Research Report

The role of the supplementary motor area (SMA) in word production

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A B S T R A C T

The supplementary motor area (SMA) is a key structure for behavioral planning and execution. Recent research on motor control conducted with monkeys and humans has put to light an anatomical and functional distinction between pre-SMA and SMA-proper. According to this view, the pre-SMA would be involved in higher level processes while the SMA-proper would be more closely tied to motor output. We extended this general framework to the verbal domain, in order to investigate the role of the SMA in speech production. We conducted two speech production experiments with fMRI where we manipulated parameters such as familiarity, complexity or constraints on word selection. The results reveal a parcellation of the SMA into three distinct regions, according to their involvement in different aspects of word production. More specifically, following a rostrocaudal gradient, we observed differential activations related to lexical selection, linear sequence encoding and control of motor output. A parallel organization was observed in the dorsolateral frontal cortex. By refining its anatomical and functional parcellation, these results clarify the roles of the SMA in speech production.

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1. Introduction

In this article, we investigate the role of the supplementary motor area (SMA) in word production. It has been shown that the SMA is directly involved in the selection, planning and production of voluntary hand movements (Lau et al., 2004; Picard and Strick, 2001). A parallel role of the SMA in speech production has been suggested, although it is still poorly understood (Crosson et al., 2001; Indefrey and Levelt, 2004; Krainik et al., 2003; Ziegler et al., 1997). We conducted two fMRI experiments in which participants were scanned while they produced words. We manipulated parameters such as familiarity, length or semantic context in order to modulate the difficulty of word selection, linear sequence encoding or production.

It is generally thought that three main steps are involved in the production of a spoken word (Levelt, 1989). First of all,

the specific word that will be produced has to be selected; secondly, the phonological, phonetic and articulatory plan for the word has to be constructed; and, finally, this plan has to be overtly articulated. The first stage, namely *word selection*, is a competitive process by which an appropriate word is selected among a cohort of candidate items. These items are thought to be activated by the message the speaker intends to communicate, given his/her communicative intentions and the specific task instructions he/she follows. The second stage is the process by which the phonemes that compose the word are selected and organized in a structured sequence that will guide the articulators. We will refer to this process as *linear encoding* to indicate that it computes the serial order in which the components of the item to be produced are ordered. It is important to stress that linear encoding is the construction by the speech production system of a linear order for the linguistic material (e.g., phonemes or syllables). The final stage of articulation is the motor execution of the sequence constructed at the previous stage.

These distinctions among cognitive stages have driven the identification of the neural basis of word production. In a meta-analysis of 82 imaging studies involving speech production, Indefrey and Levelt (2004) identified a set of regions that were activated during a variety of naming and word generation tasks, suggesting that they contribute to the "core processes of language production". Those regions included the bilateral SMA, the left posterior IFG, the left insula, the left precentral cortex and additional temporal and subcortical areas.

Imaging data thus show the SMA among the regions involved in the control of speech production. As a further testimony of its importance, spontaneous (Bleasel et al., 1996; Pai, 1999; Ziegler et al., 1997) or surgical (Krainik et al., 2003; Laplane et al., 1977) lesions of the SMA, as well as intracerebral electrical stimulation (Chauvel et al., 1996), yield a variety of speech disorders. These range in severity from speech reduction and slowing to the production of repetitive vocalization patterns or complete mutism. On the other hand, it is well known that the SMA plays an important role in motor control (see below). Speech production requires, just as motor control, choices and planning at different levels. A number of the aspects of motor control that are known to modulate the activation of the SMA are likely to have equivalents in the planning and execution of speech output (MacNeilage and Davis, 2001).

It has become clear, from convergent anatomical and functional data in monkeys and in man, that the SMA actually encompasses at least two (and sometimes three, Vorobiev et al., 1998) distinct regions: the pre-SMA and the SMA-proper. In humans, the boundary between these regions corresponds roughly to the coronal plane that includes the anterior commissure ($Y = 0$, "VCA line") in Talairach space (Picard and Strick, 1996; Rizzolatti et al., 1996). The pre-SMA is connected to prefrontal cortex (Bates and Goldman-Rakic, 1993) and is involved in a variety of situations requiring higher-level planning such as sequence learning (e.g., Hikosaka et al., 1996), retrieving sensorimotor associations or transiently buffering retrieved sequences of motor elements (Halsband et al., 1993), intervening in internal pace-

maker systems (Ferrandez et al., 2003), etc. (for a review see Picard and Strick, 2001). By contrast, the SMA-proper (sometimes referred simply as SMA, Picard and Strick, 2001) has a somatotopic organization (Chainay et al., 2004) and projects directly to the primary motor cortex and the spinal cord (He et al., 1995). Accordingly, it is thought to subserve aspects of motor execution.

There are some indications that this dichotomy between pre-SMA and SMA-proper could be honored in the domain of language. Segments of the SMA showing a dependence on higher-level task-dependent parameters (e.g., Crosson et al., 2001) tend to be anterior to those showing a correlation with speech rate or with the contrast between overt and covert speech (Huang et al., 2002; Palmer et al., 2001). Crosson et al. (2001) evaluated the relative involvement of medial (including the SMA) and lateral parts of the premotor cortex in the selection process during word production. In their tasks, the critical manipulation was the degree of external guidance on selection. External guidance was minimal in the case of free generation (i.e., produce as many exemplars of a given category as possible) and it was maximal in the case of word repetition. The results showed that the volume of activity in the pre-SMA decreased as external guidance increased, indicating the involvement of the pre-SMA in guiding the selection of the words to be produced (an interpretation that is parallel to that applied to hand motor studies; Deiber et al., 1991; Frith et al., 1991).

Other parallels between speech and motor control can be established on the basis of neuropsychological observations. Ziegler et al. (1997) investigated the word production performance of a patient with a disconnected SMA following a cerebral hemorrhage. Her performance in a number of word production tasks (e.g., repetition and articulatory learning) was impaired overall, but especially so with long pseudo-words compared to short pseudo-words and words. By contrast, she was not affected by the complexity of the syllables composing the pseudo-words. These observations suggested that the lesion resulted in a deficit in transferring the representation planned at the encoding stage to the later stages of articulatory motor programming and execution (Smith and Jonides, 1998; Ziegler et al., 1997). This interpretation is close to that used to account for deficits of gestural sequence reproduction observed in patients with lesions affecting their SMA (Halsband et al., 1993).

In short, it is likely that the involvement of the different functional structures that have been described within the medial frontal wall areas (SMA) is as intricate and complex for speech production as it is for other domains. However, our understanding of this fractionation in the verbal domain remains very incomplete. This is mostly due to an insufficient knowledge about the dissection of the SMA into more specialized modules implicated in the different aspects of word production.

We report two experiments aimed at clarifying the role of the SMA in word production. We tested on a single group of participants whether the parcellation of the SMA into pre-SMA and SMA-proper in motor control studies would hold in the case of language production tasks. This was done by attempting to relate the functional subdivisions of this area

to the cognitive processes of word production: word selection, linear encoding and articulation. In Experiment 1, we investigated the processes of linear sequence encoding and articulation. The experimental design was based on a manipulation of the familiarity and the complexity of the items to be produced. Those parameters have previously been shown to modulate the activation of the SMA in motor tasks and to play a key role in the planning of speech output. In Experiment 2, we investigated the processes of word selection and articulation. We asked participants to select and produce words while we manipulated the degree of external guidance of the selection, as well as the requirement to actually utter the selected word.

2.   Experiment 1

In this experiment, we asked participants to read or to repeat words in series of experimental blocks. We reasoned that the conjunction of the activations observed in both tasks would provide information about the speech production processes. Although modality-*specific* input processes should not be visible in the conjunction analysis, modality-*independent* comprehension processes may be visible in this analysis. Importantly, these processes (e.g., access to semantic meaning) have been shown to activate areas outside our main region of interest (Demonet et al., 2005). For example, semantic access during auditory perception has been linked to a network of areas including the superior temporal gyrus (Thierry et al., 2003), the inferior frontal gyrus, the inferior temporal cortex and the temporoparietal junction (Giraud and Price, 2001). Similarly, activation and neuropsychological studies of visual word perception have evidenced a semantic access network involving the left angular gyrus and the left temporal lobe (see data and discussion in Binder et al., 2003; Jobard et al., 2003). Although the word production tasks we used in Experiment 1 do not require explicit access to semantics, it is possible that such (presumably) modality-independent access occurs for word items. However, even if this were to be the case, it can be expected that the activations produced by theses processes will fall outside our main region of interest in the medial frontal areas.

We manipulated two factors which are known to be variably correlated with the activation of subsets of the SMA: familiarity and length. Familiarity has been shown to modulate the activation of the SMA in motor (e.g., Jantzen et al., 2002) and in speech tasks (Raichle et al., 1994). It was operationalized as a lexicality manipulation: we compared word and pseudo-word production. Words involve highly familiar syllabic sequences, whereas pseudo-words involve novel syllabic sequences. The second factor we manipulated was the complexity (or length) of motor sequences (see Boecker et al., 1998; Catalan et al., 1998). This parameter was operationalized by comparing mono- and bi-syllabic items to tri- and quadri-syllabic items. If pre-SMA and SMA-proper are recruited in the course of word production, the activation of these areas should be sensitive to the factors of familiarity and length, or to a combination of the two.

