Internal modeling of upcoming speech: A causal role of the right posterior cerebellum in non-motor aspects of language production

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The Cerebellum and Self-monitoring in Language Production

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Abstract

Some language processing theories propose that, just as for other somatic actions, self-monitoring of language production is achieved through internal modeling. The cerebellum is the proposed center of such internal modeling in motor control, and the right cerebellum has been linked to an increasing number of language functions, including predictive processing during comprehension. Relating these findings, we tested whether the right posterior cerebellum has a causal role for self-monitoring of speech errors. Participants received 1Hz repetitive transcranial magnetic stimulation during 15 minutes to lobules Crus I and II in the right hemisphere, and, in counterbalanced orders, to the contralateral area in the left cerebellar hemisphere (control) in order to induce a temporary inactivation of one of these zones. Immediately afterwards, they engaged in a speech production task priming the production of speech errors. Language production was impaired after right compared to left hemisphere stimulation, a finding that provides evidence for a causal role of the cerebellum during language production. We interpreted this role in terms of internal modeling of upcoming speech through a verbal working memory process used to prevent errors.

Keywords: language production, cerebellum, internal modeling, self monitoring, verbal working memory

1. Introduction

Evidence indicates that sensory and motor information forms an integral part of language acquisition, representation, and processing beyond auditory and visual perception or articulation (e.g., Pulvermuller & Fadiga, 2010). This has motivated research into commonalities in the neural structures and dynamics responsible for lower (i.e., sensory-motor) and higher order cognitive abilities (i.e., language) (e.g., Pickering & Garrod, 2013; Hickok, 2012). Here we aimed at further contributing to this endeavor by investigating the causal role of the cerebellum in a particular aspect of language processing, namely self-monitoring of language production beyond its pure motor aspects.

1.1 Functional Topography of the Cerebellum

During the last century, the conception of the cerebellum has progressively evolved from that of a pure motor control device to that of a modulator of the cognitive functions tied to any area in cortex to which it is reciprocally connected (e.g., Andreasen & Pierson, 2008; Mariën et al., 2001; Stoodley & Schmahmann, 2010). The cerebellum has reciprocal links through pontine and dentate nuclei and thalamus mainly to frontal and association areas of the cerebral cortex (e.g., Mariën & Manto, 2015). These links include not only frontal motor areas, but also language-related areas such as Broca's region (Desmond et al., 2005; Mariën et al., 2001). As highlighted by Murdoch (2010), "this reciprocal connectivity forms a series of segregated neural loops that are hypothesized to facilitate linguistic function in the same way that the cerebellum enhances motor functions (Leiner et al., 1989)."

In parallel with the expansion regarding the functionality of the cerebellum, there has been substantial progress in our knowledge concerning its functional topography (e.g., Stoodley & Schmahmann, 2010). Of special importance for the present purposes are two functional topographic distinctions: regions involved in motor versus non-motor functions, and regions involved in linguistic functions.

Based on connectivity and functional activation patterns, Stoodley and Schmahmann (2009; 2010; see also Desmond & Fiez, 1998 and Ito, 2008 for similar topographical distinctions) distinguish three topographic functional regions: a "sensorimotor region" comprising the anterior lobe (I-V), lobule VIII, and lobule VI to a lesser extent; a "cognitive region" comprising lobules VI, VII and dentate nucleus -though it has been observed that within the dentate, motor and non-motor domains can also be distinguished (e.g., Dum & Strick, 2003); and a "limbic region" comprising vermis and fastigial nucleus (see figure 1a). In the particular case of language production both pure motor (speech articulation) and more cognitive aspects (linguistic processing) can be distinguished. In line with the functional topographic division outlined above, there is evidence for the anterior lobe being implicated in articulatory processes (e.g., Urban et al., 2003; Ackermann et al., 1992), and the posterior lobe being implicated in higher order processes such as phonological, semantic and word generation when factoring out articulation (e.g., Stoodley & Schmahmann, 2009).

Anatomical and functional evidence also speak to the localization of linguistic function within the cerebellum. Several authors have argued that language processing is mostly confined to the right cerebellum (e.g., Stoodley & Schahmann, 2010; Mariën et al., 2001). Anatomically, projections between the

cerebral and cerebellar cortices are largely (though not exclusively) contralateral (e.g., Brodal, 1979). The lateralization is also supported by fMRI findings that linguistic functions are mainly localized in the right hemisphere of the cerebellum, though often involving a small component of the contralateral lobule (e.g., Stoodley & Schmahmann, 2009). Finally, most clinical reports suggest that language impairments such as impaired verbal fluency and agrammatism generally arise following right cerebellar hemisphere lesions (Gebhart et al., 2002; Hassid, 1995; Hokkanen et al., 2006; Marien et al., 2001; Riva and Giorgi, 2000; Silveri et al., 1994; Zettin et al., 1997; Scott et al., 2001). In this context, it should be mentioned that a small number of neuropsychological studies have also reported linguistic deficits following left cerebellar hemisphere lesions (e.g., Fabbro et al., 2000; Cook et al., 2004; Murdoch & Whelan, 2007). Though one possibility is that the pathophysiological mechanism underlying these lesions was crossed cerebellocerebral diaschisis (e.g., Cook et al., 2004), it is equally possible that they reflect ipsilateral cerebellar cerebral diaschisis, implying that the cerebellum might be bilaterally involved in language processing (Murdoch & Whelan, 2007). Another exception to the lateralization of linguistic function is to be found in prosodic and auditory language processing, that both seem to be left lateralized within the cerebellum (e.g., Callan et al., 2007; Petacchi et al., 2005). These latter findings suggest an even more fine-grained functional cerebellar specialization mirroring the cortical hemispheric specialization. Nevertheless, though the involvement of the left cerebellar hemisphere in linguistic function certainly merits further investigation, the global impression provided by the previous literature, especially in what concerns the cognitive components of

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language production, is that the right hemisphere has a predominant, though not exclusive, role for linguistic functions.

