

Bilingual language processing: A meta-analysis of functional neuroimaging studies

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Abstract

Notwithstanding rising interest, a coherent picture of the brain's representation of two languages has not yet been achieved. In the present meta-analysis we analysed a large number of functional neuroimaging studies focusing on language processing in bilinguals. We used activation likelihood estimation (ALE) to enucleate activation areas involved in bilingual processing and control of different types of linguistic knowledge – lexico-semantics, grammar, phonology – in L1 and L2. Results show that surprisingly, compared to L2, lexico-semantic processing in L1 involves a widespread system of cortico-subcortical regions, especially when L2 is acquired later in life. By contrast, L2 processing recruits regions exceeding the L1 semantic network and relating to executive control processes. Only few regions displayed selective activation for grammar and phonology. Analyses of language switching highlight a functional overlap between domain-general and bilingual language control networks. Collectively, our findings point to a shared neural network for L1 and L2 with few differences depending on the linguistic level. The emerging picture identifies under-investigated issues, offering clear directions for future research.

Keywords: Bilingualism; GingerALE; Language; Meta-analysis; fMRI; PET;

Language is generally considered to be the biological trait that makes us distinctly human. Even more remarkable is the unique ability to acquire, store and use more than one language efficiently, known as “bilingualism”. Rather than an all-or-none-phenomenon, bilingualism is a multifaceted construct sensitive to a number of distinct but interacting variables, including the age at which a second language is acquired (AoA), the level of attained second language knowledge (proficiency), and the amount of second language input (exposure) (De Bruin, 2019; Luk & Bialystok, 2013; Perani et al., 1998). In the present study, “bilingualism” indicates the regular use of two languages, “multilingualism” the regular use of multiple (i.e., more than two) languages, and “second language (L2)” any language other than the native (L1). In the last two decades, the advent of functional neuroimaging technologies and their application to brain-cognition relationships has remarkably advanced the understanding of language representation and processing in the living, intact brain. Substantial progress in the cognitive neuroscience of language has recently come from meta-analyses, an increasingly popular tool for synthesizing primary data across multiple studies in order to test hypotheses on large datasets and draw clear and unidirectional inferences (Fox et al., 1998). By accounting for inter-study variability, meta-analyses of neuroimaging data allow one to identify regions consistently activated across studies and thus to produce more generalizable results (Kober & Wager, 2010; Müller et al., 2018). The application of meta-analytic approaches to the functional neuroanatomy of language has allowed to reach important milestones such as the understanding of the distributed nature of the cortical network for semantic processing (e.g., Binder et al., 2009; Visser, Jefferies, & Lambon Ralph, 2012) as well as the more localized fronto-temporal network for phonological processing (e.g., Vigneau et al., 2006; see also Hickok & Poeppel, 2007).

When turning to bilingualism, however, a coherent picture of the brain’s capacity to acquire, store and use more than one language efficiently is currently lacking, notwithstanding the growing attention to the functional basis of bilingual language processing in recent years. To provide some

figures, a rough search through PubMed conducted on May, 29, 2018 with “bilingualism AND “neuroimaging” OR “fMRI OR PET OR NIRS” as keywords showed that the number of articles published on this topic has constantly increased, reaching in the last 4 years >40 articles per year (*i.e.*, ~1 paper per week). Despite this rising and continued interest, the available evidence is patchy and largely inconsistent. This is also because, compared to the study of monolingualism, the study of bilingualism needs to take into account additional cognitive factors such as the ability to control and switch between languages (Calabria et al., 2018) and variable socio-linguistic aspects of bilingual experience inherent to the studied populations, such as the age at which a second language (L2) is acquired (AoA), the amount and quality of first (L1) and second language (L2) input (exposure), and the level of attained L2 knowledge (proficiency). It is well known that these factors impact brain structure and function, even if their individual and cumulative effects are still debated and possibly confounded by other qualitative differences in bilingual experience (Abutalebi & Green, 2007; Perani & Abutalebi, 2005; Li & Grant, 2017; Berken et al., 2017; Liu & Cao, 2016; Perani et al., 2003). The neurocognitive organization of bilingual language processing is also widely affected by language-specific characteristics. Indeed, broad inferences about the neural correlates of different languages are often drawn on the basis of single experiments investigating only one linguistic component – *i.e.*, semantics, grammar or phonology. However, the degree of inter-linguistic similarity might be, in part, a by-product of the level under investigation; in other words, two languages may be more or less similar depending on the linguistic level one focuses on: For instance, while for an English-Italian speaker the difference in the phonological inventory of the two languages is much larger than that in the semantic system, the opposite might be true for a Japanese-Italian speaker, who would use the two languages hinging upon a largely overlapping phonemic repertoire (Kavanagh, 2007; Kramer, 2009), but in very different socio-cultural contexts. The situation is further complicated by both the heterogeneity of languages spoken by participants across studies and the extreme variability in the task adopted to

investigate the same linguistic level. Phonological processing, for example, has been investigated with consonant-vowel identification (*e.g.*, Berken et al., 2015), rhyming judgment (*e.g.*, Cao et al., 2013), phonology *n*-back task (Koyama et al., 2013), and so on.

To systematize the available neuroimaging evidence on the cerebral organization of the representation/processing of multiple language combinations in the brain, we performed a meta-analytic study of bilingual language processing with the aim to identify how the bilingual brain processes the different types of linguistic knowledge in L1 and L2. We performed the first comprehensive meta-analysis on neuroimaging data by comparing the neural correlates of different linguistic levels for L1 and L2 in bilingual speakers. In particular, we analyzed: (a) Lexico-semantics – *i.e.*, the ability to associate meaning to linguistic structures; (b) grammar – *i.e.*, the ability to recognize and produce the distinctive grammatical structures of a language; (c) phonology – *i.e.*, the ability to recognize and produce the distinctive sound patterns of a language. Since our aim was to identify the neural correlates of linguistic knowledge, production and comprehension studies were included in the same analyses (*e.g.*, Opitz et al., 2003; Pickering & Garrod, 2007; Segaert et al., 2012), as well as the different tasks investigating the three linguistic levels (for all studies, the performed tasks, participants demographic data, included contrasts and number of foci are reported in detail in Table 1). This allowed us to identify the cortical regions that are selectively associated with the representation of linguistic knowledge in L1 and L2, and to partial out idiosyncratic activation related to the (production or comprehension) system used to access it.

By testing findings from positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) investigations, we aim at answering multiple research questions: How does the bilingual brain process lexico-semantic, grammar, and phonological knowledge in L1 and L2? To what extent do similarities and differences in the processing of L1 and L2 depend on the linguistic level considered? Is linguistic knowledge in L1 and in L2 processed by means of the same neural substrates?

To answer such questions, we ran a series of meta-analyses on lexico-semantics, grammar and phonology separately, in order to both highlight L1-L2 similarities and differences for each level and disclose potential commonalities across levels. Bilinguals' proficiency and AoA, key factors related to individual linguistic history, were also considered. Another variable which is increasingly recognized as a neurally discriminating factor is language exposure or frequency of L1/L2 usage. Growing evidence suggests that increased amounts of grey matter as well as more efficient structural and metabolic connectivity are associated with continuous bilingual practice and extensive immersion in bilingual environments (e.g. Abutalebi et al., 2015; Perani et al., 2017; Pliatsikas et al., 2017). However, as language exposure is still scantily investigated or its characterization largely flawed in current research, this factor was not included in the present meta-analysis.

Bilingual competence raises a further issue, *i.e.*, how bilinguals handle different languages while avoiding cross-linguistic interference. A bilingual speaker needs to switch between and control for different languages in order to select and produce the intended linguistic items and structures. It has been proposed that bilinguals successfully resolve cross-language competition and achieve language selection by actively inhibiting their dominant language (L1) (Green, 1998). This inhibitory control mechanism, which allows bilinguals to be fluent in their weaker language (L2), is orchestrated by a networked system related to domain-general executive functions (Abutalebi & Green, 2007; Abutalebi & Green, 2016) and assumed to be engaged differentially depending on how well and how often an L2 is used. Hence, although not strictly linguistic, regions and circuits of the language control network are integral to bilingual language processing. For this reason, studies employing language control tasks were included in the present meta-analysis.

We adopted a widely used meta-analytic technique for imaging data – activation likelihood estimation (ALE) – to enucleate the activation areas involved in bilingual processing and control of different types of linguistic knowledge – lexico-semantics, grammar, phonology – in L1 and L2. ALE

methods combine the results of multiple neuroimaging studies with published coordinates and estimate the probability of spatial convergence of the reported peaks of activations (Turkeltaub et al., 2002).

Materials and methods

Data collection and preparation

The current meta-analysis is based on the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) Statement guidelines (<http://www.prisma-statement.org/>; Liberati et al., 2009; Moher et al., 2009). The aim of PRISMA is to improve the quality and reliability of systematic reviews and meta-analyses by providing a set of common rules and recommendations for authors. PRISMA guidelines suggest to follow a 27-item checklist and report a flow diagram of the literature search and paper inclusion (Fig. 1). We performed a set of specific coordinate-based meta-analyses of functional neuroimaging studies investigating language processing in bilingual individuals. Articles were selected through an on-line literature search in the following databases: Scopus, Pubmed, Web of Science. To be as inclusive as possible, the following input search keywords were employed: “(Bilingual or bilingualism) and (neuroimaging or brain imaging or fMRI or PET)”. Only studies written in English and published from January 1990 to March 2017 were included. This preliminary search returned a total of 1448 results. Three additional studies were identified through other resources (*i.e.*, Hanulová et al., 2011; Tanner et al., 2014; Bartolotti et al., 2017) yielding a total of 1451 results. Duplicates were removed from this initial set leading to a total of 739 results. Based on title and abstract, a first screening was independently conducted by two authors based on the following inclusion criteria: (1) fMRI or PET studies; (2) Healthy bilingual adults (18–50 years). Only peer-reviewed published journal articles were included. Unagreed cases were discussed and eventually resolved by the two authors who performed the screening, leading to a total of 189 eligible articles. These articles were then read in full to verify whether they could be included in the final sample. During this second screening stage, a further inclusion criterion was added: (3) Reported activation for L2>L1 or L1>L2 and/or

forward/backward language switching > baseline contrasts¹. No restriction was set on the specific languages spoken by each bilingual sample. Studies on healthy multilingual adults were also included, but the extracted coordinates were restricted to activation foci involving only L1 and L2 effects. At this screening stage, further exclusion criteria were applied to identify only those studies reporting spatial coordinates of the specific patterns of activation for L1 and L2 processing and language switching. Excluded were: (1) Review or meta-analysis studies; (2) Studies with absence of coordinates reported from whole brain activation in Talairach (Talairach & Tournoux, 1988) or Montreal Neurological Institute (MNI; Collins et al., 1998) stereotaxic space (*i.e.*, Regions-Of-Interest-based studies or small-volume corrections applied to the analysis); (3) Studies of brain connectivity, *i.e.* resting-state fMRI and multi-voxel pattern analysis; (4) Results coming from tasks investigating cognitive processes other than linguistic (e.g. working memory).

The final sample included 52 articles (see Fig. 1). We assume that these studies were approved by their respective ethics committees prior to data collection.

– Fig. 1 –

Data classification

Reported coordinates were extracted and divided into four main sets based on the linguistic levels investigated in each study: (1) Lexico-Semantics; (2) Grammar; (3) Phonology; (4) Language Switching (for a detailed list of the tasks included in each level, see Table 1). In some cases, experimental manipulations and tested contrasts belonged to more than one linguistic level. In such cases, the study's coordinates were included in multiple sets. Because AoA and proficiency are known to affect the neural signatures of L1 and L2 processing, for each set of coordinates, peaks of activation were sorted into additional subsets according to the age of acquisition (early vs. late) and proficiency

(high vs. low) of L2. For Grammar and Phonology, AoA group contrasts did not include a sufficient number of peaks, thus violating power guidelines (Müller et al., 2018). Accordingly, the contrasts belonging to these levels were collapsed over AoA. A small group of coordinates (from 6 studies) was removed due to lack of information or ambiguous statements on AoA and proficiency. Whereas six years was used as the age threshold to discriminate between early and late bilinguals (see DeKeyser, 2000; Granena & Long, 2013; Johnson & Newport, 1989), a single measure of L2 proficiency could not be consistently identified across the studies examined. Therefore, the distinction between high and low proficient bilinguals was made on the basis of the participants' description reported in each study and the original authors' classification. As very few studies (12) used participants described as low proficient, with the consequence that there were not enough peaks to run the analyses, only studies with highly proficient bilinguals were included in the meta-analysis (overall $n = 52$). The contribution of relative language exposure to the neural representation of first and second language could not be assessed, since only 16 of the 52 articles included in the meta-analysis (*i.e.*, ~31 %) reported measures of language exposure or use.

