Review

The bilingual brain: Flexibility and control in the human cortex

Augusto Buchweitz [a,*], Chantel Prat [b]

[a] *School of Languages and Brain Institute of Rio Grande do Sul (InsCer), Pontifical Catholic University of Rio Grande do Sul (PUCRS), Porto Alegre, RS, Brazil*
[b] *Department of Psychology and Institute of Learning and Brain Sciences, University of Washington, Seattle, WA, USA*

Abstract

The goal of the present review is to discuss recent cognitive neuroscientific findings concerning bilingualism. Three interrelated questions about the bilingual brain are addressed: How are multiple languages represented in the brain? how are languages controlled in the brain? and what are the real-world implications of experience with multiple languages? The review is based on neuroimaging research findings about the nature of bilingual processing, namely, how the brain adapts to accommodate multiple languages in the bilingual brain and to control which language should be used, and when. We also address how this adaptation results in differences observed in the general cognition of bilingual individuals. General implications for models of human learning, plasticity, and cognitive control are discussed.
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This paper presents a review and discussion of the cognitive neuroscientific findings concerning bilingualism. In it, we review cutting-edge research with the goal of addressing three interrelated questions about the bilingual brain: How are multiple languages represented in the brain? how are languages controlled in the brain? and what are the real-world implications of experience with multiple languages?

The present review capitalizes on what neuroimaging research conducted over the past several decades has taught us about the nature of language and complex human thought processing, namely, that thought processing is accomplished through the functioning of large-scale, highly distributed neural networks. From this viewpoint, we will integrate findings from neuropsychological research about disruptions in bilingual language production (lesion studies) with brain imaging research about the bilingual brain. Taken together, these findings will be used to generate inferences about how the brain adapts to accommodate the use and representation of multiple languages; how this adaptation results in differences observed in the general cognition of bilingual individuals; and how the consequences that bilingualism brings to human cognition can be beneficial in real-world settings. Although the primary goal of this review is to summarize how bilingualism is accomplished at the neural level, it also aims to show that our understanding of

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the cognitive neuroscience of bilingualism has important, more general implications for models of human learning, plasticity, and cognitive control.

1. Background

1.1. Defining bilingualism

Bilingualism is a multi-dimensional human phenomenon. It may be assessed along a continuum of the level of skill development and the frequency of use of the language. There is a practical, current definition of bilingualism put forth by Grosjean, which reads as follows [1,2]: Bilingualism is the regular use of more than one language, and thus bilinguals are people who need and use more than one language in their everyday lives. Bilingualism is also a common, worldwide phenomenon. Recent data by the European Commission [3] show that over half of Europeans can hold a conversation in at least one additional language, and approximately a quarter are able to speak at least two additional languages.

Also, the age at which one learns a second language (age of acquisition) defines *early* and *late* bilinguals. Early bilinguals are those who acquire their second language sometime before the "critical" or "sensitive" period for language learning, typically defined as adolescence; late bilinguals are those who acquire their second language after adolescence. With the help of functional brain imaging, questions about the implications of age of acquisition, language proficiency, and cognitive processes can be addressed in terms of their neural substrates. These factors must be kept in mind in the interest of the review that follows.

1.2. Basic principles of language and the (bilingual) brain

Over the past two decades, the use of neuroimaging methods that measure metabolic activity to study language processes has dramatically increased (see [4] for a review of 100 studies published in 2009 alone). Brain imaging research has helped establish the fact that language processes in both monolinguals and bilinguals are the product of many specialized brain centers working collaboratively. For example, listening to story passages is associated with activation of the primary auditory cortex, of the inferior frontal cortex (associated with syntactic parsing), and of the medial frontal cortex (associated with coherence-monitoring processes), among other areas of the brain [5]. The importance of collaboration among the centers can be inferred by the fact that most linguistic manipulations (e.g., syntactic complexity, phonological challenges in tongue-twister sentences) typically result in changes of activation observed across multiple centers [6–8]. In this sense, the nature of a bilingual's cognitive processing (for example, comparison of the brain activation for reading an alphabetic and a non-alphabetic language) must be reflected in features characterized in the bilingual brain; these features include magnitude and expansion of activation and synchronization of activity in different brain areas (functional connectivity).

One of the core questions with respect to the bilingual brain is whether the neural systems that underpin language representation in each language are separate or overlapping. Bilingual aphasia studies (which generally aimed at investigating language production during patient recovery) showed language deficits isolated to one language and thus suggested that at some level the two languages are distinct in the brain [9,10]. fMRI investigations of bilingual comprehension in healthy bilinguals, however, have demonstrated that there is a large amount of shared representation between two languages, especially in skilled and early bilinguals [11]. One reason why fMRI and neuropsychological studies may seem to diverge in terms of their accounts of neural instantiations of multiple languages is that aphasia/lesion investigations are largely based on the follow-up of the recovery of production, and tend to lend themselves to more modular views of brain functioning (damage to area X results in deficit Y, therefore area X may have been responsible for function Y).

Lesion studies of the bilingual brain show a diverse and heterogeneous pattern of recovery of languages [12]. Approximately half of bilingual patients show parallel recovery of their first and second languages; whereas, the other half recover either the first or the second language first or better [13–15]. It is important to note that Pitres, in the 19th century, had proposed that languages could be localized in similar areas of the cortex and independently impaired by the same lesion [10].

