

PERSPECTIVE

Neuroimaging of language control in bilinguals: neural adaptation and reserve

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Speaking more than one language demands a language control system that allows bilinguals to correctly use the intended language adjusting for possible interference from the non-target language. Understanding how the brain orchestrates the control of language has been a major focus of neuroimaging research on bilingualism and was central to our original neurocognitive language control model (Abutalebi & Green, 2007). We updated the network of language control (Green & Abutalebi, 2013) and here review the many new exciting findings based on functional and structural data that substantiate its core components. We discuss the language control network within the framework of the adaptive control hypothesis (Green & Abutalebi, 2013) that predicts adaptive changes specific to the control demands of the interactional contexts of language use. Adapting to such demands leads, we propose, to a neural reserve in the human brain.

Keywords: language control, bilingualism, neural adaptation, neural reserve

Introduction

Humans use language to coordinate actions in the world. The effective use of language demands a control system that adjusts utterances to circumstance and aborts planned utterances if necessary. Speakers of two or more languages have additional linguistic means to coordinate actions with others but *a priori* there is no reason to presume that the neural basis of language control differs between monolingual and bilingual speakers. However, the use of two or more languages not only affords novel opportunities for language use and interaction, it also imposes additional demands on the control system. Understanding how the brain orchestrates its response to such demands has been a major focus of neuroimaging research on bilingualism (Abutalebi & Green, 2007; Abutalebi, 2008; Hervais-Adelman, Moser-Mercer & Golestani, 2011; Luk, Bialystok, Craik & Grady, 2011). Since the publication of our original neurocognitive language control model (Abutalebi & Green, 2007) many new exciting findings based on structural and functional data have been published in this field and we updated the model of the language control network and proposed the ‘adaptive control hypothesis’ that predicts that the language control network adapts to the specific demands of interactional contexts in which the languages are used (Green & Abutalebi, 2013).

Such adaptation may have narrow consequences: for example, it may lead bilingual speakers to become

more proficient at handling linguistic interference (e.g., overcoming competition from the first language name of an object one wishes to name in the second language) but not to advantages in controlling other kinds of non-verbal interference (for example, interference on a Simon-type task). However, the control of language, as we have argued previously (Green, 1986; 1998; Abutalebi & Green, 2007), is likely to recruit evolutionary earlier systems (subcortical structures and the cerebellum) that subserve the control of action in general (Green & Abutalebi, 2013). Cognitive control is required any time an habitual action must be overcome to achieve a preferable outcome, to resist interference, or to respond effectively to a change in the environment. In consequence, the adaptive control hypothesis predicts that effects attributable to bilingualism may lead to correlated changes in other non-verbal domains. We allude to a burgeoning research area on non-verbal control but focus on the clinical implications for cognitive decline such as the potential neuro-protective effects of lifelong bilingualism. Such effects may be detectable as structural adaptive changes in the brain. Structural information informs us about the long-term effects of adaptation and is more informative than functional data because a decrease in structural integrity is usually observed in degenerative diseases of the brain such as dementia (Perani & Abutalebi, 2015). In the present review, we first illustrate the neural regions involved in language control as reported by both functional and structural neuroimaging studies. In doing

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so we update and bolster the neural basis of our model of the language control network. In the second part, we focus on the adaptation of this control network and its implication on neural reserve as reported by structural brain data.

The neural basis of language control

The cognitive processes underlying language control cover the intention to speak in a given language, selection of the target response (the word in the intended language), inhibition of words from the non-target language, and monitoring speech for potential intrusions (viable candidate words in the other language) (Costa, Miozzo & Caramazza, 1999; Kroll, Bobb & Wodniecka, 2006; Abutalebi & Green, 2007) as well as language disengagement and engagement (i.e., ceasing to speak in one language and switching to another, Green & Abutalebi, 2013). A network of cortical and subcortical brain areas, tightly related to executive control, orchestrates the above-mentioned processes. This network is built up from the dACC/pre-SMA complex (i.e., dorsal anterior cingulate cortex/pre-supplementary motor area), the left prefrontal cortex, the left caudate (LC) and the inferior parietal lobules bilaterally (Abutalebi & Green, 2007) together with control input from the right prefrontal cortex, the thalamus and the putamen of the basal ganglia and the cerebellum (Green & Abutalebi, 2013) and see Figure 1 for illustration. We discuss each of these areas in turn and data that bear on their operation.