Lexico-Semantics (both collapsed over AoA and split into early vs. late AoA), Grammar (collapsed over AoA) and Phonology (collapsed over AoA) sets were further split into two separate subsets each, based on coordinates from $L1 > L2$ and $L2 > L1$ contrasts. In order to identify general switching mechanisms, Language Switching coordinates (both collapsed over AoA and split into early vs. late AoA) were not divided according to the language switching direction.

Overall, a total of 13 subsets was obtained: (1) Lexico-Semantics (A, B); (2) Grammar (C,D); (3) Phonology (E,F); (4) Language Switching (G) (Table 1a); (5) Lexico-semantics split into early vs. late AoA (H, I, J, K); (6) Language Switching split into early vs. late AoA (L, M) (Table 1b). We reported results from these subsets in light of their explorative contribution to the investigation of functional brain activity in bilinguals for different levels of language processing.

Data analysis

We performed analyses for each subset of coordinates through the GingerALE 2.3.6. software (BrainMap.org) using the Activation-Likelihood Estimation (ALE) method and the Non-Additive correction to minimize within-experiment effects as described in Turkeltaub et al. (2012) (see Eickhoff et al., 2009; Eickhoff et al., 2012., Turkeltaub et al., 2012). GingerALE takes peaks of activation coordinates from neuroimaging studies, applies an inclusive brain mask and a subject-size-based Full-Width-Half-Maximum (FWHM), estimates the probability of the coordinates' spatial distribution, and then computes the convergence of these probabilities. Coordinates reported in Talairach space were first converted to MNI space with the GingerALE conversion tool. The number of participants was then specified for each selected contrast, this parameter being required for estimating the FWHM of the gaussian function used during ALE maps estimation (Eickhoff et al., 2009). For each subset, the analyses were performed thresholding ALE maps at uncorrected $p < 0.001$ and setting a minimum cluster size of 150 mm^3 (the same cluster extent threshold has been adopted by several other ALE meta-analyses, e.g. Liu & Cao 2016; Wu et al., 2012; DeWitt & Rauschecker, 2012).

Results

Lexico-semantic level

The L1>L2 contrast collapsed over AoA resulted in a large number of significant clusters of functional activation (Table 2a, Figure 2a). Cortical regions included the bilateral inferior frontal gyrus (BA 44, 45, 47), the left medial frontal gyrus (BA 8), the left middle temporal (BA 21) and parahippocampal gyri (BA 28), the left precuneus (BA 7), the bilateral superior and left inferior parietal lobules (BA 7,

3), the right angular gyrus (BA 39), the right fusiform gyrus (BA 37), the left posterior cingulate (BA 23), the left superior occipital gyrus (BA 19). Subcortical regions included the left thalamus, the left amygdala and the right caudate head. The left anterior lobe of the cerebellum was involved as well.

The L2>L1 contrast was also associated with a widespread network of regions (Table 2a, Figure 2a) including the left inferior frontal gyrus (BA 45, 47), the left superior frontal gyrus (BA 8), the bilateral precentral gyri (BA 4, 6), the bilateral insular cortices, the globus pallidus bilaterally, and the right anterior cerebellar vermis.

As shown in Table 2b and Figure 2b, the L1>L2 contrast for early bilinguals revealed a significant activation in clusters localized in a large number of frontotemporal and parietal regions, including the bilateral inferior frontal gyrus (BA 44, 45, 47), the left medial frontal gyrus (BA 8), the left middle temporal (BA 21) and parahippocampal gyri (BA 28), the left precuneus (BA 7), the parietal lobule (BA 3, 7), the right angular gyrus (BA 39) and the fusiform gyrus bilaterally (BA 37), the left posterior cingulate (BA 23), and the left thalamus subcortically. In late bilinguals, the same contrast showed only few significant clusters localized in the pars orbitalis of the bilateral inferior frontal gyrus and in the right caudate.

When the L2>L1 contrast was considered only for early bilinguals (see Table 2b, Figure 2c), the left inferior frontal gyrus (BA 45), the left insula, and the right middle occipital gyrus (BA 19) emerged as significant. In late bilinguals, significant clusters for the same contrast were observed in the left precentral gyrus (BA 6), the left superior (BA 8) and inferior frontal gyri (BA 45, 47), the bilateral globus pallidus, the insula bilaterally, and in the right anterior cerebellar vermis.

– Fig. 2 (a, b) –

Grammar level

As reported in Table 2a and Figure 3, the L1>L2 contrast revealed significant activation in clusters of the left inferior frontal gyrus (BA 44, 47), the right supplementary motor area (BA 6), the left precentral gyrus (BA 6), the right middle temporal gyrus (BA 21), the insula bilaterally, and the left inferior parietal lobule (BA 7) and the right body of the caudate nucleus.

The L2>L1 contrast (Figure 3), on the other hand, revealed significant clusters only in the left inferior frontal gyrus (BA 44), left middle occipital gyrus, left globus pallidus and right putamen (in both cases extended to the body of the caudate nucleus), and in the left posterior lobe of the cerebellum.

– Fig. 3 –

Phonological level

The L1>L2 contrast revealed significant activation in clusters of the left inferior frontal gyrus (BA 47) and bilateral middle temporal gyrus (BA 21, 22) (Table 2a, Figure 4).

For the opposite contrast (L2>L1) significant activation was observed in the left inferior frontal gyrus (BA 44), right middle frontal gyrus (BA 9), left superior frontal gyrus (BA 8), left precentral gyrus (BA 6), left superior parietal lobule (BA 7), and the right anterior cerebellar vermis (Table 2a, Figure 4).

– Fig. 4 –

Language control (switching)

Significant activation patterns related to language switching collapsed over AoA were detected in a large number of cortical and subcortical areas, including: the bilateral inferior frontal gyrus (extending to the precentral gyrus) (BA 44), the right superior frontal gyrus (BA 8), the right supplementary motor area (6), the left postcentral gyrus (4), the left anterior cingulate cortex (BA 24), the left insula, the left

caudate head, the right superior temporal gyrus (BA 22), the left lingual gyrus (extending to the middle occipital gyrus) (BA 18) and fusiform gyrus (BA 19), the left inferior parietal lobule (BA 40), the bilateral precuneus (BA 7), the right cuneus (BA 18), and the right superior and inferior occipital gyri (BA 17, 19) (see Table 2a, Figure 5a).

When considering only early bilinguals, language switching was associated with activation of the right superior frontal gyrus (extending bilaterally to the left superior frontal gyrus) (BA 6), the bilateral inferior frontal gyrus (BA 44), the bilateral middle frontal gyrus (BA 9), the left precentral gyrus (BA 6), the right superior temporal gyrus (BA 22), occipital regions such as the bilateral middle occipital gyrus (BA 18, 19), and the right cuneus (BA 18), as well as the left caudate head and the left posterior cerebellar lobe (see Table 2a and Figure 5b).

A widespread network of regions was activated in late bilinguals as well. Whereas some areas did not differ from those significantly recruited by early bilinguals, the left anterior cingulate gyrus (BA 24), the bilateral precuneus (BA 7), the left angular gyrus (BA 39), the left inferior parietal lobule (BA 40), the right insula and the right fusiform gyrus (BA 19), were significant in late bilinguals only (Figure 5b). Among the regions shared between early and late bilinguals, we found cerebellar and occipital areas, but also the fusiform gyrus, the precentral gyrus, and the inferior frontal gyrus.

In order to verify that the reported results are specifically related to the language control network and not driven by the task heterogeneity occurring in the selected studies, we ran a further analysis on a subset of studies homogeneous for the task adopted. We focused on picture naming – being the most frequently employed task among studies on language control. The results were fully consistent with those previously described for language switching, with overlapping brain regions in the two analyses (see Table 1c and Table 2c), thus indicating that our findings properly highlight the brain network underlying language control.

– Fig. 5 (a, b) –

Discussion

The present meta-analytic study aimed at examining the neural correlates of first and second language processing in the bilingual brain. A conception of language as a multi-componential construct integrating separable interacting systems – *i.e.*, (lexico)-semantics, grammar and phonology – allowed us to identify: a) The specific brain structures underpinning each linguistic level in the L1 and/or L2 network; b) the neural substrates of the language control network, an essential component of the neurocognitive bilingual architecture.

In what follows, we first focus on findings concerning the representation of L1 and L2, and then discuss the neural signatures of language control. We conclude by answering the main questions that inspired this work: What are the neural correlates of L1 and L2 processing in the bilingual brain for the different levels under investigation? To what extent do similarities and differences in L1/L2 processing depend on such levels? Instead of focusing on shared neural activation patterns, we will separately discuss the activations that selectively characterize each linguistic level.

Lexico-semantic level

The results of the meta-analyses for the L1>L2 activations collapsed over AoA highlight a widespread system of cortico-subcortical regions selectively recruited when lexico-semantic tasks are employed. At the cortical level, significant clusters of activation have been detected in: i) The left lateral and ventral temporal lobe; ii) bilateral portions of the parietal cortex; iii) bilateral frontal regions such as the inferior frontal gyrus, and iv) the left posterior cingulate. At the subcortical level, lexico-semantic processing was associated with the activation of the right caudate, the left thalamus, and the left amygdala. The emergence of a large set of areas for lexico-semantic processing is in line with the recent view that the representation and control of semantic knowledge in healthy adults is supported by a widely distributed neural network (Binder et al., 2009; Jefferies, 2013; Lambon Ralph, 2014).

Temporal structures are core regions for the convergence and association of information and play a key role in storing semantic knowledge. Neuroimaging evidence in healthy individuals suggests that the temporal pole underpins multimodal semantic processing (Visser et al., 2012). Lesions to the middle temporal gyrus have been shown to produce semantic deficits (e.g., Hillis & Caramazza, 1991; Dronkers et al., 2004), and atrophy of the fusiform gyrus in dementia patients has been associated with both verbal and nonverbal semantic impairments (Ding et al., 2016; see also Binder et al., 2009). The fusiform gyrus is adjacent to multiple modality-specific regions such as the emotional (limbic) system (Rice et al., 2015), as well as to memory-relevant temporal structures like the hippocampal formation and the parahippocampal cortex. The fusiform gyrus is thus thought to be responsible for amodal object representations. The parietal lobe is a higher-order association region consistently linked with semantic processing (e.g., Coslett & Schwartz, 2018; Fernandino et al., 2016). In particular, a critical role of inferior parietal structures for lexico-semantic knowledge emerges from studies investigating vocabulary acquisition and size, both in monolinguals (e.g., Lee et al., 2007; Richardson et al., 2010) and bilinguals (e.g. Mechelli et al., 2004; see also Abutalebi et al., 2015). Moreover, Grogan et al. (2012) showed that bilinguals speaking two (or more) foreign languages have increased grey matter density in the right posterior supramarginal gyrus relative to those speaking a single foreign language. The authors interpreted the alterations in grey matter as a result of the cumulative vocabulary size of multilingual individuals. With respect to the reported engagement of frontal regions, neuroimaging evidence has consistently shown a significant association between the activation of the bilateral inferior frontal gyrus and the processing of semantic information in a variety of tasks (e.g., Demb et al., 1995; Poldrack et al., 1999; Price, 2010). The left inferior frontal gyrus (especially Broca's area) has been suggested to support semantic decisions and semantic choices among alternatives; in particular, this region would be involved in amodal semantic processing by selecting semantic knowledge when competing alternatives are available, or by facilitating semantic integration in the absence of selection

demands (Thompson-Schill, 2003; see also Thompson-Schill, 2005 for a more domain-general role of this area). Right inferior frontal activation has been reported, for instance, by Schmidt and Seger (2009), who investigated the neural processing of linguistic materials varying for familiarity and figurative meaning, and documented in Peelle et al. (2009), whereby participants had to evaluate whether lists of features correctly described target objects. Moreover, a multimodal imaging study by Hosoda and colleagues (2013) found that individual differences in L2 vocabulary size correlated with grey matter volume in the right inferior frontal gyrus, as well as with the structural connections of that region with other components of the executive control network, thus underlying a tight relationship between language control and L2 vocabulary learning. According to the inhibitory control (IC) model (see Abutalebi & Green, 2016; Calabria et al., 2018), the right inferior frontal cortex would be responsible for inhibiting responses from the stronger language (*i.e.*, typically L1) (see Branzi et al., 2015; Videsott et al., 2010). Although less obvious for language processing, the engagement of the posterior cingulate cortex during semantic tasks is documented in the literature. In a semantic priming experiment with a lexical decision task, O'Hare et al. (2008) reported that the activation of the posterior cingulate cortex was modulated by semantic priming, concluding that this region works as a mediator between the stimulus category and the response program. More recently, Krieger-Redwood et al. (2016) have investigated the functional coupling between posterior cingulate cortex and the dorsolateral prefrontal cortex during semantic decisions of varying difficulty, suggesting that the co-activation of these regions may underlie the ability to perform semantic judgements.