The combination of the study of patients and normal bilinguals has given support to a more dynamic view of bilingual recovery that acknowledges differences between representation and control (language production) in recov-
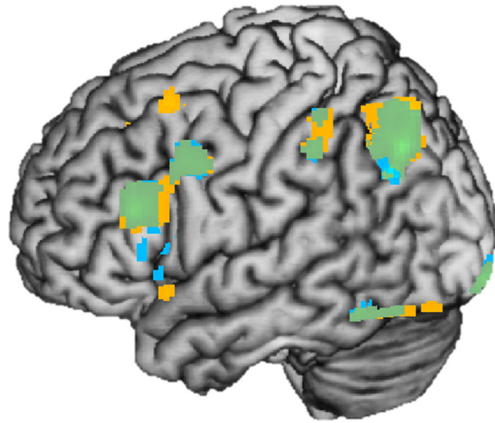
Fig. 1. Network of brain activation showing shared semantic representation for word reading in bilinguals: orange voxels show activation for L2 word reading (English); blue voxels show activation for L1 word reading (Portuguese); green voxels show overlap between L1 and L2 [29]. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

ery patterns [16]. It is the understanding of the difference between representation and control processes that may reconcile the apparently more modular view that stems from lesion studies with the view of a shared representation identified in functional imaging studies of the bilingual brain.

To understand the extent to which multiple language processes rely on shared neural mechanisms, researchers must answer at least two interrelated questions: (1) how are multiple languages represented in the bilingual brain, and (2) how are multiple languages controlled in the bilingual brain? These two questions guide the organization of the present review. The issue of real-world implications is addressed at the end of the review.

2. Neural representation of meaning: one concept, one neural representation

"Common principles underlie the representation of words in the two languages [. . .] and a common tissue underlies both" [17].

The convergence of brain networks engaged for bilingual semantic (conceptual) processes is determined by the level of proficiency of the bilingual [18]. Proficient bilinguals (independently of age of acquisition) show a striking similarity in brain activation across different languages [11,19]. Though a seminal study showed that late bilinguals recruited different language-processing areas of the brain than early bilinguals [20], the overall understanding is that semantic processes are represented in similar areas of the brain in proficient bilinguals.[1] A study of the degree of overlap between L1 and L2 used machine learning techniques to investigate the neural substrates of semantic representations of L1 and L2 in proficient bilinguals who spoke Portuguese and English [21]. The study showed reliable classification accuracies for the classification of brain activity for nouns across languages. For example, the pattern of activation elicited by the Portuguese (L1) word "cabana" could be used to reliably identify the brain activation for the homologous words in L2 (e.g., the English word "hut"), and vice-versa. This finding indicates that the semantic properties of words are similarly represented at the neural level in proficient bilinguals. It was possible to identify the word a bilingual was thinking about based solely on the brain activation for that same word in another language.

Behavioral studies have shown that bilinguals establish a conceptual mapping of the meaning of words that does not rely on the translation of words (lexical mapping) to the first language [22]. Proficient bilinguals are equally able to name pictures and categorize word exemplars (e.g., a hammer is a tool) in the first language (L1) and in the second language (L2) [23,24], and they suffer a Stroop effect from naming an ink color in one language when the word names a different color in another language [25]. Thus, neuroimaging and behavioral research alike show that there is a shared semantic representation in bilinguals, that is, shared concepts and shared cortical tissue [17]. Fig. 1

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[1] In the Kim et al. study [20] the level of the proficiency of the bilinguals was not accounted for.

underscores the large overlap in brain activation between two languages in a study of proficient bilinguals performing a word-reading task [21].

There is an important distinction to be made between the cognitive processes involved in word-level semantic (vocabulary) and syntactic (lexicon) representations. The process of accessing vocabulary refers to the sound-meaning association made between spoken and read (and signed) words and their semantic properties. Mostly, the semantic properties of these words (e.g. meaning) are accessed through reading and listening tasks, and the findings of studies that investigate these processes are related to the representation of individuals' vocabulary, not lexicon [27]. The lexicon, in turn, refers to the word-level rules that people must learn to correctly inflect words in their language (in the case of bilinguals, in multiple languages), such as learning that regular verbs in English take the past-tense suffix "-ed." These processes are discussed in the latter section of this review, which addresses the issue of language rule-based processes and language control in bilinguals.

The fact that conceptual representations converge across languages has consequences for bilingual production. A shared representation may be at the basis of cross-language interference, such as the cross-language Stroop effect in proficient bilinguals of alphabetic languages [25,28] (see also the discussion below about slower naming in bilinguals). Bilinguals have to access a representation and then choose its instantiation. In this sense, there is an important issue of language control that may be associated with representation; that is, how do bilinguals choose the appropriate word for the context of use?

It intuitively makes sense that the representation for concrete objects (e.g. bicycle), highly imageable concepts (e.g. beach) and even abstract, but common, nouns (e.g. democracy) are shared across languages. As the bilingual becomes proficient in L2, why have two neural representations for, say, the concept represented by the English word "hammer?" Would two semantic representations be required only because the concept is represented by a different letter-sound combination in the Spanish "martillo?" Intuitively the answer seems to be "no," and brain imaging also suggests that the answer is "no" (see discussion about the machine learning study [29]). Of course, there may be cultural factors that interfere in the representation of concrete nouns. Cultural factors may result in different neural representations simply because cultural factors may generate different concepts for the same physical object which, in turn, may be culturally-bound to different semantic categories. Consider the following situation: A bilingual grows up in a culture in which animals are not deities, and then learns another language in a profoundly religious culture, in which one or more animals are treated as deities. Does the bilingual develop new meaning associations and different, culturally-bound representations and semantic categories for the animal? What happens, then, to the original, or first, neural representation for the animal? To our knowledge, the issue of culturally-bound neural representations for the same animate, or inanimate, representation remains to be answered by brain imaging.