2.1.   Results

2.1.1.   Task-related networks
The reading task relative to fixation yielded bilateral activations in the pre-SMA and the precentral cortex, extending to the left anterior superior temporal gyrus (see Table 1 and Fig. 1). The same regions were activated by the repetition task, with an additional extension to Broca's area and the corresponding right-hemispheric region, and to the posterior part of the superior temporal gyrus. Accordingly, the overall contrast of both active tasks minus fixation, masked by each task relative to fixation, showed a common activation network that included the bilateral pre-SMA (TC 3 9 54; Z = 4.26) and the precentral cortex extending to the left STG.

2.1.2.   Effects of the experimental factors
We studied the influence of familiarity within the task-related networks described above. We found no region with a larger response for words than for pseudo-words. No significant activation was observed for pseudo-words relative to words when pooling the two tasks. Applying the same statistical method, we found no activations for long relative to short stimuli when pooling both tasks, or separately for each task.

The absence of main effects for familiarity and length may seem surprising given the modulations of pre-SMA and SMA activation by these factors observed in other experimental settings (e.g., in motor tasks). One possible explanation for the absence of effect of familiarity is that short sequences – one or two syllables – do not need much linear encoding processes to be produced, irrespective of how familiar they are. If this were the case, we should not expect a familiarity effect for them. This would reduce the likelihood of observing a main effect of familiarity altogether. However, in this hypothesis, we would expect an effect of familiarity for sequences that require more linear encoding: long items of three or four syllables. To test for this hypothesis, we assessed whether the pre-SMA and other

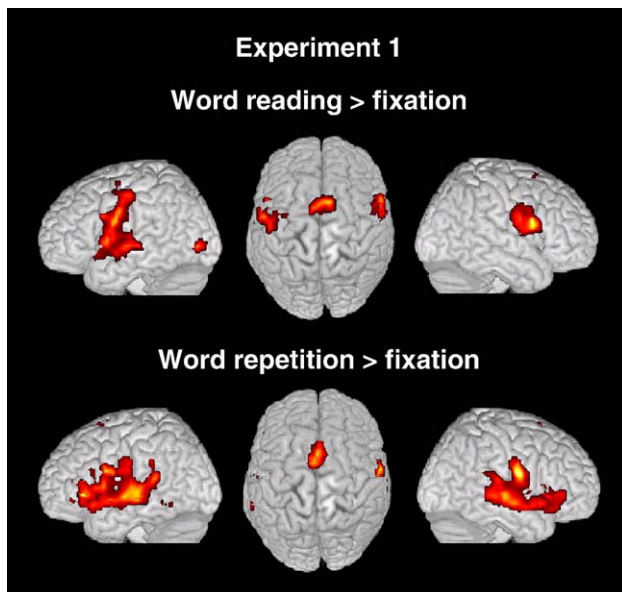| Table 1 – Frontal activation peaks from Experiment 1				
Area	Voxel Z score	TC		
		x	y	z
Reading > fixation				
Pre-SMA	4.13	9	9	60
Left precentral	4.00	−51	−3	24
Right precentral	4.51	57	9	21
Repetition > fixation				
Pre-SMA	3.84	0	9	51
Left precentral and Broca's area	4.15	−33	30	0
Right precentral and inferior frontal	4.15	60	−6	21
Pseudo-words > words during repetition				
Left anterior insula	3.30	−24	30	9
Pseudo-words > words in long > short stimuli				
Pre-SMA	3.07	0	12	57
Left precentral	3.13	−54	6	15

Fig. 1 – Brain activations during word reading (top) and during word repetition (bottom) relative to fixation in Experiment 1. The SMA and ventral precentral cortex are common to both tasks (statistical thresholds are given in the text).

structures would show a greater effect of familiarity for long than for short words, irrespective of the input modality. We searched the common activation network for voxels with a significant interaction of familiarity by length. This analysis showed activations in a set of frontal regions commonly activated by both tasks: the pre-SMA and the left precentral cortex (see details on Table 1 and Fig. 2). At the peak voxel of the pre-SMA (TC 0 12 57, Z = 3.07), the BOLD signal showed no main effect of task, familiarity or length (as seen previously), but an interaction between familiarity and length. This interaction did not differ significantly across tasks (P = 0.83). It reflects the fact that there was no difference between the activation induced by short words and short pseudo-words, while long pseudo-words yielded larger activation than long words (P = 0.006). Notice also that although the long words seem to produce less activation than the short non-words, this difference was only marginal (P < 0.1) and will not be discussed any further.

2.2. Summary and discussion

In this experiment, we isolated large-scale task-related networks that converge with a number of previous studies of word reading (Fiebach et al., 2002; Fiez et al., 1999; Hagoort et al., 1999; Jobard et al., 2003; Price, 1998) and word repetition (Burton et al., 2001; Demonet et al., 1992; Price et al., 1996). The intersection of activations common to both tasks revealed the word production network. This network included the medial frontal cortex (SMA), which was strongly activated during active tasks relative to fixation, with no difference of activation level between tasks. This activation extended behind and in front of the VCA line, thus spanning both the pre-SMA and the SMA-proper.

In addition to this overall activation, the pre-SMA showed an influence of utterance familiarity, mostly observed for long items. This interaction of familiarity and length peaked anterior to the VCA line (TC Y = 12). Even when lowering the voxelwise threshold to P < 0.05, it did *not* extend behind the VCA line into the SMA-proper. In other words, the interaction of familiarity and length affected only the part of the overall speech production area that is anterior to the VCA line, i.e., the pre-SMA. A similar pattern emerged in the lateral frontal cortex (Fig. 2). Inspecting lateral activations at a low threshold (P < 0.05), the contrast of active tasks vs. fixation showed activations extending between about Y = 40 and Y = −20. Only the anterior sector of this cluster, between Y = 40 and Y = 0, showed an interaction of familiarity and length.

The overt articulation of an item requires encoding an abstract sequence that will be converted into a motor plan that guides articulation. The interaction may be interpreted as a reflection of the relative difficulty imposed on sequence encoding by longer or unfamiliar items. The proposed hypothesis is that short item encoding (one or two syllables) is easy enough that it was not sensitive to the familiarity of the
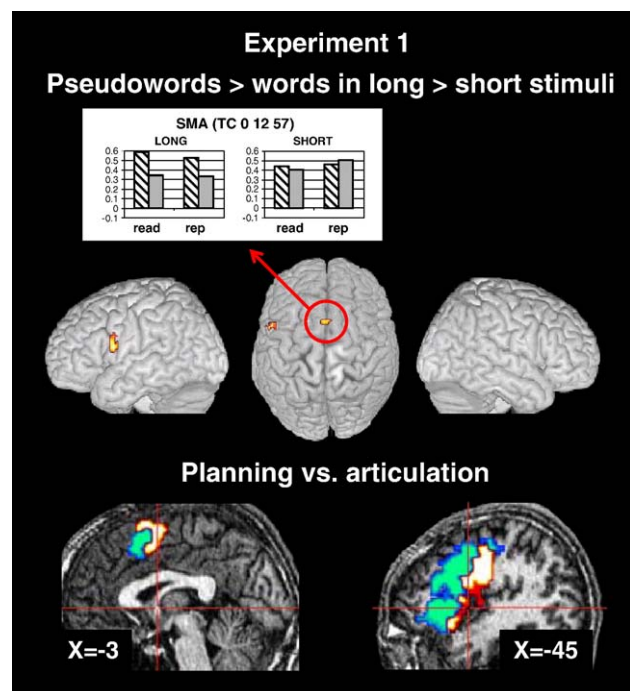

Fig. 2 – (Top) In Experiment 1, the effect of familiarity was stronger for long than for short items in the SMA and left inferior frontal cortex, irrespective of input modality. The histogram shows the percent BOLD signal change relative to fixation in the SMA (pseudo-words: hatched bars; real words: grey bars). For long items only, the activation was stronger for pseudo-words than for real words. (Bottom) SMA and lateral frontal activations, shown at a low statistical threshold (voxelwise P < 0.05). In the SMA, activations induced by active tasks minus fixation (yellow) extended both behind and in front of the VCA line, while the interaction of length and lexical status (green) was restricted to the pre-SMA. A similar pattern prevailed in the lateral frontal cortex.

sequences. By contrast, long items require considerably more linear encoding; hence, for these items, familiarity becomes a determining factor of difficulty and activity. This hypothesis will be detailed in the General discussion, in relation with other findings.

In short, Experiment 1 confirmed the involvement of both the pre-SMA and the SMA-proper in the common speech output system. Moreover, it suggested that the region just anterior to the VCA line was more involved in the linear encoding of the utterance than the SMA-proper. Finally, it suggested the existence of a parallel organization in the lateral frontal cortex.

In Experiment 1, the auditory or visual stimulus indicated unambiguously the word that had to be produced. Consequently participants were not required to select it explicitly (i.e., production was always "externally guided", in the terminology used by Crosson et al., 2001). Minimizing the processes of word selection allowed us to concentrate on the investigation on later stages of word production, such as linear encoding and articulation. This limitation is overcome in the Experiment 2, where we investigated the functional areas of the pre-SMA/SMA cortex that are involved in word selection and word articulation.

3. Experiment 2

In Experiment 2, participants were asked to produce words in response to visual cues. In one of the conditions, participants were visually presented with the name of a semantic category (e.g., "ANIMAL"). They were asked to select a word denoting a member of the category and to produce it (e.g., "a dog"). In the other conditions, participants were given basic level names which they had to produce (e.g., "dog" → "a dog"). We hypothesized that the contrast between trials requiring the active selection of a particular lexical item with those that did not require such a selection would activate anterior zones of the medial frontal cortex, within the pre-SMA sector.[1] The production of the response was always delayed with respect to the visual presentation of the stimulus. Also, we contrasted trials on which a response had to be produced (Go trials) to trials requiring no actual response (No-Go trials). The contrast between Go and No-Go trials was expected to activate more posterior parts of the medial frontal cortex, possibly SMA-proper. In order to distinguish the selection and the execution process, we used a trial structure with relatively long delays between the moment in time where the stimulus was presented and the moment where the response was triggered (see below for details).