The L1>L2 contrast also reveals significant activations in the right caudate, the left thalamus and the amygdala as subcortical structures. The role of the caudate nucleus in semantic processing has been documented both in healthy and clinical populations (Canini et al., 2016; Cousins, Ash, Irwin, & Grossman, 2017) and is likely related to semantic control processes. Thalamic lesions have been associated with lexico-semantic impairments as well, with a possible functional disconnection between

lexical units and the conceptual system (Pergola et al., 2013; Raymer et al., 1997). The amygdala, on the other hand, is well known to be primarily engaged in emotion processing (e.g. Phelps & LeDoux, 2005). In the present case, a higher involvement of this structure in L1 than L2 may be due to the stronger link between cognition and emotion which speakers usually have in their native language, with special reference to the reported stronger connection between emotional experience and semantic system (e.g., Hayakawa, Costa, Foucart, & Keysar, 2016; Hsu, Jacobs, & Conrad, 2015; see also, Sulpizio, Toti, Del Maschio, Costa, Fedeli, Job, & Abutalebi, 2019). Interestingly, a higher activation of the amygdala for L1 vs. L2 has been also reported in the absence of any emotion manipulation by Hernandez (2009), who asked Spanish-English bilinguals to name pictures of common objects of low emotional significance: The author argues that the effect could be ascribed to a higher emotionality of the native language.

As a counterweight to the widespread pattern of activation for the L1>L2 contrast, the results of the L2>L1 contrast collapsed over AoA showed very few regions specifically engaged in lexico-semantic processing: The bilateral globus pallidus, the right insula, and the right cerebellum. These latter regions are not part of the semantic network usually reported for monolinguals (e.g., Binder et al., 2009; Price, 2010), and their recruitment is arguably to be attributed to control-related functions. The globus pallidus is part of the basal ganglia, which play a key role in modulating executive control processes (e.g., Graybiel, 2000) and have found to be expanded in bilinguals compared to monolinguals (Burgaleta et al., 2016; Pliatsikas et al., 2017). Liu et al. (2010) reported increased bilateral activation of the globus pallidus in bilinguals for naming pictures in L2 vs. L1, suggesting that this subcortical structure is related to the monitoring of different stages of speech production, from language selection to auditory-motor feedback during articulation. In particular, a role of the globus pallidus has been proposed in lexical selection processes, in associating lexical information with contextual data, and in controlling lexical access in two (or more) languages (Wallesch & Papagno, 1988; Wallesch, 1990). An

alternative account proposes that, during speech production, the globus pallidus subserves semantic monitoring (Crosson, 1985). The importance of the globus pallidus in verbal fluency is corroborated by clinical evidence which reveals severe fluency deficits in pallidotomy patients (e.g., Whelan et al., 2004). The right insula too has been sporadically associated with L1 or L2 semantic processing. An interesting finding comes from a study by Sass and colleagues (2009), who conducted a semantic priming experiment in which the prime-target semantic distance was manipulated and the activation of the right insula was reported for semantically-related distant pairs but not for close pairs (e.g., anvil-nail vs. picture-frame). The authors suggested that the right insula supports semantic processing by contributing to identify semantic alternatives; this being the case, rather than being specific of word meaning extraction, its activation would reflect task-dependent attentional demands (see also Sabb et al., 2007). This interpretation might also hold for bilingual language processing, since semantic access and lexical selection among semantic alternatives in L2 might require additional cognitive effort. Finally, it is interesting to remark that, as for the L1>L2 contrast, a significant activation of the left (pre-)frontal region emerged for the L2>L1 contrast. Although this finding might seem puzzling, it is noteworthy that the activations emerging from the two contrasts involve different anatomical regions – BA 44 in the L1>L2 analysis and BA 46 in the L2>L1 analysis –, which are usually associated with different functional responses. Anatomically, whereas BA 44 corresponds approximately to the opercular part of the inferior frontal gyrus, BA 46 occupies the most rostral portion of the inferior frontal gyrus and the middle third of the middle frontal gyrus. The left BA 46 is known to be involved in language control functions such as verbal working memory (e.g. Gabrieli, Poldrack, & Desmond, 1998; Petrides, 2005). In bilinguals, increased neural activity in this area has been reported for early-exposed bilinguals vs. monolingual controls during a semantic judgment task (Kovelman, Shalinsky, Berens, & Petitto, 2008). The authors interpreted activation differences in this area as resulting from increased attentional and verbal working memory demands for dual language processing and cross-

linguistic integration of semantic information.

On the whole, our results for lexico-semantic processing in L1 show a widespread pattern of activation that nicely fits with the semantic network highlighted by meta-analytic studies on monolingual language processing (e.g. Binder et al., 2009). When further inspecting results by separately looking at early and late bilinguals, late learners seem to use additional semantic control structures like the caudate. On the other hand, results for lexico-semantic processing in L2 reveal the activation of regions which exceed the classical semantic network, and may support the processing of semantic information by means of top-down processes such as selective attention and monitoring.

It is important to note that, when separately looking at early and late bilinguals, the subcortical activity associated with L2 processing has been detected especially in late bilinguals. Although the AoA group contrasts for the lexico-semantic level should be interpreted with caution, our findings suggest that the age of L2 onset may specifically contribute to brain function irrespective of the high proficiency level attained (see Berken et al., 2017; Liu & Cao, 2016), individual variability in language learning aptitude and development of lexico-semantic functions being granted (see Grant & Li, 2015). The findings of a larger set of activated regions in L1 than L2, on the other hand, are rather unexpected, since previous evidence and reviews have usually reported larger networks for L2 than L1 (e.g. Abutalebi & Green, 2007). On the basis of the present results, one possibility might simply be that word processing in an individual's native language is mediated by the access to a more sophisticated and richer lexico-semantic system, supported by a larger neural network. However, if this were the case, one would have expected the results not to be affected by L2 AoA. Since instead an extensive activation for L1 is mainly associated with simultaneous bilingualism or early experience with L2, an alternative explanation is needed. Specifically, the extensive L1-related activation might have two complementary reasons, grounded on the speakers' bilingual experience. First, the conceptual system might be shared across bilinguals' languages, and, when processing a linguistic stimulus, an early

proficient bilingual would access the whole set of semantic features associated with that stimulus in the two languages (e.g., Kroll et al., 2010). Hence, by incorporating knowledge from two languages and cultures, the semantic system of a bilingual individual with extensive and long-lasting experience with two languages may be richer than that of a monolingual. Second, in lifelong proficient bilinguals, each language possibly maintains full activation without interfering with the others because the extensive acquaintance with the two systems would allow the bilingual brain to organize the L1 and L2 knowledge in separate lexical spaces (Hernandez et al., 2005). This would reduce the level of lexical competition between languages, yielding a more efficient lexico-semantic mapping.

Grammar level

Unlike the lexico-semantic domain, grammatical competence in bilinguals has been investigated more sporadically with functional neuroimaging methods, and thus our results come from a rather meager number of experiments (overall n of studies analyzed = 8). Although caution is recommended, we believe these results deserve some further discussion.

When we examined the L1>L2 contrast collapsed over AoA, the following regions displayed selective activation for grammar processing: The left inferior frontal gyrus (pars orbitalis and opercularis), the left precentral gyrus, the left inferior parietal gyrus, the insula, the right supplementary motor area, the middle temporal gyrus, and the right caudate. The specific pattern of activations for grammar processing for the L2>L1 contrast, on the other hand, is confined to the pars opercularis of the left inferior frontal gyrus, the bilateral putamen, the left caudate, and the posterior portion of the cerebellum bilaterally. Overall, these patterns of activation show that procedural-related circuits – i.e., frontal/basal-ganglia networks – mediate grammar processing in both L1 and L2. No involvement of medial temporal structures typically associated with declarative systems is found for L2 processing. It thus seems that grammatical processing in both languages occurs by means of similar neural mechanisms, at least in high proficient bilinguals. Although not specifically recruited for grammatical

information processing, the activation of the left inferior frontal gyrus is consistent with substantial neuroimaging evidence indicating this region as the main locus of morphological and syntactic parsing in both mono- and bilinguals (Bick et al., 2011; Bozic & Marslen-Wilson, 2010; Lehtonen et al., 2009; Moro et al., 2001). The clusters of activation in the precentral gyrus include the premotor cortex and the supplementary motor area, regions involved in multiple cognitive domains besides motor control and action coordination. In the neurolinguistic literature, the involvement of the supplementary motor area is usually reported when participants are required to organize and coordinate sequences of linguistic elements in higher order integrated structures (e.g., Alario et al., 2006; Meltzer et al., 2009; Segaert et al., 2012). In a recent proposal, Cona and Semenza (2017) argued that the supplementary motor area is a domain-general hub for merging single elements into a sequence in which are codified temporal and ordinal attributes of individual constituents. This proposal nicely fits with a specific involvement of the supplementary motor cortex in grammar computations. For sequencing behavior another relevant region is the cerebellum, which together with the premotor cortex/supplementary motor area and the left inferior frontal gyrus forms a cortico-cerebellar network supposedly involved in bilingual speech planning and production (Abutalebi & Green, 2016). At the structural level, a study on inflectional competence by Pliatsikas and colleagues (2014a) reported increased cerebellar grey matter volumes for late but highly proficient bilinguals contrasted with a group of monolinguals. A positive association between grey matter density and behavioral performance on a masked priming task was found only for bilinguals, thereby emphasizing the importance of this structure for the establishment and use of an L2 grammar. There is also fMRI evidence from the same group of participants that the patterns of activation in late, high-proficient bilinguals and monolingual controls are statistically indistinguishable during the masked priming task, suggesting that putative differences associated with early language experience tend to disappear as L2 proficiency increases, even in the cerebellum (Pliatsikas, Johnstone, & Marinis, 2014b). Further, cerebellar damages have been associated with

grammatical impairment both in language production and comprehension (e.g., Justus, 2004; Schmahmann & Sherman, 1998). It is however still debated whether the cerebellum is directly involved in language processing, or if it works by interfacing the outcome of linguistic computation with that of other cognitive processes. Specifically, the cerebellum might contribute to the coupling of procedural operations (e.g., computation of syntactic rules) with long-term stored materials (e.g., lexical knowledge) (e.g., Marien et al., 2014; Silveri & Miscagna, 2000). It has also been recently proposed that this structure might be implicated in generating predictions on incoming signals (Sokolov et al., 2017), thus contributing, in language processing contexts, to anticipate the linguistic and extra-linguistic information.