In sum, the combination of these two topographic functional distinctions leaves posterior lobules VI and Crus I and II in the right cerebellar hemisphere as prime candidates for hosting processes of language production beyond its pure motor aspects. A further question is exactly what type of cognitive function(s) the cerebellum is involved in. Concerning language, this function should be rather indirect (i.e., not directly concerning linguistic representations or their access) since damage to the cerebellum is not strongly tied to central disturbances of production and comprehension (e.g., Ito, 2008; Desmond & Fiez, 1998). More generally, several authors highlight that although many functions have been ascribed to the cerebellum, the uniformity of its synaptic organization suggests that a single, characteristic computation may be common to all (e.g., Medina & Mauk, 2000). This hypothesis of neural computation homogeneity has lent itself to hypotheses of cognitive computation homogeneity across different regions of the cerebellum (i.e., motor and cognitive regions). One example of this which we will focus on in the present study is that the cerebellum is devoted to internal modeling of self-generated actions, whether motor or cognitive in nature (e.g., Ito, 2008).

1.2 Internal modeling of upcoming speech

In the domain of motor control it is widely held that control of somatic movement involves internal modeling, allowing for the correction of motor commands by producing expectations of their sensory consequences before their effective output as physical actions (i.e., corollary discharge or efference copies;

McCloskey, 1981; Jeannerod, 1988). These sensory outcome predictions are then compared with the actual sensory input; whatever matches the outcome predictions is inhibited (i.e., reafference cancellation). In that way, a means is provided to detect any unpredicted sensorial data entailing that correction of the motor command is required (Wolpert, Ghahramani & Jordan, 1995). The posterior lobes of the cerebellum (laterality depending on the task) constitute the hypothetical center of this internal modeling of motor actions (Blakemore & Sirigu, 2003; Blakemore et al., 1998; Blakemore et al., 2001; Imamizu et al., 2000; Miall & King, 2008). Cerebellar activity is modulated by the presence and predictability of the consequences of self-generated movements (e.g., Blakemore et al., 1998; 2001). Ito (2008) proposed to extend the domain of internal models from sensori-motor actions to mental activities based on a review of anatomical (i.e., appropriate neural wiring between the cerebellum and the cerebral cortex), functional (appropriate mental activity involving the cerebellum) and neuropsychological data (the association of some mental disorders with cerebellar dysfunction).

The idea of internal models has also been incorporated into theories and empirical investigations of language processing (Pickering & Garrod, 2013; Pickering & Garrod, 2014; Hickok, 2012; Lesage at al.,2012; Argyropoulos et al., 2011; 2013; 2015). In the domain of language production, certain theories propose that internal models are used to self-monitor (prevent and detect speech errors) some or all levels of our utterances. For example, Hickok (2012) conceives of internal models of speech motor control, and proposed that higher levels (phonological encoding) of such control are modeled through temporo-parietal cortex; while the lower level (phonetic encoding) would be modeled

through the cerebellum. Empirical evidence suggestive of a role for internal modeling of articulation actions (i.e., detecting and correcting errors in the programming and execution of speech articulation) can be found in the literature (e.g., Houde, Nagarajan, Sekihara, & Merzenich, 2002; Heinks-Maldonado, Mathalon, Gray, Ford, 2005; Ghosh, Tourville, & Guenther, 2008). More hypothetical and less explored is the hypothesis that also levels beyond pure motor aspects of language might be monitored through internal models as proposed by Pickering and Garrod (e.g., Alario & Hamamé, 2013; Hartsuiker, 2013; Pickering & Garrod, 2013; Pickering & Garrod, 2014; Strijkers, Runnqvist, Costa & Holcomb, 2013). Given the above-mentioned (section 1.1) lack of central disturbances following cerebellar lesions, one might wonder whether it makes sense to hypothesize about cerebellar involvement in such a general mechanism as internal modeling. However, internal modeling of upcoming speech, while indeed being a mechanism of a general nature in the sense that it is supposed to always co-occur with the preparation of speech, is arguably a process whose incorrect functioning could be difficult to detect in comparison with many other components of language processing. This is because the consequences of internal modeling only become apparent when the speaker is preparing an erroneous utterance, which is not the default situation. In contrast, other general processes such as lexical access, phonological and phonetic encoding etc. are not only always present during language processing, but they are essential to it as no language comprehension/production can take place without them. Elsewhere it has been argued that high-level linguistic disturbances subsequent to cerebellar lesions may be more accurately detected and characterized by high-level assessments that evaluate the proficiency of more complex language processes

beyond single word hierarchies (Murdoch, 2010). Such high-level assessments would consist in tasks demanding frontal lobe support in the manipulation of novel situations, lexical- semantic operations, the development of language strategies, and the organization and monitoring of responses (Copland et al., 2000). As we will describe below, our experimental task was designed keeping in mind this potential difficulty of detecting internal modeling functioning.

Insert Figure 1 about here

1.3 The current study

Here we wanted to test whether monitoring language production levels beyond pure motor aspects of speech is achieved through internal modeling, and whether the cerebellum has a necessary role in such modeling. We used repetitive transcranial magnetic stimulation rTMS at a frequency of 1Hz, which is known to temporarily inactivate the stimulated area. Guiding our predictions by the two functional topographic distinctions reviewed above, we expected that disrupting cerebellar function in the right posterior lobules Crus I and II might lead to an impaired speech production monitoring (see Figure 1a). As a control condition (and in counterbalanced orders), the same participants received stimulation to the contralateral area in the left hemisphere of the cerebellum, which should be less related to the linguistic processing of language production. Participants engaged in a speeded language production task designed to prime the production of errors (see Figure 1b). By creating a situation of high load on the speech production monitor through the speeded nature of the task and by priming speech errors, we aimed at providing the ideal circumstances for observing a high-level linguistic impairment that would most probably be

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undetectable with standard language test batteries (e.g., Copland et al., 2000; Murdoch, 2010). To have an additional marker of self-monitoring beyond global error rates, we manipulated the lexical status of the primed error outcomes. Previous research has shown that speakers are more likely to produce errors resulting in new words than pseudowords, indicating that lexicality is a filter used to intercept errors during speech production (Baars, Motley, & MacKay, 1975; Hartsuiker, Corley & Martensen, 2005; Nooteboom, 2005). Returning to our task, the following three predictions can be made: 1) Impaired language processing of any sort (including monitoring) would be apparent through slower response times and/or higher error rates; 2) Impaired self-monitoring for accuracy would be indexed by an overall increased error-rate; 3) Impaired self-monitoring for lexicality would result in a modulation of errors as a function of their lexical status.