If at the level of words, bilingual brain activation seems to converge, brain activation for more complex comprehension processes, for example, sentence-level comprehension, shows differences associated with the workload of the task. Differences in brain activation between L1 and L2 have been found in more activation of prefrontal regions associated with increased cognitive workload in a listening comprehension task [30], and a frontal–parietal network of areas associated with phonological processes in a reading comprehension task (phonological rehearsal [31]). Studies also show recruitment of additional brain networks to accommodate the demands of different writing conventions (different writing systems and scripts) [32]. In sum, the level of dynamic distribution of brain activation in L2 compared to L1 is accounted for by differences in proficiency levels in the two languages, by workload, and by linguistic distance [31,33–37].

In addition to different activation associated with workload and writing systems, it is noteworthy that the investigation of bimodal bilinguals (signed and spoken languages) may afford a new insight into converging processes across languages: in this case, processes associated with different languages conveyed in different modalities. A recent study showed that despite large similarities in the brain activation associated with spoken and sign language production, bimodal bilinguals, in comparison with monolinguals, showed more right-hemisphere temporal and occipital activation during a sign-language task. The additional right-hemisphere areas recruited may support cognitive processes associated with sign language production. Interestingly, in early bimodal bilinguals, linguistic aspects of facial expressions are processed by the same left-hemisphere areas that process language in monolinguals [38]. The study of the bimodal bilingual brain, though still in a very early stage, may advance the understanding of the human brain's remarkable flexibility to acquire entirely different language systems using very similar brain networks.

2.1. Single word-reading network: a predictive role for the occipitotemporal cortex in skilled L2

The refinement of brain imaging studies has afforded a more detailed understanding of specific word-level processes in monolinguals and bilinguals. One of the developments of L1, and now L2 brain imaging studies, is a specific role for an area of the occipitotemporal cortex involved in word-reading processes, the area is called the visual word form area (VWFA) [39,40]. Activation in this general occipitotemporal area is predictive of the development of L1 reading skill [41]; the activation is fine-tuned to reading skill development.

The role of the occipitotemporal cortex in L1 reading has been clearly established. Activation of the VWFA shows invariance across visual (surface, non-linguistic) features but is sensitive to orthographic regularity: more robust fMRI activation is associated with words and with pseudowords than nonwords (letter strings that form combinations that are unlikely to happen in a given language) [42]. The VWFA becomes specifically tuned to the recurring properties of a writing system [41].

Recent research on bilingualism has identified a predictive role for activation of this same area for L2. Tan and colleagues [43] showed that activation of the caudate-fusiform circuit predicts the level of second language learning. Activation of specific areas associated with a simple lexical decision task correlated positively with reading performance (prediction of reading ability). The areas that predicted this performance were left caudate nucleus and left middle fusiform gyrus. The coordinates for the left fusiform gyrus activation were $x = -46$; $y = -57$; $z = -11$ [43]; the location of activation was in the vicinity of the visual word form area (VWFA), which is located at approximately $x = -43$; $y = -54$; $z = -12$ with a standard deviation of $\sim$5 mm [41].

The finding of Tan and colleagues [43] is in agreement with the hypothesis that the VWFA constitutes a special case of "perceptual expertise." According to McCandliss and colleagues [41], the response properties of the VWFA should evolve in parallel with the rise of cognitive hallmarks of expertise. In terms of brain imaging, this means that different levels of activation of the VWFA in bilinguals may provide a biological marker of increasing expertise in reading in the second language. In terms of the neurocognitive perspective, as bilinguals automatize and develop L2 reading skills, the activation of specialized centers such as the VWFA reflects this development. Others [44] also showed overlapping activation of the VWFA in skilled L1 and L2 reading of logographic scripts. Fig. 2 illustrates the center of activation reported for brain imaging studies that investigated the role of the VWFA in L1 and L2 reading.

In this section, it was shown that semantic information is highly distributed and highly overlapping in proficient bilinguals. Moreover, different factors that modulate brain activation in comprehension tasks were discussed. Generally, brain imaging studies show that there are brain indices that corroborate the hypothesis that bilinguals share their conceptual representations across languages, and there are indices that may serve as predictors of L2 skill (much like in L1 studies). Yet a crucial issue remains: the use of either the first or second language must be coordinated. As Grosjean [1,2] argues, a bilingual is not two monolingual people in one. Multiple languages share cortical tissue and influence one another. In this sense, studies have investigated the presence of a "language switch" in bilinguals [45] and shown the importance of executive and attentional processes for bilingual control in situations of production. In the following section, brain imaging studies of the bilingual ability to switch and control between languages is discussed from the point of view of brain imaging findings.

3. Language control in the bilingual brain

At the interface between the representations of multiple languages and control of these representations, a system of "rules" for manipulating linguistic forms must somehow be stored in the brain. In essence, these rule representations contain within them a control structure, or "program" for executing a linguistic manipulation. To execute these programs, a rule system must solve at least two neurocomputational problems. First, such rules must be represented in an abstract form. For instance, native English speakers should have a neural representation of the rule "to pluralize noun X, add 's' to the end of X."[2] Second, a mechanism for "plugging in" the specific variable of interest (in this case a noun) must be in place. For instance, when attempting to pluralize the word "dog," the brain must somehow feed that word form "dog" into the "X" slot of the abstract rule representation to come up with the plural form "dog + s = dogs." This procedure, which has been called "variable binding" in the computer science world, has received a considerable amount of attention [46].