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[1] In this category-member naming task, participants actively search for words that meet a certain semantic criterion. In contrast, word search during natural speech production is generally thought to involve an automatic lexical process on the part of the speaker (Kurata et al., 2000). The present task was chosen despite this potential limitation because it provides the opportunity for a strong manipulation of the external guidance on word selection. We will come back to this point in the General discussion.

3.1. Results

The presentation of stimulus words induced large activations relative to the average cerebral BOLD signal, in a reading network similar to that described in the first experiment and other studies, with left-predominant activations in frontal, parietal and occipitotemporal regions. The presentation of the Go signal, which triggered the oral response, induced activations reflecting the perception of the signal, and the production of the response. The activated network included bilateral frontal, occipital and superior temporal regions. Those overall activations were not the focus of this experiment and need not be reported in greater detail (data available on request). Our aim was to isolate medial frontal cortex activations related to lexical selection, and if possible to distinguish them from activations related to speech output.

3.1.1. Word selection
In order to isolate regions involved in the selection of a word within a specified category, we studied activations during the delay period, contrasting the Selection condition (e.g., ANIMAL → "a dog") minus the No-Selection condition (e.g., car → "a car"). This contrast activated a large network (see Table 2 and Fig. 3), including strongly left-predominant dorsolateral frontal cortex and the left pre-SMA. The left dorsolateral frontal activations included the superior frontal gyrus, the middle frontal gyrus and inferior frontal sulcus, and the ventral inferior frontal gyrus.

3.1.2. Word articulation
In order to isolate regions involved in word articulation, we restricted the analysis to No-Selection trials, and contrasted activations induced by the Go signal (which triggered speech output) relative to the No-Go signal (for which no response was produced). This contrast showed bilateral activations in the SMA-proper and the posterior segment of the pre-SMA, and in bilateral precentral cortex (see Table 2 and Fig. 3).

3.2. Summary of Experiment 2

The results can be summarized as follows. First, the activation network related to speech production (Go vs. No-Go contrast)

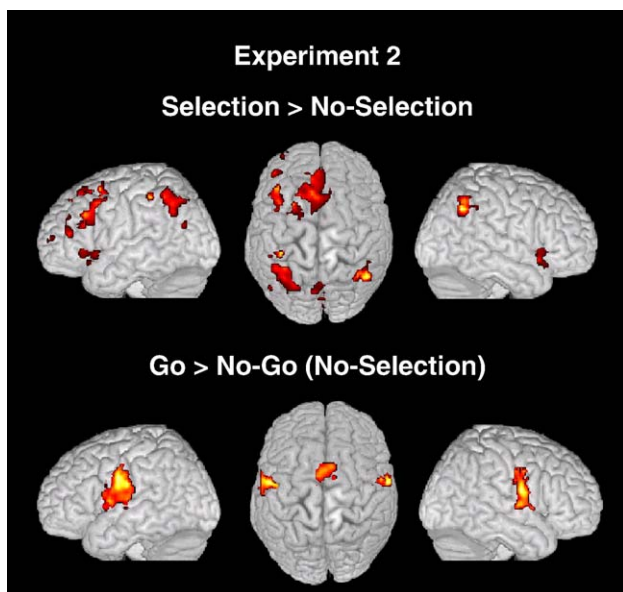| Table 2 – Frontal activation peaks from Experiment 2				
Area	Voxel Z score	TC		
		x	y	z
Lexical selection				
Left superior frontal	4.22	−24	15	51
Left middle frontal	3.97	−39	27	33
Left inferior frontal	3.00	−33	30	−3
Left pre-SMA	3.74	−6	24	54
	3.63	−6	48	48
Speech production				
SMA-proper	2.90	−6	−12	51
Posterior pre-SMA	2.87	9	9	50
Left precentral	3.32	−51	−6	33
Right precentral	3.30	63	−6	21

Fig. 3 – Brain activations during Experiment 2. (Top) Brain activation during the delay period, for trials requiring the active selection of a response word (Selection trials), relative to trials with a specified response word (No-Selection trials). Frontal activations mainly include dorsolateral prefrontal and anterior SMA regions. (Bottom) Activations corresponding to the production of a response word (Go trials), relative to trials on which no response was required (No-Go trials). SMA activations were centered around the VCA line, and dorsolateral activations were located in premotor cortex (statistical thresholds are given in the text).

largely replicated the common output network identified in Experiment 1, including bilateral pre-SMA and SMA-proper around the VCA line, and the precentral cortex. The network observed in Experiment 2 was smaller in extension to that observed in Experiment 1, a difference that could be due to the different designs (blocked vs. event-related) used in the two experiments.

Second, the network related to word selection evidenced extensive left-predominant activations, including regions clearly more anterior than those involved in speech output. The interpretation of this clear-cut functional dissociation within the medial frontal cortex is addressed in the General discussion.

4.　Additional data on motor control

In a recent study of somatotopy in the SMA-proper, Chainay et al. (2004) studied the activations related to simple movements of the lips relative to rest. As their data were potentially relevant to the present study, we conducted a new analysis in which we entered those data in a random effect group analysis using the same statistical threshold as for Experiments 1 and 2. This analysis revealed bilateral activations in the SMA-proper (left: $Z = 3.52$; right: $Z = 3.90$) and in the precentral gyrus (left: $Z = 4.99$; right: $Z = 5.15$).

5.　General discussion

The main goal of this study was to clarify the roles of the SMA in single word production. In view of the variety of contributions of this area to the control of motor behavior in general, its contributions to speech processing were expected to be diverse. We hoped to reduce to some extent this functional diversity to anatomical distinctions within the SMA (pre-SMA and SMA-proper). Our interpretation was guided by the cognitive distinction between word selection, word encoding, and articulation.

5.1.　Word selection vs. word production

We identified a functional distinction between SMA regions activated by word selection (roughly anterior to $Y = 12$) and regions activated in relation to linear encoding and articulation (posterior to this limit). Selection-related activations were identified in Experiment 2 by contrasting Selection vs. No-Selection trials. They extended from about $Y = 45$ to about $Y = 12$ mostly in the left hemisphere, corresponding to the rostral sectors of the pre-SMA and possibly also to the rostral cingulate zone (Picard and Strick, 2001). They differed clearly from (a) the regions where the interaction between length and familiarity was observed in Experiment 1 (which peaked bi-laterally at $Y = 12$, see below for more extensive discussion) and (b) the bilateral output-related activations observed both in Experiment 1 (active tasks vs. fixation) and in Experiment 2 (Go vs. No-Go trials). The latter were observed in more posterior sectors of the medial frontal lobe, from about $Y = 12$ to about $Y = –12$ (again, see the next section for more extensive discussion). It is commonly assumed that the boundary between the pre-SMA and the SMA-proper coincides with the VCA line (Picard and Strick, 1996; Rizzolatti et al., 1996). If we follow this partly conventional view, selection-related activations spanned the anterior side of the pre-SMA, whereas linear encoding and articulation-related activations spanned both the posterior part of the pre-SMA and the SMA-proper. This view is summarized on Fig. 4.

There are converging indications from anatomical and functional data both in monkeys and in humans that the pre-SMA should be considered as a prefrontal executive region rather than as a premotor structure. This area has strong connections with dorsolateral prefrontal cortex but not with primary sensorimotor cortex (Geyer et al., 2000). Accordingly, it is not functionally involved in motor-related functions per se. For instance, it shows effector-independent activations (Kurata et al., 2000), and it is involved in higher-level executive processes such as task-shifting (Nagahama et al., 1999), working-memory manipulations (Petit et al., 1998) or selection of movement direction or side (Deiber et al., 1991) (see references in the Introduction). The pre-SMA, at Talairach coordinates close to the present ones, has also been associated to semantic word generation (Amunts et al., 2004; Crosson et al., 2001).

In light of our findings and the available convergent evidence, we propose that the pre-SMA anterior to $Y = 12$ is involved in the non-motoric process of word selection, as
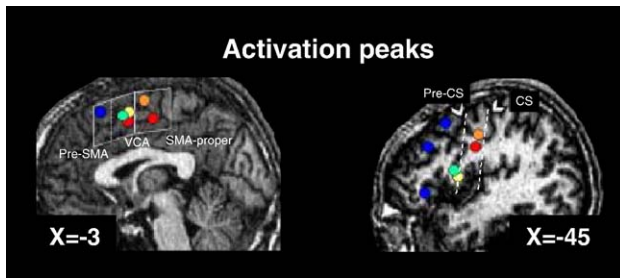
Fig. 4 – Summary of peak activations in the SMA and dorsolateral frontal cortex. Word generation peaks in the anterior part of the pre-SMA (blue). The interaction of utterance length and familiarity (an index of linear sequence encoding) peaks in the posterior part of the pre-SMA (green). Word production induces activations both in the posterior part of the pre-SMA and in the SMA-proper (yellow: Experiment 1; red: Experiment 2). Activation by simple movements of the lips peaks in the SMA-proper (orange). A parallel rostrocaudal gradient of activations related to word selection, phonological planning and overt speech output appears in the dorsolateral cortex (statistical thresholds are given in the text).

recruited in the experimental tasks that we used. As noted above, the meta-linguistic character of the word generation task used in Experiment 2 makes it somewhat different from word selection conducted in natural speech production. When generating a word from a category, speakers are actively searching their lexicon with a prespecified criterion. When producing error-free natural speech, word selection is most often conducted without an explicit search. Yet it is also the case that lexical selection in natural settings sometimes requires an active search on the part of the speaker: for instance, when resolving short-lived tip-of-the-tongue states or during the pervasive dysfluencies that speakers may experience. Differentiating functional components within the process of word selection are certainly an important issue for future research.