2. Methods

The study received appropriate ethical approval (filed under "ID-RCB-2009-A01059-48" at "Comité de Protection des Personnes Sud Méditerranée I") and was performed in accordance with the declaration of Helsinki.

2.1. Participants

Sixteen (ten females, six males) right-handed native speakers of French took part in the study in exchange for a monetary compensation. The average age of participants was 24 (SD 3), with an average of 16 (SD 2) years of education. No participant reported any history of language or neurological disorders.

2.2. Materials

Target stimuli consisted of 160 printed French words (see appendix A). For illustrative purposes the examples in the text are given in English. Across

subjects, each word was used twice in combination with another word (e.g., *mole sail, mole fence*). When exchanging the first letters of these combinations, one of them resulted in a new word pair (*sole mail*, lexical error outcome) and the other in a non-word pair (*fole mence*, non-lexical error outcome). All combinations for which initial sound exchange resulted in new word-pairs (*mole sail*) were used also in the exchanged format (*sole mail*). A given subject was only presented with one combination for each word (lexical or non-lexical outcome), and was only presented with one of the words differing in only the first sound (*mole* or *sole*). This resulted in the creation of four experimental lists with 80 word pairs (40 lexical and 40 non-lexical error outcome). Each subject received one such list divided in two separate blocks of 40 pairs each (20 lexical and 20 non-lexical outcome). Stimuli pertaining to the two blocks were matched for lexical frequency of the first word in the combination, overall lexical frequency, neighborhood density, word length, and phonetic distance.

During the experiment, each target word combination was preceded by three priming word pairs. The first two shared the initial consonants and the third pair had further phonological overlap with the error being primed (*sun mall – sand mouth – soap mate – mole sail*). In each of the two experimental blocks, subjects were also presented with 70 filler pairs that had no specific relationship to the target pairs. One to three such filler pairs were presented to subjects before each sequence of primes and target. Thus, each subject was presented with 460 unique word combinations divided in two blocks of 230 word pairs each (40 targets, 120 primes and 70 fillers). Each experimental block contained three sub-blocks in which these 230 words were repeated three times in different orders. Subjects were instructed to read all target word pairs aloud,

all prime pairs silently, 41% of the filler pairs aloud, and 59% of the filler pairs silently.

2.3. Procedure

2.3.1. Pre-stimulation protocol.

Participants first received written and oral information about the rTMS technique, and they underwent a brief examination by a neurologist. They were then asked to fill in a questionnaire and sign an informed consent. Next, they were familiarized with the experimental task through written and oral instructions and through several practice trials.

2.3.2. rTMS protocol.

A frameless stereotaxic system was used to position the TMS coil on the scalp in order to stimulate a precise anatomical region-of-interest. All volunteers participated in a separate MRI session where a high resolution anatomical scan was acquired. During the TMS session, a Polaris Spectra infrared camera (Northern Digital Inc., Canada) tracked participants' head and registered it to their MRI scan. The neuronavigation (Navigation Brain System, Nexstim 2.3, Helsinki, Finland) was used both to target and to visualize the sites during stimulation. The areas targeted for stimulation (i.e., lobules Crus I and II of the right cerebellum and the contralateral area of the left cerebellum) were marked on each participant's MRI and checked by a neurologist. Topographic mapping studies of the human motor cortex, using a figure of eight coil with 4.5 cm loop diameter, suggest a practical spatial resolution of TMS of 0.5 cm (e.g., Brasil-Neto et al., 1992). This suggests we can be rather confident that we stimulated at least part if not the complete region of interest, while not affecting untargeted areas. The choice of stimulation control-site is an important asset of the current study:

besides serving as a control for any non-specific effects of the stimulation, it also keeps the variable of physical discomfort constant across conditions. This is especially important since cerebellar TMS has been reported to induce muscle discomfort and twitching (e.g., Théoret et al., 2001; Harrington & Hammond-Tooke, 2015), making it difficult to dissociate any impact on behavior from a general attention decline induced by this discomfort. Repetitive transcranial magnetic stimulation (rTMS) was effectuated with a figure-of-eight coil at 1Hz at 60% of maximum stimulator output intensity, using a Medtronic Magpro X100 TMS system. Each session was carried out in two parts: (1) 15 min stimulation (900 pulses) followed by 3*5 min of experimental task; (2) 15 min stimulation (to the opposite hemisphere) followed by 3*5 min of experimental task. The order of stimulation (left/right first) was counterbalanced across participants. The duration of the off-line effects of low frequency rTMS is estimated to be between 60 and 100% of the duration of the stimulation (e.g., Nyffeler et al., 2006; Eisenegger et al., 2008; Chen et al., 1997). This means that we could be rather confident that the effects of inactivation would last between 9-15 minutes of the experimental task following the stimulation of each hemisphere, and that the effects of stimulating one hemisphere would not carry over to performance on the experimental task after stimulating the other hemisphere.

2.3.3. Experimental task protocol.

Participants wore headphones and they were told to silently read word pairs, but to name aloud the last word pair they had seen whenever an exclamation mark was presented. All targets and 41% of the filler items were followed by an exclamation mark presented for 500 ms. Each word pair was presented for 700 ms and was followed by a blank screen for 200 ms. In order to

encourage participants to speak fast, a tone sounded 500 ms after the presentation of the exclamation mark. The next item was presented 1000 ms after the beginning of the tone. Stimulus presentation was controlled using Eprime software. Productions were recorded both through Eprime and with a separate recorder and were processed off-line.