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[2] There are many exceptions to these rules in most languages which are presumably stored in our episodic memories.
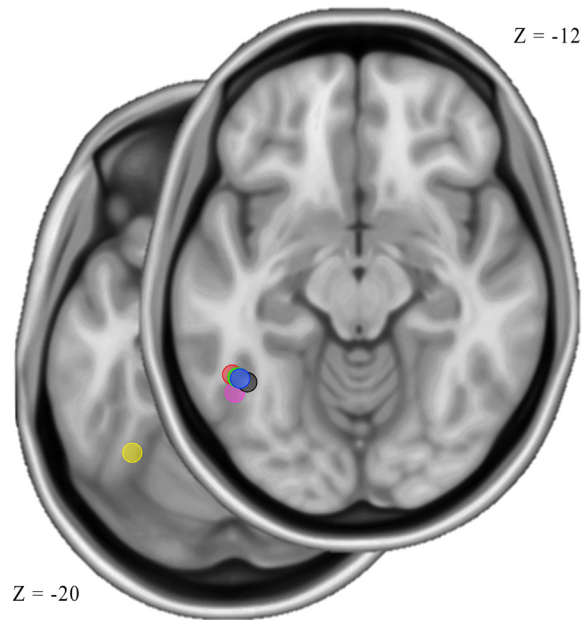
Fig. 2. The occipitotemporal cortex in skilled L2 and L1 reading. The figure illustrates the coordinates reported by studies of L1 and L2 brain activation for word-reading processes. Top slice $z = -12$; bottom slice $z = -20$. *L2 reading coordinates*: yellow $x = -37$; $y = -54$; $z = -20$ [111]; blue $x = -46$; $y = -51$; $z = -9$ [44]; red $x = -46.0$; $y = -57$; $z = -11$; *L1 reading coordinates*: pink $x = -45$; $y = -51$; $z = -9$ [44]; black $x = -43$; $y = -54$; $z = -12$ [41]; green area is the overlap between red and blue centroids (all centroids in MNI coordinates). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

In this review, we argue that the neural computations necessary for executing grammatical rules are not qualitatively different from those necessary for executing non-linguistic rules (e.g., to calculate an exponent function X^Y, multiply the base (X) by itself Y times). However, one of the remarkable features of language is the complexity of the relational contingencies that are considered in the rule representations and the additional arbitrary rules that make up irregular forms and must be learned/memorized. For instance, while all English speakers have a representation of the rule "add 'ed' to create the past tense of a verb," skilled readers realize during syntactic parsing that verbs such as "examined" can be *either* active past tense forms (e.g., The lawyer <u>examined</u> the evidence) or can be reduced-relative passive participles (e.g., The evidence <u>examined</u> in court was incriminating), and can calculate the probability that "examined" is one of the two forms by taking into account contextual variables such as the animacy of the initial noun phrase of the sentence [47,48]. Thus, ideal linguistic rule execution must be extremely flexible and include dynamic consideration of contextual relations.

Bilingual language control clearly adds at least one layer of complexity to such a system. During language production, for instance, bilinguals must "select" the appropriate **set** of rules for manipulating information in the target language of interest (e.g., To pluralize a noun, if language = English, then + "s" to the end of the noun (X); else, if language = Italian, then if noun (X) ends in "o" or "e," replace with "i," or if word ends in "a," replace with "e.").[3] Thus, we argue that "target language" in the bilingual mind must serve as an ever present "contingency" variable, upon which the appropriate selection of subsequent rules and representations for comprehending and producing language depends. To investigate this analogy further, research describing the overlapping neural underpinnings of linguistic (primarily syntax) and non-linguistic rule-based behaviors is summarized below, along with the implications of this body of work for theories of bilingual language control.

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[3] Below we discuss multiple ways that this type of information might actually be represented. We are not arguing that such rules must be represented separately from the contexts in which they are learned. However, there must be some mechanism by which the rule can be abstracted (for instance by comparing all of the words in a semantic network that end in "s" to those that don't) and applied to novel stimuli.
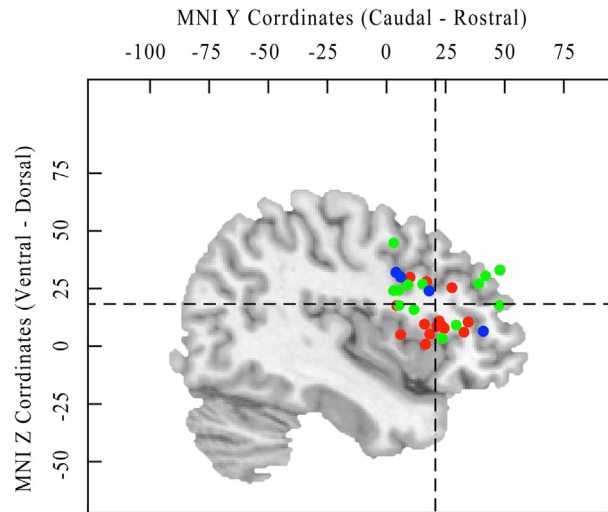
Fig. 3. Centroids of prefrontal cortex activation taken from 25 neuroimaging investigations of rule-based learning and execution (in blue), of syntactic processes (in red), and of bilingual language control (in green). See Table 1 for references. The foci of activations are overlaid on the Montreal Neurological Institute (MNI) Colin 27 template. Any stereotactic coordinates that were originally given in the Talairach–Tourneaux system were converted to the MNI system using the non-linear transformation algorithm provided in the GingerALE software [56]. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.1. The role of the prefrontal cortex in language control and rule-based behaviors