5.2. Word encoding vs. word articulation

The straightforward distinction between anterior-selection and posterior-production areas described in the previous section is complemented by a finer-grained dichotomy within the posterior activations. This dichotomy was most clearly evidenced in relation to the manipulation of the critical parameters of familiarity and length in Experiment 1. Just anterior to the VCA, i.e., in the most posterior segment of the pre-SMA, we found a region sensitive to the interaction of stimulus familiarity and stimulus length, with strongest activations for long pseudo-words. This activation peaked anterior to the VCA line ($Y = 12$) and it did not extend into the SMA-proper. This posterior pre-SMA region was associated with activations in the SMA-proper whenever actual speech output was required. However, activation in the SMA-proper was not sensitive to the parameters of length, familiarity or to their interaction, suggesting a functional fractionation between posterior pre-SMA and SMA-proper. Furthermore, the SMA-proper appeared in the Go vs. No-Go contrast in

Experiment 2, and in the contrast of reading or repetition vs. fixation in Experiment 1. It also appeared during simple lip movements in the study by Chainay et al. (2004) for which we proposed a new data analysis.

The task-independent interaction between familiarity and length observed in Experiment 1 can be taken as a marker of the post-selection encoding processes that precede articulatory execution. A variety of studies have shown stronger pre-SMA activation for the production of novel compared to well-practiced motor sequences, underlying the role of pre-SMA in the early stages of motor sequence learning (Halsband et al., 1993; Hikosaka et al., 1999, 2002; Tanji, 2001; Tanji and Hoshi, 2001) and in motor sequence complexity (Boecker et al., 1998). In the case of Experiment 1, the overt articulation of an item requires converting an abstract planned sequence into an effective motor plan for articulation. At this stage, novel (pseudo-words) and longer items impose more processing than familiar (word) and shorter items. Note that pseudo-words are novel items that participants have never encountered before, yet they are composed of known fragments such as the syllables of the language. If the syllable is seen as the unit of articulatory output (Dogil et al., 2002), then the novelty of the pseudo-words lies in the sequencing of otherwise well known motor-programs. Since there was minimal learning in the verbal experiments reported here (pseudo-words were presented only once in each modality), the production of a pseudo-word can be seen as the production of sequence of syllables in the early stages of its learning. We propose that an interaction between length and familiarity (rather than main effects of this variables) was observed because of the minimal amount of encoding required by short items composed of 1 or 2 syllables. By contrast, long items (3 or 4 syllables) require more encoding and hence their processing is sensitive to the familiarity of the sequence.

Activations in SMA-proper posterior to the VCA would reflect actual motor speech execution. As mentioned in the Introduction, the posterior segment of the SMA is directly connected to sensorimotor cortex and to the spinal cord, and is probably involved in more peripheral aspects of movement and speech control, as confirmed by Chainay et al. (2004).[2]

In short, then, our data indicate that the SMA is diversely involved in a variety of verbal processes during word production. This area should be decomposed in at least three regions along the rostrocaudal axis: anterior pre-SMA, posterior pre-SMA and SMA-proper, as shown by the spatial distribution of activation peaks (Fig. 4). The division between the latter two regions would roughly be the VCA

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[2] Hagoort et al. (1999) found stronger activations in the SMA-proper (TC – 3 – 19 51) for words than for pseudo-words. This post hoc difference was attributed to the presence of higher frequency syllables in real words than in pseudo-words in their experimental materials. The authors suggested that the SMA would be involved in accessing precompiled articulatory routines for high-frequency syllables. According to this view, the posterior pre-SMA would be sensitive to the familiarity of sequences, while the SMA-proper would be sensitive to the familiarity of individual syllables (i.e., motor programs).

line. Interestingly, the division of the medial frontal wall areas in three (rather than two) functionally distinct areas has been proposed by Vorobiev et al. (1998) on the basis of cytoarchitectonic data in normal human brains. Our functional interpretation of the activation in these three regions during language production links them to the processes of word selection, word encoding and word articulation, respectively.

5.3. Parallel speech networks in SMA and lateral frontal cortex

Picard and Strick (2001) have emphasized the close anatomical and physiological similarity between the SMA-proper and the *caudal* dorsal premotor cortex (PMd$_c$), and between the pre-SMA and the *rostral* dorsal premotor cortex (PMd$_r$). Our results indicate that the mesial frontal cortex likely contributed to word processing in tight association with a set of dorsolateral frontal regions. Indeed, the contrasts that allowed us to identify three distinct sectors within the SMA also revealed dorsolateral frontal activations. As visible on the right side of Fig. 4, those activations obeyed a rostrocaudal organization parallel to that prevailing in the SMA. If we adhere to the functional analysis proposed before, we observe from front to back activations related to word selection (green), to linear encoding (blue and anterior red) and to articulation (yellow and posterior red).

5.4. Parcellation of the dorsolateral cortex

While the precise organization of the SMA in relation to speech is still poorly understood, the parcellation of the dorsolateral cortex is better known, on the basis of classical neuropsychological lesion study and of functional imaging. As there is good agreement of the present data with this background knowledge, this point will be discussed briefly. First, the activations related to peripheral stages of speech output overlap precisely with the region of the mouth in studies of the motor homunculus (e.g., Gerardin et al., 2000; Lotze et al., 2000). Second, the region sensitive to the interaction of length and familiarity, associated with linear encoding (presumably including phonological encoding), corresponds to the posterior boundary of Broca's area as it merges in the precentral sulcus (BA 44/6). This region has been repeatedly associated with phonological processing in a wide variety of language tasks (see e.g., Burton et al., 2000; Davachi et al., 2001; Demonet et al., 1992, 1996; Paulesu et al., 1993; Poldrack et al., 1999; Xu et al., 2001). Also, transcranial magnetic stimulation of this area, but not of more anterior sectors of Broca's area, interfered with phonological working memory (for intraoperative stimulation data see also Duffau et al., 2003; Nixon et al., 2004). Third, selection-related activations include anterior sectors of Broca's area. This region corresponds mostly to Brodmann's area 45. The involvement of this region in controlled semantic processes has been well documented (Amunts et al., 2004; Gabrieli et al., 1998; Roskies et al., 2001), even if there are slight anatomical discrepancies among studies (with some authors emphasizing the role of BA 44 rather than BA 45: Thompson-Schill et al., 1997, 1999). Interestingly, Gold and Buckner (2002) observed that during a

controlled *semantic* task, this region was associated with activations of the left middle temporal gyrus (TC – 51 – 55 2), close to those we observed during word selection (see also Thompson-Schill et al., 1999). In contrast, during a controlled *phonological* task, the association was with a precentral region (TC – 55 – 1 28) at almost the same coordinates as the phonological region that we discussed above.

5.5. Overall mesial–lateral organization

The functional meaning of the antero-posterior gradient is relatively clear, going from executive to encoding to motor processes. By contrast, given that our study was not designed to address this issue, an interpretation of the relationship between the mesial and dorsal components at each of those levels can only be speculative (Crosson et al., 2001; Deiber et al., 1991; Goldberg, 1985; Passingham, 1993). Some clarification may be gained from studies of brain-lesioned patients. Lateral and mesial lesions yield a variety of impairments of word production (Devinsky and D'Esposito, 2004; Laplane et al., 1977, on lateral lesions see: Lecours et al., 1983, on mesial lesions see: Robinson et al., 1998; Ziegler et al., 1997). Two general features seem to characterize language deficits after mesial frontal lesions, as compared to lateral lesions (Krainik et al., 2003; Laplane et al., 1977). First, there is a typical recovery profile, with an excellent functional prognosis: initial speech reduction or even complete mutism, fast initial improvement, slower recovery of the residual reduction of spontaneous speech. Second, performance is often strikingly dependent on task demands. Speech output is much better when there are strong external constraints (e.g., repetition, sentence completion, word reading) than in spontaneous speech. A proposal that may account for both the similarity and the divergences between dorsal and mesial lesions emphasizes the role of the SMA as providing the drive for sustained movement and cognition (Alexander, 2003), i.e., roughly the "intention" to speak (Lau et al., 2004). According to this hypothesis, the SMA would harness the left lateral frontal cortex through projections traversing the periventricular white matter. The fact that those projections are bilateral could explain the effective functional compensation by the non-dominant SMA after left-hemispheric mesial frontal lesions (Krainik et al., 2003, 2004). Such organization might prevail at several hierarchical levels (selection, phonological encoding, motor output) to ensure the production of a normal speech flow.

6. Conclusion

The two experiments we report clarify the role of the SMA in the verbal domain. The patterns of activation that we observed within the SMA allow us to draw a functional distinction of three regions that can be directly associated with specific stages that are postulated in current models of word production: (a) anterior pre-SMA activation can be related to effortful word selection process; (b) posterior pre-SMA appears to be involved in encoding of word form information (possibly including the control of syllable sequencing); and (c) the activation of SMA-proper is observed in

relation to overt articulation. These activation profiles were not restricted to the mesial parts of the frontal lobe. A parallel parcellation was shown in lateral frontal cortex, which is compatible with previous findings concerning the involvement of this area in verbal tasks. Our interpretation of these findings provides a clear extension of previous observations in motor control experiments concerning the role of subregions within the SMA.