2.4. Data processing

2.4.1. Errors.

A person naïve to the purpose of the experiment transcribed orthographically all productions. The transcriptions were scored as correct, errors, partial responses (e.g., only one word produced), dysfluencies or omissions. The errors were classified as "priming related errors" or "other errors". "Priming related errors" included full exchanges (*mole sail => sole mail*), partial exchanges (anticipations, e.g., *mole sail => sole sail,* perseverations, e.g., *mole sail => mole mail*, other partial exchanges, e.g., *mole sail => sole saint*), repaired and interrupted exchanges (*mole sail => so...mole sail*), full and partial competing errors (*mole sail => star milk/star sail*), and other related errors (*mole sail => mail sole*). "Other errors" included diverse phonological substitutions that were unrelated to the priming manipulation (e.g., *mole sail => hole saint/ro..mole sail/...saint*).

2.4.2. Response times.

Another person naïve to the purpose of the experiment measured the response times for all individual recordings using the software check-vocal (Protopapas, 2007).

2.5. Statistical analyses

The data were analyzed using the lme4 package (Bates et al., 2015) in R version 3.2.2 (R Development Core Team, 2015). Errors were analyzed using generalized linear mixed models (GLMM) with a binomial link function (e.g., Jaeger, 2008), estimating the conditional probability of a response given the random effects and covariate values. Response times were analyzed with linear mixed models (LMM), estimating the influence of fixed and random covariates on the response. One difference between GLMMs and LMMs concerns the type of hypothesis testing that can be used, which is related to the knowledge about the dispersion parameter in both cases. In GLMMs of binomial data, the dispersion parameter is fixed at 1 (e.g., Chen & Conomos, 2015), while in linear mixed models the residual variance has to be estimated. For this reason, z-scores can be used in GLMMs while t-values are used in LMMs. Because both z-scores and p-values are related to the standard normal distribution, p-values can reliably be obtained from z-scores. The summary output of the GLMM function of lme4 in R provides p-values based on asymptotic Wald tests, which is common practice for generalized linear models (e.g., Bolker et al., 2009). The Wald statistic is asymptotically distributed as a standard normal distribution and uses the z-score to calculate the p-value. In contrast, the summary output of the LMM function only provides t-values. Consequently, we report p-values for error-rates and t-values for response times. Following common practice (e.g., Fisher 1925), we take t-values to approximate z-scores and assume that absolute values above 1.96 reflect significant effects.

A common protocol was used for building and comparing both GLMMs and LMMs. In order to determine which fixed effects and interactions to include in the models, a forward selection procedure was used in which each of the

variables was entered into the analysis individually, followed by interaction terms, and only variables or interaction terms that were significant (i.e., with a T-value above 1.96 or a p-value below .05) were kept in the analyses. In those cases where a newly added variable was significant and changed the significance of another variable, the anova function of R was used to compare both models and non-significant p-values were taken to indicate that the more parsimonious model should be preferred.

In all models, Participants and Items were included as crossed random effects (i.e., intercept estimates), allowing to tease apart the influence of subjects/items on their repeated observations from the influence of the fixed effects of theoretical interest. Errors (i.e., both related and other errors) were fitted with a first series of models to evaluate a non-specific impairment of self-monitoring after right hemisphere stimulation. These models included the fixed factors hemisphere and block. Next, the subset of priming-related errors were fitted in separate models to evaluate the output-tied lexicality bias (i.e., the tendency to make more lexical than non-lexical errors) and its interaction with hemisphere. These models thus included the fixed factors lexicality, hemisphere, and block.

For response times, a Box–Cox test (Box & Cox, 1964) indicated that a logarithmic transformation was the most appropriate to approximate a normal distribution, and this is what was used. For clarity, however, we also report approximate estimates of the effect sizes in milliseconds obtained by running identical models with the untransformed response times. The fixed factors included in the models were hemisphere and block as well as the interactions.

2.6. Results

2.6.1. Errors.

Mean error-rates for overall errors and the subset of priming-related errors are reported in Tables 1a and b respectively, and the final models are summarized in Tables 1c and d respectively. Out of the 3840 target trials, there were 500 errors (13% of the data). As shown in Figure 2a, there were more errors after stimulation to the Right hemisphere (14.2% of 1920 target trials) compared to the Left hemisphere (11.8% of 1920 target trials). Overall, there was a progressive decrease in errors in each experimental block (1st: 15.3%, 2nd: 12.9%, 3rd: 10.9%). For the subset of 161 priming related errors (4.2%), more errors were made in the lexical outcome condition (6.4% overall: 7.3% RH and 5.5% LH) than in the non-lexical outcome condition (2%: 2.1% RH and 1.9% LH); thus, there was a lexical bias effect. No other significant effects of interest were found.

Table 1a. Overall mean error-rates in each experimental condition; numbers in parenthesis represent the standard error of the mean.

Block	Right hemisphere	Left hemisphere
1	15.6 (1.4)	15.0 (1.4)
2	14.2 (1.4)	11.6 (1.3)
3	12.8 (1.3)	8.9 (1.1)

Table 1b. Mean error-rates of priming-related errors in each experimental condition; numbers in parenthesis represent the standard error of the mean.