Given the overlap in computational demands described above, it is not surprising that the bilateral prefrontal cortical regions have been found to play an important role in *both* linguistic and non-linguistic rule-based behaviors. One of the benefits of using rule-based behaviors as a model for understanding language control is that a considerable amount of research using single-cell recordings in animals has contributed to our understanding of the dynamics of non-linguistic rule learning and execution. Converging evidence from these studies [49], as well as from neuroimaging investigations of healthy individuals [50] suggests the importance of the lateral prefrontal cortices in abstract rule learning and execution. Highly overlapping prefrontal regions have also repeatedly been associated with syntactic processes in healthy monolinguals [51,52], and with impairments in syntactic processing in patients with brain damage [53]. Finally, and of particular relevance to this paper, investigations of bilingual language control have shown that these areas are also activated in paradigms that require controlled switching between languages [45,54]. Consistent with these findings are neuropsychological investigations showing that damage to the lateral prefrontal cortex can lead to pathological switching deficits in bilingual individuals [55]. To demonstrate the overlap between the findings in these three fields, Fig. 3 displays a series of centroids in the left lateral prefrontal cortex obtained from neuroimaging investigations of rule-based learning and execution (in blue), of syntactic processes (in red), and of bilingual language control (in green). The coordinates are reported in Table 1.

While the similarity in these findings is compelling, the fact that the lateral prefrontal cortices are heavily involved in many aspects of higher-level cognition may leave one wondering about the precise nature of their involvement in rule-based behaviors, and how it relates to bilingual language control. To explore this further, we will again anchor our discussion in the literature on rule-based behavior. Research on rule representation, for instance, has shown that as the complexity of the relations encoded in the rule increases, the more rostrally the prefrontal cortical contributions can be found [57,58]. In general, this complexity is measured in terms of the number of relations, or the hierarchy of variables that must be considered for the rule. This research suggests then that the prefrontal cortex is central to representing the relations among variables considered in a rule, and as the relations become more interdependent, the representation of the rules moves rostrally in the lateral prefrontal cortex.

Recently, a series of papers making the link between syntactic processes and rule learning in artificial grammar paradigms have argued that the role of the inferior frontal gyrus in syntactic processes stems from its importance in processing such hierarchical relations in sequence [59,60]. Of particular interest is a review paper arguing for a "rostro-caudal gradient of structured sequence processing in the left inferior frontal gyrus" [60] for linguistic infor-

mation. In their review, the authors also argue that linguistic processes requiring increasingly hierarchical relational considerations (e.g., sentence and discourse-level semantic processes) involve more rostral regions of the lateral prefrontal cortex, whereas relations with more basic contingencies (e.g., those involved in phonological combinations) involve more caudal regions of the lateral prefrontal cortex. Taken together, these results seem to suggest that the prefrontal cortex plays an important role in representing the relations between variables in rules (both linguistic and non-linguistic in nature) in an abstract, hierarchical manner, with more abstract relations being represented in more rostral regions of the brain, and that the inferior frontal gyrus, in particular, seems to be important when these rules involve a timed, or sequential component, such as in syntactic processes.

How, then, might language control structures (i.e. grammatical rules) be differentially represented in the bilingual brain? At least two possibilities arise. In the first case, rules for each language are represented in parallel, with the desired, or target, language acting as a type of "prime" in the bilingual brain that biases activation of one rule over another. Another possibility is that linguistic rules in the bilingual brain are complex rules that contain control structures for manipulating variables in both languages, with an additional "contingency" level related to target language. This type of "If language is X" contingency (such as the example of pluralization given earlier in this section), would add an additional level of hierarchical relations to consider during grammatical processing in bilinguals. Based on the research previously discussed, this added level of complexity should result in grammatical rules in bilinguals being represented more rostrally in the left lateral prefrontal cortex than the same rules would be represented in monolinguals. To the best of our knowledge, this has not been directly experimentally investigated; however, Kovelman and colleagues [61] compared patterns of activation in monolinguals and bilinguals when performing a syntactic parsing task and found that bilinguals had greater activation than monolinguals in the most rostral portion of the left inferior frontal cortex (see [61, Fig. 1A]). Also note that in Fig. 3, four of the most anterior (or rostral) centroids of activation come from language switching experiments (in green). We see this as an interesting area of future exploration; perhaps one that might be well addressed using multi-voxel pattern analysis techniques such as those described in [21,62,63].

3.2. The role of the basal ganglia in rule-based behaviors and language control

When considering the overlapping circuitry of linguistic and non-linguistic rule-based behaviors, the importance of the connectivity between the basal ganglia and prefrontal cortex cannot be overlooked. The basal ganglia are a set of interconnected nuclei located at the base of the forebrain that, through a complex circuit of inhibitory and excitatory signals, can influence the neural inputs to the frontal lobe [64]. This privileged position allows the basal ganglia to function as a "gate," allowing them to control the inputs received by the frontal lobes, which in turn function as one of the key information integration regions of the cortex.

Because they are rich in dopamine projections, the basal ganglia are one of the most plastic regions of the brain, and thus have been widely implicated in models of *learning* in general, and *rule-learning* specifically [65]. Experiments with animals have shown, for instance, that basal ganglia damage impairs learning of stimulus-response associations [66]. In humans, diseases affecting the basal ganglia (e.g., Parkinson's or Huntington's disease) have also been shown to impair the acquisition of complex stimulus-response associations [67]. Taken together, these findings suggest that the basal ganglia may be particularly important during the acquisition phase of rule-based behaviors.