7. Experimental procedures

7.1. Experiment 1

7.1.1. Subjects
Ten subjects (5 females, 5 males), aged 25–43 years, with university education, fully right-handed according to the Edinburgh Inventory, participated in the study. All were drug-free, had no neurological or psychiatric history and had normal anatomical MRIs. All gave their written informed consent. The experiment was approved by the Ethical Committee of the Hôpital de Bicêtre. These participants were also tested in Experiment 2 (the order of the experiments was counterbalanced, see Methods section of Experiment 2). They received full instructions for the two protocols before scanning.

7.1.2. Procedure
The experiment comprised two runs. In one of them, words and pseudo-words were presented visually and participants were asked to read them aloud. In the other, stimuli were presented auditorily and the task was to repeat them aloud. Half of the participants received the reading task first and the other half received the repetition task first. Each of these two experimental runs was organized in short blocks of 8 stimuli. Length and lexicality were kept constant in each block. That is, there were blocks of either long or short words and blocks of either long or short pseudo-words. Each run included a total of 15 blocks: 3 blocks for each combination of length × lexical status (12 blocks in total), plus 3 additional resting blocks of the same duration, with no linguistic stimuli. Items and blocks were presented in a different quasi-random order to each subject. The probability of transition from one block type to another was homogeneous. Finally, an experimental sequence used for one participant was used for another participant in the exact reversed order.

Fig. 5 – Structure of the trials in Experiment 1.

The structure of the experimental trials is represented on Fig. 5. Each trial started with a 500 ms central fixation point, followed by stimulus presentation. On auditory trials, stimuli were presented binaurally over headphones (the fixation point remained on the screen). Participants were instructed to repeat out loud the stimulus as soon as it had finished. On visual trials, stimuli were displayed foveally for 1500 ms. Participants were asked to read aloud the stimulus as soon as it disappeared. The instructions emphasized repeatedly the requirement that responses should be uttered as whispers, while any movement of the head was strictly avoided.[3] The next trial started 3000 ms after the onset of the previous one, irrespective of the duration of the participants' response (i.e., the onset of the trials was not time-locked to the participant's responses). The experiment was controlled by the software E-Prime (http://www.pstnet.com/products/e-prime/).

7.1.3. Materials
We selected 24 short and 24 long familiar common nouns. Short words comprised 1 or 2 syllables. They were on average 4.0 phonemes long and 5.5 letters long. Long words comprised 3 or 4 syllables. They were on average 7.8 phonemes long and 9.5 letters long. Word frequency did not differ between long and short words (short words: mean log[Freq + 1] = 1.51; long words: mean log[Freq + 1] = 1.34; New et al., 2001; frequencies in occurrences per million computed from a corpus of 15 million words). For each word, we created a pseudo-word that closely matched its surface properties: the matched word and pseudo-word had the same CV-structure, the same number of phonemes, syllables and letters. The frequency of syllables did not differ across conditions (log frequencies: short words 3.67, long words 3.79, short non-words 3.52, long non-words 3.64) (data based on the syllabification corpus of Goslin and Frauenfelder, 2000). A complete list of materials is provided in the Appendix.

A group of 10 participants (matched to the population tested in the imaging experiment) named these words and pseudo-words in a behavioral pretest involving reading and repetition in a counterbalanced order. Naming latencies and errors were recorded. Given the very small number of errors, these were not analyzed further. The pattern of naming latencies was very similar in reading and repetition (see Table 3), with somewhat larger effects in the reading task.

This observation is confirmed by repeated measures analysis of variance (ANOVA) of the naming latency data. In reading, we observed main effects of familiarity ($F[1–9] = 89.4$, MSE = 343361, $P < 0.01$) and length ($F[1–9] = 198.4$, MSE = 214330, $P < 0.01$) and an interaction between the two factors ($F[1–9] = 45.1$, MSE = 64964, $P < 0.01$). The interaction can be interpreted as an indication of a larger familiarity effect for long items. Similarly, in the repetition task, there was a main effect of familiarity ($F[1–9] = 66.0$, MSE = 133056, $P < 0.01$), a main effect of length ($F[1–9] = 116.8$,

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[3] The production of overt speech in an fMRI scanner is a potential source of artifacts due to movements of the articulators and of the head. However, in a review and a specific study devoted to this issue, Barch et al. (1999) argue in favor of using overt rather than covert responses in word production experiments. In their study, movements were small, and did not consist in a drift away from the initial position, but rather in oscillations around this position. Moreover, the signal to noise ratio decrease from the covert to the overt condition was evaluated at around 10% only, and artifacts were very much reduced in group vs. individual analyses. Finally, cognitive effects on activation levels were shown to be much smaller in the covert than in the overt condition overall (see also Birn et al., 1999; Palmer et al., 2001; Rosen et al., 2000).

Table 3 – Production latencies for the materials of Experiment 1 broken down by familiarity and length (M: average naming latency; SD: standard deviation)

	Reading				Repetition			
	Short		Long		Short		Long	
	M	SD	M	SD	M	SD	M	SD
Words	587	71	653	87	746	74	821	89
Pseudo-words	692	73	919	80	815	73	983	83
Familiarity effect	105		266		69		161	

MSE = 148231, P < 0.01) and an interaction between the two factors (F[1–9] = 38.0, MSE = 21390, P < 0.01). Importantly for us, the time variations among conditions are well below the sensitivity of the fMRI signal.

7.1.4. Imaging parameters

In each run, 124 functional volumes sensitive to blood oxygen level-dependent (BOLD) contrast were acquired with a T2-weighted gradient echo, echo planar imaging sequence on a 1.5 T Signa Imager [TR (relaxation time) = 3000 ms, α (flip angle) = 90°, TE (echo time) = 60 ms, field of view = 240 × 240 mm, in plane resolution = 3.75 × 3.75 mm]. Each volume comprised 20 axial slices of 5 mm thickness covering most of the brain. Care was taken to scan the supplementary motor area (SMA) entirely. The first four volumes were discarded to reach signal equilibrium. High-resolution T1-weighted images [3D fast gradient-echo inversion recovery sequence, TI (inversion time) = 400 ms, TR = 11 ms, TE = 2 ms, α = 20°, field of view = 240 × 240 mm, slice thickness = 1.5 mm, in-plane resolution = 0.94 × 0.94 mm] were also acquired for anatomical localization.

7.1.5. Statistical analysis of imaging data

Functional images were analyzed with the Statistical Parametric Mapping software (SPM99). To correct for motion, functional scans were realigned using the first image as a reference. The anatomical image was linearly transformed to Talairach space (Talairach and Tournoux, 1988) using the standard template of the Montreal Neurological Institute. Functional scans were then normalized using the same transformation, and then smoothed with a Gaussian spatial filter (5 mm FWHM). The resulting images had cubic voxels of 3 × 3 × 3 mm. For single-subject analyses, there were 10 types of blocks: 8 active blocks resulting from the combination of task (reading or repetition), familiarity (word or pseudo-word) and length (short or long), as well as 2 resting blocks (one in each task). The activation on each of the 10 types of blocks was modeled by a combination of the standard SPM hemodynamic function and its temporal derivative. Only the former function was used for statistical contrasts. Two additional variables of non-interest modeled constant differences across the two sequences. Long-term signal variations were eliminated with a high-pass filter set at 240 s. Low-pass filtering was achieved by convolution with a Gaussian of 4 s FWHM. Data were submitted to a random-effect group analysis with subjects as random variable. The analysis was performed in two steps. First, to delineate the word production network common to both the repetition and the reading tasks, we isolated large-scale task-related networks by contrasting tasks minus their control fixation condition using a voxelwise P < 0.01, and a threshold for cluster extent of P < 0.05 corrected for multiple comparisons within the volume of the whole brain. Second, we looked for the influence of familiarity, utterance length and the interaction of familiarity and length within those networks, correcting for multiple comparisons within the appropriate volume activated by tasks vs. fixation. Contrasts used for masking analyses were

also at the P < 0.01 threshold. In the text and tables, we only report activations in mesial and lateral frontal regions, which are the focus of this study, with their extensions in contiguous areas when required. Whole brain activation networks are visible in figures, and the complete data set is available on request.

7.2. Experiment 2

7.2.1. Methods

7.2.1.1. Subjects.
This experiment was carried out with the same subjects and during the same testing session as Experiment 1. Most methodological parameters were therefore identical. The order of the experiments was counterbalanced: half of the participants were tested first on Experiment 1, and the other half were tested first on Experiment 2. We used the same participants in both experiments to ensure maximum comparability across experiments. The tasks and the structure of the trials were very different from one experiment to another and the materials were non overlapping.

7.2.1.2. Materials.
For Selection trials, we selected 6 names of semantic categories (animals, weapons, fruits, pieces of furniture, tools and articles of clothing). A pretest conducted with 10 independent participants indicated which were the 3 most frequent category members given for each of those semantic categories. We reasoned that these would be the most likely responses in the Selection trials during the experiment proper. For No-Selection trials, we selected 36 names of basic level exemplars, 18 for the Go and 18 for the No-Go condition. Exemplars were drawn from 12 semantic categories (3 exemplars from each). Mostly different categories were used in the Go (birds, boats, geographical terms, kitchen utensils, trees, and vehicles) and the No-Go (body parts, buildings, insects, jewels, kitchen utensils, music instruments) conditions. We chose the materials for the No-selection (Go and No-Go conditions) trials such that (a) they were not among the items frequently given in the Selection responses and (b) they were matched with the most frequent Selection responses on a number of relevant psycholinguistic variables (frequency of occurrence, as well as length in syllables, phonemes and letters). Constraining the materials in this way was intended to make the expected response words in the three conditions as comparable as possible. A complete list of the materials is provided in the Appendix.