	Right hemisphere			Left hemisphere		
Block	Lexical	Non-lexical	Av.	Lexical	Non-lexical	Av.
1	8.4 (1.6)	1.6 (0.7)	5.0 (0.9)	6.6 (1.4)	1.9 (0.8)	4.2 (0.8)

2	7.8	2.2	5.0	5.6	2.5	4.1
	(1.5)	(0.8)	(0.9)	(1.3)	(0.9)	(0.8)
3	5.6	2.5	4.1	4.4	1.3	2.8
	(1.3)	(0.9)	(0.8)	(1.1)	(0.6)	(0.7)

Table 1c. All errors (significant effects)

	Effect estimate	Std.err	z-value	p-value
(Intercept)	-2.25	0.22	-10.28	<0.01
Hemisphere (Right)	0.21	0.10	2.06	0.04
Block (2)	-0.24	0.12	-2.00	0.05
Block (3)	-0.46	0.12	-3.77	<0.01

Table 1d. Priming related errors (significant effects)

	Effect estimate	Std.err	z-value	p-value
(Intercept)	-3.10	0.21	-14.55	<0.01
Lexicality (non-lexical)	-1.25	0.22	-5.80	<0.01

2.6.2. Response Times.

Mean response times are reported in Table 2a and the final model is summarized in Table 2b. After excluding the 500 errors (13%), 38 dysfluencies (1%), 57 partial responses (1.5%) 38 non-responses (1%), and 74 recording failures (1.6%), the remaining 3133 correct responses (81.6% of the data) were included in the response time analysis. In the first experimental block, participants were slower after right (457ms) compared to left hemisphere (435ms) stimulation (see figure 2b). No other significant effects of interest were found.

Table 2a. Mean response times in each experimental condition; numbers in parenthesis represent the standard error of the mean.

Block	Right hemisphere	Left hemisphere
1	457 (4.9)	435 (4.3)
2	441 (4.9)	448 (4.7)
3	440 (4.9)	443 (5)

Table 2b. Response times in trials with correct responses (significant effects)

	Effect estimate	In ms	Std.Error	t value
(Intercept)	6.06	438	0.04	159.35
Hemisphere (Right)	0.05	25	0.01	4.66
Block (2)	0.03	14	0.01	2.56
Block (3)	0.00	5	0.01	0.26
Hemisphere (Right) x Block (2)	-0.07	-32	0.02	-4.53
Hemisphere (Right) x Block (3)	-0.05	-27	0.02	-3.49

Insert Figure 2 about here

3. General Discussion

The aim of this paper was to explore the causal role of the right posterior cerebellum in language production. Specifically, we tested the hypothesis that self-monitoring of not exclusively motor related aspects of language might be achieved through internal models of upcoming speech, instantiated through the cerebellum. To this end, participants received rTMS to the right and left posterior hemispheres of the cerebellum in counterbalanced orders, and then engaged in a task that maximized the load of speech production monitoring by requiring speeded responses and by priming the production of speech errors. Furthermore, to have an index of a particular type of self-monitoring beyond

global error-rates, we manipulated the lexical status of the potential error outcomes (pseudoword errors are intercepted more often than word errors). The following three predictions were made: 1) Impaired language processing of any sort (including self-monitoring) would be apparent through slower response times and/or higher error rates; 2) Impaired self-monitoring for accuracy would be indexed by an overall increased error-rate; and 3) Impaired self-monitoring for lexicality would result in a modulation of errors as a function of their lexical status. In line with our first two predictions, we observed that after stimulation to the right hemisphere of the cerebellum compared to the left hemisphere, participants committed more errors (all three blocks) and took longer in starting to produce correct responses (first block). Contrary to our third prediction, this effect was independent of the lexical status of the error outcome (this non-confirmed prediction will be further discussed below).

In general terms, an implication of the right cerebellar lobules Crus I and II in cognitive aspects of language production had already been highlighted by functional activation studies and neuropsychological studies (e.g., Stoodley & Schmahmann, 2009; Mariën et al., 2001). An important contribution of our study is that it shows within the same participants that this area has a causal role in language production, and that in a context in which compensatory changes or rewiring has not had a chance to occur (e.g., as might occur following a stroke). Furthermore, by including a dependent variable (error-rates) that can be directly linked to a particular (though admittedly broad) cognitive process (self-monitoring), this study helps constraining the functional role that the cerebellum might have in the process of producing language. It should be noted that an increase in response times as observed in the first block is also consistent with

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an impaired self-monitoring ability: for example, a delay in the interception and inner repair of speech errors might lead to such a pattern. However, though parsimony favors a common origin of the increased error-rates and the response time delay, other possible accounts such as impairment in the temporal organization of the sound structure of utterances (e.g., Ackermann et al., 2007) remain equally possible for the response time delay.

Theoretically, these data are consistent with the view that internal models are used to self-monitor speech production (e.g., Pickering & Garrod, 2013; Pickering & Garrod, 2014; Hickok, 2012). In what follows we will try to shed some light at the issue of what level(s) of language production might be subject to this internal modeling. A first candidate level, which would not assume the current results to reflect the involvement of any linguistic processing proper, is articulation. Trouble with the control of motor production might indeed lead to certain speech errors in the form of pure dysfluencies or mispronunciations, though many problems of speech motor control will rather be reflected in properties that do not affect accuracy such as lengthening of certain segments, vocal quality, pitch, tone, volume, strength, steadiness, speed etc. However, the errors included in our analyses involved *phonological* units (speakers added, deleted, or exchanged phonemes), which, in our opinion, is not predicted by an impaired motor control function. Furthermore, speech motor control is not expected to be affected by the stimulation to Crus I and II of the right hemisphere (e.g., Stoodley and Schmahmann, 2009). Disorders related to articulatory aspects of language production such as dysarthria has been shown to involve lesions in the upper paravermal region of the right cerebellar hemisphere, the site of coordination of articulatory movements of the tongue and orofacial muscles (e.g.,

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Ackermann et al., 1992; Urban et al., 2003). Even though TMS lacks focal precision at the millimeter level as discussed previously (section 2.3.3), the posterior areas we targeted here should be at a sufficient distance from the anterior regions responsible for speech motor control.

A second candidate level to locate our effects can be found moving a little further along the cognitive continuum of language production. As mentioned in the Introduction (1.2), the language production model of Hickok (2012) conceives a role of the cerebellum for the internal modeling of phonetic aspects of language production. However, this explanation is not satisfactory either to account for the observed error pattern involving phonological units.