Whereas the analysis of the L1>L2 contrast showed a significant involvement of the left insula, the opposite contrast revealed the specific contribution of the bilateral putamen. The left insula is functionally connected with different syntactically-related cortical areas, such as the left inferior frontal gyrus and the supplementary motor area (Ardila, Bernal, & Rosselli, 2014), and – although non systematically – it has been found to be involved in morphological and syntactic processing in monolinguals (e.g., Henderson et al., 2016; Schell et al., 2017; Tyler et al., 2004). For instance, in a study aimed at isolating the functional correlates of syntactic processing, Moro et al. (2001) identified the insula as one of the region selectively engaged in syntactic computation. Further evidence comes from clinical studies: Relating functional activity and grey matter integrity with linguistic performance in patients with left hemisphere damage, Tyler et al. (2011) showed that the patients' syntactic abilities were associated with neural activity and tissue integrity also in the left insula. Functional neuroimaging studies of healthy adults have suggested the implication of the putamen in a variety of grammar-related tasks, including violations of the expectancy of grammatical categories (Friederici, Ruschemeyer, Hahne, & Fiebach, 2003), syntactic ambiguity reading (Stowe, Paans, Wijers, & Zwarts, 2004), and artificial grammar learning (Forkstam, Hagoort, Fernandez, Ingvar, & Petersson, 2006; Lieberman,

Chang, Chiao, Bookheimer, & Knowlton, 2004). In bilinguals, putaminal activation has been detected for grammatical judgements in L2 (Wartenburger et al., 2003), but also sentence production (Dodel et al., 2005) and translation (Price, Green, & Von Studnitz, 1999). Significant reshaping (i.e., bilateral expansion) of the putamen in both simultaneous (Burgaleta et al., 2016) and highly immersed bilinguals (Pliatsikas et al., 2017) relative to monolinguals has also been reported. It is reasonable to hypothesize that the involvement of the putaminal structure for L2 vs. L1 processing under the morpho-syntactic domain is related to the use of a typically weaker L2 while suppressing interference from grammatical structures of the native language, especially in production contexts.

Phonological level

The activations of the L1>L2 contrast for phonology collapsed over AoA are mainly localized in the left inferior frontal gyrus and the right middle temporal gyrus. It should be noted, however, that functional neuroimaging evidence for phonological processing in bilinguals is scanty, similar to grammar processing (overall n of studies analyzed = 12).

The involvement of middle temporal structures in processing sounds and sound structure is well established (Yang & Small, 2015). The dual-stream model of speech processing identifies the middle temporal gyrus as a key component of the ventral stream (e.g., Hickok & Poeppel, 2004, 2007). According to such model, a ventral stream – involving inferior and middle temporal cortices – processes the speech signal for comprehension, whereas a dorsal stream – involving the parietal operculum and the posterior regions of frontal lobe (*i.e.*, the posterior part of the inferior frontal gyrus, the insula, and part of the precentral gyrus) – plays a role in mapping auditory speech information into articulatory/motor representations. In such framework, the bilateral middle temporal gyrus plays a role as a sound-to-meaning interface, by mapping phonological material into semantic representations. A larger involvement of this structure in L1 than L2 suggests that sound-to-meaning mapping in the second language might remain effortful even in bilinguals described as high proficient. It remains to be

investigated whether variations in early language experience or plasticity associated with differences in L2 AoA may modulate the process, possibly contributing to make sound-to-meaning mapping similar in both L1 and L2.

The meta-analysis for the L2>L1 contrast shows a larger set of regions: Bilateral frontal regions (i.e., the left inferior and superior frontal gyri, the left precentral gyrus and the right middle frontal gyrus), the left superior parietal gyrus, and the cerebellum. Despite proficient knowledge of L2 grammar and vocabulary, mastering non-native sounds may be challenging, and an early L2 onset does not automatically lead to native-like mastery (Flege & MacKay, 2011; Pallier et al., 1997; Thompson, 1991). As shown by ample experimental work, previous language experience acts as a “filter” through which foreign speech is processed (e.g. Bohn & Flege, 1990). It has been proposed that the neural commitment to the acoustic properties of L1 may interfere with the perception of new sounds at an early phonetic level, as L2 learners tend to rely on acoustic cues perceptually salient in L1 but not reliable for sound categorization in L2 (Kuhl, 2000; Iverson et al., 2003). An involvement of frontal regions emerged for phonological processing in both L1 and L2. In dual-stream models of speech processing (e.g., Hickok & Poeppel, 2004, 2007), these regions are key components of the dorsal stream. While for L1, the activation was limited to the left inferior frontal gyrus, for the L2 there was a larger recruitment of dorsal-stream regions, which might suggest that this route is less efficient in integrating auditory information with motor representations in the non-native language. The engagement of frontal structures such as the inferior and middle frontal gyri, which are known to play a prominent role in inhibitory control processes (Aron et al., 2014; Sharp et al., 2010), may also indicate that the phonological competition that occurs between two languages present additional challenges for the bilingual, who must inhibit phonological activation of the non-target (dominant) language. Strictly speaking, the superior parietal lobule is not a language-specific region; it has been proposed to play a critical role in integrating internally and externally driven information (Cavanna & Trimble, 2006;

Utevsky et al., 2014), thus contributing to attentional and memory operations. A larger involvement of this structure in L2 than L1 phonological processing might therefore be associated with the additional resources required by a more effortful phonological computation in a foreign language. Cerebellar-parietal connections have been shown to underpin phonological storage in healthy monolingual adults, especially during the late stages of verbal encoding (Macher et al, 2014), and focal or degenerative cerebellar disease has been reported to impair verbal fluency by specifically affecting phonemically-related retrieval strategies while sparing semantic processing (Leggio et al., 2000). Besides computational and retrieval strategies, the cerebellum is also known to be involved in motor speech planning and temporal aspects of speech perception both in young children and adults (Ackermann et al., 2007; Kuhl et al., 2014). Most recently, activity in the right posterolateral cerebellum has been shown to correlate with the predictability of the phonological content of upcoming word stimuli (Lesage et al., 2017).

Language control (switching)

An intervention of the executive control system in bilingual language processing has been attributed to the need of selectively attending to one language for communication, monitoring speech from other languages' intrusions, and switching between languages in different contexts (Green, 1998; Abutalebi & Green, 2007; Calabria et al., 2018; Kroll et al., 2008). It is well documented that damage to the executive control system usually results in pathological language switching (Abutalebi, Miozzo, & Cappa, 2000; Kong et al., 2014). As outlined by Abutalebi et al. (2013), the most potent task to study language control are those experimental designs where participants have to switch between their languages.

Here, by collapsing activations over AoA, we show that language switching elicits activation in various cortical and subcortical areas bilaterally, both within and outside the classical left perisylvian language network. These areas include the superior and inferior frontal gyri, the precentral gyrus, the postcentral gyrus, the superior temporal gyrus, the cuneus, the middle occipital gyrus, the fusiform gyrus, the an-

terior cingulate cortex, the insula, and the caudate. Activations in these regions have also been reported in studies investigating executive control with non-linguistic conflict tasks (e.g., Grahn, Parkinson, & Owen, 2008; Botvinick et al., 2001; McGuire & Botvinick, 2010; Miller & Cohen, 2001), pointing to an engagement of the executive control network across verbal and non-verbal domains.

As mentioned earlier, the left prefrontal cortex, and specifically the left inferior frontal gyrus, has been consistently associated with domain-general inhibitory control and response selection (Branzi et al., 2015; Hernandez et al., 2000; van Heuven et al., 2008), whereas its right counterpart is arguably related to response inhibition (Aron et al., 2007). Intraoperative electrocortical stimulation of the left inferior frontal gyrus has been shown to induce unintended language switching in bilingual patients (Kho et al., 2007). Two further key components of the control network underscored by the present meta-analysis are the anterior cingulate cortex and the inferior parietal lobule. Increased neural activity during switching tasks may reflect increased monitoring demands necessary to perform a difficult task such as using an L2 while preventing L1 intrusion. The anterior cingulate is assumed to be a key structure of the executive control network that underpins the prioritization of information for goal-directed behavior (e.g. Botvinick et al., 2001). In particular, especially the dorsal anterior cingulate has been identified as responsible for recruiting executive control through the monitoring of conflicting information, whilst other executive control components would actually implement executive control to overcome interference (Botvinick et al., 2001; Kerns et al., 2004). The regular coordination between languages has been shown to tune the anterior cingulate cortex for conflict monitoring (e.g. Abutalebi et al., 2013; Del Maschio et al., 2018, see also 2019a) across verbal and non-verbal domains (Abutalebi et al., 2007, 2012; De Baene et al., 2015). The pre-supplementary motor area, rostral to the primary motor cortex and dorsal to the anterior cingulate region, has been specifically associated with the initiation of speech during language switching (see Luk et al., 2012). In an fMRI experiment, for instance, Abutalebi et al. (2013) asked trilingual speakers to name pictures in their L1, L2, and L3 and switch among

languages; they showed that, independently of language proficiency, pre-supplementary motor/anterior cingulate response increases when switching between languages; this finding indicates a direct involvement of pre-supplementary motor/anterior cingulate area in monitoring the language context for bilinguals and, more in general, its involvement in task monitoring. Functional and structural neuroplastic changes in this area are assumed to result from the continuous challenge of coordinating between languages while avoiding cross-linguistic interference (Abutalebi & Green, 2007; Green & Abutalebi, 2013; Del Maschio, Fedeli, Sulpizio, & Abutalebi, 2019b). The inferior parietal lobule is deemed relevant for integrating motor, perceptual and cognitive streams of information (Gottlieb, 2007) and response-to-stimulus mapping (De Baene et al., 2012), and has also been implicated in bilinguals' language switching (Wang et al., 2009). Specifically, the left inferior parietal lobule has been proposed to bias language selection away from the non-target language, whereas its right counterpart would be responsible for driving selection towards the intended language (see Abutalebi & Green, 2016). Clinical evidence on bilingual aphasics suggests that pathological fixation to one language or uncontrolled language switching may occur after damage to the left inferior parietal cortex (Abutalebi & Green, 2007).

Lesion and neuroimaging studies on monolingual adults indicate that the insular cortex is implicated in a number of linguistic and non-linguistic control functions (Ardila et al., 2014; Oh, Duerden, & Pang, 2014; Price, 2010). This region has indeed direct connections to speech and language centers like Broca's area, but is also the core of the salience network, which plays a key role in the detection of relevant stimuli and initiation of dynamic switching between the executive control network and the default mode network (Gogolla, 2017; Menon & Uddin, 2010). The significance of insular activations in high proficient bilinguals may result from the specific neurocognitive demands of bilingual language processing, including executive control functions such as switching, but also saliency and attention.

As our findings indicate, the control of two languages is accomplished through a combination of interwoven activities in a neural network that comprises subcortical structures as well, in particular

the left caudate. Lesions to this region have been frequently associated with breakdown of language control (Aglioti & Fabbro, 1993; Aglioti et al., 1996; Green & Abutalebi, 2008), and left caudate activity has been detected in healthy participants engaged in language control tasks such as translation (Lehtonen et al., 2005), language selection (Branzi et al., 2015; Crinion et al., 2006) and language switching (Abutalebi et al., 2013; Zou et al., 2012). In particular, the left caudate has been suggested to be involved in the resolution of response conflict: In their fMRI study with trilingual speakers, Abutalebi et al. (2013) showed that the involvement of the left caudate was modulated by the proficiency of the to-be-used language, reporting the greatest increase of this structure for switching from the most (L1) to the least proficient language (L3). The left caudate plays thus a role in selecting the lexical item in the required language while facing the interface from the alternative language (see also, Abutalebi et al., 2008).

When we inspected language switching by separately looking at early and late bilinguals, two further regions emerged: The bilateral middle frontal gyrus in early bilinguals, and the cerebellum in both early and late bilinguals, but more prominently in the latter group. Direct evidence of the involvement of the middle frontal gyrus in early bilinguals' switching has been provided by a recent intracranial recording study by Sierpowska and colleagues (2018). The authors investigated language switching in Spanish-Catalan bilinguals and found that a transitory lesion to the middle frontal gyrus caused switching errors. Interestingly, increased cortical thickness in the middle frontal gyrus has been found in conscript interpreters vs. controls after three months of intense language training (Mårtensson et al. 2012), suggesting a role of relative language use as a source of neural plasticity in this region. The cerebellum is highly connected with key regions of the language control network (Green & Abutalebi, 2013; Sulpizio, Del Maschio, Del Mauro, Fedeli, & Abutalebi, 2020), including the inferior frontal cortices (Aron et al., 2007; Krienen & Buckner, 2009). This fronto-cerebellar circuit has been proposed to represent a target of adaptive change in bilingual speakers (Abutalebi & Green, 2016), as increased

grey matter volume in the cerebellum of immersed, late bilinguals relative to monolinguals seem to confirm (Pliatsikas et al., 2014a). As already noted, it is plausible that cerebellar activation mediates the prediction of future input while maintaining ongoing representations (Ito, 2008; Lesage et al., 2012). It has been shown that grey matter density in the right cerebellum significantly predicts the bilinguals' ability to resist speech interference from L1 while processing an utterance in L2 (Filippi et al., 2011).