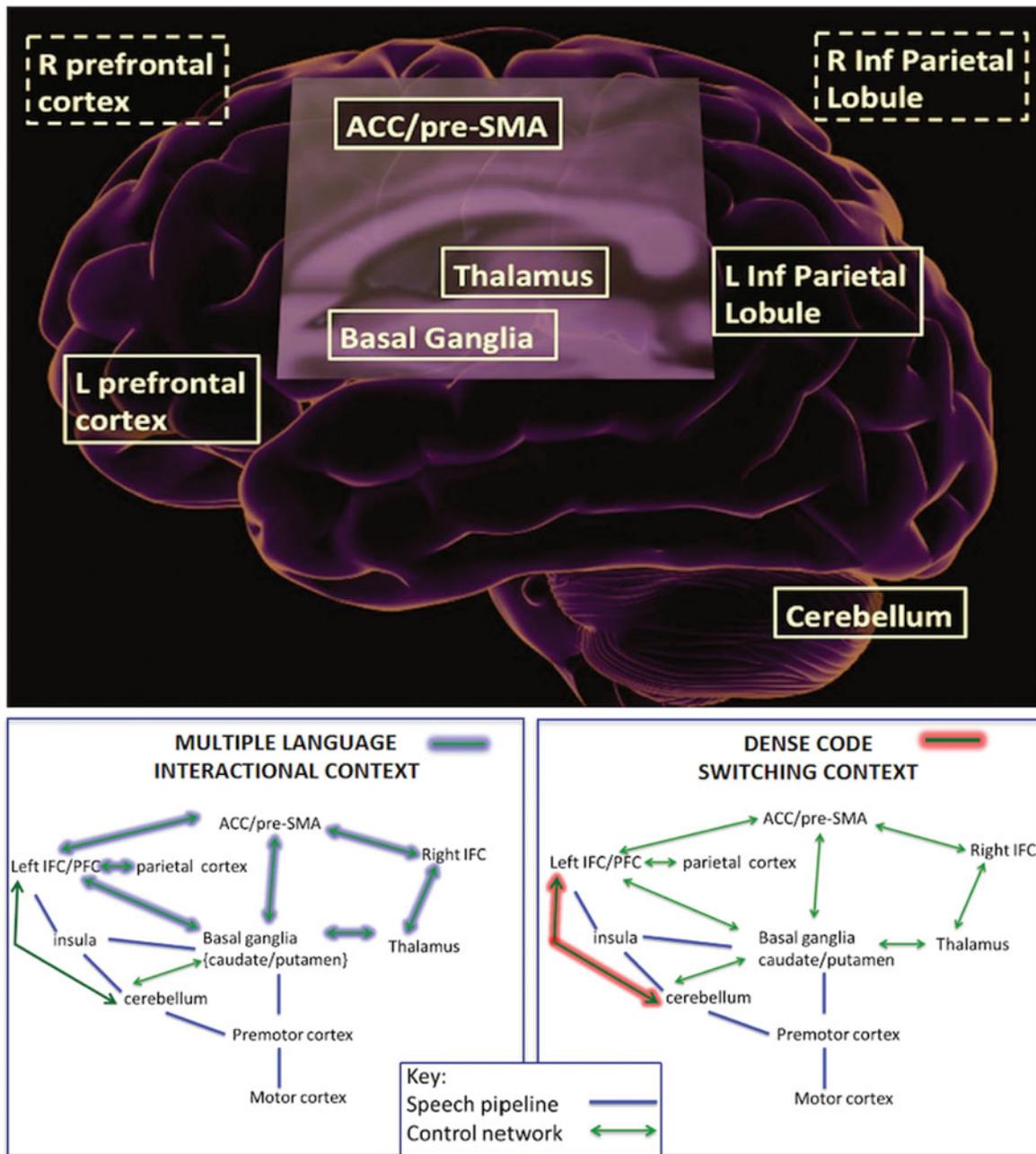
The dACC/pre-SMA complex

ACC (anterior cingulate cortex) activity is usually related to conflict and error monitoring and its involvement in cognitive control is quite unequivocal (Botvinick, Nystrom, Fissell, Carter & Cohen, 1999; Botvinick, Braver, Barch, Carter & Cohen, 2001). Both the dorsal ACC (dACC) and the pre-supplementary motor area (pre-SMA) are associated with conflict monitoring with the latter area (i.e., pre-SMA) also involved in initiating speech in language switching (see Luk, Green, Abutalebi & Grady, 2012 for further discussion). Functional activity of the dACC/Pre-SMA has been consistently reported during language switching and language selection tasks in bilinguals (Abutalebi, Brambati, Annoni, Moro, Cappa & Perani, 2007; Wang, Xue, Chen, Xue & Dong, 2007; Abutalebi, Annoni, Zimine, Pegna, Seghier, Lee-Jahnke, Cappa & Khateb, 2008; Abutalebi, Della Rosa, Green, Hernandez, Scifo, Keim, Cappa & Costa, 2012; Guo, Liu, Misra & Kroll, 2011; Hosoda, Hanakawa, Nariai, Ohno & Honda, 2012; Branzi, Della Rosa, Canini, Costa & Abutalebi, 2015) and for cross-linguistic conflict resolution (Rodriguez-Fornells, van der Lugt, Rotte, Britti, Heinze & Muentel, 2005; van Heuven,

Schriefers, Dijkstra & Hagoort, 2008). Recently, it has been shown that the dACC/Pre-SMA plays a major role in tasks involving conflict resolution subserving selection of the targeted response in both linguistic and non-linguistic contexts (Abutalebi et al., 2012; Branzi et al., 2015). In the Abutalebi et al. study (2012) an advantage on a flanker task was reported for bilinguals as compared to monolinguals. Moreover, bilingual performance correlated with increased grey matter density in the dorsal ACC, and functional activity indicated a more efficient use of this structure by bilinguals. Interestingly, in a different study with elderly subjects, Abutalebi, Guidi, Borsa, Canini, Della Rosa, Parris and Weekes (2015a) reported that increased grey matter density in the dorsal ACC is also present for senior bilinguals as compared to age-matched monolinguals. As to functional