Finally, moving upwards in the cognitive continuum of language production, also a third candidate level can be excluded since we found no evidence for an implication of the cerebellum in the monitoring of lexical processing. That is, speakers intercepted and repaired internally non-lexical items about to be produced to the same extent regardless of stimulation site. Of course, being based on a null effect, this interpretation should be taken with caution. In sum, our data suggest that the cerebellum, besides having a role for speech motor control of phonetic aspects of speech, is also implicated in the supervision of phonological aspects but not of higher levels of language production.

One possibility is that our findings reflect a difficulty of maintaining a phonological speech goal (i.e., auditory target in terminology of Hickok, 2012), perhaps due to interference with verbal working memory. That is, the referent of comparison in the internal modeling process might be more easily disrupted because of verbal working memory failure, resulting in phonological errors of

both lexical and non-lexical types going undetected. Supporting this interpretation is the fact that selective activation in tasks involving verbal working memory in conjunction with language has been reported in posterior parts of the cerebellum, predominantly in the right hemisphere, within a network that also involves Broca's area and the supplementary motor area (SMA) (e.g., Desmond & Fiez, 1998). Desmond and Fiez propose that the cerebellum might serve to enhance working memory performance by comparing the output of subvocal articulation with acoustically based phonological representations in a short-term store. This is supposed to occur especially as the memory load increases and the need for more accurate and efficient rehearsal becomes more critical, as was presumably the case in our study in which speakers were instructed to say aloud the latest word pair they had read whenever an unpredictable beep sounded. Relevant for the ability of self-monitoring, discrepancies between actual versus intended motor trajectories are hypothesized to result in an error-correction that would serve to maintain the integrity of the rehearsed items. (e.g., Desmond et al., 1997; Desmond & Fiez, 1998). This interpretation suggests that an accurate model of language production and self-monitoring should integrate both domain-general cognitive computations such as internal modeling, and interfacing cognitive systems such as verbal working memory.

4. Conclusion

In conclusion, the research presented here supports a causal role of the right posterior cerebellum for language production beyond its pure motor aspects. A plausible specification of this role is that the cerebellum is involved in

internal modeling of upcoming speech that is used to detect errors, concretely by maintaining in verbal working memory acoustically based phonological representations which can afterwards be compared with the output of subvocal articulation processes.

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Appendix A.

LEXICAL				NON-LEXICAL			
Set A		Set B		Set A		Set B	
malade	sinus	durée	pédale	légion	barreau	bouton	coussin
dentier	répit	raison	maquette	ciment	belote	loto	jonction
faveur	semelle	ragot	fumeur	poker	sapin	primeur	colosse
tenue	voiture	marine	fission	musée	peinture	fournée	bordée
rosier	gâteau	coteau	poupon	lavoir	moisson	boulette	jointure
matin	passage	tonus	boucan	monteur	filleul	poulet	taverne
pillage	sommier	lutin	bocal	tracas	recteur	couture	poison
cadeau	rocher	garage	palette	cuisson	manière	têtard	lamelle
verger	bison	nature	ration	gardon	façon	croupier	filon
ministre	seringue	crochet	briquet	tonton	rouleau	paresse	fraction
titre	voile	clé	bol	vieux	brique	mâche	pomme
ciel	fil	gag	troupe	robe	coeur	lueur	cote
lierre	poupe	foire	prime	masque	fosse	plaque	gerbe
flic	coin	douche	salle	veste	singe	place	fable
butte	lave	gaule	tare	boule	lampe	four	dague
dame	rose	banque	marque	roc	panne	braise	contre
serre	valve	natte	pièce	course	forge	grange	touche
mec	bise	note	puits	vase	pion	liège	tête
rage	cap	dune	lieu	selle	fiche	suite	disque
casse	tube	soir	lac	soupe	foudre	cause	gousse
gosier	râteau	blé	col	lecteur	joker	toison	boulet
patin	massage	loir	sac	lanière	fêtard	gamelle	ponton
sillage	pommier	mise	bec	maçon	journée	pilon	bouture
radeau	cocher	rap	cage	bouleau	moto	traction	piment
berger	vison	tag	groupe	poussin	savoir	carreau	roulette
sinistre	meringue	vitre	toile	fonction	troupier	pelote	fracas
saveur	femelle	verre	salve	molosse	lardon	lapin	fusée
fagot	rumeur	poire	frime	cordée	frimeur	ceinture	région
farine	mission	souche	dalle	pointure	conteur	boisson	caresse
poteau	coupon	gare	taule	caverne	mouton	tilleul	buisson
cil	fiel	salade	minus	pelle	risque	crique	pousse
pierre	loupe	rentier	dépit	case	sueur	coupe	frange
foin	clic	maison	raquette	verbe	tour	bosse	montre
lutte	bave	venue	toiture	sable	poudre	linge	bourse
rame	dose	purée	dédale	vague	foule	rampe	soeur
barque	manque	bonus	toucan	pause	mouche	casque	fraise
patte	nièce	butin	local	tâche	piège	gorge	canne
pote	nuits	parage	galette	fête	lobe	lion	vote
lune	dieu	rature	nation	doc	geste	biche	dieux
tasse	cube	brochet	criquet	glace	fuite	flaque	somme
cause	panne	selle	pomme	clé	pièce	butte	cap
soupe	coeur	vase	cote	ciel	tare	mec	lave