Among bilinguals, a critical factor which is supposed to drive differences in the neural signatures of language control is how well and how often a second language is spoken. Indeed, the processing demands entailed by the simultaneous management of more than one language have been shown to be particularly taxing in low proficient or less exposed individuals, who seem to heavily rely on the active suppression of their L1 when using a second language (e.g., Consonni et al., 2013; Sugiura et al., 2015). Since our sample comprised only highly proficient bilinguals, we were unable to test the effects of L1/L2 proficiency or usage differences among participants

Further considerations

Although highly informative, the findings here reported should be considered in light of several limitations. First, there is heterogeneity in the number of activation peaks for each linguistic level investigated. In particular, the analyses for lexico-semantics and language control are based on a large number of peaks, whereas the analyses for grammar and phonology are not. This reflects a structural flaw of the available literature which reverberates on the strength of our conclusions. At the same time, the emerging picture may drive future investigations: Functional neuroimaging research on bilingualism should focus more on how bilinguals process grammar and/or phonology in their first and second language. Our study offers anyhow a useful tool to sketch empirical predictions on these two linguistic domains, as well as a comprehensive view of past research directions.

Another issue that deserves further investigation regards language distance, that is the relative degree of similarity between (two) languages, a construct closely related to language complexity. Since

no general agreement exists on scalar measures for linguistic distance, very few studies investigated the impact of language distance on L1 and L2 neural processing, making the issue not currently suitable for a meta-analysis. However, the available data suggest that an allegedly larger distance between languages tend to be associated with a more extensive recruitment of control-related regions during language processing (cf. Ghazi-Saidi and Ansaldo, 2017 and Raboyeau et al., 2010).

A final concern refers to important individual differences in bilingual competence which are known to affect the functional architecture of the bilingual brain, *i.e.*, AoA, proficiency and exposure. Our results show that little fMRI work has been conducted on the impact of L2 AoA variability on phonological and grammar processing, bilinguals with low levels of L2 proficiency, and differences in language exposure. The analyses here conducted have been inevitably restricted to high proficient bilinguals, as only 12 studies with low proficient individuals evenly distributed across linguistic levels emerged from the literature search. A larger consistency across studies in qualifying bilinguals' proficiency, as well as a higher reliance on objective measures, are also recommended for future research. The matter becomes even more complicated when considering the case of language exposure, whose effects are barely explored in the functional literature of bilingual language processing. The importance of exposure or use for structural brain plasticity and reserve has been demonstrated (e.g. Abutalebi et al., 2015; Del Maschio et al., 2019c; Olsen et al., 2015; Perani et al., 2003; Pliatsikas et al., 2017). But for unknown reasons the study of the functional basis of exposure has not yet fully captured the attention of researchers.

Conclusions

The results of our quantitative investigation show that, overall, first and second language are processed through the same neural structures, as clearly indicated by the absence of extensive selective activation either for L1 or L2. At the same time, some differences emerged as a function of the different linguistic levels considered: Even if limited, heterogeneity was more manifest at the lexico-semantic level, with

surprisingly native language processing recruiting a larger set of cortical and subcortical regions with respect to L2. This finding may suggest that word processing in an individual's native language is mediated by the access to a richer lexico-semantic system supported by a more widespread neural network. L1-L2 differences with respect to grammar and phonology were quite scarce. Note, however, that such finding could be affected by the scanty overall number of studies investigating these two linguistic levels.

Moreover, concerning executive control, the present study also provides clear evidence on the neural infrastructure that enables the bilinguals' capacity to correctly use a target language while avoiding interference from those unintended. In line with previous reviews, we can confirm that language control is accomplished by relying by a widespread and domain-general executive network involving structures such as the prefrontal cortices, the inferior parietal lobules, and the left caudate nucleus (see Abutalebi & Green, 2007; Green & Abutalebi, 2013).

To conclude, the present study used a meta-analytic approach to draw clear and unidirectional inferences on language representation and control in the bilingual brain. At the same time, the emerging picture identifies under-investigated issues, offering clear directions for future research.

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Table 1a. Characteristics of the studies included in the different sets analyzed, collapsed over AoA

Set A: Linguistic level: Lexico-Semantics; Contrast: L1>L2							<i>171 foci</i>
<i>Study (n=18)</i>	<i>L1</i>	<i>L2</i>	<i>Subjects</i>	<i>Age</i>	<i>Task</i>	<i>AoA</i>	<i>Incl. contrasts</i>
Abutalebi et al., 2007	Dialect	German	12	24.5	Word reading	<3	5
Abutalebi et al., 2008	German	French	12	25.4	Picture naming	11.6	1
De Bleser et al., 2003	Dutch	French	11	18-21	Picture naming	10	1
Fu et al., 2018	Chinese	English	21	22	Picture naming	10	1
Hernandez et al., 2009	Spanish	English	12	21.4	Picture naming	<5	1
Jamal et al., 2012	Spanish	English	12	18-29	Word reading	<6	1
Klein et al., 2006	English	French	10	--	Word repetition	5.9	1
Liu et al., 2010	Chinese	English	24	24	Picture naming	12	1
Nakamura et al., 2010	Japanese	English	24	21-38	Semantic judgement	>10	1
Nichols & Joanisse, 2016	Chinese (Mandarin)	English	22	22.18	Picture-word matching	13.8	1
Nosarti et al 2010	Italian/English	Italian/English	30	31-39	Word reading	11	3
Palomar-García et al., 2015	Spanish	Catalan	23	20.22	Picture naming	02-05	2
Perani et al., 1998	Spanish	Catalan	12	19-27	Discourse listening	Early childhood	1
Rodriguez-Fornells et al., 2002	Spanish	Catalan	22	18-30	Lexical decision	1	1
Román et al., 2015	Spanish	Catalan	23	25.1	Semantic judgement	3	1
Ruschemeyer et al., 2005	Russian	German	7	30.5	Semantic judgement	>12	2
Videsott et al., 2010	Ladin	Italian/German	20	27.3	Picture naming	>15	1
Vingerhoets et al., 2003	Dutch	French/English	12	27.6	Word production, picture naming, sentence reading	13.5; 10.3	3
Set B: Linguistic level: Lexico-Semantics; Contrast: L2>L1							<i>164 foci</i>
<i>Study (n=22)</i>	<i>L1</i>	<i>L2</i>	<i>Subjects</i>	<i>Age</i>	<i>Task</i>	<i>AoA</i>	<i>Incl. contrasts</i>
Abutalebi et al., 2008	German	French	12	25.4	Picture naming	11.6	1
Berken et al., 2015	French	English	13	25.2	Sentence reading	14	1
De Bleser et al., 2003	Dutch	French	11	18-21	Picture naming	10	1
Fu et al., 2018	Chinese	English	21	22	Picture naming	10	1
Hernandez et al., 2009	Spanish	English	12	21.4	Picture naming	<5	1
Hsiesh et al., 2017	Chinese	Japanese	28	24.64	Lexical decision	20.72	2
Jamal et al., 2012	Spanish	English	12	18-29	Word reading	<6	1
Jeong et al., 2016	Japanese	English	30	23.35	Picture naming	12.3	3
Klein et al., 2006	English	French	10	--	Word repetition	5.9	1
Liu et al., 2010	Chinese	English	24	24	Picture naming	12	1
Nakamura et al., 2010	Japanese	English	24	21-38	Semantic judgement	>10	1
Nichols & Joanisse, 2016	Chinese (Mandarin)	English	22	22.18	Picture-word matching	13.8	1
Nosarti et al., 2010	Italian/English	Italian/English	30	31-39	Word reading	11	2

Park et al., 2012	Macedonian	English	8	25	Lexical decision	>6	1
Perani et al., 1998	Spanish	Catalan	12	19-27	Discourse listening	Early childhood	1
Perani et al., 2003	Spanish/Catalan	Catalan/Spanish	11	20-27	Word production	3	2
Van Heuven et al., 2008	Dutch	English	12	24.1	Lexical decision	>10	2
Videsott et al., 2010	English	Italian	20	27.3	Picture naming	5	1
Vingerhoets et al., 2003	Dutch	French/English	12	27.6	Word production, picture naming, sentence reading	13.5; 10.3	2
Wartenburger et al., 2003	Italian	German	12	--	Semantic judgement	18-20	1
Xu et al., 2017	Chinese	English	12	26.5	Lexical decision	>6	1
Yang et al., 2011	Chinese	English	17	19-28	Lexical decision	12	1

Set C: Linguistic level: Grammar; Contrast: L1>L2

57 foci

<i>Study (n=6)</i>	<i>L1</i>	<i>L2</i>	<i>Subjects</i>	<i>Age</i>	<i>Task</i>	<i>AoA</i>	<i>Incl. contrasts</i>
De Grauwe et al., 2014	German	Dutch	24	24.62	Lexical decision	20.1	1
Lehtonen et al., 2009	Finnish	Swedish	16	26.3	Lexical decision	Early childhood	1
Perani et al., 1998	Spanish	Catalan	12	19-27	Discourse listening	Early childhood	1
Ruschemeyer et al., 2005	Russian	German	7	30.5	Grammatical judgement	>12	2
Saur et al., 2009	German/French	German/French	12	26	Grammatical judgement	<3	1
Saur et al., 2009	German/French	German/French	12	26	Grammatical judgement	>10	2
Suh et al., 2007	Korean	English	16	22.9	Grammatical judgement	High school	2

Set D: Linguistic level: Grammar; Contrast: L2>L1

47

<i>Study (n=6)</i>	<i>L1</i>	<i>L2</i>	<i>Subjects</i>	<i>Age</i>	<i>Task</i>	<i>AoA</i>	<i>Incl. contrasts</i>
Berken et al., 2015	French	English	13	25.2	Sentence reading	14	1
Lehtonen et al., 2009	Finnish	Swedish	16	26.3	Lexical decision	Early childhood	1
Perani et al., 1998	Spanish	Catalan	12	19-27	Discourse listening	Early childhood	1
Saur et al., 2009	German/French	German/French	12	26	Grammatical judgement	>10	2
Wartenburger et al., 2003	Italian	German	12	--	Grammatical judgement	18-20	1
Yokoyama et al., 2006	Japanese	English	36	--	Grammatical judgement	11.8	1

Set E: Linguistic level: Phonology; Contrast: L1>L2

37 foci

<i>Study (n=5)</i>	<i>L1</i>	<i>L2</i>	<i>Subjects</i>	<i>Age</i>	<i>Task</i>	<i>AoA</i>	<i>Incl. contrasts</i>
Kim et al., 2016	Korean/Chinese	Chinese/English	27	21-21.9	Rhyming judgement	14.5	2
Kim et al., 2017	Korean/Chinese	Chinese/English	13-16-20-17	21-21.8-22.8	Rhyming judgement	10.4-12.1	2
Palomar-García et al., 2015	Spanish	Catalan	23	20.22	Word listening	02-05	2
Perani et al., 1998	Spanish	Catalan	12	19-27	Discourse listening	Early childhood	1
Ruschemeyer et al., 2005	Russian	German	7	30.5	Sentence listening	>12	1

Set F: Linguistic level: Phonology; Contrast: L2>L1

103 foci

<i>Study (n=10)</i>	<i>L1</i>	<i>L2</i>	<i>Subjects</i>	<i>Age</i>	<i>Task</i>	<i>AoA</i>	<i>Incl. contrasts</i>
Berken et al., 2015	French	English	13	25.2	Sentence reading	14	1
Callan et al., 2004	English	Japanese	22	23-42	Syllable identification	High school	1
Callan et al., 2006	Japanese	English	13	21-49	Vowel/consonant identification	Late acquired	3
Cao et al., 2014	Chinese	English	26	18-34	Rhyming judgement	12	2
Kim et al., 2016	Korean/Chinese	Chinese/English	27	21-21.9	Rhyming judgement	14.5	2
Kim et al., 2017	Chinese/English	Korean/Chinese	13-16-20-17	21-21.8-22.8	Rhyming judgement	10.4-12.1	1
Klein et al., 2006	English	French	10	--	Word repetition	5.9	1
Koyama et al., 2013	Japanese/English	Japanese/English	14	26.2-29.3	Phonological matching	>12	1
Nosarti et al., 2010	Italian/English	Italian/English	30	31/39	Word reading	11	3
Perani et al., 1998	Spanish	Catalan	12	19-27	Discourse listening	Early childhood	1

Set G: Linguistic Level: Switching

212 foci

<i>Study (n=17)</i>	<i>L1</i>	<i>L2</i>	<i>Subjects</i>	<i>Age</i>	<i>Task</i>	<i>AoA</i>	<i>Incl. contrasts</i>
Abutalebi et al., 2007	Italian	French	12	30.2	Language switching	<3	1
Coderre et al., 2016	Spanish	English	14	24	Language switching	6	2
De Baene et al., 2015	Spanish	Basque	32	22.4	Language switching	<3	2
de Bruin et al., 2014	Dutch	English	17	21.82	Language switching	10,13	3
Fu et al., 2018	Chinese	English	21	22	Language switching	10	1
Garbin et al., 2011	Spanish	Catalan	19	20	Language switching	<4	3
Guo et al., 2011	Chinese	English	24	--	Language switching	12	4
Hernandez et al., 2001	English	Spanish	6	21.7	Language switching	<5	4
Hernandez et al., 2009	Spanish	English	12	21.4	Language switching	<5	1
Hosoda et al., 2012	Japanese	English	20	26.1	Language switching	11	8
Klein et al., 1995	English	French	12	22	Language switching	5	1
Lei et al., 2014	Korean	Chinese	8	25-28	Language switching	1	2
Price et al. 1999	German	English	6	30.5	Language switching	8.8	4
Reverberi et al., 2015	German	English	21	23.1	Language switching	Late acquired	3
Rinne et al., 2000	Finnish	English	8	32-56	Language switching	Late acquired	2
Weissberger et al., 2015	Spanish	English	21	21	Language switching	5.1	1
Zhang et al., 2015	Chinese	English	22	21.3	Language switching	11.9	4

Table 1b. Characteristics of the studies included in the analysis for Lexico-semantic and Language Control (Switching), split by AoA.