7.2.1.3. Procedure.
Each trial started with the visual presentation of a stimulus word for 1000 ms (see Fig. 6). On Selection trials, stimuli consisted of upper-case category names (e.g., ANIMAL), and subjects were instructed to covertly select an adequate exemplar (e.g., "a dog"), and to be ready to utter this word. On No-Selection trials, stimuli consisted of lower-case exemplar names (e.g., car), and subjects were instructed to be ready to utter this word, also with a determiner (e.g., "a car"). The stimulus word was followed by a fixation cross that had a duration of 4800 ms or 7200 ms. After this fixation delay, a cue appeared, indicating whether a response should be given (Go trials: question mark) or not (No-Go trials: cross). The cue was presented for 1000 ms. When a verbal response was required, the word with the appropriate indefinite article was to be produced (in French un/une for masculine and feminine nouns, respectively). This ensured that participants accessed the lexical representation of the words (in order to retrieve their gender) and that they were not reading words simply through surface processing (Damian et al., 2001).

Selection trials were always associated with Go cues, whereas No-Selection trials were associated with Go and No-Go cues with
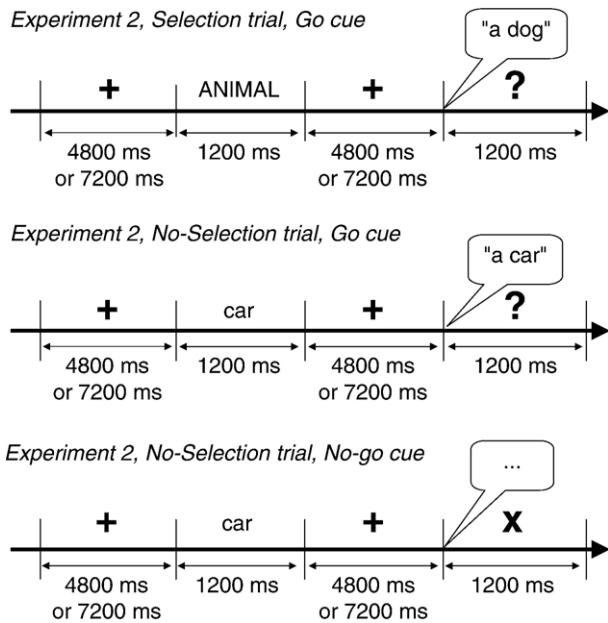
Fig. 6 – Structure of the trials in Experiment 2.

also activated by the first term of the contrasts relative to the average BOLD signal (P < 0.01).

Appendix A.
Materials used in Experiment 1

equal probability. Overall, the 3 experimental conditions (i.e., Selection Go, No-Selection Go and No-Selection No-Go) had an equal probability of 1/3.

The next trial started either 4800 ms or 7200 ms after the cue had disappeared (see Fig. 6). Overall, then, experimental trials had one of three possible durations (given by combining the precue and the post-cue durations): 11,600 ms, 14,000 ms and 16,400. This variable timing was intended to: (a) separate as much as possible in time the processes related to response selection and the processes related to response execution, (b) to provide variability for the event-related statistical model and (c) to improve participant's attention during the responses preparation phase.

The order of presentation of the trials was a quasi-random order determined for each participant, and obeying the following constraints. Two occurrences of a given category were separated by at least 5 trials; there were no more than 2 trials in a row from any of the 3 experimental conditions; there were no more than three trials in a row with the same precue delay, the same post-cue delay or with the same cue type (i.e., Go and No-Go). Following these constraints, we produced 8 experimental lists each one with a different sequence of trials. The experiment included a total of 54 trials, i.e., 18 trials of each type.

7.2.1.4. Imaging parameters and statistical analysis. The general acquisition parameters, image processing and statistical methods were the same as in Experiment 1, except for the following points. A series of 162 functional volumes was acquired (plus four initial discarded volumes), each comprising 17 axial slices of 5 mm thickness, covering the SMA, with a TR of 2400 ms. Activation was modeled by fitting six regressors, each time-locked and corresponding to the hemodynamic response to one component of the trials: the stimulus word, the delay period in the Selection and No-Selection conditions, the Go and the No-Go signal in the No-Selection condition and the Go Signal in the Selection condition. The high-pass filter was set at 120 s. The same statistical thresholds as in Experiment 1 were used: P < 0.01 voxelwise and corrected P < 0.05 for cluster extent. To ensure that those differences did not result from deactivations in the subtracted condition, we checked that the observed areas were

Words			Pseudo-words	
Length	Word	English translation	Length	Pseudo-word
Short	Voiture	Car	Short	Liatule
	Pureté	Purity		Varté
	Valeur	Value		Chenuf
	Canard	Duck		Fonard
	Bras	Arm		Tra
	Clou	Nail		Blin
	Chance	Chance		Tof
	Ancre	Anchor		Adre
	Culte	Cult		Golque
	Chaise	Chair		Fime
	Tonneau	Barrel		Vinou
	Papier	Paper		Lilier
	Défaut	Default		Guno
	Église	Church		Atruce
	Enclume	Anvil		Ocride
	Hasard	Luck		Eloffe
	Accord	Agreement		Ocar
	Pigeon	Pigeon		Névain
	Montre	Watch		Vougre
	Luge	Sled		Vinne
	Arbre	Tree		Eltre
	Cage	Cage		Sose
	Nez	Nose		Ko
	Stade	Stadium		Stèse
	Écureuil	Squirrel		Aipirail
	Cigarette	Cigarette		Mitaurate
	Compartiment	Compartment		Poufarvané
	Établissement	Institution		Oletristin
	Compositeur	Composer		Guvojatar
	Température	Temperature		Santourésol
	Calendrier	Calendar		Felougrier
	Opération	Operation		Ochératui
	Conversation	Conversation		Tumarvelion
	Gendarmerie	Police headquarters		Joucartémi
Long	Individu	Individual	Long	Ulitimo
	Rhinocéros	Rhinoceros		Litonusonne
	Téléphone	Telephone		Tomélaze
	Pyramide	Pyramid		Pelontar
	Univers	Universe		Apidel
	Pistolet	Gun		Nurvafi
	Cheminée	Chimney		Guritté
	Escalier	Staircase		Urgadio
	Institutrice	School-teacher		Arpépadril
	Appartement	Apartment		Ucarderent
	Microscope	Microscope		Cadrustal
	Examen	Exam		Acritein
	Tabouret	Stool		Riquéja
	Professeur	Professor		Drafulaire

Appendix B.
Materials used in Experiment 2

	Semantic category	Stimulus presented	Most likely response in pretest	English	Log freq	No. let	No. phon
Selection trials	Animals	ANIMAL	Un chat	A cat	1.48	4	2
	Animals	ANIMAL	Un chien	A dog	1.28	5	3
	Animals	ANIMAL	Un lion	A lion	1.82	4	3
	Weapons	ARME	Un couteau	A knife	1.39	7	4
	Weapons	ARME	Un fusil	A rifle	2.30	5	4
	Weapons	ARME	Un pistolet	A gun	2.30	8	7
	Fruits	FRUIT	Une banane	A banana	1.05	6	5
	Fruits	FRUIT	Une poire	A pear	0.88	5	4
	Fruits	FRUIT	Une pomme	An apple	0.44	5	3
	Furniture	MEUBLE	Un lit	A bed	0.54	3	2
	Furniture	MEUBLE	Une armoire	A cabinet	0.87	7	6
	Furniture	MEUBLE	Une table	A table	1.44	5	4
	Tools	OUTIL	Un marteau	A hammer	1.57	7	5
	Tools	OUTIL	Un tournevis	A screwdriver	1.85	9	8
	Tools	OUTIL	Une scie	A saw	1.25	4	2
	Clothes	VÊTEMENT	Un pantalon	Trousers	1.45	8	6
	Clothes	VÊTEMENT	Une jupe	A skirt	1.37	4	3
	Clothes	VÊTEMENT	Une robe	A dress	1.01	4	3
Average					1.35	5.56	4.11

	Semantic category	Stimulus presented	Expected response	English	Log freq	No. let	No. phon
No selection Go trials	Birds	Moineau	Un moineau	A sparrow	0.56	7	5
	Birds	Pie	Une pie	A magpie	0.89	3	2
	Birds	Pigeon	Un pigeon	A pigeon	0.79	6	4
	Boats	Barque	Une barque	A small boat	1.25	6	4
	Boats	Chalutier	Un chalutier	A trawler	0.41	9	7
	Boats	Paquebot	Un paquebot	A liner	0.88	8	5
	Geography	Île	Une île	An island	1.79	3	2
	Geography	Océan	Un océan	An ocean	1.31	5	4
	Geography	Ville	Une ville	A city	2.36	5	3
	Kitchen	Bol	Un bol	A bowl	1.11	3	3
	Kitchen	Saladier	Un saladier	A salad bowl	0.35	8	7
	Kitchen	Verre	Un verre	A glass	2.07	5	3
	Trees	Bouleau	Un bouleau	A birch	0.31	7	4
	Trees	Chêne	Un chêne	An oak tree	1.20	5	3
	Trees	Sapin	Un sapin	A pine tree	0.92	5	4
	Vehicles	Avion	Un avion	An airplane	1.55	5	4
	Vehicles	Moto	Une moto	A motorcycle	0.96	4	4
	Vehicles	Voiture	Une voiture	A car	2.09	7	6
Average					1.15	5.61	4.11