|							
boule	fosse	veste	gerbe	lierre	valve	rage	bise
lueur	singe	suite	fable	flic	salle	gag	marque
robe	lampe	vieux	dague	natte	coin	titre	fil
masque	contre	course	brique	note	lieu	serre	rose
grange	forge	mâche	touche	dune	prime	foire	troupe
liège	pion	four	tête	casse	voile	douche	puits
braise	fiche	roc	disque	dame	bol	gaule	lac
plaque	foudre	place	gousse	soir	tube	banque	poupe
ciment	peinture	couture	bordée	tenue	sinus	pillage	briquet
bouton	moisson	poker	jointure	durée	gâteau	coteau	bocal
tracas	filleul	croupier	taverne	rosier	sommier	tonus	seringue
légion	recteur	tonton	poison	matin	rocher	lutin	fission
loto	manière	gardon	lamelle	cadeau	voiture	garage	ration
musée	façon	primeur	filon	verger	poupon	nature	bison
boulette	rouleau	têtard	fraction	crochet	fumeur	ministre	boucan
paresse	coussin	cuisson	barreau	faveur	maquette	malade	répit
fournée	jonction	poulet	belote	ragot	palette	dentier	passage
monteur	colosse	lavoir	sapin	marine	semelle	raison	pédale
coupe	sœur	linge	sueur	pote	fiel	blé	taule
bosse	foule	verbe	geste	lune	cage	mise	nuits
case	vote	flaque	poudre	tasse	salve	rap	dieu
rampe	lobe	vague	dieux	patte	col	tag	loupe
casque	montre	pause	canne	cil	nièce	vitre	dose
sable	fuite	tâche	mouche	pierre	manque	verre	bave
lion	piège	fête	tour	foin	dalle	poire	groupe
biche	fraise	doc	risque	lutte	cube	souche	frime
gorge	frange	glace	pousse	rame	bec	gare	sac
pelle	somme	crique	bourse	loir	toile	barque	clic
ceinture	piment	cordée	bouture	patin	femelle	gosier	toiture
boisson	mouton	pointure	joker	sillage	râteau	butin	coupon
tilleul	fracas	maçon	fusée	radeau	mission	salade	dépit
lecteur	région	toison	ponton	berger	minus	rentier	pommier
lanière	moto	gamelle	lardon	brochet	dédale	maison	cocher
caverne	troupier	pilon	frimeur	saveur	massage	venue	raquette
bouleau	roulette	traction	fêtard	fagot	toucan	purée	rumeur
poussin	caresse	carreau	buisson	farine	galette	parage	criquet
fonction	journée	pelote	boulet	poteau	vison	rature	local
molosse	conteur	lapin	savoir	bonus	meringue	sinistre	nation

Figure1

A
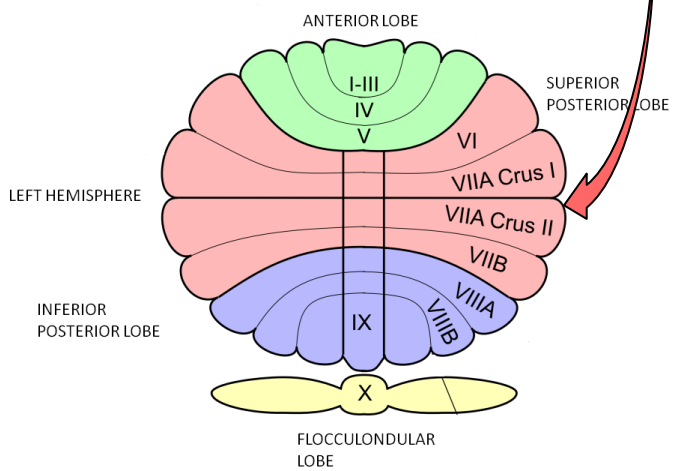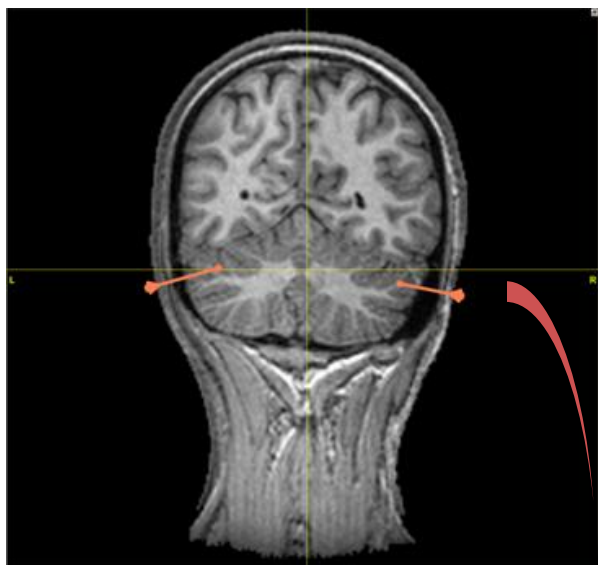
B
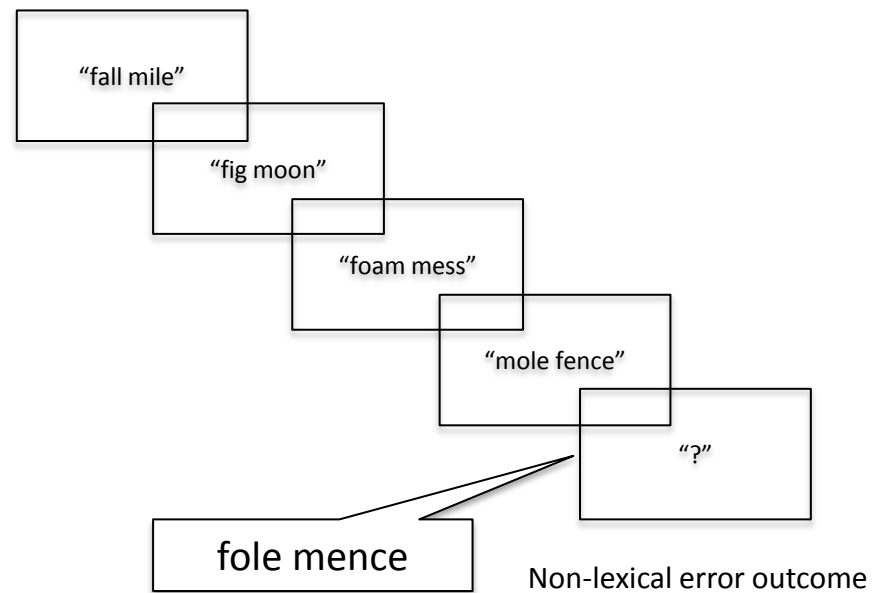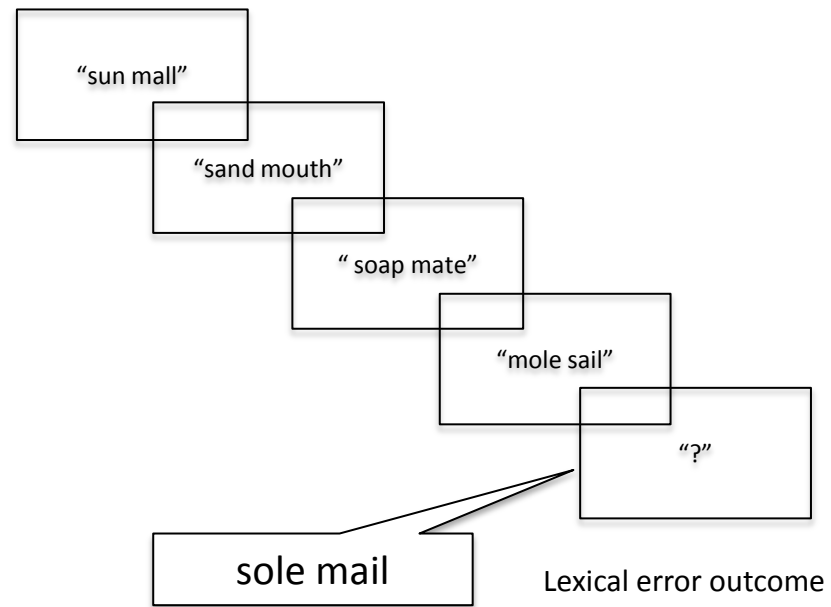
Figure 1. Schematic representation of the stimulation sites and the experimental task.