activity, however, dACC/Pre-SMA activity is not limited to bilingual language processing but may be found also in monolinguals. For example, Abutalebi, Della Rosa, Ding, Weekes, Costa and Green (2013a) reported that during language switching bilinguals, when switching from L2 to L1, activate the dACC/Pre-SMA to the same degree as do monolinguals, when switching from verbs to nouns in their single language. This evidence underlines that the dACC/Pre-SMA is commonly used for monitoring correct responses during language conditions where a certain amount of control is needed such as in a switching task. However, bilinguals develop more grey matter density in this area because they are constantly faced with language conflict, something that the monolingual brain rarely experiences.

The left prefrontal cortex

A complete description of the functions of the left prefrontal cortex would go beyond the scope of this review, but undoubtedly there is ample consensus that the prefrontal cortex is a chief player in cognitive control (Miller & Cohen, 2001). In more general terms, it has been suggested that the dorsolateral prefrontal cortex (DLPFC) is tuned for adaptation of response-sets as a function of efficient selection of the target stimulus in contexts with interfering information (Ridderinkhof, Ullsperger, Crone & Nieuwenhuis, 2004; Collette, Olivier, Van der Linden, Laureys, Delfiore, Luxen & Salmon, 2005). The prefrontal cortex comprises many different areas: chief among them the superior, middle, and inferior frontal gyri, the frontal eye fields and the orbitofrontal cortex. For bilinguals, the left middle and inferior frontal gyrus (LIFG) are thought to be part of the language control network, specifically involved in overriding automatic processes and controlling interference from irrelevant information (such as prepotent responses from the dominant language). The LIFG is also commonly involved in bilingual language control as evidenced in studies



Note that boxes with dotted lines denote brain regions in the right hemisphere (R = right; L = left; Inf = inferior; IFC = inferior frontal cortex).