	Semantic category	Stimulus presented	Expected response	English	Log freq	No. let	No. phon
No selection No-Go	Body parts	Bras	–	Arm	2.46	4	3
	Body parts	Jambe	–	Leg	1.58	5	3
	Body parts	Oreille	–	Ear	1.82	7	4
	Buildings	Maison	–	House	2.48	6	4
	Buildings	Pavillon	–	Villa	1.26	8	6
	Buildings	Pont	–	Bridge	1.79	4	2
	Insects	Fourmi	–	Ant	0.62	6	5
	Insects	Mouche	–	Fly	1.13	6	3
	Insects	Moustique	–	Mosquito	0.29	9	6
	Jewel	Bague	–	Ring	1.00	5	3
	Jewel	Bracelet	–	Bracelet	0.82	8	6
	Jewel	Collier	–	Necklace	1.00	7	5
	Kitchen	Casserole	–	Pot	1.11	9	6
	Kitchen	Fourchette	–	Fork	0.85	10	6

Appendix B (*continued*)

	Semantic category	Stimulus presented	Expected response	English	Log freq	No. let	No. phon
	Kitchen	Plat	–	Dish	1.69	4	3
	Music	Guitare	–	Guitar	0.93	7	5
	Music	Piano	–	Piano	1.33	5	5
	Music	Violon	–	Violin	0.96	6	5
Average					1.28	6.44	4.44

REFERENCES

Alexander, M.P., 2003. Transcortical motor aphasia: a disorder of language production. In: D'Esposito, M. (Ed.), Neurological Foundations of Cognitive Neuroscience. MIT Press, Cambridge, MA, pp. 165–174.

Amunts, K., Weiss, P.H., Mohlberg, H., Pieperhoff, P., Eickhoff, S., Gurd, J.M., Marshall, J.C., Shah, N.J., Fink, G.R., Zilles, K., 2004. Analysis of neural mechanisms underlying verbal fluency in cytoarchitectonically defined stereotaxic space—The roles of Brodmann areas 44 and 45. NeuroImage 22, 42–56.

Barch, D.M., Sabb, F.W., Carter, C.S., Braver, T.S., Noll, D.C., Cohen, J. D., 1999. Overt verbal responding during fMRI scanning: empirical investigations of problems and potential solutions. NeuroImage 10, 642–657.

Bates, J.F., Goldman-Rakic, P.S., 1993. Prefrontal connections of medial motor areas in the rhesus monkey. J. Comp. Neurol. 336, 211–228.

Binder, J.R., McKiernan, K.A., Parsons, M.E., Westbury, C.F., Possing, E.T., Kaufman, J.N., Buchanan, L., 2003. Neural correlates of lexical access during visual word recognition. J. Cogn. Neurosci. 15, 372–393.

Birn, R.M., Bandettini, P.A., Cox, R.W., Shaker, R., 1999. Event-related fMRI of tasks involving brief motion. Hum. Brain Mapp. 7, 106–114.

Bleasel, A., Comair, Y., Lüders, H., 1996. Surgical ablations of the mesial frontal lobe in humans. In: Lüders, H. (Ed.), Supplementary Sensorimotor Area. Lippincott-Raven, Philadelphia, pp. 217–235.

Boecker, H., Dagher, A., Ceballos-Baumann, A.O., Passingham, R.E., Samuel, M., Friston, K.J., Poline, J., Dettmers, C., Conrad, B., Brooks, D.J., 1998. Role of the human rostral supplementary motor area and the basal ganglia in motor sequence control: investigations with H2 15O PET. J. Neurophysiol. 79, 1070–1080.

Burton, M.W., Small, S.L., Blumstein, S.E., 2000. The role of segmentation in phonological processing: an fMRI investigation. J. Cogn. Neurosci. 12, 679–690.

Burton, M.W., Noll, D.C., Small, S.L., 2001. The anatomy of auditory word processing: individual variability. Brain Lang. 77, 119–131.

Catalan, M.J., Honda, M., Weeks, R.A., Cohen, L.G., Hallett, M., 1998. The functional neuroanatomy of simple and complex sequential finger movements: a PET study. Brain 121 (Pt. 2), 253–264.

Chainay, H., Krainik, A., Tanguy, M.L., Gerardin, E., Le Bihan, D., Lehericy, S., 2004. Foot, face and hand representation in the human supplementary motor area. NeuroReport 15, 765–769.

Chauvel, P.Y., Rey, M., Buser, P., Bancaud, J., 1996. What stimulation of the supplementary motor area in humans tells about its functional organization. Adv. Neurol. 70, 199–209.

Crosson, B., Sadek, J.R., Maron, L., Gokcay, D., Mohr, C.M., Auerbach, E.J., Freeman, A.J., Leonard, C.M., Briggs, R.W., 2001. Relative shift in activity from medial to lateral frontal cortex during internally versus externally guided word generation. J. Cogn. Neurosci. 13, 272–283.

Damian, M.F., Vigliocco, G., Levelt, W.J.M., 2001. Effects of semantic context in the naming of pictures and words. Cognition 81, B77–B86.

Davachi, L., Maril, A., Wagner, A.D., 2001. When keeping in mind supports later bringing to mind: neural markers of phonological rehearsal predict subsequent remembering. J. Cogn. Neurosci. 13, 1059–1070.

Deiber, M.P., Passingham, R.E., Colebatch, J.G., Friston, K.J., Nixon, P.D., Frackowiak, R.S.J., 1991. Cortical areas and the selection of movement: a study with PET. Exp. Brain Res. 402, 393–402.

Demonet, J.F., Chollet, F., Ramsay, S., Cardebat, D., Nespoulous, J.L., Wise, R., Rascol, A., Frackowiak, R., 1992. The anatomy of phonological and semantic processing in normal subjects. Brain 115, 1753–1768.

Demonet, J.F., Fiez, J.A., Paulesu, E., Petersen, S.E., Zatorre, R.J., 1996. PET studies of phonological processing: a critical reply to Poeppel. Brain Lang. 55, 352–379.

Demonet, J.F., Thierry, G., Cardebat, D., 2005. Renewal of the neurophysiology of language: functional neuroimaging. Physiol. Rev. 85, 49–95.

Devinsky, O., D'Esposito, M., 2004. Language, aphasia, and other speech disorders. In: Devinsky, O., D'Esposito, M. (Eds.), Neurology of Cognitive and Behavioral Disorders. Oxford Univ. Press, Oxford.

Dogil, G., Ackermann, H., Grodd, W., Haider, H., Kamp, H., Mayer, J., Riecker, A., Wildgruber, D., 2002. The speaking brain: a tutorial introduction to fMRI experiments in the production of speech, prosody and syntax. J. Neurolinguist. 15, 59–90.

Duffau, H., Capelle, L., Denvil, D., Gatignol, P., Sichez, N., Lopes, M., Sichez, J.P., Van Effenterre, R., 2003. The role of dominant premotor cortex in language: a study using intraoperative functional mapping in awake patients. NeuroImage 20, 1903–1914.

Ferrandez, A.M., Hugueville, L., Lehericy, S., Poline, J.B., Marsault, C., Pouthas, V., 2003. Basal ganglia and supplementary motor area subtend duration perception: an fMRI study. NeuroImage 19, 1532–1544.

Fiebach, C.J., Friederici, A.D., Muller, K., von Cramon, D.Y., 2002. fMRI evidence for dual routes to the mental lexicon in visual word recognition. J. Cogn. Neurosci. 14, 11–23.

Fiez, J.A., Balota, D.A., Raichle, M.E., Petersen, S.E., 1999. Effects of lexicality, frequency, and spelling-to-sound consistency on the functional anatomy of reading. Neuron 24, 205–218.

Frith, C.D., Friston, K., Liddle, P.F., Frackowiak, R.S., 1991. Willed action and the prefrontal cortex in man: a study with PET. Proc. Biol. Sci. 244, 241–246.

Gabrieli, J.D.E., Poldrack, R.A., Desmond, J.E., 1998. The role of left prefrontal cortex in language and memory. Proc. Natl. Acad. Sci. Am. 95, 906–913.

Gerardin, E., Sirigu, A., Lehericy, S., Poline, J.B., Gaymard, B., Marsault, C., Agid, Y., Le Bihan, D., 2000. Partially overlapping neural networks for real and imagined hand movements. Cereb. Cortex 10, 1093–1104.

Geyer, S., Matelli, M., Luppino, G., Zilles, K., 2000. Functional neuroanatomy of the primate isocortical motor system. Anat. Embryol. (Berl) 202, 443–474.

Giraud, A.L., Price, C.J., 2001. The constraints functional neuroimaging places on classical models of auditory word processing. J. Cogn. Neurosci. 13, 754–765.

Gold, B.T., Buckner, R.L., 2002. Common prefrontal regions coactivate with dissociable posterior regions during controlled semantic and phonological tasks. Neuron 35, 803–812.

Goldberg, G., 1985. Supplementary motor area structure and function: review and hypotheses. Behav. Brain Sci. 8, 567–616.

Goslin, J., Frauenfelder, U.H., 2000. A comparison of theoretical and human syllabification. Lang. Speech 44, 409–436.

Hagoort, P., Indefrey, P., Brown, C., Herzog, H., Steinmetz, H., Seitz, R.J., 1999. The neural circuitry involved in the reading of German words and pseudowords: a PET study. J. Cogn. Neurosci. 11, 383–398.

