2009. "Relating structure to function: Heschl's Gyrus and acoustic processing", *Journal of Neuroscience* 29:61-69.
- Weintraub, Sandra, M.M Mesulam, and L. Kramer. 1981. "Disturbances in prosody: a right-hemisphere contribution to language", Archives of Neurology 38: 742–744.

- Wise, Richard S., Sophie K. Scott, Catrin S. Blank, Cath J. Mummery, Kevin Murphy, and Elizabeth A. Warburton. 2001. "Separate neural subsystems within 'Wernicke's area'", *Brain* 124: 83-95.
- Wise, Richard, Francois Chollet, Uri Hadar, Karl Friston, Elaine Hoffner and Richard Frackowiak. 1991. "Distribution of cortical neural networks involved in word comprehension and word retrieval", *Brain* 114:1803–1817.
- Wennekers, Thoma., Max Garagnani and Friedemann Pulvermüller. 2006. "Language models based on Hebbian cell assemblies", *Journal of Physiology Paris* 100:16–30.
- Werker, Janet F. and Chris E. Lalonde. 1988. "Cross-language speech perception: Initial capabilities and developmental change", *Developmental Psychology* 24:672-683.
- Westermann, Gert and Eduardo R. Miranda. 2004. "A new model of sensorimotor coupling in the development of speech", *Brain and Language* 89: 393–400.
- Xiao, Zhunagwei, John X. Zhang, Xiaoyi Wang, Renhua Wu, Xiaoping Hu, Xuchu Weng and Li Hai Tan. "Differential activity in left inferior frontal gyrus for pseudowords and real words: An event-related fMRI study on auditory lexical decision", *Human Brain Mapping*, 25: 212–221.
- Yang, Jing, Kathleen M. Gates, Peter Molenaar and Ping Li. 2015. "Neural change underlying successful second language word learning: An fMRI study", Journal of Neurolinguistics 33: 29-49.
- Zakrzewska, Marta and Aneta Brzezicka. 2014. "Working memory capacity as a moderator of load-related frontal midline theta variability in Sternberg task", *Frontiers in Human Neuroscience* 8: 399.
- Zaehle, Tino, Torsten Wustenberg, Martin Meyer, and Lutz Jancke. 2004. "Evidence for rapid auditory perception as the foundation of speech processing: a sparse temporal sampling fMRI study", European Journal of Neuroscience 20: 2447– 2456.
- Zafar, Shahila and K. Meenakshi. 2012. "Individual Learner Differences and Second Language Acquisition: A Review", Journal of Language Teaching and Research 3: 639-646.
- Zatorre, Robert J., Alan Evans, Ernst Meyer and Albert Gjedde. 1992. "Lateralization of phonetic and pitch discrimination in speech processing", *Science 256: 846–849*.

- Zatorre, Robert J., Pascal Belin and Virginia B. Penhune. 2002. "Structure and function of auditory cortex: music and speech", *Trends in Cognitive Science* 6: 37–46.
- Zarahn, Eric, Brian Rakitin, Diane Abela, Joseph Flynn and Yaakov Stern. 2005. "Positive evidence against human hippocampal involvement in working memory maintenance of familiar stimuli", *Cerebral Cortex*, 15:303-16.
- Zhang, Hui, Paul A. Yushkevich, Daniel C. Alexander and James C. Gee. 2006. "Deformable registration of diffusion tensor MR images with explicit orientation optimization", *Medical Image Analysis* 10: 764-785.
- Zhang, Hui, Paul A. Yushkevich, Daniel Rueckert, James C. Gee. 2007. "Unbiased white matter atlas construction using diffusion tensor images", *Lecture Notes in Computer Science*, 4792/2007: 211-218.
- Zuo, Xi.-Nian, Clare Kelly, Adriana Di Martino, Maarten Mennes, Daniel S. Margulies, Saroja Bangaru, Rrebecca Grzadzinski, Alan C. Evans, Yu-Feng Zang, F. Xavier Castellanos, and Michael P. Milham. 2010. "Growing together and growing apart: regional and sex differences in the lifespan developmental trajectories of functional homotopy", *The Journal of Neuroscience* 30: 15034–15043.