Figure 1. Brain Regions related to language control (top) and their functional interactions in two different situational contexts (bottom) as outlined by the adaptive control model (Green & Abutalebi, 2013). In a multiple language interactional context (bottom, left) both languages can be active and in order to speak in one language the speaker has to maintain the goal, detect salient cues, control interference and eventually inhibit responses with task engagement and disengagement. This engages more extensively the following components of the control network: bilaterally the inferior frontal and parietal cortices, the ACC/pre-SMA, and the basal ganglia and the thalamus. The network is still engaged in a dense code-switching context (bottom, right) but since this particular condition relies also on opportunistic planning, a cerebellar-left prefrontal connection is heavily engaged (see for more details, Green & Abutalebi, 2013).

investigating language switching (Hernandez, Martinez & Kohnert, 2000; Lehtonen, Laine, Niemi, Thomson, Vorobyev & Hughdal, 2005; Abutalebi et al., 2008; van Heuven et al., 2008; Branzi et al., 2015). Left prefrontal

related activity has been reported not only for language switching tasks (where the need of language control is maximized) but also during simple language production tasks such as word generation, picture naming and verbal

fluency (see Abutalebi & Green, 2007). The interesting finding is that these areas are more engaged when it comes to producing the weaker language (typically L2) (De Bleser, Dupont, Postler, Bormans, Speelman, Mortelmans & Debrock, 2003; Kovelman, Baker & Petitto, 2008; Marian, Spivey & Hirsch, 2003; Parker Jones, Green, Grogan, Pliatsikas, Filippopolitis, Ali, Lee, Ramsden, Gazarian, Prejawa, Seghier & Price, 2012; Perani, Abutalebi, Paulesu, Brambati, Scifo, Cappa & Fazio, 2003). We referred to this effect as the ‘prefrontal effect’ in bilingual language production and it mirrors the cognitive effort bilinguals have to put in whenever processing the weaker language (Abutalebi & Green, 2007). This extra effort is necessary to select responses from the weaker language. Indeed, contrary to the dACC/Pre-SMA, the left prefrontal cortex is not involved in conflict monitoring but rather in the complicated process of response control such as response selection and suppression (Green & Abutalebi, 2013).

The right inferior frontal cortex

In recent years, evidence has been mounting that the left prefrontal cortex is more related to response selection and its right counterpart is rather associated to response inhibition (Aron, Behrens, Smith, Frank & Poldrack, 2007). It is plausible then that its engagement is triggered during language switching and indeed it is connected via the thalamus to two subcortical nuclei structures implicated in language control (caudate and putamen). In detail, the right inferior frontal gyrus has been related to domain-general inhibitory control (Aron, Robbins & Poldrack, 2004; Aron, Robbins & Poldrack, 2014). Related to our purposes is work indicative of the after-effects of naming in one language rather than another. Videsott, Herrnberger, Hoenig, Schilly, Grothe, Wiater, Spitzer and Kiefer (2010) reported the surprising datum that during a naming task in multilinguals (Videsott et al., 2010), the right middle frontal gyrus is more engaged when it comes to naming in the stronger languages (L1 and L2) while it was less active during naming in the weaker languages such as L3 and L4. Moreover, activity in the right dorsolateral prefrontal cortex specifically correlated to naming accuracy as a measure of language proficiency with the strong languages but not with the weaker languages. The authors did not further discuss the exact mechanism of how this finding related to response inhibition. However, a direct examination of the ‘after effects’ of naming (i.e., naming a set of pictures in L1 after having named them in L2 and vice versa) does suggest an explanation for right prefrontal engagement (Branzi et al., 2015; and see below for discussion). Naming in L1 after having named in L2 was significantly associated to increased activity in the right prefrontal cortex while an opposite pattern of activity (i.e., significant deactivation)

was found for naming in L2 after having named in L1. One explanation here is that the extra activity observed for naming in L1 after having named in L2 arises because of the necessity to override the inhibition of the prepotent L1 during the previous L2 naming block.