Halsband, U., Ito, N., Tanji, J., Freund, H.J., 1993. The role of premotor cortex and the supplementary motor area in the temporal control of movement in man. Brain 116 (Pt. 1), 243–266.

He, S.Q., Dum, R.P., Strick, P.L., 1995. Topographic organization of corticospinal projections from the frontal lobe: motor areas on the medial surface of the hemisphere. J. Neurosci. 15, 3284–3306.

Hikosaka, O., Sakai, K., Miyauchi, S., Takino, R., Sasaki, Y., Putz, B., 1996. Activation of human presupplementary motor area in learning of sequential procedures: a functional MRI study. J. Neurophysiol. 76, 617–621.

Hikosaka, O., Nakahara, H., Rand, M.K., Sakai, K., Lu, X., Nakamura, K., Miyachi, S., Doya, K., 1999. Parallel neural networks for learning sequential procedures. Trends Neurosci. 22, 464–471.

Hikosaka, O., Nakamura, K., Sakai, K., Nakahara, H., 2002. Central mechanisms of motor skill learning. Curr. Opin. Neurobiol. 12, 217–222.

Huang, J., Carr, T.H., Cao, Y., 2002. Comparing cortical activations for silent and overt speech using event-related fMRI. Hum. Brain Mapp. 15, 39–53.

Indefrey, P., Levelt, W.J.M., 2004. The spatial and temporal signatures of word production components. Cognition 92, 101–144.

Jantzen, K.J., Steinberg, F.L., Kelso, J.A., 2002. Practice-dependent modulation of neural activity during human sensorimotor coordination: a functional Magnetic Resonance Imaging study. Neurosci. Lett. 332, 205–209.

Jobard, G., Crivello, F., Tzourio-Mazoyer, N., 2003. Evaluation of the dual route theory of reading: a metanalysis of 35 neuroimaging studies. NeuroImage 20, 693–712.

Krainik, A., Lehericy, S., Duffau, H., Capelle, L., Chainay, H., Cornu, P., Cohen, L., Boch, A.L., Mangin, J.F., Le Bihan, D., Marsault, C., 2003. Postoperative speech disorder after medial frontal surgery—Role of the supplementary motor area. Neurology 60, 587–594.

Krainik, A., Duffau, H., Capelle, L., Cornu, P., Boch, A.L., Mangin, J.F., Bihan, D.L., Marsault, C., Chiras, J., Lehericy, S., 2004. Role of the healthy hemisphere in recovery after resection of the supplementary motor area. Neurology 62, 1323–1332.

Kurata, K., Tsuji, T., Naraki, S., Seino, M., Abe, Y., 2000. Activation of the dorsal premotor cortex and pre-supplementary motor area of humans during an auditory conditional motor task. J. Neurophysiol. 84, 1667–1672.

Laplane, D., Talairach, J., Meininger, V., Bancaud, J., Orgogozo, J.M., 1977. Clinical consequences of corticectomies involving the supplementary motor area in man. J. Neurol. Sci. 34, 301–314.

Lau, H.C., Rogers, R.D., Haggard, P., Passingham, R.E., 2004. Attention to intention. Science 303, 1208–1210.

Lecours, A.R., Lhermitte, F., Bryans, B., 1983. Aphasiology. Baillière Tindall, London.

Levelt, W.J.M., 1989. Speaking: From Intention to Articulation. MIT Press, Cambridge, MA.

Lotze, M., Erb, M., Flor, H., Huelsmann, E., Godde, B., Grodd, W., 2000. fMRI evaluation of somatotopic representation in human primary motor cortex. NeuroImage 11, 473–481.

MacNeilage, P.F., Davis, B.L., 2001. Motor mechanisms in speech ontogeny: phylogenetic, neurobiological and linguistic implications. Curr. Opin. Neurobiol. 11, 696–700.

Nagahama, Y., Okada, T., Katsumi, Y., Hayashi, T., Yamauchi, H.,

Sawamoto, N., Toma, K., Nakamura, K., Hanakawa, T., Konishi, J., Fukuyama, H., Shibasaki, H., 1999. Transient neural activity in the medial superior frontal gyrus and precuneus time locked with attention shift between object features. NeuroImage 10, 193–199.

New, B., Pallier, C., Ferrand, L., Matos, R., 2001. A lexical database for contemporary French on internet: Lexique. Ann. Psychol. 101, 447–462.

Nixon, P., Lazarova, J., Hodinott-Hill, I., Gough, P., Passingham, R., 2004. The inferior frontal gyrus and phonological processing: an investigation using rTMS. J. Cogn. Neurosci. 16, 289–300.

Pai, M.C., 1999. Supplementary motor area aphasia: a case report. Clin. Neurol. Neurosurg. 101, 29–32.

Palmer, E.D., Rosen, H.J., Ojemann, J.G., Buckner, R.L., Kelley, W.M., Petersen, S.E., 2001. An event-related fMRI study of overt and covert word stem completion. NeuroImage 14, 182–193.

Passingham, R., 1993. The Frontal Lobes and Voluntary Action. Oxford Univ. Press, Oxford.

Paulesu, E., Frith, C.D., Frackowiak, R.S., 1993. The neural correlates of the verbal component of working memory. Nature 362, 342–345.

Petit, L., Courtney, S.M., Ungerleider, L.G., Haxby, J.V., 1998. Sustained activity in the medial wall during working memory delays. J. Neurosci. 18, 9429–9437.

Picard, N., Strick, P.L., 1996. Medial wall motor areas: a review of their location and functional activation. Cereb. Cortex 6, 342–353.

Picard, N., Strick, P.L., 2001. Imaging the premotor areas. Curr. Opin. Neurobiol. 11, 663–672.

Poldrack, R.A., Wagner, A.D., Prull, M.W., Desmond, J.E., Glover, G.H., Gabrieli, J.D., 1999. Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. NeuroImage 10, 15–35.

Price, C.J., 1998. The functional anatomy of word comprehension and production. Trends Cogn. Sci. 2, 281–288.

Price, C.J., Wise, R.J.S., Warburton, E.A., Moore, C.J., Howard, D., Patterson, K., Frackowiak, R.S.J., Friston, K.J., 1996. Hearing and saying—The functional neuro-anatomy of auditory word processing. Brain 119, 919–931.

Raichle, M.E., Fiez, J.A., Videen, T.O., MacLeod, A.K., Pardo, J.V., Fox, P.T., Petersen, S.E., 1994. Practice-related changes in human brain functional anatomy during non-motorlearning. Cereb. Cortex 4, 8–26.

Rizzolatti, G., Luppino, G., Matelli, M., 1996. The classic supplementary motor area is formed by two independent areas. In: Lüders, H. (Ed.), Supplementary Sensorimotor Area. Lippincott-Raven, Philadelphia, pp. 45–56.

Robinson, G., Blair, J., Cipolotti, L., 1998. Dynamic aphasia: an inability to select between competing verbal responses? Brain 121 (Pt. 1), 77–89.

Rosen, H.J., Ojemann, J.G., Ollinger, J.M., Petersen, S.E., 2000. Comparison of brain activation during word retrieval done silently and aloud using fMRI. Brain Cogn. 42, 201–217.

Roskies, A.L., Fiez, J.A., Balota, D.A., Raichle, M.E., Petersen, S.E., 2001. Task-dependent modulation of regions in the left inferior frontal cortex during semantic processing. J. Cogn. Neurosci. 13, 829–843.

Smith, E.E., Jonides, J., 1998. Neuroimaging analyses of human working memory. Proc. Natl. Acad. Sci. U. S. A. 95, 12061–12068.

Talairach, J., Tournoux, P., 1988. Co-Planar Stereotaxic Atlas of the Human Brain. 3-Dimensional Proportional System: An Approach to Cerebral Imaging. Thieme Medical Publishers Inc. Stuttgart New York: George Thieme Verlag, Translated by Mark Rayport. New York.

Tanji, J., 2001. Sequential organization of multiple movements: involvement of cortical motor areas. Annu. Rev. Neurosci. 24, 631–651.

Tanji, J., Hoshi, E., 2001. Behavioral planning in the prefrontal cortex. Curr. Opin. Neurobiol. 11, 164–170.

Thierry, G., Giraud, A.L., Price, C., 2003. Hemispheric dissociation in access to the human semantic system. Neuron 38, 499–506.

Thompson-Schill, S.L., D'Esposito, M., Aguirre, G.K., Farah, M.J., 1997. Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. Proc. Natl. Acad. Sci. U. S. A. 94, 14792–14797.

Thompson-Schill, S.L., D'Esposito, M., Kan, I.P., 1999. Effects of repetition and competition on activity in left prefrontal cortex during word generation. Neuron 23, 513–522.

Vorobiev, V., Govoni, P., Rizzolatti, G., Matelli, M., Luppino, G., 1998. Parcellation of human mesial area 6: cytoarchitectonic evidence for three separate areas. Eur. J. Neurosci. 10, 2199–2203.

Xu, B., Grafman, J., Gaillard, W.D., Ishii, K., Vega-Bermudez, F., Pietrini, P., Reeves-Tyer, P., DiCamillo, P., Theodore, W., 2001. Conjoint and extended neural networks for the computation of speech codes: the neural basis of selective impairment in reading words and pseudowords. Cereb. Cortex 11, 267–277.

Ziegler, W., Kilian, B., Deger, K., 1997. The role of the left mesial frontal cortex in fluent speech: evidence from a case of left supplementary motor area hemorrhage. Neuropsychologia 35, 1197–1208.