Set H: Linguistic level: Lexico-Semantics; AoA: Early; Contrast: L1>L2							131 foci
<i>Study (n=8)</i>	<i>L1</i>	<i>L2</i>	<i>Subjects</i>	<i>Age</i>	<i>Task</i>	<i>AoA</i>	<i>Incl. contrasts</i>
Abutalebi et al., 2007	Dialect	German	12	24.5	Word reading	<3	5
Hernandez et al., 2009	Spanish	English	12	21.4	Picture naming	<5	1
Jamal et al., 2012	Spanish	English	12	18-29	Word reading	<6	1
Klein et al., 2006	English	French	10	--	Word repetition	5.9	1
Palomar-García et al., 2015	Spanish	Catalan	23	20.22	Picture naming	2-5	2
Perani et al., 1998	Spanish	Catalan	12	19-27	Discourse listening	Early childhood	1
Rodríguez-Fornells et al., 2002	Spanish	Catalan	22	18-30	Lexical decision	1	1
Román et al., 2015	Spanish	Catalan	23	25.1	Semantic judgement	3	1
Set I: Linguistic level: Lexico-Semantics; AoA: Late; Contrast: L1>L2							40 foci
<i>Study (n=10)</i>	<i>L1</i>	<i>L2</i>	<i>Subjects</i>	<i>Age</i>	<i>Task</i>	<i>AoA</i>	<i>Incl. contrasts</i>
Abutalebi et al., 2008	German	French	12	25.4	Picture naming	11.6	1
De Bleser et al., 2003	Dutch	French	11	18-21	Picture naming	10	1
Fu et al., 2018	Chinese	English	21	22	Picture naming	10	1
Liu et al., 2010	Chinese	English	24	24	Picture naming	12	1
Nakamura et al., 2010	Japanese	English	24	21-38	Semantic judgement	>10	1
Nichols & Joanisse, 2016	Chinese (Mandarin)	English	22	22.18	Picture-word matching	13.8	1
Nosarti et al 2010	Italian/English	Italian/English	30	31-39	Word reading	11	3
Ruschemeyer et al., 2005	Russian	German	7	30.5	Semantic judgement	>12	2
Videsott et al., 2010	Ladin	Italian/German	20	27.3	Picture naming	>15	1
Vingerhoets et al., 2003	Dutch	French/English	12	27.6	Word production, picture naming, sentence reading	13.5; 10.3	3
Set J: Linguistic level: Lexico-Semantics; AoA: Early; Contrast: L2>L1							32 foci
<i>Study (n=6)</i>	<i>L1</i>	<i>L2</i>	<i>Subjects</i>	<i>Age</i>	<i>Task</i>	<i>AoA</i>	<i>Incl. contrasts</i>
Hernandez et al., 2009	Spanish	English	12	21.4	Picture naming	<5	1
Jamal et al., 2012	Spanish	English	12	18-29	Word reading	<6	1
Klein et al., 2006	English	French	10	--	Word repetition	5.9	1
Perani et al., 1998	Spanish	Catalan	12	19-27	Discourse listening	Early childhood	1
Perani et al., 2003	Spanish/Catalan	Catalan/Spanish	11	20-27	Word production	3	2
Videsott et al., 2010	English	Italian	20	27.3	Picture naming	5	1
Set K: Linguistic level: Lexico-Semantics; AoA: Late; Contrast: L2>L1							134 foci
<i>Study (n=16)</i>	<i>L1</i>	<i>L2</i>	<i>Subjects</i>	<i>Age</i>	<i>Task</i>	<i>AoA</i>	<i>Incl. contrasts</i>
Abutalebi et al., 2008	German	French	12	25.4	Picture naming	11.6	1
Berken et al., 2015	French	English	13	25.2	Sentence reading	14	1
De Bleser et al., 2003	Dutch	French	11	18-21	Picture naming	10	1
Fu et al., 2018	Chinese	English	21	22	Picture naming	10	1
Hsiesh et al., 2017	Chinese	Japanese	28	24.64	Lexical decision	20.72	2

Jeong et al., 2016	Japanese	English	30	23.35	Picture naming	12.3	3
Liu et al., 2010	Chinese	English	24	24	Picture naming	12	1
Nakamura et al., 2010	Japanese	English	24	21-38	Semantic judgement	>10	1
Nichols & Joanisse, 2016	Chinese (Mandarin)	English	22	22.18	Picture-word matching	13.8	1
Nosarti et al., 2010	Italian/English	Italian/English	30	31-39	Word reading	11	3
Park et al., 2012	Macedonian	English	8	25	Lexical decision	>6	1
Van Heuven et al., 2008	Dutch	English	12	24.1	Lexical decision	>10	2
Vingerhoets et al., 2003	Dutch	French/English	12	27.6	Word production, picture naming, sentence reading	13.5; 10.3	2
Xu et al., 2017	Chinese	English	12	26.5	Lexical decision	>6	1
Yang et al., 2011	Chinese	English	17	19-28	Lexical decision	12	1
Wartenburger et al., 2003	Italian	German	12	--	Semantic judgement	18-20	1

Set L: Linguistic Level: Switching; AoA: Early

212 foci

<i>Study (n=9)</i>	<i>L1</i>	<i>L2</i>	<i>Subjects</i>	<i>Age</i>	<i>Task</i>	<i>AoA</i>	<i>Incl. contrasts</i>
Abutalebi et al., 2007	Italian	French	12	30.2	Language switching	<3	1
Coderre et al., 2016	Spanish	English	14	24	Language switching	6	2
De Baene et al., 2015	Spanish	Basque	32	22.4	Language switching	<3	2
Garbin et al., 2011	Spanish	Catalan	19	20	Language switching	<4	3
Hernandez et al., 2001	English	Spanish	6	21.7	Language switching	<5	4
Hernandez et al., 2009	Spanish	English	12	21.4	Language switching	<5	1
Klein et al., 1995	English	French	12	22	Language switching	5	1
Lei et al., 2014	Korean	Chinese	8	25-28	Language switching	1	2
Weissberger et al., 2015	Spanish	English	21	21	Language switching	5.1	1

Set M: Linguistic Level: Switching; AoA: Late

197 foci

<i>Study (n=8)</i>	<i>L1</i>	<i>L2</i>	<i>Subjects</i>	<i>Age</i>	<i>Task</i>	<i>AoA</i>	<i>Incl. contrasts</i>
de Bruin et al., 2014	Dutch	English	17	21.82	Language switching	10,13	3
Fu et al., 2018	Chinese	English	21	22	Language switching	10	1
Guo et al., 2011	Chinese	English	24	--	Language switching	12	4
Hosoda et al., 2012	Japanese	English	20	26.1	Language switching	11	8
Price et al. 1999	German	English	6	30.5	Language switching	8.8	4
Reverberi et al., 2015	German	English	21	23.1	Language switching	Late acquired	3
Rinne et al., 2000	Finnish	English	8	32-56	Language switching	Late acquired	2
Zhang et al., 2015	Chinese	English	22	21.3	Language switching	11.9	4

Table 1c. Characteristics of the studies included in the analysis for Lexico-semantics and Language Control (Switching), collapsed over AoA (picture-naming tasks only)

Supplementary Set: Linguistic Level: Switching (only naming)							<i>186 foci</i>
<i>Study (n=8)</i>	<i>L1</i>	<i>L2</i>	<i>Subjects</i>	<i>Age</i>	<i>Task</i>	<i>AoA</i>	<i>Incl. contrasts</i>
De Baene et al., 2015	Spanish	Basque	32	22.04	Language switching	<3	2
Garbin et al., 2011	Spanish	Catalan	19	20	Language switching	<4	3
Hernandez et al., 2001	English	Spanish	6	21.07	Language switching	<5	4
Hernandez et al., 2009	Spanish	English	12	21.04	Language switching	<5	1
de Bruin et al., 2014	Dutch	English	17	21,82	Language switching	10,13	3
Fu et al., 2018	Chinese	English		21	Language switching	10	1
Guo et al., 2011	Chinese	English	24	--	Language switching	12	4
Reverberi et al., 2015	German	English	21	23.01	Language switching	Late acquired	3

Table 2a. Results for activations for each linguistic level collapsed over age of acquisition.

Volume (mm3)	Region	L/R	MNI Coordinates			BA	Peak ALE value
			x	y	z		
<i>Set A: Linguistic level: Lexico-Semantics; Contrast: L1>L2</i>							
12824	Inferior Frontal Gyrus (op.)	L	-54	16	14	44	0.028
1488	Superior Parietal Lobule	L	-24	-48	52	7	0.020
1360	Thalamus	L	-6	-8	12	-	0.015
1032	Middle Temporal Gyrus	L	-66	-34	4	21	0.019
936	Cerebellum	L	-38	-64	-10	-	0.019
752	Superior Occipital Gyrus	L	-20	-74	36	19	0.015
520	Parahippocampal Gyrus	L	-14	-10	-16	28	0.014
480	Inferior Frontal Gyrus (orb.)	R	46	36	-4	47	0.013
480	Angular Gyrus	R	46	-70	40	39	0.017
448	Superior Parietal Lobule	R	34	-66	62	7	0.013
384	Posterior Cingulate	L	-3	-49	28	23	0.016
352	Precuneus	L	-4	-62	38	7	0.015
296	Inferior Parietal Lobule	L	-48	-26	48	3	0.013
256	Medial Frontal Gyrus	L	-3	27	49	8	0.011
224	Inferior Frontal Gyrus (tri.)	R	52	40	14	45	0.012
184	Fusiform Gyrus	R	46	-64	-8	37	0.011
168	Amygdala	L	-22	4	-22	28	0.011
160	Caudate	R	14	18	0	-	0.011
<i>Set B: Linguistic level: Lexico-Semantics; Contrast: L2>L1</i>							
8504	Precentral Gyrus	L	-56	10	10	6	0.034
3016	Superior Frontal Gyrus	L	-4	22	48	8	0.019

1624	Insula	L	-32	26	-6	-	0.017
920	Pallidum	L	-14	6	-4	-	0.014
864	Insula	R	30	20	-8	-	0.012
576	Pallidum	R	14	8	-6	-	0.018
488	Cerebellum	R	32	-60	-32	-	0.014
312	Inferior Frontal Gyrus (orb.)	L	-46	48	-6	47	0.012
240	Inferior Frontal Gyrus (tri.)	L	-52	40	0	45	0.013
192	Precentral Gyrus	R	36	-20	34	4	0.012

Set C: Linguistic level: Grammar; Contrast: L1>L2

608	Caudate	R	12	18	4	-	0.010
568	Inferior Frontal Gyrus (op.)	L	-54	12	26	44	0.011
536	Insula	L	-40	4	10	-	0.009
504	Precentral Gyrus	L	-54	10	2	6	0.011
496	Middle Temporal Gyrus	R	60	-10	-20	21	0.012
496	Insula	R	44	2	8	-	0.012
448	Supplementary Motor Area	R	4	-3	51	6	0.010
400	Inferior Parietal Lobule	L	-28	-72	48	7	0.011
224	Inferior Frontal Gyrus (orb.)	L	-32	20	-18	47	0.009