The basal ganglia have also been implicated in *rule-execution* processes, however. Specifically, because of their ability to dynamically "gate" signals to the frontal lobes, which are in turn important for representing the abstract relations contained in rules, the basal ganglia may function to route specific variables of interest into abstract rule representations. In one of the few experiments to date that has separated rule encoding from rule execution, Stocco and colleagues [68] found that the basal ganglia were involved in rule execution, at precisely the point in time in which the target variables to be manipulated were "plugged in" to the abstract rule representation. In summary, with respect to rule-based behaviors, the basal ganglia seem to be important both for rule-learning and rule execution.

In terms of linguistic rules, Ullman and colleagues were among the first researchers to ascribe a linguistic role to the basal ganglia [69–71]. Using constructs rooted primarily in a memory framework, Ullman compared syntactic processes to other types of procedural or implicit knowledge, which have also been linked to basal ganglia functioning [72,73]. This view is supported by several neuropsychological findings, which have convincingly demonstrated that language impairments normally associated with cortical lesions (i.e., aphasias) can also originate from basal ganglia damage [74,75], and by neuroimaging experiments on healthy adults which have shown that the basal ganglia are important for syntactic processes [76,77].
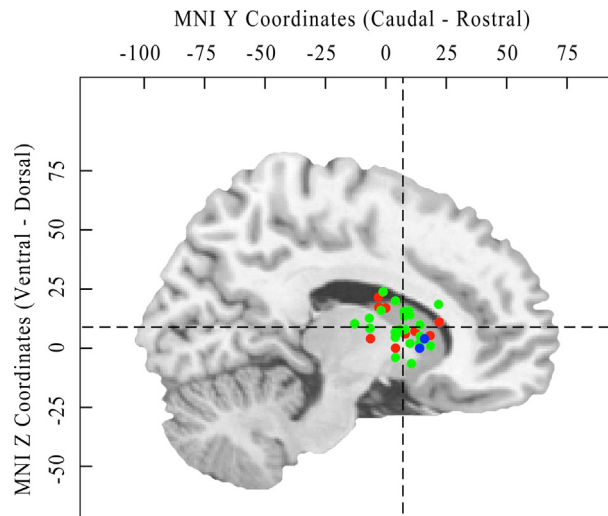
Fig. 4. Centroids of basal ganglia activation taken from 25 neuroimaging investigations of rule-based learning and execution (in blue), of syntactic processes (in red), and of bilingual language control (in green). See Table 1 for references. The foci of activations are overlaid on the Montreal Neurological Institute (MNI) Colin 27 template. Any stereotactic coordinates that were originally given in the Talairach–Tourneaux system were converted to the MNI system using the non-linear transformation algorithm provided in the GingerALE software [56]. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

More recently, however, the basal ganglia have been implicated in models of linguistic control, both within languages in monolinguals and between languages in bilinguals. For instance, Friederici and colleagues [78] proposed that the basal ganglia become involved in language processes during situations in which automatic processing is not sufficient to achieve fluent comprehension. Consistent with these ideas, a series of recent neuroimaging investigations of individual differences in monolinguals found that when comprehension becomes increasingly difficult, higher-working-memory-capacity individuals exhibit greater modulation of activation in the basal ganglia than do lower-capacity individuals [77,79]. Thus, one of the variables that has been widely related to good reading comprehension (verbal working memory capacity) has been repeatedly associated with greater recruitment of the basal ganglia during complex comprehension paradigms.

A recent review paper described how a neurocomputational model of basal ganglia function [68] can be applied to a model of language control in the bilingual brain [80]. In particular, they claim that target language in the bilingual brain serves as an ever present "condition," determining the contextually appropriate subsequent linguistic actions and variables to be selected. This theory is also consistent with converging findings from neuroimaging investigations of bilingual language use and from investigations of deficits in bilingual patients with basal ganglia damage. For instance, neuropsychological studies have shown that control over target language use can become impaired with lesions to the basal ganglia [81]. In addition, Stocco and colleagues reported the findings of 16 fMRI investigations of bilingual language use (typically measured by language switching paradigms) in which activation foci were reported within the basal ganglia nuclei [80]. To consolidate the results suggesting a shared role for the basal ganglia in rule-based behaviors, centroids from neuroimaging investigations of non-linguistic rule-based behaviors (in blue), syntactic processing (in red), and bilingual language control (in green) are depicted in Fig. 4. Citations and MNI coordinates for the centroids of activation in Fig. 4 and are listed in Table 1.

Note that these centroids are largely clustered around the head of the caudate nucleus (part of the striatum), which functions as the primary "input" station for signals being routed to the prefrontal cortex.

In summary, converging evidence suggests that the lateral prefrontal cortices and the basal ganglia are jointly involved in controlling language in the bilingual brain. To better understand the functional relevance of these findings, we examine the roles that these regions play in linguistic and non-linguistic learning and execution of rule-based behaviors. Based on the shared computational demands involved in all rule-based behaviors, and the demonstrated overlap in neural underpinnings, we feel that this analogy is useful for characterizing the neural underpinnings of bilingual language control. In the subsequent sections, we discuss some of the more practical implications of this rule-based model.

Table 1
References and MNI coordinates for activation centroids depicted in Figs. 3 and 4.