The inferior parietal lobules

The inferior parietal lobules comprise two distinct gyri – the supramarginal gyrus and the angular gyrus – and it has been well established that the inferior parietal lobules are recruited in the context of attentional tasks during short-term memory processing (Majerus, D’Argembeau, Martinez Perez, Belayachi, Van der Linden, Collette, Salmon, Seurinck, Fias & Maquet, 2010), for reevaluating conflicting choices (Rushworth, Paus & Sipila, 2001) and for detecting events captured by attentional functions (Kiehl, Stevens, Laurens, Pearlson, Calhoun & Liddle, 2005). The most inferior portion of the inferior parietal lobules (i.e., the temporo-parietal junctions) has been reported to be involved in bottom-up attentional orienting (Shomstein, 2012).

In the history of bilingualism, the left angular gyrus has been granted a particular status: it was labeled already in the 1920s as the multilingual talent area (Pötzl, 1925). Pötzl reported that bilinguals and multilinguals with lesions to this area were not able to switch among their languages. Based on this clinical evidence and on functional neuroimaging work on language switching (e.g., Price, Green & von Studnitz, 1999), Abutalebi & Green (2008) in their neurocognitive model of language switching proposed a characterization of the inferior parietal lobules for language control. During language switching, the left inferior parietal lobule would be involved in biasing language selection away from the language not in use, while its right counterpart would be responsible in biasing selection towards the language in use (Abutalebi & Green, 2008).

As to structural neuroimaging, Mechelli, Crinion, Noppeney, O’Doherty, Ashburner, Frackowiack and Price (2004) reported higher grey matter density in the posterior region of the supramarginal gyrus for young adult bilinguals as compared to monolinguals. Further, higher L2 proficiencies in bilinguals correlated to increased grey matter density – a finding most plausibly attributed to an increase in L2 vocabulary knowledge. Likewise, Abutalebi, Canini, Della Rosa, Green and Weekes (2015b) confirmed the persistence of this correlational effect also for bilingual seniors (as compared to monolinguals). The effects of language proficiency upon this area were also reported in a follow-up study with multilingual children (Della Rosa, Videsott, Borsa, Canini, Weekes, Franceschini & Abutalebi, 2013): increased proficiency correlated with increasing grey matter densities over a one year period. Further research is needed to establish

the functional roles of different regions within the supramarginal gyrus in order to establish a more direct link to structural changes and the demands of speech production in bilingual speakers.

Subcortical structures: the left caudate, putamen and thalamus

Traditionally, subcortical structures (i.e., basal ganglia) are associated with motor control, emotional control and cognitive control such as cognitive sequence planning (Graybiel, 2000). Through its linkage to anterior and posterior regions of LIFG (Ford, Triplett, Sudhyadhom, Gullett, McGregor, Fitzgerald, Mareci, White & Crosson, 2013) the thalamus is likely to play an important role in language production in bilingual speakers by aiding the selection of relevant lexical and semantic representations. For present purposes though we focus on two subcortical nuclei that have been consistently advocated to be involved in language control in bilinguals: the left head of the caudate nucleus (LC) and the left putamen. As to the LC, it should be mentioned that breakdown of language control has been frequently observed after lesions to this structure (see Green & Abutalebi, 2008, for review). As to imaging studies, experimental paradigms that do rely on control of languages such as translation (Price et al., 1999; Lehtonen et al., 2005), language selection (Crinion, Turner, Grogan, Hanakawa, Noppeney, Devlin, Aso, Urayama, Fukuyama, Stockton, Usui, Green & Price, 2006; Abutalebi et al., 2008; Branzi et al., 2015), language switching in production (Zou, Ding, Abutalebi, Shu & Peng, 2012; Abutalebi et al., 2013a) and in comprehension (Abutalebi et al., 2007) are all characterized by the specific engagement of LC activity. Contrary to the ACC activity which seems not to be specific to bilingual language processing, LC activity has been reported to be specific under the tasks studied (Abutalebi et al., 2013a). The authors compared a group of multilinguals to a group of monolinguals during a switching paradigm (switching between languages for multilinguals and switching between nouns and verbs of the single language for monolinguals). Both groups activated similarly the ACC (as measured by the BOLD effect) but a different picture emerged for the LC: monolinguals deactivated the LC while multilinguals actively engaged the LC. Moreover, the lower the proficiency of their languages was, the more LC activity was necessary.