Set D: Linguistic level: Grammar; Contrast: L2>L1

688	Inferior Frontal Gyrus (op.)	L	-52	10	22	44	0.009
256	Middle Occipital Gyrus	L	-29	-97	-3	18	0.009
184	Pallidum	R	20	4	0	-	0.008
168	Putamen	L	-20	8	6	-	0.008
160	Cerebellum	L	-6	-88	-26	-	0.009
160	Cerebellum	L	-34	-82	-20	-	0.009

Set E: Linguistic level: Phonology; Contrast: L1>L2

984	Inferior Frontal Gyrus (orb.)	L	-34	12	-16	47	0.020
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592	Middle Temporal Gyrus	R	62	-42	2	22	0.016
392	Middle Temporal Gyrus	R	62	-12	-18	21	0.011

Set F: Linguistic level: Phonology; Contrast: L2>L1

3248	Inferior Frontal Gyrus (op.)	L	-56	10	10	44	0.033
1632	Precentral Gyrus	L	-48	2	34	6	0.019
1008	Cerebellum	R	34	-68	-28	-	0.015
424	Superior Parietal Lobule	L	-28	-62	44	7	0.016
296	Middle Frontal Gyrus	R	46	10	48	9	0.010
240	Superior Frontal Gyrus	L	-4	14	54	8	0.010

Set G: Linguistic Level: Switching

3712	Inferior Frontal Gyrus (op.)	L	-50	14	20	44	0.026
1600	Superior Frontal Gyrus	R	4	20	56	8	0.030
1288	Lingual Gyrus	L	-8	-96	0	18	0.022
1152	Precuneus	L	-6	-76	46	7	0.019
784	Anterior Cingulate	L	-2	14	26	24	0.025
656	Precuneus	R	6	-70	42	7	0.024
632	Inferior Parietal Lobule	L	-42	-54	48	40	0.021
600	Postcentral Gyrus	L	-52	-4	40	4	0.021
560	Fusiform Gyrus	L	-40	-80	-8	19	0.022
456	Superior Occipital Gyrus	R	22	-96	10	17	0.019
288	Supplementary Motor Area	R	2	2	66	6	0.018
272	Cuneus	R	10	-100	14	18	0.017
264	Caudate	L	-12	22	-4	-	0.019
248	Superior Temporal Gyrus	R	66	-16	-6	22	0.018

248	Inferior Frontal Gyrus (op.)	R	32	14	30	44	0.017
208	Inferior Occipital Gyrus	R	32	-80	-10	19	0.016
184	Superior Frontal Gyrus	R	24	32	46	8	0.016
176	Insula	L	-34	20	-8	-	0.015

Table 2b. Results for activations of Lexico-semantics and Language Control (Switching) split by age of acquisition (early vs. late bilinguals)

Volume (mm3)	Region	L/R	MNI Coordinates			BA	Peak ALE value
			x	y	z		
<i>Set H: Linguistic level: Lexico-Semantics; AoA: Early; Contrast: L1>L2</i>							
11736	Inferior Frontal Gyrus (op.)	L	-54	16	14	44	0.028
1824	Thalamus	L	-6	-8	12	-	0.015
1808	Precuneus	L	-24	-48	52	7	0.020
1288	Middle Temporal Gyrus	L	-66	-34	4	21	0.019
1088	Cerebellum	L	-38	-64	-10	-	0.019
648	Superior Parietal Lobule	R	34	-66	62	7	0.013
624	Parahippocampal Gyrus	L	-14	-10	-16	28	0.014
480	Precuneus	L	-4	-62	38	7	0.015
480	Angular Gyrus	R	45	-70	40	39	0.017
456	Inferior Parietal Lobule	L	-48	-26	48	3	0.013
448	Posterior Cingulate	L	-3	-49	28	23	0.016
400	Precuneus	L	-20	-74	34	31	0.013
288	Inferior Frontal Gyrus (orb.)	R	46	34	-4	47	0.012
288	Medial Frontal Gyrus	L	-3	27	49	8	0.011
272	Inferior Frontal Gyrus (tri.)	R	52	40	16	45	0.012
256	Fusiform Gyrus	R	46	-64	-8	37	0.011
248	Parahippocampal Gyrus	L	-22	4	-22	34	0.011
208	Fusiform Gyrus	L	-50	-54	-10	37	0.010
<i>Set I: Linguistic level: Lexico-Semantics; AoA: Late; Contrast: L1>L2</i>							
1856	Inferior Frontal Gyrus (orb.)	L	-48	38	-10	47	0.021
352	Inferior Frontal Gyrus (orb.)	R	50	22	-10	38	0.013
152	Caudate	R	14	18	0	-	0.011
<i>Set J: Linguistic level: Lexico-Semantics; AoA: Early; Contrast: L2>L1</i>							
1368	Insula	L	-34	16	-4	-	0.011
248	Inferior Frontal Gyrus (tri.)	L	-50	40	2	45	0.007
152	Middle Occipital Gyrus	R	46	-70	14	19	0.008
<i>Set K: Linguistic level: Lexico-Semantics; AoA: Late; Contrast: L2>L1</i>							
9040	Precentral Gyrus	L	-56	10	10	6	0.027
3920	Superior Frontal Gyrus	L	-4	22	48	8	0.033
936	Insula	R	30	20	-8	-	0.012

648	Inferior Frontal Gyrus (tri.)	L	-46	32	-14	45	0.018
600	Pallidum	R	-14	8	-6	-	0.018
504	Pallidum	L	-14	6	-2	-	0.014
432	Insula	L	-32	26	-6	-	0.015
200	Inferior Frontal Gyrus (orb.)	L	-46	48	-8	47	0.011
168	Cerebellum	R	4	-54	-16	-	0.011

Set L: Linguistic Level: Switching; AoA: Early

2256	Superior Frontal Gyrus	R	4	20	56	8	0.028
1080	Inferior Frontal Gyrus (op.)	L	-58	10	12	44	0.017
728	Middle Occipital Gyrus	L	-18	-88	-6	18	0.019
568	Middle Occipital Gyrus	R	48	-76	4	19	0.015
544	Superior Temporal Gyrus	R	66	-16	-6	22	0.014
544	Superior Frontal Gyrus	R	24	32	46	8	0.027
416	Fusiform Gyrus	L	-38	-80	-8	19	0.016
352	Precentral Gyrus	L	-52	-2	40	6	0.019
344	Inferior Frontal Gyrus (op.)	R	60	22	18	44	0.015
336	Cerebellum	L	-44	-66	-16	-	0.018
296	Caudate	L	-12	22	-4	-	0.014
240	Middle Frontal Gyrus	R	36	28	44	9	0.014
232	Cuneus	R	10	-100	16	18	0.016
216	Middle Frontal Gyrus	L	-46	20	22	46	0.014
176	Inferior Frontal Gyrus (tri.)	R	64	28	0	45	0.012

Set M: Linguistic Level: Switching; AoA: Late

1912	Precuneus	L	-12	-68	50	7	0.018
1768	Anterior Cingulate Gyrus	L	-2	14	26	24	0.025
1240	Lingual Gyrus	L	-8	-96	0	17	0.022
1032	Precuneus	R	6	-70	42	7	0.024
808	Inferior Frontal Gyrus (op.)	L	-50	14	20	44	0.019
520	Supplementary Motor Area	R	2	2	64	6	0.017
512	Insula	R	32	22	-2	-	0.014
456	Inferior Frontal Gyrus (op.)	R	32	14	30	44	0.017
416	Cuneus	R	22	-98	8	17	0.015
408	Inferior Parietal Lobule	L	-42	-54	46	40	0.017
296	Cerebellum	L	-26	-78	-12	19	0.014
288	Precentral Gyrus	L	-50	-8	42	4	0.015
256	Cerebellum	L	-34	-64	-32	-	0.013
248	Inferior Frontal Gyrus (op.)	L	-46	6	32	44	0.013
224	Precuneus	R	20	-66	24	7	0.015
208	Angular Gyrus	L	-50	-54	34	39	0.014
160	Fusiform Gyrus	R	32	-80	-12	19	0.013

Table 2c. Results of activations for Language Control (Switching) collapsed over age of acquisition

(picture-naming tasks only)

Volume (mm ³)	Region	L/R	MNI Coordinates			BA
			x	y	z	
<i>Supplementary Set: Linguistic Level: Switching (only naming)</i>						
1344	Superior Frontal Gyrus	R	6	20	56	0.018
1288	Inferior Frontal Gyrus (op.)	L	-58	10	12	0.017
1040	Postcentral Gyrus	R	-52	-4	40	0.021
1008	Cuneus	L	10	-100	14	0.017
928	Supplementary Motor Area	L	2	2	64	0.018
904	Calcarine Fissure	L	-8	-96	0	0.018
776	Fusiform Gyrus	L	-40	-80	-8	0.021
624	Precuneus	R	-10	-72	36	0.015
504	Inferior Occipital Gyrus	R	32	-80	-10	0.016
328	Lingual Gyrus	L	-18	-90	-4	0.015
328	Supplementary Motor Area	L	-12	22	66	0.015

312	Fusiform Gyrus	L	-26	-78	-12	0.014
304	Insula	R	34	18	4	0.014
288	Inferior Occipital Gyrus	R	46	-78	-6	0.015
272	Precentral Gyrus	L	-36	2	42	0.013
256	Superior Temporal Gyrus	R	66	-14	-4	0.015
248	Caudate	L	-12	22	-4	0.016
232	Middle Occipital Gyrus	R	48	-76	4	0.016
232	Cuneus	R	20	-66	24	0.015
176	Middle Cingulate	L	-2	-36	38	0.011

Figure 1. PRISMA flow diagram of the literature search. PRISMA = Preferred reporting items for systematic reviews and meta-analyses (<http://www.prismastatement.org/>).

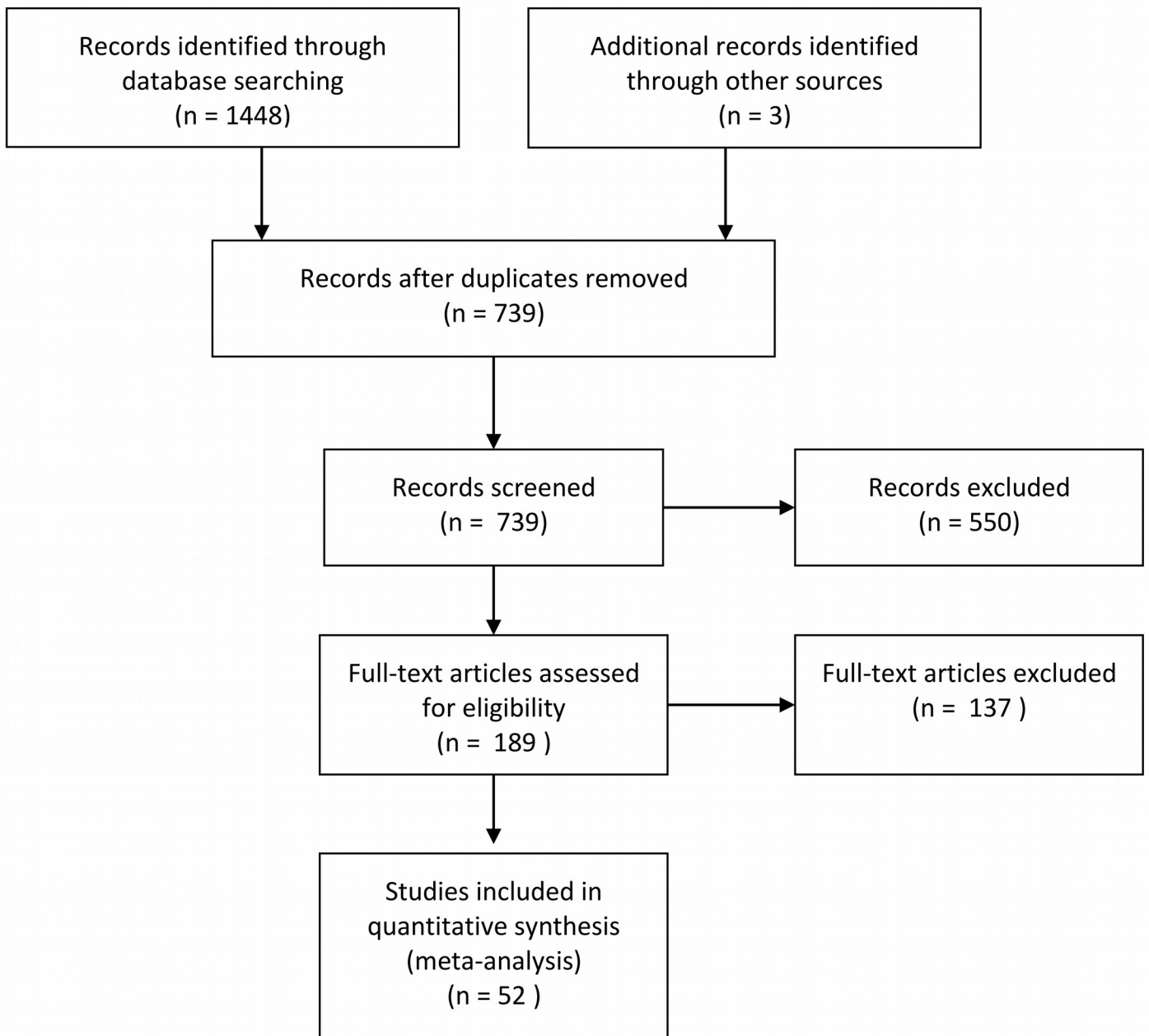


Figure 2. Lexico-semantic. a) Activations collapsed over Age of Acquisition (AoA); red = L1>L2, blue = L2>L1; b) Activations for early (red) and late (blue) bilinguals (L1>L2); c) Activations for early (red) and late (blue) bilinguals (L2>L1)