Study	Region	Coordinates (x, y, z)	Type
Abutalebi et al. [82]	Caudate	−16 6 7	Bilingual language control
	Caudate	16 8 13	
	Caudate	−18 −1 24	
	Caudate	−10 4 5	
	Caudate	14 4 7	
Abutalebi et al. [83]	Caudate	−2 10 16	Bilingual language control
	Caudate	−28 −13 10	
	Caudate	28 −7 8	
	Caudate	14 −7 13	
Bahlmann et al. [84]	Caudate	−28 18 5	Non-linguistic rules
	Caudate	14 12 7	
	Caudate	−16 −6 4	
	IFG	−46 4 18	
	IFG	−34 28 25	
	IFG	−28 18 5	
Ben-Shachar et al. [85]	IFG	−43 21 9	Syntax
	IFG	−41 10 30	
	IFG	−27 22 11	
Ben-Shachar et al. [51]	IFG	−45 23 9	Syntax
	IFG	−31 24 8	
Bunge et al. [50]	IFG	−42 6 30	Non-linguistic rules
	IFG	−45 18 24	
Crinion et al. [86]	Caudate	−6 8 8	Bilingual language control
	Caudate	−6 6 8	
	Caudate	−4 14 2	
Friederici et al. [78]	IFG	−36 16 1	Syntax
	IFG	−46 16 10	
Ghosh et al. [87]	Caudate	14 −3 17	Syntax
Grogan et al. [88]	Caudate	16 10 14	Bilingual language control
	Caudate	12 −2 16	
	Caudate	−14 14 10	
	Caudate	−8 4 20	
Hernandez et al. [89]	IFG	−53 12 16	Bilingual language control
	IFG	−51 3 24	
	IFG	−40 5 24	
	IFG	−57 5 18	
Klein et al. [90]	Caudate	−15 11 −7	Bilingual language control
Lehtonen et al. [91]	Caudate	−16 4 −4	Bilingual language control
Meschyan & Hernandez [92]	Caudate	24 10 16	Bilingual language control
Moro et al. [76]	Caudate	−24 −3 22	Syntax
	IFG	−28 35 11	
	IFG	−28 33 6	
Price et al. [93]	Caudate	−16 19 1	Bilingual language control
	Caudate	−18 22 19	
	Caudate	18 14 5	
	Caudate	18 8 16	
Ruge & Wolfensteller [94]	Caudate	12 16 4	Non-linguistic rules
	IFG	−44 4 32	
Santi & Grodzinsky [95]	IFG	−48 17 28	Syntax
	IFG	−42 6 5	
Stocco et al. [96]	Caudate	12 14 0	Non-linguistic rules
Strange et al. [97]	IFG	−36 41 7	Non-linguistic rules
Venkatraman et al. [54]	IFG	−46 9 27	Bilingual language control
	IFG	−57 15 27	
Wang et al. [98]	IFG	−39 42 31	Bilingual language control
	IFG	−57 30 9	
	IFG	−27 48 33	
	IFG	−39 39 27	
	IFG	−57 24 3	
	IFG	−36 48 18	
	IFG	−51 3 45	
Wartenburger et al. [26]	Caudate	−20 8 6	Syntax
	Caudate	−20 0 17	
	Caudate	20 4 0	

3.3. Implications for L2 learners: learning through experience versus learning form explicit instructions

Much of the existing research on rule learning has used paradigms in which participants or animals must extract the rules of an experiment through trial-and-error learning (e.g. [49,99]). Interestingly, investigations of single-cell recordings in animal models have shown that the prefrontal cortex and basal ganglia are dynamically involved in such learning paradigms. Specifically, the basal ganglia (and in particular the striatum) begin to activate in rule-relevant contexts quite quickly, whereas the prefrontal cortical neurons change their patterns of activation much more slowly (e.g. [99]). These results are consistent with the idea that the basal ganglia, which are more dopamine rich and more plastic than the cortex, seem to initiate the mappings of stimulus–response pairings, whereas the prefrontal cortex may eventually store the abstracted representations of such mappings.

Although it is difficult to determine in animal models, the difference between the prefrontal cortical region and basal ganglia's involvement in rule learning may also map on to explicit (prefrontal cortex) and implicit (basal ganglia) rule awareness. To explore this, in human studies, it is possible to explicitly give participants the "rule" (or instructions) for performing a task initially, rather than having them learn through trial-and-error. Successive trials then involve practice with retrieving and applying the rule, rather than extracting it. In one such study, it was shown that the processing of a "cue" indicating a rule resulted in immediate activation in the rostral part of the prefrontal cortex [94]. Activity in the basal ganglia (in particular in the striatum), on the other hand, correlated with learning to apply the rule, as indicated by increased reaction time during the subsequent application of that rule. Taken together, these findings suggest that the basal ganglia and prefrontal cortices are differentially involved when individuals learn through experience versus when learning through explicit instructions.

These findings have obvious implications for models of second language acquisition and second language learning in the bilingual brain. For instance, one might predict that the rules of languages that are acquired early, through experience with the language, are more likely to be represented in the basal ganglia than are rules of languages that are learned explicitly, for instance in the classroom environment, which may be more likely to be represented in the prefrontal cortex. Consistent with this hypothesis, Zanini and colleagues [100] reported greater syntactic impairments in the native language than in a later learned L2 in bilingual Parkinson's patients, whose basal ganglia functioning is largely impaired due to dopamine depletion. Perhaps then, a key difference between early and late L2 learning can be explained in terms of the different neural circuitry involved in acquiring rules through experience versus learning rules explicitly. To our knowledge, this has not been explored directly. We see this as an exciting area for future research.