Apart from the LC, the putamen is involved during language production. Left putaminal activity may reflect control of articulatory processes (see Abutalebi et al., 2013b; and also Burgaleta, Sanjuán, Ventura-Campos, Sebastian-Galles & Ávila, 2016, for volumetric increases in this structure, along with the thalamus in simultaneous bilinguals). Indeed, in highly demanding language control conditions, such as simultaneous interpreting,

activation in the putamen varied with the duration of the overlap between listening and speaking (Hervais-Adelman, Moser-Mercer, Michel & Golestani, 2014). Such modulation most likely reflects the extra effort required to suppress at the output level the words of the language not in use while simultaneously hearing speech in that language.

The cerebellum

As we noted above, language control recruits phylogenetically earlier structures involved in the control of action. The cerebellum is a further critical structure. It is linked to all the key regions of the language control network (Green & Abutalebi, 2013) including the right inferior frontal cortex (e.g., Aron, Behrens, Smith, Frank & Poldrack, 2007) which, via the thalamus, directly accesses caudate and putamen regions of the basal ganglia (Smith, Surmeier, Redgrave & Kimura, 2011). Formerly treated as primarily concerned with motor control, researchers now recognize its contribution to a wide range of language and cognitive functions (see Tyson, Lantrip & Roth, 2014 for a review). A fronto-cerebellar circuit, for example, links the right cerebellum to the left inferior frontal cortex (Krienen & Buckner, 2009). Lack of cerebellar activation impairs speech production in bilingual speakers indicating its important contribution to morphosyntactic processing (Marien, Engelborghs, Fabbro & De Deyn, 2001; Silveri, Leggio & Molinari, 1994). Adaptive changes in the cerebellum might then be expected as non-native speakers acquire the grammatical rules of their L2. Indeed grey matter cerebellar volume, though not specifically right cerebellar volume, in immersed, proficient L2 speakers does correlate with efficient processing of L2 morphosyntax (Pliatsikas, Johnstone & Marinis, 2014). The cerebellum's precise functional contributions to morphosyntactic processing are unknown. Functional imaging studies using sentence production and comprehension tasks have yet to elucidate these but it is plausible that cerebellar activation mediates the prediction of future input based on past knowledge (Ito, 2008). In fact, disrupting right cerebellar activation (using repetitive transcranial magnetic stimulation) does delay eye movements to a target object predicted by sentence content (Lesage, Morgan, Olson, Meyer & Miall, 2012). The ability to make predictions entails maintaining an ongoing representation. Effective maintenance ensures resistance to interference and may underlie the finding that grey matter density in a region of the right cerebellum significantly predicts the ease with which bilingual speakers resist speech interference from their first language while comprehending an utterance in their second language (Filippi, Richardson, Dick, Leech, Green, Thomas & Price, 2011).

Distinct levels of control?

One interesting question is, of course, if language control is exerted at a single level or at multiple levels (see De Groot & Christoffels, 2006). The ongoing debate is whether language control acts upon a specific stimulus to be selected, such as a single word, or rather acts upon the entire language system. One way to investigate this is to detect whether the language control system is differently engaged when control is exerted upon a restricted set of lexical representations that were, for instance, previously used in a paradigm where both languages have to be alternatively used (such as picture naming in L1 and L2). This would provide a glimpse of local control. In detail, local control properly refers to the after-effects of naming a given picture in one language upon subsequent naming of that very same picture in the other language.