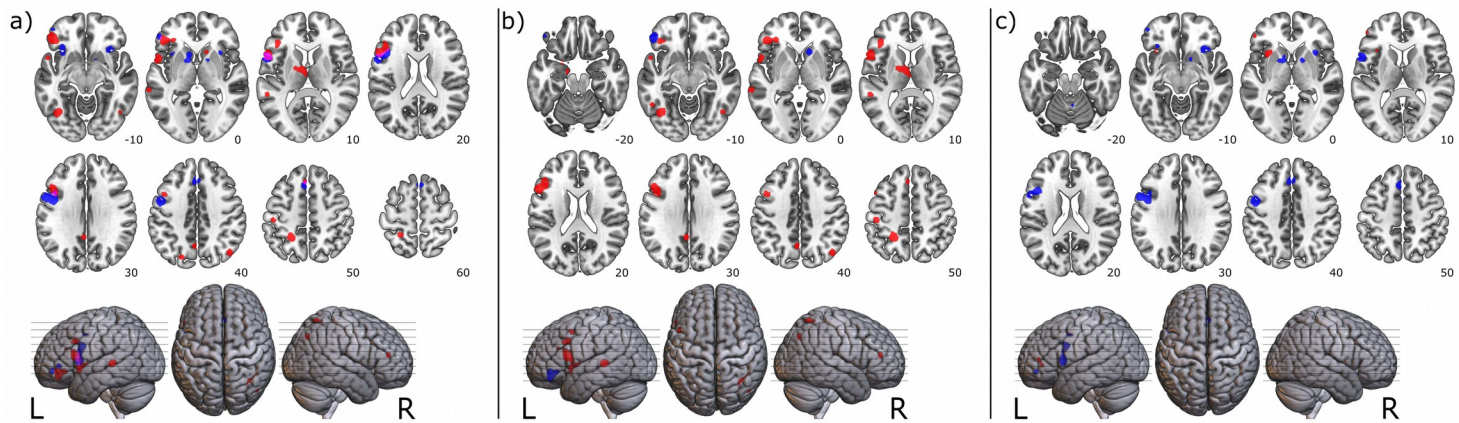


Figure 3. Grammar. Activations are collapsed over Age of Acquisition (AoA). Red = L1>L2; Blue = L2>L1

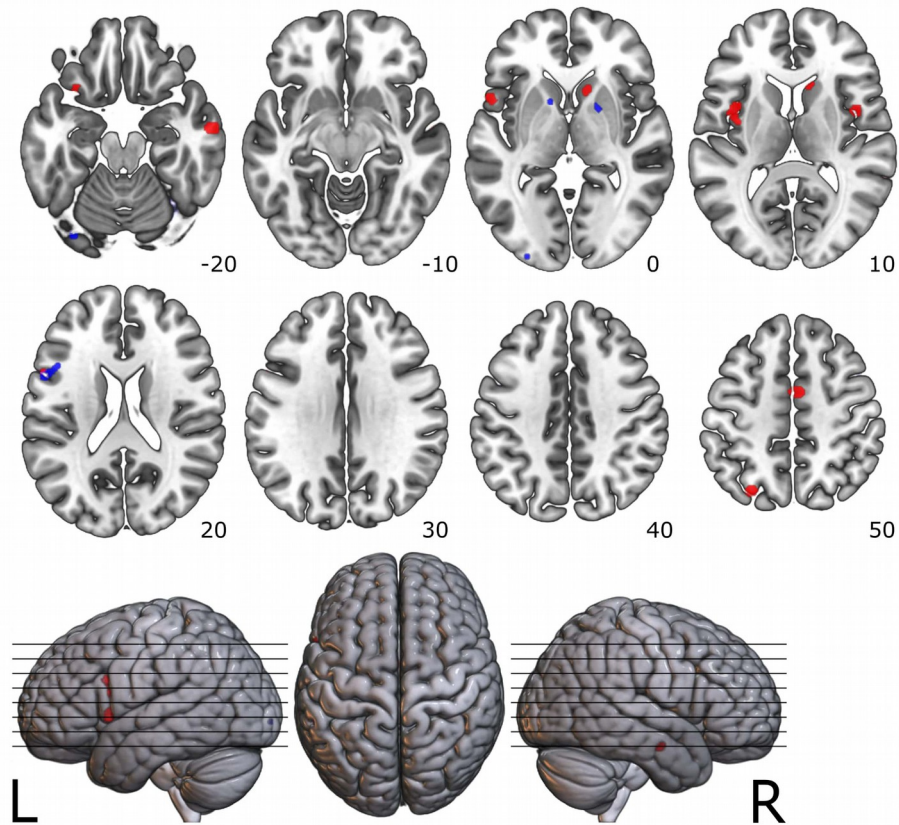


Figure 4. Phonology. Activations are collapsed over Age of Acquisition (AoA). Red = L1>L2; Blue = L2>L1

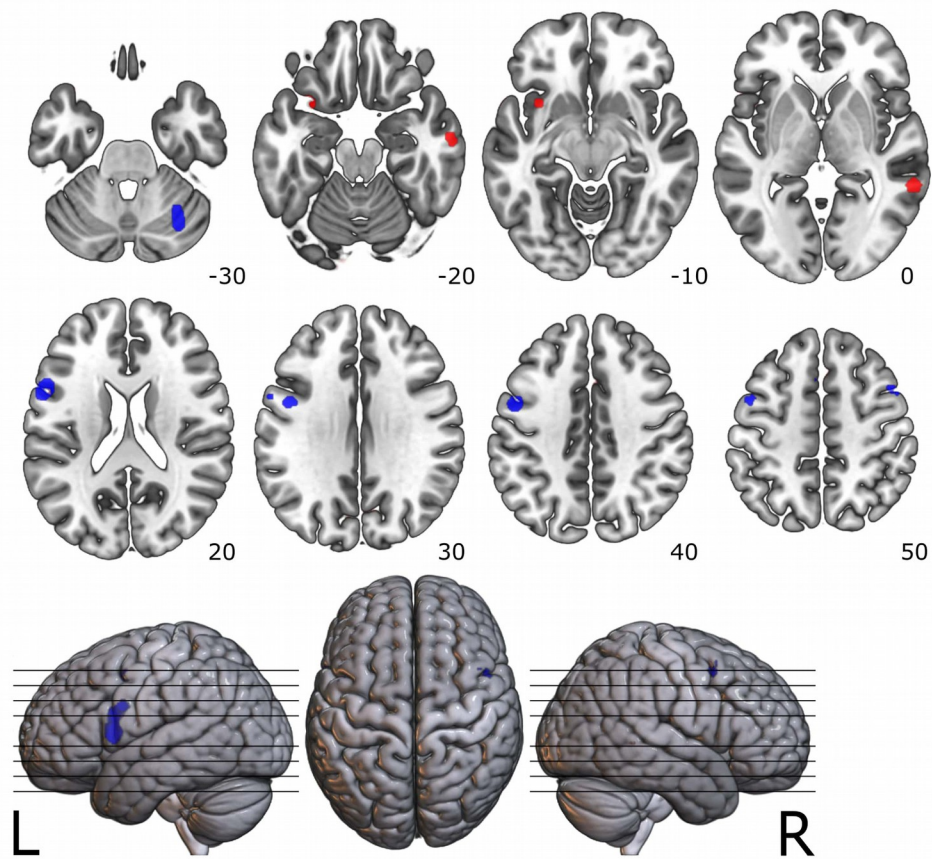
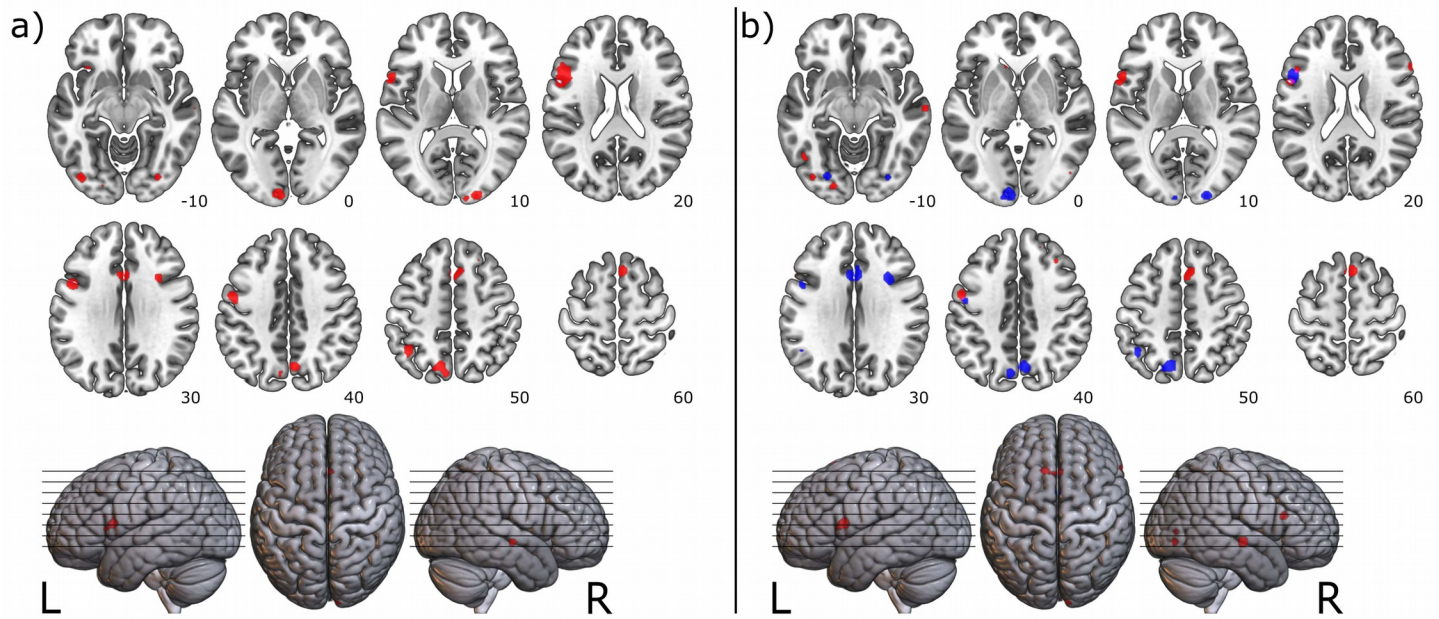


Figure 5. Language Control (Switching); a) Activations collapsed over Age of Acquisition (AoA); b) Activations for early (red) and late (blue) bilinguals



Footnotes

¹ A contrast is the difference in BOLD signal between two experimental conditions.