A, top: Areas targeted for stimulation in the right and left cerebellum marked in the MRI of one experimental subject. A, bottom: Division of the cerebellum into ten lobules (adapted from Schlerf et al., 2014). B, top: An example sequence of events in a trial priming for a lexical error outcome. B, bottom: An example sequence of events in a trial priming for a non-lexical error outcome.

Figure 2

A

Right hemisphere   Left hemisphere
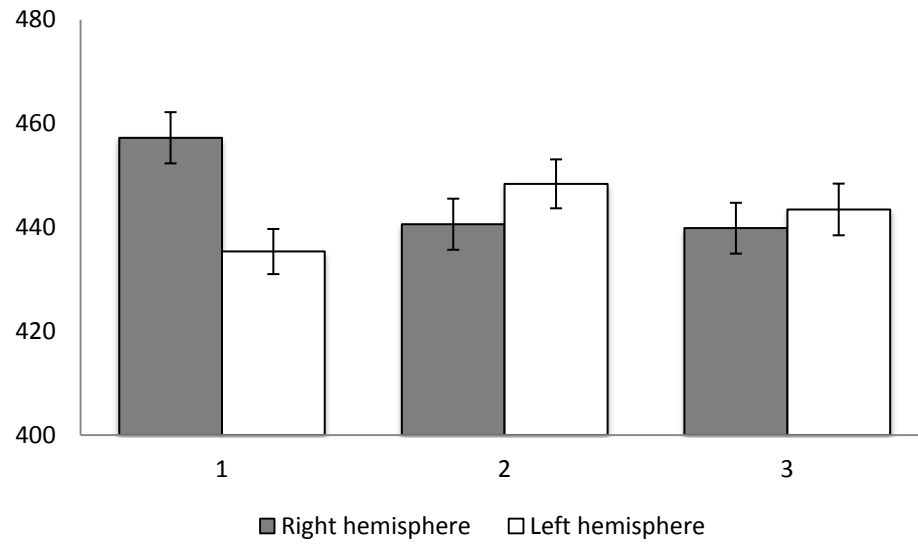
B

Right hemisphere   Left hemisphere
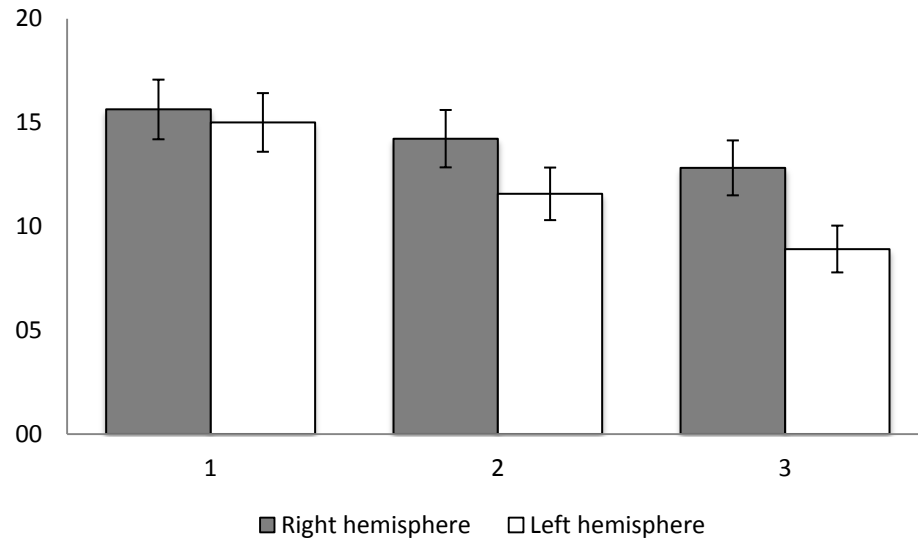
Figure 2. Error-rates and Response times

(A) Percent of overall errors out of the 1920 trials in each hemisphere broken

down by cerebellar hemisphere of stimulation and experimental block. (B)

Response times, similar break down. Error bars represent standard errors of the

mean.