3.4. Implications for theories of the bilingual advantage in executive functioning

Among the most intriguing findings over the past decade of research on bilingualism are those that have demonstrated a bilingual advantage over monolinguals on a number of tasks that measure non-linguistic executive functioning (see [101] for a review). Because these results are primarily found in early bilinguals, who are unlikely to "select" into a bilingual developmental experience, they suggest that something about the unique bilingual language experience gives rise to improvements in more general executive processes. The most parsimonious explanation of this phenomenon is that learning and controlling multiple languages "trains" a neural circuit that is also utilized for more general executive functioning. Until recently, however, such a circuit had yet to be specified.

Recently, Stocco and colleagues [96] proposed that the network for "conditionally" routing signals to the frontal cortex through the basal ganglia is strengthened in bilinguals. Their review summarized research demonstrating the shared importance of fronto-striatal loops in tasks that measure components of executive functioning, such as set shifting, as well as in tasks that measure bilingual language control, such as language switching. They propose that because target language of interest serves as an ever present "condition" in the bilingual mind, the ability of the basal ganglia to flexibly (as a function of this condition) route signals to the frontal cortex is strengthened in bilinguals, and that this strengthening gives rise to the observed bilingual benefit in tasks that measure cognitive flexibility and susceptibility to interference.

To test this hypothesis, Stocco and Prat [102] compared patterns of behavioral performance and brain activation in an fMRI investigation of instructed mathematical rule execution in bilinguals and monolinguals. Using a rapid instructed task learning paradigm [103] found that bilingual individuals were able to execute novel mathematical rules more quickly than were monolinguals. This improved performance was associated with increased activation in the basal ganglia in bilingual individuals over monolinguals, at the precise moment in which the variables of interest

were being "plugged in" to novel rule templates. These findings are consistent with the hypothesis that target language of interest functions as an ever present "variable" (or condition) in the bilingual mind, and that practice with flexible (or conditionally-based) rule application gives rise to general benefits in flexible rule application in bilingual individuals.

3.5. Implications for education and developmentally delayed populations

The research discussed in this review demonstrates that in addition to the benefits associated with having multiple methods of communicating in an increasingly globalized world, bilingual development gives rise to generalized improvements in the functioning of a brain circuit that supports perhaps the most essential and limited aspects of human cognition. These improvements include better executive function abilities and the benefit of a cognitive reserve that seems to protect an individual from cognitive decline that occurs with aging. Given the preponderance of evidence to support these benefits of bilingualism, one might ask why all children aren't being raised bilingually? The answer to this is might be rooted in an out-dated, and largely scientifically unsubstantiated notion that bilingual language development results in language delays.

This mismatch between science and popular opinion is particularly important with respect to recommendations for raising children with developmental language impairments such as those with selective language impairment (SLI) or autism spectrum disorder (ASD). Parents of children with these disorders are traditionally advised to raise their children monolingually, in order to simplify their language input and "maximize" their success in learning an L1 (see [104] for a transcribed interview about prescribed language practices with the parent of a child with ASD). Not only can such changes in home language practices come with great socio-cultural costs [105], the research presented in the previous section suggests that raising children in bilingual homes to be monolingual may provide a disadvantage with respect to their more general cognitive functioning. This is particularly important with respect to children with ASD, who also exhibit impairments in cognitive flexibility and susceptibility to interference in their everyday functioning, as well as in the very tasks (e.g., card sorting, and the Simon task) in which bilinguals have a demonstrated advantage. Thus, the recommendation that a child with ASD be raised in a single language environment may be removing a type of natural training of, or buffer against, their more general cognitive impairments. At least, it is denying these children an opportunity to further develop higher-level cognitive skills.

In order to evaluate the cost–benefit ratio of raising a child with language impairments bilingually, one must carefully examine the claim that developing two languages further impairs these children. To date, most of the evidence suggests the contrary. For instance, Paradis and colleagues [106] showed that bilingual children with SLI exhibited the same level of performance when evaluating grammatical tense morphemes in each of their languages that monolingual children with SLI did. Several experiments have shown that bilingual children with ASD exhibit the same level of communicative abilities that monolingual children with ASD do [107–109]. In fact, one investigation of 80 toddlers diagnosed with ASD showed that children from bilingual families were more likely to vocalize and gesture than were those from monolingual families [110]. To the best of our knowledge, no one has yet looked at differences in executive functioning in children with ASD from monolingual and bilingual backgrounds. The research summarized here strongly predicts, however, that all other things being equal, bilingual children with ASD should outperform their monolingual counterparts, particularly in tasks that measure cognitive flexibility and susceptibility to interference. In summary, we feel that it is plausible that bilingual language control trains a neural circuit with broader implications for cognitive functioning, and that this training has broad implications for education and intervention in developmentally delayed populations.

4. Future directions: investigation of bilingual mechanisms in an increasingly bilingual world

The present review provided a discussion of recent brain imaging research that explored the fascinating human ability to learn more than one language. The issues of representation of meaning and control of the use of different languages were addressed in the light of biological indices of brain function that corroborate earlier behavioral findings, and that debunk notions of negative effects of bilingualism. Brain imaging research undoubtedly needs to continue to explore the cognitive mechanisms of an increasing population of bilingual speakers. Although the benefits of bilingualism are clear, the underlying mechanisms of a cognitive reserve and executive function advantage must be further developed. The understanding of these mechanisms may help to underscore the importance of learning more

than one language, and may help propagate cognitive advantages to developmentally delayed populations. One practical question is how education systems should evolve to keep up with the increasing presence of foreign languages and foreign students, and perhaps guide a multi-cultural generation. It seems likely that education and understanding of human cognition can benefit from brain imaging studies on how to learn languages and new rule-based systems.

Acknowledgements

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