On the other hand, the notion of global control refers to when there is a switch in language to naming stimuli not previously seen or named. In this case control would be exerted upon the whole language system (i.e., global control) because stimuli are new and supposedly activate the whole language system (De Groot & Christoffels, 2006), as opposed to control necessary to manage stimuli previously named in the other language (i.e., translation equivalents).

Local versus global control was assessed in the study by Branzi et al. (2015) alluded to above. An interesting functional dissociation between the brain areas responsible for language control was reported: the LIFG, RIFG, LIPL and RIPL were all found to be engaged in a similar fashion for both local and global control, especially for naming in L1. Presumably, naming in L1 (after naming in L2) is enacted by the activity in these areas ruled by demands to override previous inhibition of L1 during a preceding L2 trial, independently of the fact of whether control is exerted at the local or global level. On the other hand, activity of the dACC/pre-SMA complex was responsive only for local control and not for global control. In other words, dACC/pre-SMA activity is not strictly necessary for monitoring the entire language system but acts only on a subset of lexical stimuli (if these were used previously in the other language). Interestingly, the dACC/pre-SMA was more active for local control in L2, and not for L1, indicating that naming in L2 (after naming in L1) relies more on monitoring processes. The authors proposed that language control in bilinguals might be hierarchically organized with the dACC/pre-SMA acting as the supervisory attentional system, recruited for increased monitoring demands such as local control in L2. On the other hand, prefrontal, inferior parietal areas and the caudate would act as the response selection system, tailored for language selection for both local and global control.

Neural adaptation and neural reserve in bilinguals

It is now well reported from different populations over the world that bilingualism delays the onset of dementia by an average of 4 to 5 years (Bialystok et al., 2007; Alladi, Bak, Duggirala, Surampudi, Shailaja, Kumar Shukla, Chaudhuri & Kaul, 2013; Woumans, Santens, Sieben, Versijpt, Stevens & Duyck, 2015). Such neuroprotective effects plausibly derive from the adaptive changes required to represent and use two languages. Structural neuroimaging is a powerful tool to measure such adaptive neural changes and a number of studies now establish that the human brain adapts to the increased demands of speaking more than one language with the effects of adaptation that are most influential in areas related to language control. Such changes have been detected in the course of language learning (for a review, see Li, Legault & Litcofsky, 2014). In the left prefrontal cortex, for example, Stein, Federspiel, Koenig, Wirth, Strik and Wiest (2012) reported increased grey matter density in bilinguals (as compared to monolinguals) that correlated with an increase in L2 proficiency. As discussed above, Mechelli et al. (2004) found increased grey matter density in LIPL that correlated with L2 vocabulary knowledge. Grey matter increase in the LIPL is not restricted to individuals with high L2 proficiency but has also been associated to better performance on executive tasks in multilingual children followed-up over a one-year period (Della Rosa et al., 2013). As to the ACC, increased grey matter density correlated with better conflict monitoring in bilinguals but not in their monolingual counterparts (Abutalebi et al., 2012). Additionally, increased grey matter density in bilinguals as compared to monolinguals has also been reported in regions of the basal ganglia such as the left caudate (Zou et al., 2012) and left putamen (Abutalebi et al., 2013b). We observed above that grey matter density in a right cerebellar region predicted resistance to between-language sentence level interference in bilingual speakers (Filippi et al., 2011). These are only some of the structural neuroimaging studies available but they indicate adaptive change consequent on the learning or use of more than one language that is detectable in regions mediating language control. We do not have a deep understanding of which factors in language use trigger adaptive change but it is reasonable to assert that these neural changes potentially express themselves in a neural protection of the aging brain. Investigating elderly individuals with neuroimaging techniques is essential to testing this possibility.

To date, there are a handful of studies on structural changes in the aging bilingual brain (see Perani & Abutalebi, 2015; and Gold, 2015 for a review). Among these, Luk et al. (2011), employed diffusion tensor imaging (DTI) to investigate white matter connectivity in 14 bilingual and 14 monolingual senior adults matched

for performance on neuropsychological tests. Of interest, higher values of fractional anisotropy were found for bilinguals than monolinguals. The significant differences were found in the corpus callosum, extending anteriorly to the white matter of the frontal lobes. As to the significance of these findings, one should consider that progressive disruption of white matter is typically observed during aging (Pfefferbaum, Adalsteinsson & Sullivan, 2005; Gunning-Dixon, Brickman, Cheng & Alexopoulos, 2009). Thus, the study of Luk et al. (2011) shows that bilingualism may delay the progressive loss of white matter and hence protects the aging brain against the effects of loss of white matter such as cognitive decline.

Related to the findings of Luk et al. (2011) is the recent evidence that aging bilinguals compared to matched monolinguals have increased grey matter along the entire extension of the ACC, starting from its dorsal region and extending towards its ventral region (Abutalebi et al., 2015a). The ACC surrounds the corpus callosum and many of the cingulate projections pass through the corpus callosum (Rash & Richards, 2001).

In another study investigating grey matter density, Abutalebi, Canini, Della Rosa, Sheung, Green and Weekes (2014) reported that aging bilinguals have increased grey matter compared to monolinguals (matched for age, education, socio-economic status, and cognitive testing) bilaterally in the temporal poles and the orbitofrontal cortex. Overall, bilinguals showed also fewer effects of aging upon the brain. Strikingly, for the temporal poles (brain regions linked to lexical retrieval and semantics), the authors also reported that L2 proficiency correlated with grey matter volume: Increasing L2 proficiency predicted increasing grey matter volume. In other words, bilinguals fluent in their second language appeared to have the greatest neuroprotection. Again, it is worth underlining that the temporal poles, along with the orbitofrontal cortex, are among the first cortical areas that suffer from physiological aging-related brain atrophy (Kalpouzos, Chetelat, Baron, Landeau, Mevel, Godeau, Barré, Constans, Viader, Eustache & Desgranges, 2009), and the finding that the effects of bilingualism are most prominent in these regions may eventually explain why the onset of cognitive decline is delayed in bilinguals.

Concerning cognitive decline, it is well known that mild cognitive impairment (MCI) is usually associated with grey matter loss in the inferior parietal lobule (Saykin, Wishart, Rabin, Santulli, Flashman, West, McHugh & Mamourian, 2006; Apostolova, Steiner, Akopyan, Dutton, Hayashi, Toga, Cummings & Thompson, 2007). Indeed, reduced grey matter densities of the inferior parietal lobule are observable even in early stages of dementia (McDonald, McEvoy, Gharapetian, Fennema-Notestine, Hagler Jr., Holland, Koyama, Brewer & Dale, 2009). So it is noteworthy that Abutalebi et al. (2015a) provided direct evidence in an aging population

that bilinguals do not show aging effects bilaterally in the inferior parietal lobules as compared to matched monolinguals.

Conclusions

Language use involves utterance production with conversation as the primary site. If we treat language use as a form of skilled performance, it follows that there is a need for a close analysis of the interactional contexts of language use (Green, 2011). Conversational practices and the recurrent demands they impose are key to understanding how the regions and circuits involved in utterance production are controlled and the adaptive changes that might be expected in the brains of bilingual speakers (Green & Abutalebi, 2013). We need details for example of the extent to which bilinguals code-switch between languages within a conversational turn, restrict use of each language to distinct contexts of use, or use multiple languages in distinct conversational turns to different speakers (see Figure 1, lower diagrams). Research to understand how the bilingual brain adapts and how such adaptive change shapes the language control network contingent on the patterns of long-term use is still in its infancy but we are optimistic that new findings and methods will continue to enrich theoretical understanding and in due course help explicate how bilingual language use contributes to the various genetic and lifestyle factors that form the bases of neuroprotective effects in the elderly.

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